Vol.2 Issue-1, SEP 2021 (e-ISSN: 2582-8223)

Signalling of Jasmonic acid and its response to fruit ripening

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ARTICLE ID: 020

Abstract

Jasmonic acid (JA) is produced naturally by climacteric and non-climacteric fruits and play an important role in fruit development and ripening. They are present in low concentration in various plant parts including buds, shoots, leaves, flowers, fruits, and seeds and the largest amount in fruits. JA is biosynthesized from linolenic acid by the octadecanoid pathway in which translocation of lipid intermediates takes place from chloroplast membranes into the cytoplasm and then into peroxisomes. In the chloroplast membrane, linolenic acid is converted to OPDA with the help of the enzymes LOX, AOS, AOC and OPR. A list of the key regulators of JA signalling includes JASMONATE ZIM DOMAIN (JAZ) proteins, F-box protein COI1, Skp/ Cullin/F-box complex (SCFCOI1), a type of E3 ubiquitin ligase and also the 26S proteasome. The JAZ are negative regulators of JA-induced gene expression and are degraded through the SCFCOI1-dependent 26S proteasome pathway. JAZ proteins recruit the Groucho/Tup1-type co-repressor TPL and TPRs through an adaptor protein NINZA. MYC2 is a bHLH-type TF and has been regarded as a master regulator of JA signalling. JAs crosstalk with ethylene involving the positive and negative feedback. JA-activated TF MYC2 promotes the transcription of ACS1 and ACO1 and ethylene biosynthesis in response to JA ripening.

Introduction

India is a prominent producer of horticultural crops in the world. The country ranks second in fruit production. As per National Horticulture Database (Second Advance Estimates) published by National Horticulture Board, during 2019-20, India produced 99.07 million metric tonnes of fruits and 191.77 million metric tonnes of vegetables. Therefore, it is necessary to found new approaches regarding fruit quality and its shelf life. Plant growth and development is a complex process but well-coordinated and regulated through the action of active small molecules such as plant hormones (phytohormones). Fruits, during their development from the ovary to maturity, experience a wide range of molecular and physiological changes, where ripening-related changes are associated with colour, fruit softening, increase in specific volatiles, and alterations in the sugar/acid balance etc. JA is associated with a wide range of processes including biotic and abiotic stress tolerance, seed germination and leaf senescence shown in Fig.1.

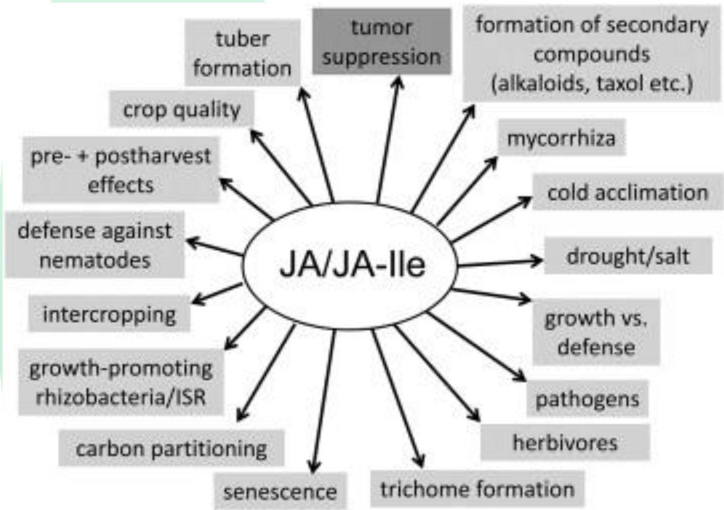

Fig.1: Various responses of jasmonates **(Wasternack, 2014)**

JASMONATES also regulates Ripening in fruits

Phytohormones act either near to or transport to other parts from their sites of synthesis to mediate physiological, biochemical and/or molecular responses of plants under optimal or stressful conditions. Jasmonic acid and its conjugates, such as methyl jasmonate (MeJA) and jasmonoyl-isoleucine (JA-Ile), collectively known as jasmonates (JAs), serve as natural plant growth regulators and are ubiquitous in the plant kingdom. Acting as stress modulators JAs can suppress or enhance plant stress responses. MeJA, initially identified in flowers of *Jasminum grandiflorum* (**Demole *et al*., 1962).** Recently, it has been shown that a significant acceleration in ripening in MeJA-treated fruit was observed, along with the accelerated changes of ethylene production, the enhanced activities and expression levels of ACS and ACO **(Tao *et al*., 2021).**

