

Review Article

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Defense Induced by Jasmonic Acid: A Review

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A number of novel JA derivatives have been synthesized, isolated, and characterized. A clearer picture of jasmonate biosynthesis and functions has emerged that in many respects resembles the synthesis and functions of prostaglandins and leukotrienes in mammals. Jasmonates are produced from a-linolenic acid from lipids of damaged plant membranes. The biosynthesis of these signalling compounds can be triggered through the activation of cell membrane receptors by pathogens, peptide signals, or wounding. These jasmonates are widely distributed in plants and affect a various processes, including fruit ripening, production of viable pollen, root growth, and plant responses to wounding, abiotic stress, infections, and insects. Many of these new compounds have potent biological activity, promising that novel types of pharmacological agents possessing new mechanisms of action could soon become available. All these effects of JA are indirect, due to the well-studied induction of the biosynthesis of secondary compounds like anthocyanins, glucosinolates, terpenoids, or phenolics via transcription factors such as the Myb, Myc, and ORCA families. JA and its derivatives are widely use in daliy life as medicinal, cosmetic, and flavoring uses and other applications in agriculture systems. During the last 20 years, the many of research and inventions have showed that JA, (p)-7-iso-JA and MJ have anticancer activity against various cancers (e.g., prostate, lymphoid, breast, blood, skin cancers, etc.).

Introduction

Plants are very delicate have no opportunity other than to adapt their growth and changing with environment and need to coordinate their growth and physiology responses. Plants present in an environment in ancient time characterized by the presence of various types of stresses both biotic and abiotic. Phytohormones play important role in plant growth, development and response to stresses. Plant hormones regulate diverse developmental processes and send the signals networks in plants under different abiotic stresses. With the advancement in plant

biology research it has been established that phytohormones have the potential to remove the deleterious effects posed by abiotic stresses (Masood *et al.*, 2012; Khan *et al.*, 2013). Plant defense 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). According to (Creelman and Mulpuri, 2002; Wasternack and Hause, 2002;

Wasternack, 2014 Jasmonates widely role in 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. Jasmonates regulate a wide range of plant processes, such as growth and development, including defense against biotic and abiotic stresses (Browse and Howe, 2008; Reinbothe *et al.*, 2009). Wasternack (2007) and Gfeller *et al.*, (2010) studied that the derivatives of a-linolenic acid viz. jasmonic acid and jasmonoyl-L-isoleucine (JAile) are accumulate in plants in response to biotic and abiotic stress. Xue and Zhang (2007) studied that Jasmonic acid regulate the leaf and root morphogenesis in soybean. Jasmonic acid was first of all isolated from the fungal cultures of *Lasiodiplodiatheobromae* while as methyl jasmonate (MeJA; Fig. 1) was obtained from the essential oil of *Jasminumgrandiforum* L. And *Rosmarinus officinalis* L. Jasmonates are present in all higher plants and the level is higher in flowers and reproductive tissues, while low in roots and mature leaves. The derivatives of jasmonic acid are various types and mainly hydroxylated forms like tuberonic acid and cucurbitic acid and other amino acid conjugates (Hamberg and Gardner, 1992). Koda (1992) revealed that tuberonic acid (12-hydroxy-JA) and its glucoside regulate the tuber formation in potato; however, recent study has indicated that the process is controlled by light, temperature and gibberellic acid (Lin *et al.*, 2013). Therefore, itwas concluded that the JAs control tuber formation indirectly through crosstalk with GA signaling (Wasternack and Hause, 2013). Recently Michelet *et al.*, 2012 found that 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

