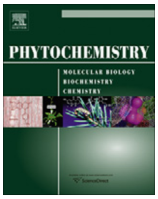
Phytochemistry 72 (2011) 1624–1634

Contents lists available at ScienceDirect

Phytochemistry

journal homepage: www.elsevier.com/locate/phytochem



Review

Reiterative and interruptive signaling in induced plant resistance to chewing insects

Jinwon Kim, Hélène Quaghebeur, Gary W. Felton *

Department of Entomology and Center for Chemical Ecology, Penn State University, University Park, PA 16802, USA

ARTICLE INFO

Article history:
Available online 5 May 2011

Keywords:
Plant defense
Plant signaling
Effectors
Saliva
Elicitors
Oviposition
Transgenerational induction
Herbivory

ABSTRACT

Our understanding of induced resistance against herbivores has grown immeasurably during the last several decades. Based upon the emerging literature, we argue that induced resistance represents a continuum of phenotypes that is determined by the plant's ability to integrate multiple suites of signals of plant and herbivore origin. We present a model that illustrates the range of signals arising from early detection through herbivore feeding, and then through subsequent plant generations.

Published by Elsevier Ltd.

Contents

1. Introduction

Plants have evolved diverse molecular strategies to prevent or overcome pests and diseases. All plants are believed to have a general immune response against pathogens, which is termed basal defense. Some plants will also exhibit a more specific type of resistance that involves the recognition of a specific effector from the pathogen by a ligand receptor from the plant. This response, based on a "gene-for-gene" recognition mechanism of the pathogen by the plant, is mediated by resistance (R) genes (Jones and Dangl, 2006). The classic zig-zag model proposed for disease resistance describes the quantitative output or amplitude of defense of the plant immune system (Jones and Dangl, 2006). In some cases, this model has been applied to plant resistance to arthropod herbivores. For example, in tomato, the *Mi* gene, a member of a large family of R genes, mediates resistance to potato aphids, whiteflies, and root-knot nematodes (Kaloshian and Walling, 2005).

---

* Corresponding author. Tel.: +1 814 865 1895; fax: +1 814 865 3048.
E-mail address: gwf10@psu.edu (G.W. Felton).

0031-9422/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.phytochem.2011.03.026

Induced resistance to herbivores has often been viewed as a discreet resistance phenotype, hence tested in bioassays by comparing the response of herbivores to induced or wounded plants vs. the uninduced or unwounded controls. While this approach has proved invaluable in identifying the response of plants to herbivory, we argue that induced resistance is not a single or discreet phenotype. In this article, we support the idea that induced resistance against arthropods represents a continuum of phenotypes that depends upon signal reiteration (and or interruption) from many varied environmental stimuli. Our working model is mostly based on emerging studies that recently uncovered subtle interactions between plants and chewing herbivores, as well as current work in our own laboratory on tomato.

We intend to describe defense signaling and the associated range of plant responses to chewing herbivores in the context of early warning, feeding and transgenerational signals.

2. Background on induced defenses in tomato

Since the pioneering work of Clarence Ryan on induced defenses in tomato (Green and Ryan, 1972), tomato has emerged as one of the best studied model systems for induced defenses against herbivores (Broadway et al., 1986; Chen et al., 2005; Cooper and Goggin, 2005; Fowler et al., 2009; Kandoth et al., 2007; Ryan, 2000; Stout et al., 1998; Thaler, 1999). Induced resistance in tomato against chewing herbivores is largely dependent upon the octadecanoid or jasmonic acid (JA) pathway (Howe et al., 1996; Li et al., 2004; Thaler et al., 2002a,c). Great progress has been made in identifying the central components of the JA signaling cascade, which include SCF^{COI1} (a 4-unit E-3 ubiquitin ligase complex coronatine insensitive 1) (COI1) associating a S-phase kinase-associated protein, a cullin, a RING-finger protein and a F-box (SCF) and jasmonate ZIM-domain (JAZ) proteins, found to repress transcription of JA-responsive genes (Chini et al., 2007; Chung et al., 2008; Katsir et al., 2008; Thines et al., 2007).

The JA pathway is part of a complex signaling network that integrates signals from a variety of biotic and abiotic components. Thus the regulation of induced defenses may be mediated through cross talk from other signaling pathways (Lorenzo and Solano, 2005; Wasternack et al., 2006), such as salicylic acid (SA) (Doares et al., 1995; Felton et al., 1999; Thaler et al., 2002b), nitric oxide (Orozco-Cardenas and Ryan, 2002), abscisic acid (Pena-Cortes et al., 1991; Thaler and Bostock, 2004), ethylene (Diaz et al., 2002), auxin (Young et al., 1994) or hydrogen peroxide (H_2O_2) (Orozco-Cardenas and Ryan, 1999; Orozco-Cardenas et al., 2001).