The Jasmonate biosynthesis pathway

Briefly presented in Fig.2, JAs are derived from a-linolenic acid liberated from membrane phospholipids by the action of phospholipase A (PLA). a-Linolenic acid is first converted to 13-hydroperoxy linolenic acid (13-HPOT) and then to 12-OPDA in the chloroplasts in a series of reactions catalyzed by 13-lipoxygenase, allene oxide synthase (AOS), and allene oxide cyclase (AOC), respectively. Both AOS and AOC are chloroplastic enzymes 12-OPDA is then transported to peroxisomes either passively or actively by the ABC (ATP-binding cassette) transporter COMATOSA (CMS). 12-OPDA is subsequently reduced by 12-OXOPHYTODIENOATE REDUCTASE3 to 3-oxo-2-2′ (Z-pentenyl)-cyclopentane-1-octanoic acid (OPC:8), which then undergoes three cycles of b-oxidation in the peroxisomes to produce Jasmonic acid. Jasmonic acid is further modified in the cytosol to produce various Jasmonic acid derivatives.

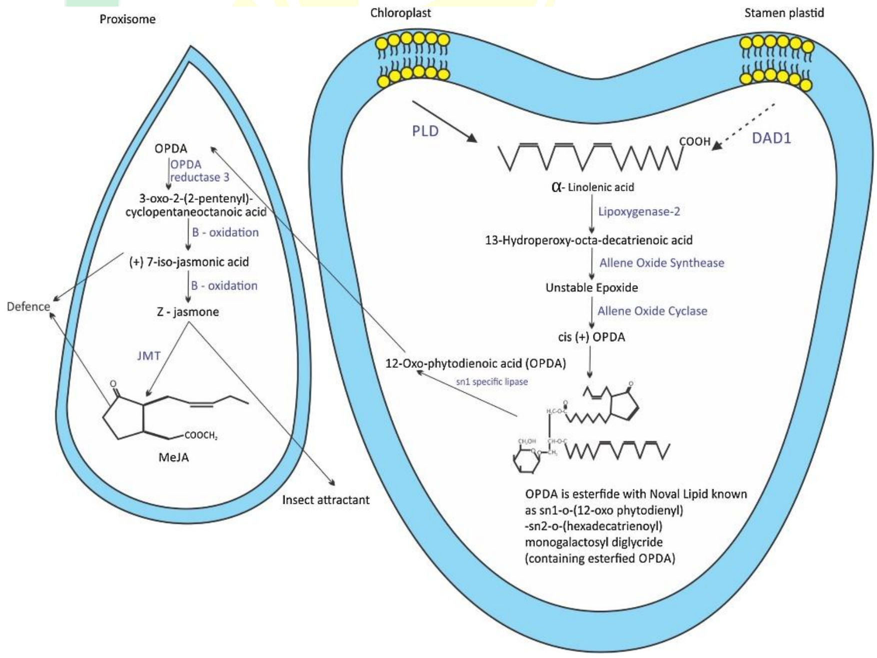

Fig. 2. Major steps involved in the synthesis of methyl jasmonates (MeJA) from α-linolenic acid. [Redrawn based **(Wasternack and Song, 2017)**]

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Jasmonate perception and signalling

Jasmonic acid (JA) perception via the COI1–JAZ co-receptor complex – mechanisms in JA-induced gene expression are presented in Fig. 3. In the resting state (left, low JA-Ile level), the binding of MYC2 to a G-box within the promoter of a JA-responsive gene does not activate transcription due to binding of the repressors Jasmonate ZIM domain proteins (JAZs) to MYC2. The co-repressors Novel Interactor of JAZ (NINJA) bound to JAZs, and TOPLESS (TPL) repress transcription via HISTONE DEACETYLASE 6 (HDA6) and HDA19. Upon stimulation (right, high JA-Ile level), JAZs are recruited by COI1 and subjected to ubiquitinylation and subsequent degradation by the 26S proteasome. Subsequently, MYC2 can activate transcription of early JA-responsive genes such as those encoding JAZ and MYC2. Transcription is mediated by the subunit 25 of the Mediator complex (MED25). ASK1, Arabidopsis SKP1 (S-phase kinase-associated protein 1) homologue; CUL, CULLIN; E2, ubiquitin-conjugating enzyme; MYC2, bHLHzip transcription factor; RBX, RING-H2 protein; SCF-complex, complex consisting of Skp1, Cullin-1 and F-box protein; Ub, ubiquitin.

