

The Essential Role of Jasmonic Acid in Plant–Herbivore Interactions – Using the Wild Tobacco *Nicotiana attenuata* as a Model

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ABSTRACT

The plant hormone jasmonic acid (JA) plays a central role in plant defense against herbivores. Herbivore damage elicits a rapid and transient JA burst in the wounded leaves and JA functions as a signal to mediate the accumulation of various secondary metabolites that confer resistance to herbivores. *Nicotiana attenuata* is a wild tobacco species that inhabits western North America. More than fifteen years of study and its unique interaction with the specialist herbivore insect *Manduca sexta* have made this plant one of the best models for studying plant–herbivore interactions. Here we review the recent progress in understanding the elicitation of JA accumulation by herbivore-specific elicitors, the regulation of JA biosynthesis, JA signaling, and the herbivore-defense traits in *N. attenuata*.

KEYWORDS: Jasmonic acid; Defense; Plant–herbivore interaction; *Nicotiana attenuata*; *Manduca sexta*

INTRODUCTION

Plants and insects have coevolved for about three hundred million years (Gatehouse, 2002). To defend themselves against herbivore attack, plants evolved sophisticated defense mechanisms. Physically, they are equipped with thorns, spines, trichomes, and sticky resins. Chemically, they produce toxic, nondigestible, or antinutritive secondary metabolites, which function as direct defenses, to poison or deter their insect enemies. They release volatile substances, which are airborne signals in the indirect defenses, to attract predators or parasitoids of the herbivores. The well-known direct defense traits include glucosinolates, cyanogenic glucosides, alkaloids, phenolics, and proteinase inhibitors (PIs). The indirect defense traits include green leaf volatiles (GLVs), terpenoids, and extrafloral nectars (Kessler and Baldwin, 2002). To balance

the developmental demands and costly defenses, as both consume energy and nutrients, many defenses are deployed only after herbivore attack, and these defense traits are thus called the inducible defenses. Most inducible defenses are regulated by jasmonic acid (JA), an important phytohormone that is synthesized by an oxylipin pathway. JA signaling interacts with other phytohormone signaling pathways and mediates the large transcriptional and metabolic reconfigurations in plants after herbivore attack (Verhage et al., 2010); thus, JA signaling is considered to be a master regulator of plant resistance to arthropod herbivores (Halitschke and Baldwin, 2004; Howe and Jander, 2008; Wu and Baldwin, 2010; Ballare, 2011).

Nicotiana attenuata is an annual native tobacco that inhabits the Great Basin Desert of Southwestern USA. It occurs ephemerally in large populations after perceiving certain unknown germination cues in wood smoke generated by wild fires. The post-fire germination behavior is beneficial as the soil is nitrogen-rich and the interspecific competition is little.

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However, *N. attenuata* also faces a large unpredictable herbivore community. *Manduca sexta*, commonly known as the tobacco hornworm, is a specialist herbivore feeding on the foliage of *N. attenuata*. During the long-time coevolution with herbivores, *N. attenuata* is equipped with effective direct and indirect defenses to cope with *M. sexta* attack. Many studies have provided important insight into the defense of *N. attenuata* against *M. sexta* and the underlying mechanism.

Here, using *N. attenuata* as the model, we review the progress in understanding the herbivore-specific elicitors, JA signaling and its role in herbivore defense, JA-induced defense traits, as well as how JA biosynthesis is regulated.

HERBIVORE-SPECIFIC ELICITORS

To respond promptly and specifically to different herbivore attackers, recognition of herbivores is critical. In many plant species, mechanical wounding and herbivore feeding switch on overlapping but different signaling pathways, and different feeding behaviors (chewing or piercing–sucking) arouse different defense responses. The recognition of insects requires perception of chemical cues secreted by insects to the wounds and/or distinguishing particular patterns of tissue damages. How plants recognize herbivore *via* mechanical and chemical cues has been intensively reviewed (Felton and Tumlinson, 2008; Bonaventure et al., 2011b; Erb et al., 2012). The elicitors that induce defense responses during folivory by chewing insects are diverse in structure. They can be enzymes (e.g., glucose oxidase, β -glucosidase) (Mattiacci et al., 1995; Musser et al., 2002), fatty acid-amino acid conjugates (FACs) (Alborn et al., 1997; Bonaventure et al., 2011b), sulfur-containing fatty acids (e.g., caeliferins) (Alborn et al., 2007), fragments of cell walls (e.g., pectins and oligogalacturonides) (Bishop et al., 1981), or peptides released from plant proteins during digestion (e.g., inceptins; proteolytic fragments of the chloroplastic ATP synthase γ -subunit) (Schmelz et al., 2006). Importantly, the activities of most of these insect-derived elicitors are usually restricted to particular plant–insect associations and only activate responses in specific but not all plant species (Schmelz et al., 2006, 2009; Bonaventure, 2011). This selectivity probably reflects the evolutionary history of both plants and their interacting insects and, hence, it is crucial to understand the mechanisms of plant–insect interactions in an evolutionary and ecological context.