H_2O_2 is generated locally at the feeding or injury site, then spreads systemically (Maffei et al., 2007; Musser et al., 2006; Orozco-Cardenas and Ryan, 1999). In tomato, the systemic, wound-induced accumulation of H_2O_2 requires intact JA- and systemin-signaling (Orozco-Cardenas and Ryan, 1999) and H_2O_2 was proposed to act as a downstream, secondary messenger to JA for the regulation of polyphenol oxidases and several proteinase inhibitors (Orozco-Cardenas and Ryan, 1999; Orozco-Cardenas et al., 2001; Sagi et al., 2004). Interestingly, H_2O_2 did not affect the expression of "early genes" involved in JA biosynthesis (e.g., lipoxygenase) (Orozco-Cardenas et al., 2001). This secondary messenger role in JA signaling contrasts to some plants such as tobacco where H_2O_2 induces SA, which subsequently inhibits JA signaling (Leon et al., 1995).

The cascade of defense proteins that are induced in response to JA or herbivory include multiple proteinase inhibitors (Broadway et al., 1986; Diez-Diaz et al., 2004; Green and Ryan, 1972; Lison et al., 2006), polyphenol oxidases (Bhonwong et al., 2009; Constabel et al., 1995; Mahanil et al., 2008; Stout et al., 1998; Thipyapong et al., 2007), ascorbate oxidase (Felton and Summers, 1993), leucine aminopeptidase (Chao et al., 1999; Narvaez-Vasquez et al., 2008; Pautot et al., 1993), arginase (Chen et al., 2007, 2004, 2005) and threonine deaminase (Chen et al., 2007, 2005). A review of the literature on induced defenses in tomato reveals that the majority of studies focus on rapid responses expressed with hours to days following wounding or feeding (Stout et al., 1996a,b). Defenses that are expressed days to weeks following herbivory or even in the next generation (delayed induced defenses) have largely been ignored. How leaf-feeding may induce defenses in the fruit is virtually unknown, although induced resistance in fruit to phytopathogens has been established (Thines et al., 2007; Fan et al., 2008).

Some plant responses to herbivory occur immediately following damage and affect the same herbivores that have inflicted the damage (rapid induced responses), whereas other responses take longer to develop and may manifest their effects on later stages of the herbivore or even subsequent herbivore generations. The latter type of response is characteristic of mechanical defenses such as leaf hairs or trichomes, because their production is not induced in mature tissues thus requiring new growth for expression. Trichomes have been recognized as important components of plant defense against herbivores for over five decades (Dalin et al., 2008). More recently there have been several studies showing that chewing-type herbivores (e.g., caterpillars, beetles) induce trichome production in new leaves (Dalin et al., 2008). However, the effect of damage on trichome production depends upon the identity of the herbivore, even among species possessing similar feeding strategies (Dalin et al., 2008; Traw and Dawson, 2002a,b). In a comparative study in black mustard, feeding by the cabbage looper *Trichoplusia ni* induced trichome production, but feeding by the small cabbage white butterfly *Pieris rapae* or the flea beetle *Phyllotreta cruciferae* did not (Traw and Dawson, 2002b). These studies suggest that the differences observed in trichome induction may be due to differences in the composition of the oral/salivary secretions of these herbivores. The density of glandular trichomes may increase in response to wounding or the application of methyl jasmonate (Boughton et al., 2005).

Trichomes in *Solanum* species and particularly in tomato *Solanum lycopersicum* are among the best studied in terms of their role in plant defense (Kennedy, 2003; Sanchez-Pena et al., 2006; Simmons et al., 2004; Wilkens et al., 1996). Seven types of glandular or non-glandular trichomes have been described in tomato, varying in relative abundance, size, cell number and shape (Luckwill, 1943). Not only are tomato trichomes morphologically diverse, but their chemical exudates also contain a wide assortment of antiherbivore defenses (Frelichowski and Juvik, 2001; Fridman et al., 2005; Li et al., 1999; Schilmiller et al., 2009; Thipyapong et al., 1997; van Schie et al., 2007; Zhang et al., 2008). Types VI and VII glandular trichomes have received the most attention as they are a formidable defense against some herbivores (Li et al., 2004; Simmons et al., 2004). The molecular mechanisms of trichome development and formation are not as well understood compared to *Arabidopsis*, but JA is a key hormone regulating the development of glandular trichomes in tomato (Li et al., 2004). The effects of herbivory on inducing trichome formation have yet to be reported in tomato.

3. Early warning signals

3.1. Help thy neighbor

Plants release a mixture of volatile compounds when attacked by insect herbivores to attract natural enemies of the herbivorous attackers (Dicke et al., 2003). These volatiles include methylesters of jasmonate and salicylate, *cis*-jasmone, green leaf volatiles (C6 aldehydes, alcohols, and esters), terpenoids and other minor