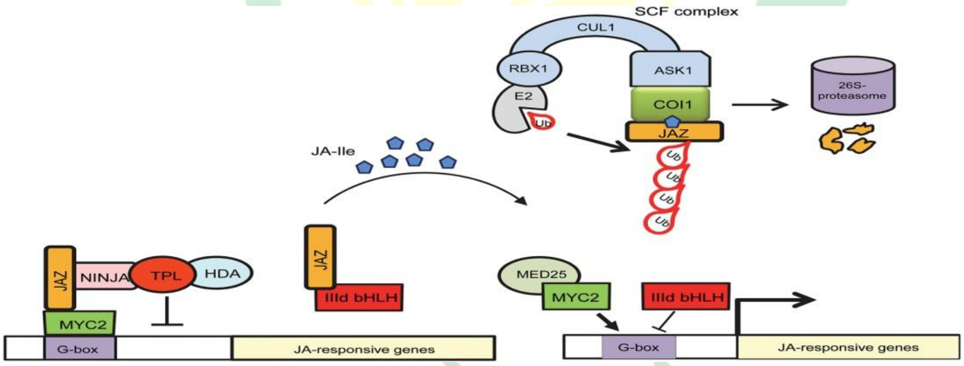

Fig.3. Mechanisms in JA-induced gene expression

Crosstalk of Jasmonate (JA) with the signalling pathways of other phytohormones (Fig.4)

• In the interaction between JA and GA and MYC2 is the main component involved.

• JAZ repressors interfere with the repressing activity of DELLA on PIF3 and this promotes growth.

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• On the other hand, DELLAs interact with JAZ repressors, relieving MYC2 from JAZ repression and contribute to JA-mediated defence responses by activation of MYC2, while reciprocal interference between JAZ and DELLAs would release their respective downstream targets (e.g., PIF3 and MYC2) to modulate the JA and GA signalling antagonism.

• MYC2 is also positively regulated by ABA. Upon perception of ET signals, the ET receptor ETR1/CTR1 complex is inactivated, and EIN3 and EIL1 are stabilized to activate ET responses.

• The JAZ inhibition on EIN3/EIL1 mediates JA and ET signaling synergy in plant resistance, whereas the reciprocal counteraction between MYC2 and EIN3/EIL1 mediates the JA and ET signalling antagonism.

• Cytokinin and JA regulate each other production under stress conditions.

• The JA signalling pathway is linked with auxin homeostasis through the modulation of YUCCA8 and YUCCA9 gene expression in Arabidopsis.

• Among JA biosynthetic genes, the expression level of DAD1 was markedly decreased in the double mutant, suggesting that ARF6 and ARF8 are required for activation of DAD1 expression.

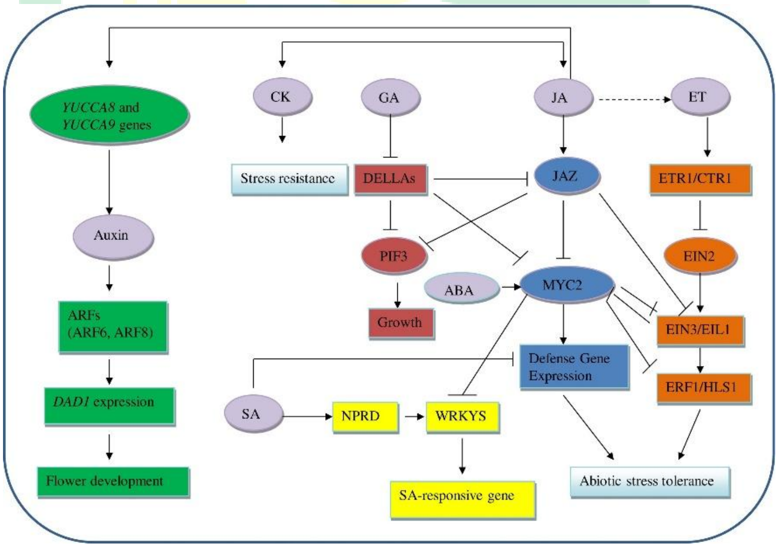

Fig.4.Crosstalk of jasmonate (JA) with the signalling pathways of other phytohormones.**(Per*etal*., 2018)**

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Abbreviations: (ETR1, ethylene response1**;** ERF1, ethylene response factor 1; CTR1, constitutive triple response 1**;** PIF3, phytochrome interacting factor3; JAZ, jasmonate ZIM domain; EIN3, ethylene insensitive; EIL, ethylene insensitive 3-like1 protein; ERF1, ethylene response factor 1; HLS1, HOOKLESS 1; ARF, Auxin response factor, WRKYS, (TF); DAD1, defective in anther dehiscence1) Positive and negative regulatory actions are indicated by arrows and lines with bars, respectively, whereas double-sided arrows indicate physical interactions.

