Review on Plant Response to Jasmonates (JAs) in Defense against Herbivory

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Abstract

Plants, being sessile throughout their life cycle, are vulnerable to various kinds of abiotic and biotic stress conditions. Jasmonic acid (JA) and its cyclopentanone derivatives are produced by plants. They are collectively known as jasmonates (JAs). Jasmonates (JAs) are universally known lipid-derived phytohormones which regulate overall plant growth under both abiotic and biotic stresses. They are helpful in developing root and reproductive system in plants. They coordinate with other plant hormones under changing environmental conditions. JAs alone or sometimes in combination with other plant hormones ameliorate stress conditions. They also participate in upregulation of antioxidant metabolism, osmolyte synthesis, and metabolite accumulation. Pretreatment and/or exogenous application of JA exhibited multi-stress resilience under changing environment as well as other biotic stress conditions.

Key Words: Jasmonates (JAs), Phytohormones, Plant-insect interaction, Signalling

Introduction

The study of Plant hormones is centuries old i.e., about the 5 classical hormones Auxin, Cytokinin, Abscisic acid, Gibberellic acid and Ethylene. However, there are many "non-traditional" plant growth regulators which include highly diverse group of oxidized compounds, collectively known as *oxylipins*. Oxylipins execute diverse functions ranging from developmental processes to stress responses in plants (Andersson *et.al.,* 2006). Plant oxylipins can be produced either enzymatically by Lipoxygenases (LOXs) or Dioxygenases (DOXs) or non- enzymatically by autoxidation of polyunsaturated fatty acids (Göbel and Feussner, 2009). One of the well characterized examples of oxylipins is Jasmonates (JAs). Jasmonates are cyclo-pentanone compounds or novel plant immune hormones which are derived from α- linolenic acid by the octadecanoid pathway. Chemical formula of JA is $C_{12}H_{18}O_3$ with molecular mass of 210.27 g/mol and density of 1.1 g/cm^3.

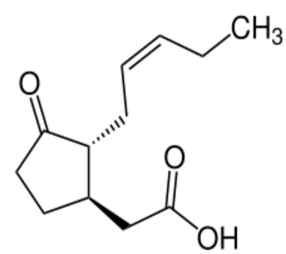

Fig 1: Wasternack and B. Hause (2013)

These multifunctional hormones are involved in plant development and defense processes (Seo *et.al*. 2001; Huang *et.al*. 2017; Per *et.al*. 2018). Besides developmental functions of plants, JAs activate plants against pathogens and environmental stresses (Pauwels *et.al.* 2009; Seo *et.al.* 2011). It has also been reported that JAs are signalling hormones induced under stress and respond quickly to them (Du *et.al*. 2013). They are involved in plant development, reproduction (Wasternack 2007; Browse 2009) floral development, growth inhibition, fruit ripening, tendril coiling, potato tuberization, trichome formation, and fungi arbuscular mycorrhizal association (Browse 2005; Balbi and Devoto 2008; Reinbothe *et.al.* 2009; Yoshida *et.al.* 2009). Per *et.al.* (2018) have reported specific role of JA under abiotic stress. However, Kazan (2015) has reviewed the diverse roles of JA and ethylene in abiotic stress tolerance. JA and ethylene regulate root development and anthocyanin accumulation which may be associated with abiotic stress tolerance. Biotic stress in plants is caused by viruses, bacteria, fungi, nematodes, parasites, and insects/pests. In order to protect themselves, plants develop a mechanism in defense. Such responses are mediated by JA, salicylic acid (SA), ethylene, polyamines, and abscisic acid (ABA) acting as primary signals in regulation of plant defense.