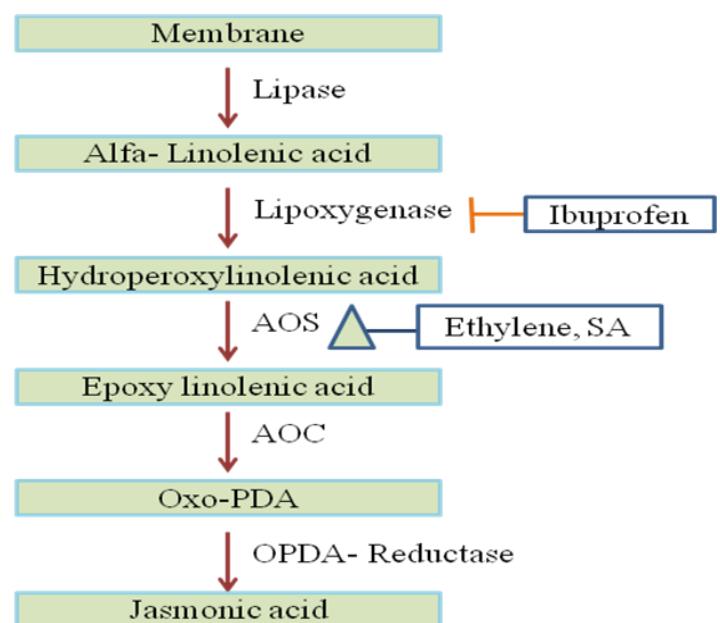
expression of hyaluronase synthase 2 (HAS2) and hyaluronase synthase 3 (HAS3) which consequently increase the synthesis of hyaluronic acid (HA). Plants are associated with diverse microbial communities that influence their health and nutrition. These organisms are known as the plant microbiome and used as more sustainably maintain or enhance global food security. To achieve this, ways to manipulate the structure of plant-associated microbial communities need to be identified. Recently, activation of the jasmonic acid (JA) plant defence pathway, that are involved in suppression of necrotrophic pathogens and herbivorous insects, was shown to alter the composition of the *Arabidopsis thaliana* root microbiome. Activation of the JA give signal to pathway increased the relative abundances of bacterial populations closely related to taxa that are reported to suppress phytopathogens and insects. This suggests that when these attack the plants may have evolved mechanisms to recruit symbionts that enhance their tolerance to biotic stress. Currently, however, it is not found whether the microbiomes of other plant species are influenced by activation of the JA pathway, and whether these effects, if any, are also present in endophytic compartments of the host. Given the intimate physical association between plants and endophytic symbionts, changes to the structure of endophytic communities may disproportionately influence host fitness. While JA give the signal has been shown to restrict endophytic colonisation of rice (*Oryza sativa*) by incompatible strains of nitrogen-fixing *Azospirillum* and suppress nodulation in *Lotus japonicus* it remains unknown whether JA gives the signal influences the overall structure of endophytic microbiomes. Wheat is one of the most important and widely grown crops worldwide. Despite this, the effects of JA signalling on wheat microbial communities have not been characterised. In this research, we used

phylogenetic marker gene sequencing to determine whether activation of the JA pathway altered the diversity of bacterial and archaeal communities associated with the wheat rhizosphere and root and shoot endophytic environments. Increased JA signalling was achieved via exogenous application of methyl jasmonate (MeJA) and confirmed by quantification of JA-associated gene transcripts. In the last year, we measured the total enzymatic activity and substrate utilisation profiles of microbial communities associated with the rhizosphere (Liu *et al.*, 2016). Phytohormones play important roles in mediating host responses to various abiotic stresses. Increasing evidence has shown that jasmonic acid (JA, or the related compound methyl jasmonate, MeJA) functions in diverse physiological processes in plants, such as the regulation of plant responses to abiotic stresses.

The exogenous application of JA to wheat seedlings for three days has been shown to significantly enhance the salt tolerance of these plants by increasing the activities of antioxidant enzymes and the concentrations of antioxidative compounds. MeJA improves salinity resistance in German chamomile by increasing the activity of antioxidant enzymes. The endogenous JA content has been shown to be markedly increased under drought and cold stresses but reduced under heat stress in rice. Expression profiling and physiological characterization on salinity stress response in barley reveal the JA-mediated adaptation to salinity stress. Zhao *et al.*, showed that a wheat allene oxide cyclase (AOC) gene enhances salinity tolerance via the JA signalling pathway⁸. The steady-state levels of two key enzymes in JA biosynthesis, lipoxygenase (LOX) and allene oxide synthase (AOS), and the content of JA are higher in salt-tolerant tomato cultivars⁹. The salt hypersensitivity of the *lox3* mutant can be complemented by MeJA¹⁰ (Zhang *et al.*, 2009).

