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Research review paper

Action of jasmonates in plant stress responses and development — Applied aspects ☆

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ABSTRACT

Jasmonates (JAs) are lipid-derived compounds acting as key signaling compounds in plant stress responses and development. The JA co-receptor complex and several enzymes of JA biosynthesis have been crystallized, and various JA signal transduction pathways including cross-talk to most of the plant hormones have been intensively studied. Defense to herbivores and necrotrophic pathogens are mediated by JA. Other environmental cues mediated by JA are light, seasonal and circadian rhythms, cold stress, desiccation stress, salt stress and UV stress. During development growth inhibition of roots, shoots and leaves occur by JA, whereas seed germination and flower development are partially affected by its precursor 12-oxo-phytodienoic acid (OPDA). Based on these numerous JA mediated signal transduction pathways active in plant stress responses and development, there is an increasing interest in horticultural and biotechnological applications. Intercropping, the mixed growth of two or more crops, mycorrhization of plants, establishment of induced resistance, priming of plants for enhanced insect resistance as well as pre- and post-harvest application of JA are few examples. Additional sources for horticultural improvement, where JAs might be involved, are defense against nematodes, biocontrol by plant growth promoting rhizobacteria, altered composition of rhizosphere bacterial community, sustained balance between growth and defense, and improved plant immunity in intercropping systems. Finally, biotechnological application for JA-induced production of pharmaceuticals and application of JAs as anti-cancer agents were intensively studied.

Contents

Abbreviations: AM, arbuscular mycorrhiza; AOC, allene oxide cyclase; 13-AOS, allene oxide synthase; *coi1*, *coronatine insensitive1*; *dad1*, *delayed anther dehiscence1*; GA, gibberellic acid; ISR, induced systemic resistance; JA, jasmonic acid; *jai1*, *JA insensitive1*; JAR1, JA-amino acid synthetase; JAZ, JASMONATE ZIM DOMAIN PROTEIN; 13-LOX, 13-lipoxygenase; MeJA, JA methyl ester; OPDA, *cis*-(+)-12-oxo-phytodienoic acid; OPR3, OPDA reductase3; PGPR, plant growth promoting rhizobacteria; PLA_1, phospholipase A1; RNS, root nodule symbiosis; SA, salicylic acid; SCF, Skp1/Cullin/F-box complex; TA, tuberonic acid; VOCs, volatile organic compounds.

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1. Introduction

Jasmonates are key signaling compounds in plant responses to biotic and abiotic stresses as well as in development. Jasmonic acid (JA) and its derivatives are synthesized from α-linolenic acid esterified in galactolipids of chloroplast membranes. α-Linolenic acid is released by a phospholipase A1 and oxygenated by a 13-lipoxygenase (13-LOX) to a 13-hydroperoxyoctadecatrienoic acid, which is converted by a 13-allene oxide synthase (13-AOS) to a highly unstable epoxide (Fig. 1). This epoxide cyclizes to *cis*-(+)-12-oxo-phytodienoic acid (OPDA) by the action of an allene oxide cyclase (AOC). The second half of JA biosynthesis takes place in peroxisomes. The final product (+)-7-*iso*-JA is in equilibrium with (-)-JA and is released into the cytosol. Among numerous metabolic conversions of JA, such as hydroxylation, *O*-glucosylation, decarboxylation, carboxylation, methylation, conjugation or sulfation of JA and hydroxylated JA, respectively, the conjugation of JA with amino acids such as L-isoleucine is the most important reaction catalyzed by JAR1 (reviewed in Wasternack, 2007; Wasternack and Hause, 2013). The product (+)-7-*iso*-JA-L-Ile is the most bioactive JA compound (Fonseca et al., 2009) and is the ligand of the SCF^{COI1}–JAZ-co-receptor complex (Sheard et al., 2010) (cf. below). All enzymes and proteins involved in JA biosynthesis and perception have been cloned from different plant species and some of them have been crystallized (e.g. 13-LOX, 13-AOS, AOC, ACYL-CoA-OXIDASE1, OPR3, JAR1 and the SCF^{COI1}–JAZ-co-receptor complex) (Kombrink, 2012; Wasternack and Hause, 2013). Regulation of JA biosynthesis takes places by a positive feedback loop, by substrate availability and by tissue specificity (Wasternack, 2007). The substrate availability is the reason, why constitutive overexpression of genes coding for enzymes of JA biosynthesis such as 13-AOS and AOC did not lead to elevated JA levels (Stenzel et al., 2003). Such transgenic lines produced increased amounts of JA only upon wounding or other environmental stimuli leading to release of α-linolenic acid. The initial rationale behind such transgenic approaches was the expectation to generate plants with increased resistance to herbivores or necrotrophic pathogens. Both responses belong to the well-studied signaling pathways, where JA is involved. Other JA-mediated processes are plant responses to desiccation stress, ozone stress, UV-stress, osmotic stress, cold stress, or light stress, but also formation of secondary metabolites and adaptation to seasonal and circadian rhythm are regulated by JA (Fig. 2). Moreover, jasmonates are involved in the regulation of beneficial plant–microbe interactions, such as interactions with arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria (PGPR). During plant development the following processes are mediated by JA: Male and female organ development, embryo development, sex determination in maize, seed germination, seedling development, root growth, gravitropism, trichome formation, tuber formation, leaf movement, and leaf senescence. Over the last two decades of JA research a remarkable improvement of information accumulated on enzymes and proteins involved in JA biosynthesis and signaling pathways of developmentally regulated processes and of

