



Review

Jasmonates in plants under abiotic stresses: Crosstalk with other phytohormones matters



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ABSTRACT

Jasmonates (JAs) are naturally occurring plant growth regulators and ubiquitous in plant kingdom. JAs are involved in the improvement of crop performance under natural and changing environmental conditions. Additionally, JAs are also known to interact with other phytohormones and thereby, modulate growth and development of plants and their abiotic stress responses. This review aimed to dissect available information on the role and underlying mechanisms of JAs in plant developmental responses and plant tolerance to major abiotic stresses, and its crosstalk with other major phytohormones in regulating the process. The major points potentially important for future research in the current direction are also summarized. The adoption of exhaustive approaches is advocated to unveil mechanisms underlying abiotic stress-mediated control of up-regulation of JA biosynthesis pathway and its genetic regulation and hormone homeostasis.

1. Introduction

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). It is also a well-known phenomenon that 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 plant kingdom (Ghasemi Pirbalouti et al., 2014). JAs have been identified as growth regulators in many plant cultivars and induce a wide variety of developmental responses (Engelberth et al., 2001). Acting as stress modulator JAs can suppress or enhance plant stress responses (Agrawal et al., 2003). MeJA-mediated up-regulation of stress defense, and secondary metabolism processes has been reported in plants (Chen et al., 2011). MeJA can also significantly

control photosynthesis and antioxidant metabolism via modulating proteome profile (Maserti et al., 2011). JAs have been well documented for their important roles in plant responses to abiotic stresses such as heavy metals (Maksymiec et al., 2005), drought (Brossa et al., 2011), salt (Dong et al., 2013; Qiu et al., 2014; Zhao et al., 2014) and heat stress (Clarke et al., 2009). JAs have been advocated to significantly contribute to plant stress responses mainly by playing role as a signal of developmentally- or environmentally-regulated expression of various genes responsible for tolerance (Kazan, 2015; Santino et al., 2013; Wasternack and Hause, 2013; Wasternack, 2014; Ahmad et al., 2016; Wasternack and Strnad, 2016). Notably, the significance of the outcomes of JAs-interaction with other plant hormones in plant stress tolerance has also been documented (Kazan and Manners, 2012; Kazan, 2015; Ahmad et al., 2016; Wasternack and Strnad, 2016; Wasternack and Song, 2017). However, literature is scanty on JA crosstalk with other major phytohormones in plants under optimal and representative abiotic stress factors. Considering the recent literature, this paper dissects the role and underlying mechanisms of JA-regulated plant growth

Abbreviations: AOS, allene oxide synthase; APX, ascorbate peroxidase; bHLH, basic helix-loop-helix; BRs, brassinosteroids; CAT, catalase; COI, coronatine insensitive; DHAR, dehydroascorbate reductase; HPO DE, hydroperoxy octadecadienoic acids; HSP, heat shock protein; JA, jasmonates; JA-Ile, jasmonoyl-isoleucine; JAZ, jasmonate zim domain; JIH, jasmonoyl-isoleucine; LOXs, lipoxygenases; MDHAR, monodehydroascorbate reductase; MeJA, methyl jasmonate; NINJA, novel interactor of JAZ; NO, nitric oxide; OPC, 3-oxo-2-(Z)-pentenyl-cyclopentane-1-octanoic acid; OPDA, 12-oxophytodienoic acid; OPR, OPDA reductase; PAL, phenylalanine ammonia lyase; PPO, polyphenol oxidase; PR, pathogenesis-related; PS, photosystem; PUFAS, polyunsaturated fatty acids; SAG, senescence-associated gene; SCF, Skp/Cullin/F-box complex; SOD, superoxide dismutase; TAD, transcription activation domain; TF, transcription factors; TPIs, thiol protein inhibitors; TPRs, TPL-related proteins; α -LA, α -linolenic acid

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and development in optimal and major abiotic stress conditions, presents crosstalks on and interaction-outcomes of JA with other phytohormones, and also includes major points potentially important for future research in the current direction.

2. Jasmonates

Jasmonates are simple lipid-derived oxylipins produced as a result of lipoxygenases-mediated oxygenation of polyunsaturated fatty acids (PUFAs). Notably, oxylipins share a high degree of structural and functional similarity to prostaglandins found in animals (reviewed by Kombrink, 2012). MeJA, one of the conjugates of JA is a fragrant volatile compound initially identified in flowers of *Jasminum grandiflorum* (Demole et al., 1962). The first isolation of JA was reported from the culture filtrate of the fungus *Lasioidiplodia theobromae* (Alderidge et al., 1971). Later, JA-specific physiological responses were observed when root growth inhibition and promotion of senescence in Osaka (Japan) and Halle (Germany), respectively were found in the early 80 s (Hause and Schaarschmidt, 2009).

