Available online at www.sciencedirect.com

SCIENCE DIRECT®

Biochimica et Biophysica Acta 1734 (2005) 91 – 111

BIOCHIMICA ET BIOPHYSICA ACTA

BBA

http://www.elsevier.com/locate/bba

Review

Herbivore-induced, indirect plant defences

Gen-ichiro Arimura, Christian Kost, Wilhelm Boland*

Max Planck Institute for Chemical Ecology, Department of Bioorganic Chemistry, Hans-Knöll-Strasse 8, D-07745 Jena, Germany

Received 14 October 2004; received in revised form 25 February 2005; accepted 1 March 2005
Available online 17 March 2005

Abstract

Indirect responses are defensive strategies by which plants attract natural enemies of their herbivores that act as plant defending agents. Such defences can be either constitutively expressed or induced by the combined action of mechanical damage and low- or high-molecular-weight elicitors from the attacking herbivore. Here, we focus on two induced indirect defences, namely the de novo production of volatiles and the secretion of extrafloral nectar, which both mediate interactions with organisms from higher trophic levels (i.e., parasitoids or carnivores). We give an overview on elicitors, early signals, and signal transduction resulting in a complex regulation of indirect defences and discuss effects of cross-talks between the signalling pathways (synergistic and antagonistic effects). In the light of recent findings, we review molecular and genetic aspects of the biosynthesis of herbivore-induced plant volatiles comprising terpenoids, aromatic compounds, and metabolites of fatty acids which act as infochemicals for animals and some of which even induce defence genes in neighbouring plants. Finally, ecological aspects of these two indirect defences such as their variability, specificity, evolution as well as their ecological relevance in nature are discussed.

Keywords: Extrafloral nectar; Herbivore-induced plant volatile; Indirect defence; Oxylipin; Signalling pathway

1. Introduction

Plants have evolved a wide spectrum of strategies to defend themselves against herbivores. Such defensive strategies can be classified as direct defences, which immediately exert a negative impact on herbivores, or indirect defences, which include higher trophic levels, thus fulfilling the defensive function [1]. Direct defences may prevent herbivores from feeding via physical barriers, such as spines, thorns, trichomes, and waxes or chemical ones, with secondary plant metabolites (e.g., phenylpropanoids, terpenoids, alkaloids, and fatty acids); or via specialized defence proteins (e.g., proteinase inhibitors, so-called PIs). On the other hand, indirect defences work by attracting the herbivores' enemies, such as parasitoids or predators, which actively reduce the number of feeding herbivores. Both strategies can be either constitutive, meaning that they are always expressed, or inducible, meaning that they appear only when needed, namely, following herbivory.

In recent years especially, induced, indirect defences have received increasing attention and have been studied on the genetic, biochemical, physiological, and ecological levels. The aim of this review is to summarize the current state of knowledge, merge results from different biological fields, and point to new possibilities for future research. Beginning

Abbreviations: ACC, 1-aminocyclopropane-1-carboxylic acid; ALA, alamethicin; CAM, calmodulin; CDPK, calcium-dependent protein kinase; DMNT, (*E*)-4,8-dimethyl-1,3,7-nonatriene; EAG, electroantennogram; EF, extrafloral; EFN, extrafloral nectar; ERF, ethylene-responsive transcription factor; FAC, fatty acid–amino acid conjugate; FAD, ω-3 fatty acid desaturase; FPP, farnesyl diphosphate; GPP, geranyl diphosphate; HIPV, herbivore-induced plant volatile; HPL, fatty acid hydroperoxide lyase; IGP, indole-3-glycerol phosphate; JA, jasmonic acid; JMT, JA carboxyl methyltransferase; LOX, lipoxygenase; MAPK, mitogen-activated protein kinase; 1-MCP, 1-methylcyclopropene; MeJA, methyl jasmonate; MKP, MAPK phosphatase; OPDA, 12-oxophytodienoic acid; ORCA, octadecanoid-derivative responsive *Catharanthus* AP2-domain; P450, P450 monooxygenases; PI, proteinase inhibitor; PLA, phospholipase A; PLD, phospholipase D; SA, salicylic acid; SAM, *S*-adenosylmethionine; SAR, systemic acquired resistance; SIPK, salicylic acid-induced protein kinase; SMT, SA carboxyl methyltransferase; TMTT, 4,8,12-trimethyltrideca-1,3,7,11-tetraene; TPS, terpene synthase; WIPK, wounding-induced protein kinase

* Corresponding author. Tel.: +49 3641 571200; fax: +49 3641 571202.
E-mail address: boland@ice.mpg.de (W. Boland).

1388-1981/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.bbalip.2005.03.001

with the first contact between plant and herbivore, and including herbivore recognition, signal elicitation, and early signalling steps, and followed by a description of the signalling cascades and biosynthesis pathways involved, we will end with an overview of the ecology and evolution of induced, indirect defensive plant traits.

