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Review

Jasmonates counter plant stress: A Review

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ABSTRACT

Jasmonates (JAs), the derivatives of lipids, act as vital signaling compounds in diverse plant stress responses and development. JAs are known to mediate defense responses against herbivores, necrotrophic pathogens, nematodes and other micro-organism besides alleviating abiotic stresses including UV-stress, osmotic stress, salt stress, cold stress, temperature stress, heavy metal stress, ozone stress etc. Jasmonate signaling does not work alone while mediating defense responses in plants but it functions in multifarious crosstalk network with other phytohormone signaling pathways such as auxin, gibberellic acid (GA), and salicylic acid. The present review gives the holistic approach about the role of jasmonates in counteracting the stress whether biotic or abiotic. Jasmonates regulate beneficial plant–microbe interactions, such as interactions with plant growth promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi.

Contents

1. Introduction

Plants being sessile have no opportunity other than to adapt their growth and form to the changing environment and need to coordinate their growth and physiology accordingly. Plants live in an environment which is most of the times, characterized by the presence of different types of stresses both biotic and abiotic. Phytohormones play a remarkable role in plant growth, development and response to stresses. Plant hormones regulate diverse developmental processes and signaling networks in plants under different abiotic stresses. With the advancement in plant biology research it has been established that phytohormones have the potential in alleviating the deleterious effects posed by abiotic stresses (Masood et al., 2012; Khan et al., 2013). Plant defense

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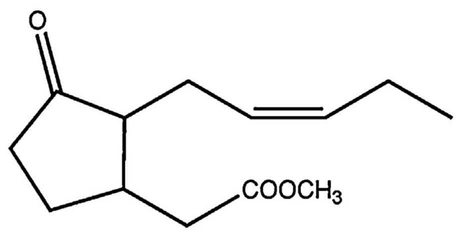

Fig. 1. Structure of methyl jasmonate.

responses are mediated by three major pathways of the phytohormones, jasmonic acid (JA), salicylic acid (SA) and ethylene (ET). The fine tuning of plant response to pathogen depends on the synergistic or antagonistic interactions between these three pathways (Takahashi et al., 2004).

Jasmonates are important cellular regulators involved in diverse developmental processes such as seed germination, root growth, gravitropism, trichome formation, embryo development, sex determination (maize), fertility, seedling development, tuber formation, leaf movement, fruit ripening and leaf senescence (Creelman and Mulpuri, 2002; Wasternack and Hause, 2002; Wasternack, 2014). Jasmonates are known to regulate a wide range of plant processes, such as growth and development, including defense against biotic and abiotic stresses (Browse and Howe, 2008; Browse, 2009; Reinbothe et al., 2009). The derivatives of α-linolenic acid viz. jasmonic acid and jasmonoyl-L-isoleucine (JA-Ile) are known to accumulate in plants in response to biotic and abiotic stress (Wasternack, 2007; Gfeller et al., 2010). Jasmonic acid is also known to regulate the leaf and root morphogenesis in soybean (Xue and Zhang, 2007).

Jasmonic acid was first of all isolated from the fungal cultures of *Lasiodiplodia theobromae* while as methyl jasmonate (MeJA; Fig. 1) was obtained from the essential oil of *Jasminum grandiforum* L. and *Rosmarinus officinalis* L. Jasmonates are present in almost all higher plants and the level is higher in flowers and reproductive tissues, while as very low in roots and mature leaves.

The derivatives of jasmonic acid are of different types and mainly hydroxylated forms like tuberonic acid and cucurbic acid and other types of amino acid conjugates (Hamberg and Gardner, 1992). According to Koda (1992) tuberonic acid (12-hydroxy-JA) and its glucoside regulate the tuber formation in potato; however, recent efforts have indicated that the process is controlled by light, temperature and gibberellic acid (Lin et al., 2013). Therefore, it was concluded that the JAs control tuber formation indirectly through crosstalk with GA signaling (Wasternack and Hause, 2013). Recently, one of the derivatives of the jasmonic acid, namely tetra-hydro-jasmonic acid (LR2412) has shown anti-aging potential in case of human skin. LR2412 is known to increase the expression of hyaluronase synthase 2 (HAS2) and hyaluronase synthase 3 (HAS3) which consequently increase the synthesis of hyaluronic acid (HA) (Michelet et al., 2012).