Biosynthesis of jasmonate

The higher amounts of B present in soil also decrease the net photosynthetic rate, closing of stomatal, internal CO₂ concentration and total chlorophyll content in leaves (Aftab *et al.*, 2011). B toxicity leads to the accumulation of reactive oxygen species (ROS) in wheat (Gunes *et al.*, 2007), barley (Inal *et al.*, 2009) and tomato (Cervilla *et al.*, 2007). Paull *et al.*, 1992; Noctar *et al.*, 1997 found that when exposed to B stress include leaf burn, decreased fruit size and number, delayed development and reduced vigor. The typical symptoms showed by plant. Exogenous application of MeJA has been shown to counter the boron toxicity in plants. When boron stressed plants of *Artemisia* were foliarly sprayed with MeJA, it trigger the synthesis of antioxidant enzymes, reduced the amount of lipid peroxidation and enhances artemisinin content.



Role of jasmonates in chilling stress

Chilling injury (CI) creates storage problems for the horticultural crops, especially growing in the tropical and sub-tropical regions. The fruits of the tropical plants exhibit chilling

injury symptoms, including browning of the skin, greater firmness in texture, and off-flavor in the fruit. It has been found that MeJA treatment reduce the chilling injury in the fruits of plants like zucchini, mango, avocado, sweet pepper, tomato and papaya (Wang and Buta, 1994; Meir *et al.*, 1998; Gonzalez-Aguilar *et al.*, 2000, 2003). JAs induce the production of a diverse array of chemicals such as proteinase inhibitors, antimicrobial secondary compounds, antioxidants, pathogenesis-related and cellular protection molecules, including proteins involved in detoxification and redox balance (Farmer and Ryan, 1990; Farmer, 2007; Cao *et al.*, 2009; Soares *et al.*, 2010; Guo *et al.*, 2013; Zhou *et al.*, 2013; Gill *et al.*, 2013). MeJA significantly application reduced the CI index and electrolyte leakage in pineapple. Browning discoloration mostly occurs by the accumulation of phenolics compounds and the polyphenol oxidase in the fruits (Paull and Rohrbach, 1985). However, when the fruits of pineapple were treated with MeJA, total phenolic content was significantly reduced as compared to the non-treated plants, which ultimately protects the fruits from the browning discoloration. It has been discovered that MeJA treatment can reduce the development of chilling injury symptoms in zucchini (Wang and Buta, 1994) and mango (Gonzalez-Aguilar *et al.*, 2000).

Boron stress and role of jasmonate

Boron (B) is an essential nutrient element for growth and development of plants. However, in excess amount it may be toxic to the plants and can cause oxidative stress and considerably reduces the stem length, fresh and dry masses of the plants as in *Artemisia annua*. Aftab *et al.*, 2011 studied that the excess amounts of B present in soil also decrease the net photosynthetic rate, closing of stomatal, internal CO₂ concentration and total chlorophyll content in leaves. B toxicity

leads to the accumulation of reactive oxygen species (ROS) in wheat (Gunes *et al.*, 2007), barley (Inal *et al.*, 2009) and tomato (Cervilla *et al.*, 2007). The typical symptoms showed by plants when exposed to B stress include leaf burn, decreased fruit size and number, delayed development and reduced vigor (Paull *et al.*, 1992; Noctor *et al.*, 1998). Exogenous application of MeJA has been shown to counter the boron toxicity in plants. When boron stressed plants of *Artemisia* were foliarly sprayed with MeJA, it started to stimulate the synthesis of antioxidant enzymes, reduced the amount of lipid peroxidation and enhances artemisinin content.