2. Cell- and long-distance signalling in plants in response to herbivory

Plants have evolved a large array of interconnected cell-signalling cascades, resulting in local resistance and long-distance signalling for systemic acquired resistance (SAR). Such responses were initiated with the recognition of physical and chemical signals of the feeding herbivores, activate subsequent signal transduction cascades, and finally lead to an activation of genes involved in defence responses that consequently enhance feedback signalling and metabolic pathways (Fig. 1). This section describes the aspects of cell signalling involved in the induction of indirect herbivore responses.

2.1. Elicitors

In the 1990s and earlier, many chemical ecologists believed that herbivorous oral secretions and regurgitants elicited insect-induced plant responses, since simple mechanical wound stimuli, in many cases, could not mimic plant responses following insect attack [2–5]. β-Glucosidase derived from regurgitate of *Pieris brassicae* larvae was identified as a potential elicitor of herbivore-induced plant

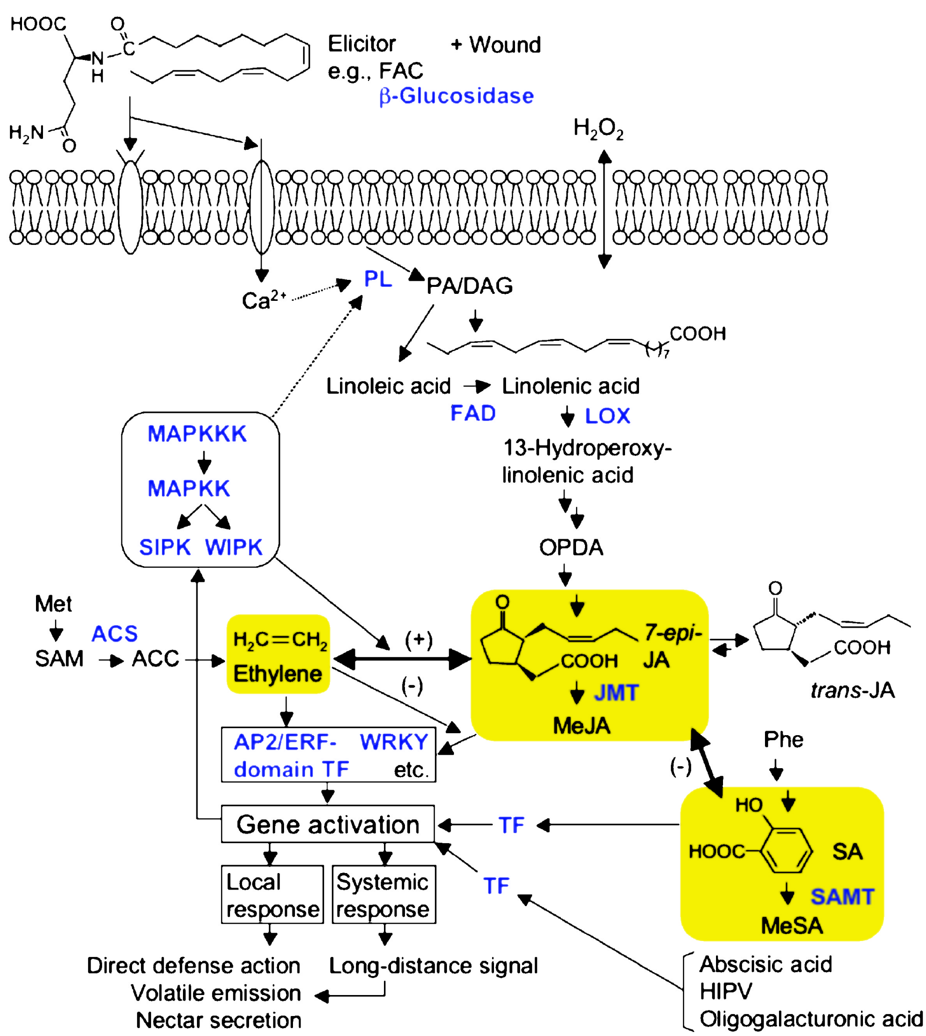

Fig. 1. Schematic representation of the signalling pathways required for herbivore-induced responses in plants. This scheme merges the evidence obtained from several plant taxa. The overall scenario may differ in certain plants; in particular the existence and the extent of synergistic and antagonist interaction between pathways may vary significantly. Elements in blue represent enzymes. Broken arrows indicate possible steps not yet described. Abbreviations: ACC, 1-aminocyclopropane-1-carboxylic acid; ACS, ACC synthase; DAG; diacylglycerol; FAC, fatty acid-amino acid conjugate; FAD, ω-3 fatty acid desaturase; HIPV, herbivore-induced plant volatiles; JA, jasmonic acid; JMT, JA carboxyl methyl transferase; LOX, lipoxygenase; MAPK, mitogen-activated protein kinase; MeJA, methyl JA; MeSA, methyl SA; OPDA, 12-oxophytodienoic acid; PL, phospholipase; PA, phosphatidic acid; SA, salicylic acid; SAM, *S*-adenosyl-methionine; SAMT, SA carboxyl methyl transferase; TF, transcription factor.