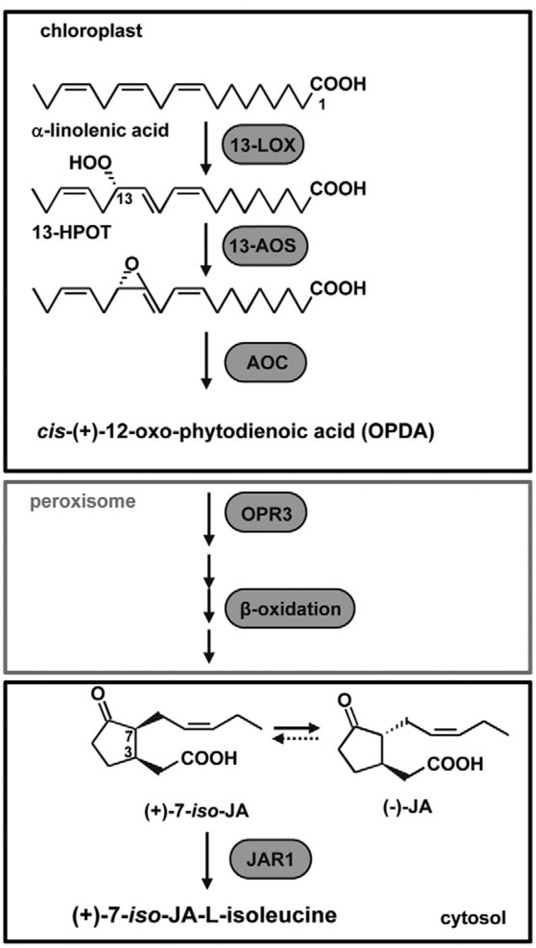

Fig. 1. Biosynthesis of jasmonic acid (JA) and (+)-7-*iso*-JA-L-isoleucine takes place in three different compartments of a plant cell. In the chloroplast, α-linolenic acid is released from membranes, oxygenated by a 13-lipoxygenase (13-LOX) to a hydroperoxyoctadecatrienoic acid (13-HPOT), which is converted to an unstable epoxide by a 13-allene oxide synthase (13-AOS) and cyclized by an allene oxide cyclase (AOC) to *cis*-(+)-12-oxo-phytodienoic acid (OPDA). Upon transport of OPDA into peroxisomes the cyclopentenone ring is reduced by an OPDA reductase3 (OPR3). Subsequently, the fatty acid β-oxidation machinery catalyzes shortening of the carboxylic acid side chain to (+)-7-*iso*-JA, which is released into the cytosol and epimerizes to (−)-JA. Conjugation with amino acids, such as isoleucine, is catalyzed by jasmonoyl–isoleucine conjugate synthase (JAR1).

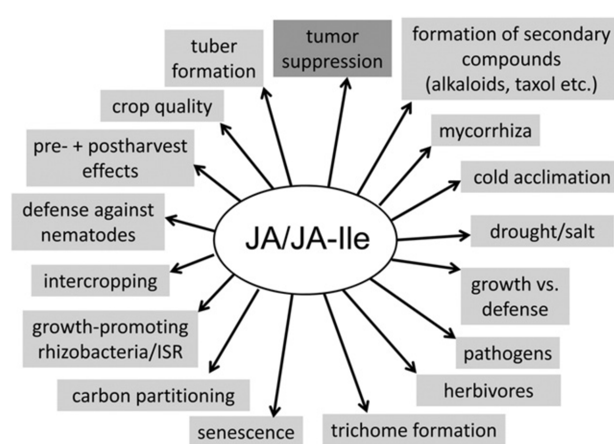

Fig. 2. Jasmonic acid (JA) and its conjugate with isoleucine are signals in various responses to biotic and abiotic stresses, in developmental processes, but also in applied aspects of agronomical importance such as crop quality, intercropping or defense against necrotrophic pathogens or herbivores. Tumor suppression by JA/JA-Ile might be of importance via pharmaceuticals prepared from plant extracts with high JA/JA-Ile content.