Jasmonates and Ethylene interaction

Jasmonic acid and ethylene can act antagonistically or synergistically in controlling stress responses or development. The JA-ethylene interaction has been linked mainly through ethylene (ET)-activated transcription factors ETHYLENE INSENSITIVE3 (EIN3) and its close homolog EIN3-Like1 (EIL1). JA-activated TF MYC2, on the one hand, promote EIN3 degradation through binding to the promoter of an F-box gene, EIN3 BINDING F-BOX PROTEIN1, to induce its expression, and on the other, physically interact with EIN3 and inhibit its DNA binding activity. In fig.5**.** JA-activated MdMYC2 promotes ethylene biosynthesis in apples through three mechanisms:

(i) Enhancing the transcription of both *MdACS1* and *MdACO1* by binding to their promoter

(ii) Enhancing the transcription of *MdERF3* by binding to its promoter, which in turn promotes the transcription of *MdACS1*

(iii) Interacting with MdERF2, which prevents MdERF2 from binding to the *MdACS1* promoter and from interacting with MdERF3, resulting in more MdERF3 being available for binding to the *MdACS1* promoter and a consequent increase in *MdACS1* transcription.

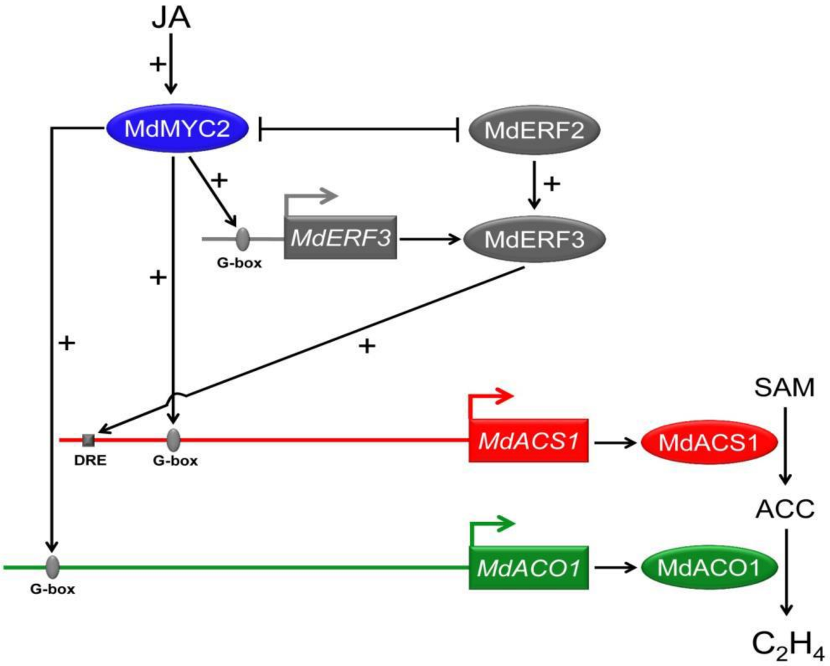

Figure.5.Model Showing the Promotion of Ethylene Biosynthesis **(Li *et al*, 2017)**

Abbreviation: (DRE, dehydration-responsive element; ERF-binding site; G-box, MYC-binding site; SAM, S-adenosyl methionine; ACC, 1-aminocyclopropane-1-carboxylic acid;C_2H_4, ethylene; JA, jasmonate)]

Conclusion:

As research on the biosynthesis and activity of plant hormones progresses, it is becoming clear that a large diversity of metabolites related to different phytohormones play a role in plant growth and development. Efforts are required to extend the shelf life without compromising its value and consumer acceptability and constitute a major challenge. MeJA involved fruit development and ripening process through regulation of anthocyanin, volatile compounds accumulation, chlorophyll and fruit softening impairment. MeJA showed molecular crosstalk with the hormone ethylene to facilitate the fruit to accomplish the appropriate physiological and developmental responses. The role of JAs in defence responses and growth protection promises to pave the way in the protection of crop plants and increase crop quality which ultimately leads to food security. Thus, the present views point out that, further studies to decipher specific JA roles and their signalling pathway-associated components during ripening is required.

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