J Plant Growth Regul (2005) 23:167–169
DOI: 10.1007/s00344-004-0051-1

JPGR
Journal of Plant Growth Regulation

JASMONATES

Introductory Remarks on Biosynthesis and Diversity in Actions

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In the early sixties jasmonic acid methyl ester (JAME) was identified as the oil-constituent of jasmin, and the free acid (JA) was first found in the culture filtrate of *Botryodiplodia theobromae*. However, only in 1980/81 did jasmonates become interesting after Sembdner's group in Halle/Saale (Germany) observed the growth-inhibition of jasmonates and Ueda's group in Osaka (Japan) described the senescence-promoting effect of jasmonates. In the middle of the eighties the biosynthetic pathway for JA was described by Vick and Zimmermann in Fargo (USA). First, jasmonate-induced alteration of gene expression was observed with barley leaves, where several proteins accumulated abundantly upon jasmonate treatment as described by Parthier's group in Halle/Saale in 1986. Since 1990, when Ryan's lab in Pullman (USA) recognized that airborne JAME is a signal for wound-induced proteinase inhibitor gene expression in tomato, numerous sets of genes were identified as being up-regulated or down-regulated by JA. The next breakthrough was the observation in Zenk's lab in Munich (Germany) that external stimuli such as elicitors applied to plant cell suspension cultures led to an endogenous increase of jasmonates followed by alkaloid synthesis. Subsequently, JA was found to be a signal in numerous abiotic and biotic stress responses and in various developmental processes. Some of them are summarized in Figure 1.

In the last decade, an enormous interest in JA has appeared, reflected in an exponentially growing number of publications. Some highlights of that period are

(i) Identification of mutants of *Arabidopsis* affected in jasmonate biosynthesis or signalling and being male sterile.

(ii) Identification of COI1 which is affected in the JA insensitive mutant *coi1* as one of the first F-box proteins of the ubiquitin/proteasome pathway found in plants

(iii) The synergistic and antagonistic signalling of jasmonate, ethylene and salicylate

(iv) Identification of the first transcription factors (ORCAs) that regulate JA-responsive gene expression.

(v) The role of jasmonate in plant-plant and plant-insect interactions.

Among other aspects, all these highlights will be discussed in the present special issue of JPGR. The most recent research on jasmonates is reviewed by experts from the corresponding fields. The 7 papers cover chemistry, physiology, molecular biology and genetics as well as applied research on jasmonates. Several aspects of JA research were reviewed in the last years. The goal of this special issue on jasmonates is to combine the numerous aspects in a parallel and new presentation.

Received: 4 October 2004; accepted: 5 October 2004; Online publication: 27 January 2005
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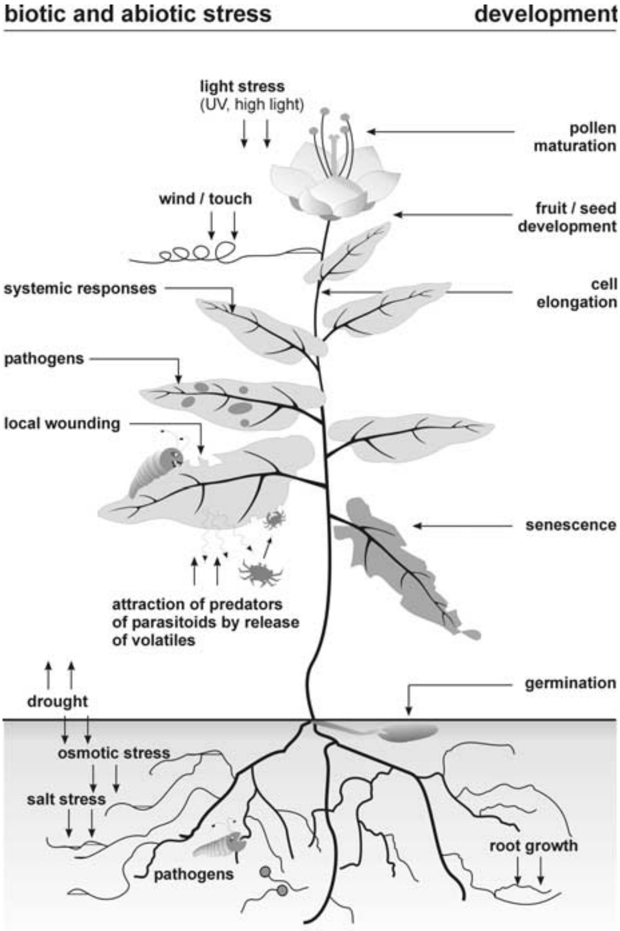

Figure 1. Diagram of the biotic and abiotic stress responses and developmental processes in which jasmonic acid and related compounds function as signals.

Figure 2. Guest Editor, Claus Wasternack

The chemistry on jasmonates and related compounds including diverse cyclopentanoid oxylipins and their mimics is discussed by Axel Mithöfer, Mathias Maitrejean and Wilhelm Boland. Here, synthesis and structure of various jasmonates, of the precursor 12-oxophytodienoic acid, and of coronatine, phytoprostanes and indanones are presented from the chemical point of view. Structure-activity relationships are shown, and the biological activities of particular compounds including quantitative and qualitative considerations lead to the question on application of JA-like compounds such as indanones.