2. Structure and biosynthesis of jasmonates

Jasmonates are fatty acid derived cyclopentanones that occur ubiquitously in the plant kingdom. Jasmonates belong to the family of oxygenated fatty acid derivatives collectively called as oxylipins, which are produced via the oxidative metabolism of polyunsaturated fatty acids. Jasmonates are synthesized in plants by means of the octadecanoid pathway (Fig. 2), and are similar to animal anti-inflammatory prostaglandins in structure and biogenesis (Wasternack and Hause, 2002). Certain stimuli activate phospholipases to release α-linolenic acid (18:3) from membrane lipids. The linolenic acid is oxygenated by lipoxygenase (LOX) to form 13(S)-hydroxy linolenic acid (13-HPOT), which is then converted to 12-oxo-phytodienoic acid (OPDA) by allene oxide synthase (AOS) and allene oxide cyclase (AOC). Jasmonic acid is synthesized from OPDA through reduction and three steps of β-oxidation after which it is catabolised further by JA carboxyl methyltransferase (JMT) to form its volatile counterpart MeJA (Song et al., 2000; Seo et al., 2001). Since JA is derived from 18:3 (octadecatrienoic acid), the series of enzymatic reactions leading to JA biosynthesis is often referred to as the octadecanoid pathway. Recently, oxylipin content analysis of *Arabidopsis* leaves revealed the existence of a novel C_{16} cyclopentenone called dn-OPDA (Weber, 2002).

3. Jasmonate metabolism

The metabolism of jasmonic acid occurs through seven different routes as is known from the information of corresponding end products of each route (Fig. 3).

1. The adenylation at the carboxylic end of JA by the enzyme JA conjugate synthase (JAR1) leads to the formation of amino acid conjugates (Staswick and Tiryaki, 2004).
2. Reduction in the keto group of the cyclopentenone ring leads to the formation of cucurbic acid (Sembdner and Parthier, 1993).

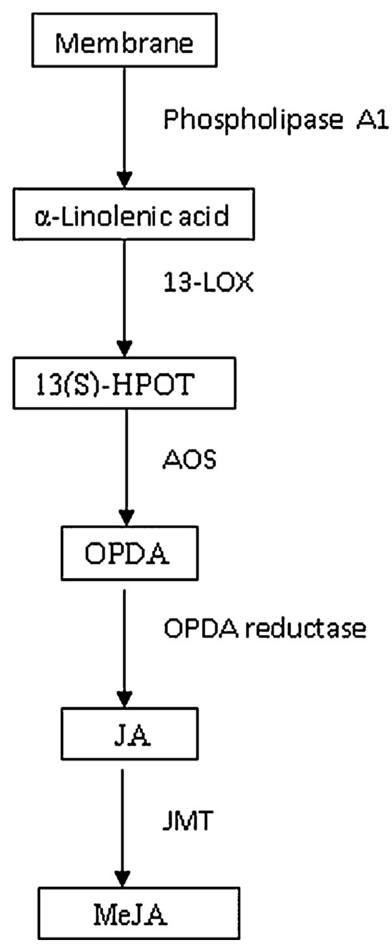

Fig. 2. Main pathway of jasmonate biosynthesis. A phospholipase A_1 releases α-linolenic acid from membrane lipids. The α-linolenic acid is oxygenated by lipoxygenase (LOX) to form 13(S)-hydroxy linolenic acid (13-HPOT), which is then converted to 12-oxo-phytodienoic acid (OPDA) by allene oxide synthase (AOS) and allene oxide cyclase (AOC). Jasmonic acid (JA) is synthesised from OPDA through reduction and three steps of β-oxidation, and is further converted to methyl jasmonate (MeJA) by JA carboxyl methyl transferase (JMT) (Cheong and Do Choi, 2003).