Methyl Jasmonate (MeJA)

It is a highly volatile compound and has identical activity in vapor and liquid phases. Plants produce jasmonic acid (JA) and MeJA in response to many biotic and abiotic stresses (particularly herbivory and wounding), which build up in the damaged parts of the plant. Exogenous application of methyl jasmonate (MeJA) can induce anatomical and chemical changes that are components of defense responses in plants. Particularly, MeJA is well-known to increase leaf trichome density to protect against insect herbivory, but surprisingly little is known about the effects of MeJA on other leaf properties and plant growth (Cui Li & Peng Wang *et.al.,* 2018). Methyl jasmonate was first isolated from the essential oil of *Jasmoinum grandiflorum* (Demole *et.al.,*1962).

Jasmonate plays important role in Plant Growth and Development in areas of seed germination, Root growth inhibition, lateral root formation, adventitious root formation, tuber formation, trichome formation, leaf senescence and in development of reproductive organs. Some of its role are described below:

Roles of Jasmonates in Symbiotic Interactions

Mutualistic symbiosis are important in nature and sustainable agriculture, the most important of which are the almost ubiquitously occurring arbuscular mycorrhiza (AM) and root nodule symbiosis (RNS). Whereas the former entails an association with obligate biotrophic fungi of the phylum Glomeromycota (Schu¨ssler et al., 2001), the latter is the interaction of the leguminous roots with nitrogen-fixing bacteria. In these two forms of intracellular (endo) symbioses, the heterotrophically growing microbial partners are accommodated within living root cells (Oldroyd et al., 2009). JA seems to be involved in the establishment and maintenance of AM, but the results are partially contradictory. The AM roots exhibit enhanced JA levels accompanied by the expression of JA-induced genes and genes encoding enzymes of JA biosynthesis (Hause et al., 2002; Isayenkov et al., 2005; Lope´z-Ra´ez et al., 2010). In tomato, however, mycorrhization led also to an accumulation of oxylipins derived from the 9-LOX pathway in colonized parts of the root (Leo´n-Morcillo et al., 2012). Here, a local induction of expression of LOXA and AOS3 occurred. Both genes are induced by JA (Garcı´a-Garrido et al., 2010), implying that it might control the spread of the fungus via 9-LOX-derived oxylipins.

This is supported by the fact that application of JA to mycorrhizal plants results in a diminished mycorrhization rate (Vierheilig, 2004; Herrera-Medina et al., 2008). However, other data show that JA application is associated with an enhanced plant–fungus interaction

(Tejeda- Sartorius et al., 2008; Kiers et al., 2010; Landgraf et al., 2012). Most probably, these contrasting data accrue from differences in the experimental designs, such as JA concentrations, timing and frequency of JA application, plant organs treated and plant nutritional status.

Role of Jasmonates in Trichome Formation

Glandular trichomes are multicellular and often involved in resistance to insects due to formation of terpenoids, flavonoids, alkaloids and defense proteins (Tian *et al*., 2012). They represent a useful tool for production of secondary metabolites (Tissier, 2012). Furthermore, glandular and non-glandular trichomes are involved in defense against herbivores via trichome density and JA-inducible defense compounds, such as PI2, monoterpenes and sesquiterpenes (Tian *et al.,* 2012).

Jasmonate Signaling during Plant-Insect Interaction

Amongst all the phytohormones, jasmonates are most important signaling molecule associated with plant defense against herbivores as they activate the expression of both direct and indirect defenses. Jasmonates are produced at insect-infested local sites and either jasmonate itself or some Jasmonic Acid (JA)-elicited compound travels to systemic leaves and elicits defense response. Upon herbivory, receptors/sensors of the host plant recognize Herbivory Associated Molecular Patterns (HAMPs) and early signaling events start with the involvement of Mitogen Activated Protein Kinases (MAPKs). JA biosynthesis is initiated in the chloroplast with the hydrolysis of chloroplast membrane lipids by phospholipases releasing free α-linolenic acid (α-LA), which gets converted to 12-oxo-phytodienoic acid (OPDA). OPDA is subsequently transported to peroxisomes where JA is produced by β-oxidation and it conjugates with isoleucine by JA amino acid synthetase (JAR) enzymes.