Anticancer activity

JA and its derivatives, which are fatty acid-derived cyclopentanones, occur widely in the plant kingdom and have been known for various biological activities. One case study Halitschke *et al.*, 2004 found that the first report on jasmonate-induced anticancer activities exhibited their capacity to cause both cell death and suppression of cell proliferation. Ferrari *et al.*, 2003 found that Jasmonates are small hydrophobic compounds that act as plant stress hormones and can increase the survival of lymphoma-bearing animals and humans, and induce death in human leukemia, lung, colon, prostate, neuroblastoma, breast, and melanoma cell lines, and also effect in leukemic cells from chronic lymphocytic leukemia (CLL) patients. MJ was studied in topical application for precancerous and cancerous skin lesions (Pedranzani, *et al.*, 2003). Accordingly (Reinbot *et al.*, 2009) indicated that a JA derivative, 3-hydroxy-2(S)-(2Z-butenyl)- cyclopentane-1(S)-acetic acid, obtained by biotransformation with the fungus *Gibberellins fujikuroi*, was able to inhibit the growth of both androgen-sensitive (LNCaP) and androgen sensitive (DU-145)

prostate cancer cells. The apoptosis evoked by this new molecule appeared to be associated with an increase in reactive oxygen species (ROS) production (Reinbothe *et al.*, 2009). A study indicated that three JA derivatives obtained by biotransformation were specifically active on several types of cancer cells (Carvajal *et al.*, 2011, 2012, 2013).

Anti-inflammatory activities

The results of studies on the potential anti-inflammatory effects of MJ derived from the red alga Gracilaria verrucosashowed that MJ was comparable to or more effective than prostaglandin-like compounds (Dang *et al.*, 2008, and Dang *et al.*, 2012). A study indicated that of MJ analogs for their anti-inflammatory activities, the α -haloenones exhibited potent activity higher than those of natural anti-inflammatory prostaglandins (Dang *et al.*, 2012). Methyl 4,5-didehydrojasmonate also exhibited in vitro anti-inflammatory potency comparable to that of the most potent natural anti-inflammatory prostaglandin 15d-D. Among all these jasmonate analogs found that α -haloenone inhibited the production of pro-inflammatory mediators (nitric oxide (NO), interleukin (IL)-1b, IL-6, and tumor necrosis factor (TNF)-a) through the down-regulation of NF- κ B activity in lipo polysaccharide (LPS)-activated murine macrophages.

Antiparasitic activities

Gold *et al.*, (Gold *et al.*, 2003) reported that jasmonates had significant antiparasitic effects on human parasites, *Plasmodium falciparum* (an intra erythrocytic protozoan parasite, which is the cause of the most severe form of malaria), and *Schistosoma mansoni* (a parasitic worm residing in blood vessels, causing a serious human infestation). Another case (Park *et al.*, 2012) indicated that MJ induced a time- and dose-dependent decrease

in the number of live *Trichomonas vaginalis*, an important human parasite of the urogenital tract. Other researchers (Ofer *et al.*, 2008) also reported on the potential of employing MJ as a treatment for trichomoniasis, including its use against metronidazole-resistant strains.

In conclusion the recent years have been highly dynamic and productive for the field of JA research, with important discoveries emerging constantly. A large number of JA derivatives have been synthesized, isolated, and characterized. Jasmonate biosynthesis and functions has emerged which have potential to synthesis and functions of prostaglandins and leukotrienes in mammalians. Jasmonates are produced from α -linolenic acid from lipids which damaged plant membranes. The biosynthesis of these signalling compounds can be triggered through the activation of cell membrane receptors by pathogens, peptide signals, or wounding. These jasmonates are widely distributed in plants and affect a variety of processes namely as fruit ripening, production of viable pollen, root growth, and plant responses to wounding, abiotic stress, infections, and insects. Many of these new compounds have already been shown to have potent biological activity, promising that novel types of pharmacological agents possessing new mechanisms of action could soon become available. All these effects of JA are indirect, due to the well-studied induction of the biosynthesis of secondary compounds like anthocyanins, glucosinolates, terpenoids, or phenolics via transcription factors such as the Myb, Myc, and ORCA families. JA and its derivatives have emerged with medicinal, cosmetic, and flavoring uses and diverse applications in agriculture systems. During the last 20 years, the vast majority of studies and inventions have evidenced that JA, (β) -7-iso-JA and MJ have anticancer activity against various cancers (e.g., prostate, lymphoid, breast, blood, skin cancers, etc).

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