FACs are components of many lepidopteran larval oral secretions (OS) (Yoshinaga et al., 2010) and they are necessary and sufficient to elicit herbivory-specific responses in several plant species including maize (*Zea mays*) and the wild tobacco *N. attenuata* (Alborn et al., 1997; Halitschke et al., 2001). Volicitin [N-(17-hydroxylinolenoyl)-L-Gln] was the first FAC identified from the OS of *Spodoptera exigua* larvae, and when applied to damaged leaves of corn seedlings, volicitin induces emission of volatile compounds that attract parasitic wasps, the natural enemies of *Spodoptera exigua* (Alborn et al., 1997). Other types of FACs have been

identified in lepidopteran larvae with some of the most abundant forms consisting of linoleic (18:2) and linolenic (18:3) acids conjugated to glutamate (Glu) or glutamine (Gln) (Yoshinaga et al., 2008). One pioneering study reported that a plasma membrane protein from maize binds volicitin (Truitt and Pare, 2004). This study suggested that a putative receptor is responsible for the perception of FACs. Similar to plant perception of microbe-associated molecular patterns (MAMPs) by various MAMP-specific receptors, recent studies have shown that after perception of FACs, plants rapidly activate a series of early responses including changes in ion fluxes across the plasma membranes (Maffei et al., 2004), activation of protein kinases (Wu et al., 2007; Kallenbach et al., 2010), and generation of reactive oxygen species (Maffei et al., 2006).

The role of FACs in induction of JA accumulation was firstly reported in *N. attenuata* (Halitschke et al., 2001). The oral secretions (OS) of the specialist herbivore, *M. sexta*, quickly and transiently induce the accumulation of JA. The OS-induced JA levels are much higher than those induced by wounding alone, indicating certain compounds in OS are herbivore-derived elicitors. In 2001, several FACs, which are composed predominantly of linoleic acid (18:2) or linolenic acid (18:3) conjugated to Glu or Gln were identified in the OS of *M. sexta* (Halitschke et al., 2001). Applying synthetic FACs to mechanical wounds at concentrations comparable to those found in *M. sexta* OS also amplified the wound-induced JA accumulation; however, ion-exchange treatment of OS, which removed all detectable FACs, resulted in the loss of JA-inducing ability. The JA-inducing activity of ion-exchanged OS could be completely restored by the addition of synthetic FACs at OS-equivalent concentrations. These results clearly show that FACs are herbivore-specific elicitors which induce JA accumulation (Fig. 1) (Halitschke et al., 2001). The metabolism of FACs after entering plants was unknown until recently one of the major FACs in *M. sexta* OS, N-linolenoyl-glutamic acid (18:3-Glu), was analyzed on wounded leaf surfaces of *N. attenuata*. It is modified within seconds by a heat labile process. Some of the major modified forms, 13-hydroxy-18:3-Glu, 13-hydroperoxy-18:3-Glu, and 13-oxo-13:2-Glu, are oxygenated products derived from 13-LIPOXYGENASE (13-LOX) activity and one of these derivatives, 13-oxo-13:2-Glu, is also an active elicitor of JA biosynthesis (Fig. 1) (VanDoorn et al., 2010a, 2010b). However, how JA biosynthesis is activated by the FACs is still not clear. The identification of new component involved in the FAC perception and signal transduction will provide important insights into this field.

Compared with the rapidly advancing field of perception and signal transduction of microbial molecular patterns and effectors, the molecular components used by plant cells to perceive herbivore signatures and to transduce and activate specific responses against folivorous insects remain largely unknown. Identification of new herbivore-specific elicitors and new regulators in perception and transduction of these elicitors will greatly expand our knowledge on how plants recognize different herbivore and response to them.

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