Plants can mount an array of inducible defense responses against herbivorous arthropods which includes the synthesis of deterrent/antifeeding metabolites (R.N. Bennett et .al., 1994; A.R. War et.al., 2012), defensive proteins (J.S. Thaler et.al., 2001) and/or increases in leaf epidermal defensive structures such as trichomes (B.M. Traw et.al., 2002). These responses are mediated by endogenous signalling molecules, e.g. phytohormones, among which jasmonic acid (JA), salicylic acid (SA) and ethylene are central regulators of plant defenses against pathogens and herbivores (C.M.J. Pieterse et.al., 2012). In particular, activation of the JA signalling pathway has been reported to confer resistance against chewing-biting and cell content feeding insects, as well as necrotrophic pathogens (L.L. Walling, 2000; J. Glazebrook: 2005) while induction of SA signalling increases the resistance against biotrophic pathogens (A. Koornneef et.al., 2008). Moreover, artificial activation of these defense-associated signalling pathways by using natural or synthetic elicitors has proven to increase plant resistance against different insects and diseases and is, therefore, regarded as a valuable strategy to control pests in agriculture (J.S. Thaler, 1999).

Role of Jasmonates in Abiotic Stress

Out of 13 billion hectares of total land, only 1.6 billion is under farm land production accounting to only 12% of arable land (Syngenta, 2014). Agriculture must evolve in order to meet the demands of the increasing population. However, every year some part of the world suffers from drought, global increase in temperature, variable precipitation that eventually hampers the quality and quantity of crops. All these visible warning signs can have erratic production patterns all over the world. Plants encounter numerous challenges in terms of competition from other plants, organisms and because of the complex environment. All these provocations have made the plants tougher and more flexible. The morphological flexibility has given them the advantage to counteract, inhabit and endure biotic and abiotic challenges. Rapid changes in the plant biochemistry and physiology are mediated by the action of several phytohormones.

By tradition cytokinin, auxins, brassinosteroids, and giberellins have always been associated to regulate developmental processes of plants, whereas, salicylic acid, JA and ethylene associate with plant defense and ABA regulates plant's response to abiotic stress. Now, it has been quite evident from many reports that all hormones affect multiple plant functions.

Thus, one can say that hormones not only participate in plant developmental processes but also have a say in plant's response to abiotic stresses like drought, osmotic stress, chilling injury, heavy metal toxicity etc. These adversities have forced the plants to either employ avoidance as a mechanism in order to surmount the stress or choose defense over growth (Band etal., 2012; Murray etal., 2012; Petricka etal., 2012; Wasternack and Hause,2013). Thus, stress activates signal transduction of hormones which may promote specific protective mechanisms.

Role of Jasmonates under Heavy Metal Induced Toxicity

Although many metal ions are essential nutrients some are toxic to both plants and animals (Hou et.al. 2007; Asgher et.al. 2015; Iqbal et.al. 2015). Excess of essential metals or even metalloid induce toxicity in plants, which may result into oxidative stress leading to physiological changes (Dhankar and Solanki 2011). JA application, however, enhanced accumulation of osmolytes while carotenoids enhanced antioxidant enzyme concentration which prevented the plants from damage by excess metal ions (Poonam et.al. 2013). Recently, Farooq et.al. (2018) have also reported that exogenous application of MJ to *Brassica napus* plants alleviated the arsenic-induced oxidative stress and improved overall plant growth and photosynthesis.

Conclusion

This research review's purpose is to help the reader understand different aspects posed by Jasmonates (JAs) in plant defense. More research and testing is required to gain a better understanding of relationship of secondary metabolites and JAs. Jasmonic acid and its methyl ester play a significant role in plant growth and developmental processes under changing environmental as well as other biotic stresses. It has been established that JAs are emerging players in alleviating the deleterious effects under adverse conditions. Thus, these findings are useful in the development of resilient plants by manipulation of JA biosynthesis.

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