2.1. Biosynthesis

Various aspects of JA biosynthesis in plants have been extensively reviewed and discussed (Acosta and Farmer, 2010; Wasternack and Hause, 2013; Wasternack and Song, 2017). The biosynthesis of JA occurs through octadecanoid pathway, in which translocation of lipid-intermediates takes place from chloroplast membranes into cytoplasm and then into peroxisomes (León, 2013) (Fig. 1). Herein, the JA biosynthesis occurs from the oxidation of phospholipid α -linolenic acid (C18:3) released from chloroplast membranes through the action of phospholipases (PLDs). In chloroplast membrane, linolenic acid is converted into 12-oxophytodienoic acid (OPDA) in three steps. In the subsequent dioxygenation steps, a chloroplastic 13-lipoxygenases (LOXs; 13-LOX and 9-LOX) oxidize α -linolenic acid (α -LA) and generate the 13-hydroperoxy derivative of LA hydroperoxy octadecadienoic acids (e.g., 13S-HPODE and 9S-HPODE) (Bannenberg et al., 2009). Thereafter, 13S-HPODE is dehydrated with the help of enzyme allene oxide synthase (AOS; EC 4.2.1.92) into the 12-oxo phytodienoic acid

(12-OPDA), also known as allene oxide. In the peroxisome, oxidation of exported OPDA to 3-oxo-2-(Z)-pentenyl)-cyclopentane-1-octanoic acid (OPC:8) is performed by the enzyme OPDA reductase (OPR; EC 1.3.1.4). Finally, the carbon side chain from the precursor molecule is shortened through three cycles of β -oxidation in the peroxisome (Ziegler et al., 2000; Bannenberg et al., 2009; Lyons et al., 2013). Three of LOXs namely, LOX2, LOX3 and LOX4 have been reported in *Arabidopsis thaliana* genome (Bell and Mullet, 1993; Caldelari et al., 2011). Both AOS and AOC are chloroplastic enzymes (Ziegler et al., 2000; Hause et al., 2003). However, OPDA is exported from chloroplast to peroxisome and potentially involves the carrier COMATOSE1/PEROXIMAL 1/PEROXISOME ABC TRANSPORTER (ABC CTS1/PXA1/PED3) (Zolman et al., 2001; Theodoulou et al., 2005; Footitt et al., 2007). JA is also metabolized into a variety of products that include the methyl ester (MeJA), amide conjugates with amino acids (JA-Ile), conjugate with sugars and hydroxylated and didehydro derivatives (Staswick, 2008). Different plant species have been used to reproduce the proteins and enzymes required for JA biosynthesis and perception and some of them have also been crystallized such as 13-AOS, AOC, ACYL-CoA-OXIDASE1, JAR1, 13-LOX, OPR3 and the SCFCO11-JAZ-co-receptor complex (Kombrink, 2012; Wasternack and Hause, 2013).

2.2. Signaling

A list of the key regulators of JA signaling includes JASMONATE ZIM DOMAIN (JAZ) proteins (ZIM-domain protein) (Thines et al., 2007), F-box protein CORONATINE INSENSITIVE 1 (COI1), Skp/Cullin/F-box complex (SCF^{COI1}), a type of E3 ubiquitin ligase (Deshaies, 1999), and also the 26S proteasome (Turner et al., 2002). The JAZ proteins have been considered as a crucial interface in the JA signaling cascade (Pauwels and Goossens, 2011). These proteins are negative regulators of JA-induced gene expression by acting as repressor of JA-signaling, and are degraded through the SCF^{COI1}-dependent 26S proteasome pathway. The molecular mechanisms by which JAZ proteins repress gene expression have been shown by Pauwels et al. (2010). These authors showed that the *Arabidopsis* JAZ proteins recruit the Groucho/Tup1-type co-repressor TOPLESS (TPL) and TPL-related proteins (TPRs) through a previously uncharacterized adaptor protein,

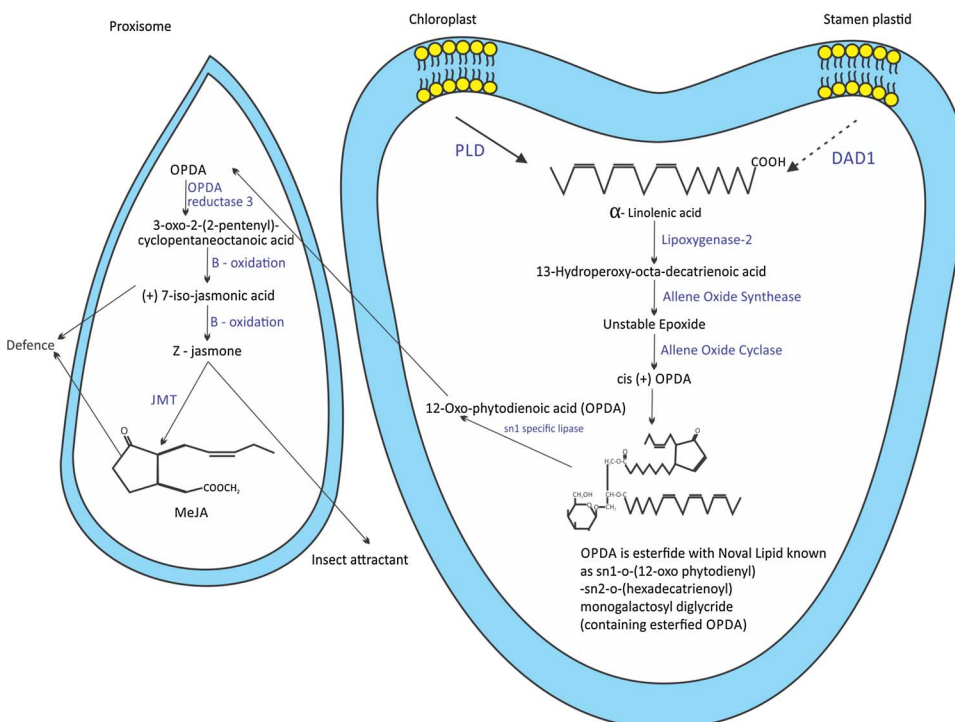


Fig. 1. Major steps involved in the synthesis of methyl jasmonates (MeJA) from α -linolenic acid. [Redrawn based on Wasternack and Song (2017)].

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