Next, Florian Schaller, Andreas Schaller and Annick Stintzi provide an overview on biosynthesis and metabolism of jasmonates. Reflecting the establishment of the biosynthetic pathway, each step in biosynthesis is discussed in terms of biochemistry and molecular biology. Discussing the intracellular location of enzymes and compounds related to this pathway, the authors cover the question of how jasmonate biosynthesis is compartmentalized and regulated. An excellent description of the enzymes and gene families coding for them is performed in a comparative manner for several plant species. Like other contributions to this special issue, the separate signalling activities of JA and 12-oxophytodienoic acid are described. Lipid bound octadecanoids and their link to JA biosynthesis are presented. Finally, this chapter shows how JA is metabolized by hydroxylation, glucosylation, methylation, amino acid conjugation or adenylation.

Jasmonate-regulated gene expression is discussed by Bea Pauw and Johan Memelink, and they present arguments for separation of causes and consequences in discussing JA signal transduction. The identification of the first jasmonate responsive transcription factors in J. Memelink's lab improved our understanding of the regulation of jasmonate-induced gene expression remarkably. In this chapter, jasmonate responsive genes, their promoters and transcription factors and regulation of these transcription factors are described. It is shown how jasmonate affects mRNA and protein abundance and activity of these transcription factors. Data are presented that highlight a crosstalk between jasmonate, ethylene and salicylate also at the level of transcription factors. The jasmonate-induced gene expression is discussed for genes coding for enzymes of terpenoid indole alkaloids, and the general impact for other jasmonate-induced genes is shown. In distinguishing primary and secondary responses, the authors introduce a signal transduction terminology used in animal research.

The question of how jasmonates serve as signals in plant-microbe interactions is addressed by Maria J. Pozo, L. C. Van Loon and C. M. J. Pieterse. Different interactions are described depending on the type of micro-organisms and the flexibility of the plants to establish an innate immunity. In the corresponding signalling pathways salicylate, ethylene and/or jasmonate orchestrate a network. The outcome of each resistance response is explained in terms of basal resistance, induced resistance and innate immunity. The key role of jasmonate in several of these resistance responses, in the priming of plant defenses and in the interactions with beneficial micro-organisms is described. The paper focuses on *Arabidopsis thaliana* and the various mutants that are affected in plant pathogen interactions by defects in signalling or synthesis of signalling components.

Next Gregg A. Howe describes all aspects of the local and systemic wound response. With preference for data from tomato, the wound response pathway and its various signals such as jasmonate, the 18 amino acid peptide systemin, the systemin precursor prosystemin and hydrogen peroxide are discussed in terms of wound-induced gene expression, preferentially of proteinase inhibitor gene expression. Emphasis is placed on genetic analysis of the wound response pathway. Three types of mutants are described. The *spr2* (*suppressor of prosystemin-mediated responses 2*) is affected in the ω-3-fatty acid desaturase, the *spr1* has incomplete systemin perception and the jasmonate insensitive *jai1* is a homolog of the coronatine/jasmonate-insensitive mutant *coi1* of *A. thaliana*. Grafting experiments with these mutants revealed new insights in long distance signalling and systemic wound responses. Another breakthrough is described for the role of jasmonate in distinct developmental processes. Whereas *coi1* of *A. thaliana* is a male sterile mutant, the homologous *jai1* is female sterile and is affected in glandular trichome development.

Plants have to tolerate or to adapt to the high number and diversity of insects on earth. Direct and indirect defense mechanisms have been evolved. Rayko Halitschke and Ian T. Baldwin summarize recent data on jasmonates and related compounds in plant-insect interactions. Jasmonates and other oxylipins are key players in plant responses to herbivores and other types of insects. The paper covers the generation of oxylipins upon herbivore attack, the role of herbivore-specific signals and plant-plant signalling. Perspectives on how transgenic manipulation of oxylipin levels can be achieved by overexpression of different enzymes of the lipoxygenase pathway such as lipoxygenase, allene oxide synthase and hydroperoxy lyase, are discussed. Examples are given on how this manipulation interferes with the plant-insect interaction and how individual signal cascades can be altered.

The numerous stimulatory or inhibitory effects of jasmonates on plant responses to biotic and abiotic stresses as well as on developmental processes led to attempts on biotechnological application of jasmonates. Indeed, increased formation of phytoalexins and alkaloids in plant cell suspension cultures following jasmonate treatment could be used. Even under field conditions jasmonates were used to increase plant defense responses against pathogens or herbivores. The advantages of jasmonate treatment could be evaluated in storage and prolonged transport of seeds and fruits. All these applied aspects of application of jasmonates are discussed by Hugo Pena-Cortés, Paula Barrios, Fernando Dorta, Victor Polanco, Carolina Sánchez, Elizabeth Sńnchez and Ingrid Ramirez. With partial overlap with other contributions, aspects of JA biosynthesis, transgenic modulation of JA levels, wound responses, plant pathogen as well as plant insect interactions are also discussed.

Two further contributions covering aspects of jasmonate in senescence (Susheng Gan, Cornell University, Ithaca, USA) and in secondary metabolism (Jörg Bohlmann, University of British Columbia, Vancouver, Canada) will be published in a forthcoming issue.

Finally, I would like to thank all of the authors for their efforts, and the thorough and careful inspection of the literature in reviewing the seven topics. We hope that each contribution will be a useful resource for many plant hormone biologists and students interested in molecular plant physiology.