

# Fatty acids and early detection of pathogens<sup>☆</sup>

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Early in interactions between plants and pathogens, plants recognize molecular signatures in microbial cells, triggering a form of immunity that may help resist infection and colonization by pathogens. Diverse molecules provide these molecular signatures, called pathogen-associated molecular patterns (PAMPs), including proteins, polysaccharides, and lipids. Before and concurrent with the onset of PAMP-triggered immunity, there are alterations in plant membrane lipid composition, modification of membrane fluidity through desaturase-mediated changes in unsaturated fatty acid levels, and enzymatic and non-enzymatic genesis of bioactive lipid mediators such as oxylipins. These complex lipid changes produce a myriad of potential molecular signatures that are beginning to be found to have key roles in the regulation of transcriptional networks. Further, research on fatty acid action in various biological contexts, including plant–pathogen interactions and stress network signaling, is needed to fully understand fatty acids as regulatory signals that transcend their established role in membrane structure and function.

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## Introduction

Fatty acids (FAs) and fatty acid-metabolites are not only major structural and metabolic constituents of the cell but they also function as modulators of a multitude of signal transduction pathways evoked by environmental and developmental stimuli. Emerging evidence identifies fatty acids as second messengers and regulators of signal transducing molecules or transcription factors. Many functions of FAs in living organisms are linked to changes in membrane lipid composition and adjustment of membrane fluidity, largely mediated by desaturases, as critical for the function of integral membrane proteins that ultimately affect cell signaling mechanisms [1,2]. In addition to structural signaling, FAs also have regulatory activities upon their release by lipases, followed by enzymatic and non-enzymatic generation of bioactive lipid mediators such as oxidatively modified lipids which specifically trigger diverse cellular processes and play an important role in numerous innate immune functions [3,4]. In a broader context, FAs can also modulate signal transduction pathways by functioning as hydrophobic hormones where they bind to and regulate the activity of receptor proteins controlling major regulatory networks that impact cell metabolism and signaling systems [1,5,6]. In addition, ample studies have established that specific FAs also interact with diverse transcription factors to provide direct or indirect regulation of primary organismal physiology [7–9]. The effects of FAs on gene expression are also being found to extend to post-transcriptional regulatory mechanisms such as directly mediating the rate of mRNA turnover for specific transcripts [1,6,10,11]. Thus, FAs because of their chemical diversity have the potential to provide an intricate regulatory capacity in many cellular processes.

In contrast to the vast body of knowledge of fatty acid signaling in animals, this information is rather limited in plants. Intriguingly however, despite shared aspects of FA signaling in plants and animals, mechanistic features unique to plants are now being recognized. Detailed understanding of FA signaling in plants will therefore provide information critical for revealing these mechanistic differences across kingdoms.

## Structural properties of fatty acids in relation to disease and defense

A FA function is specifically determined by the length, position and desaturation level of its lipophilic acyl chain; therefore it is critical to quantitatively determine how different fatty acids alter functional properties of a

multitude of signaling components and ultimately cellular responses.

Levels of free fatty acids increase in response to various stresses and play a pivotal role in plant–microbe interactions. For example, fatty acid synthesis in the obligate biotrophism of arbuscular-mycorrhizal fungi is dependent on plant-derived C16 FAs [12]. Furthermore, eggplants with enhanced levels of palmitoleic acid (16:1) exhibited increased resistance to *Verticillium dahlia*, suggesting increasing the production of plant 16:1 as a viable approach to enhance crop resistance to fungal diseases [13]. Seed fatty acid composition is also suggested to be a component of pathogen susceptibility and seed colonization. For instance colonization of soybean seeds by *Cercospora kikuchii* is found to be correlated with the oleic acid (18:1)/linoleic (18:2) ratio, and that mid-18:1 soy genotypes in the field are more extensively colonized by this fungal pathogen [14]. Interestingly, mounting evidence suggests that reduced levels of 18:1 in the chloroplast caused by a mutation in *SUPPRESSOR OF SA INSENSITIVITY OF npr1-5 (SSI2)*, encoding one of the stearoyl-ACP desaturase isoforms, results in the constitutive activation of defense responses [15–17]. Reducing the level of 18:1 leads to a stabilization of NITRIC OXIDE ASSOCIATED1 (NOA1), an enzyme that regulates nitric oxide (NO) levels and thus increases endogenous NO levels. This triggers transcriptional upregulation of NO responsive nuclear genes, thereby activating disease resistance. In fact application of NO or reduction in 18:1 levels induces the expression of similar sets of nuclear genes [18\*\*]. Thus, NOA1/18:1 may provide a direct mechanistic link between membrane integrity and transcriptional regulation of plant defense responses. 18:1 is also found to be a stimulator of the signaling enzyme phospholipase D (PLD $\delta$ ), which has an anti-cell-death function [19]

Polyunsaturated FAs (PUFAs), major constituents of membrane lipids, are released from membranes by lipases in response to attacks by biotic agents. These FAs play a pivotal role in plant–microbe interactions either directly as free FAs or through the function of oxylipins, the vast and diverse family of oxygenated derivatives of PUFAs (Figure 1). As free FAs, 18:2 levels partly regulate development, seed colonization, and mycotoxin production by *Aspergillus spp.* [20]. Moreover, elevation of 18:2 levels elicit enhanced resistance to attack by the fungal pathogen, *Colletotrichum gloeosporioides* [21].

Trienoic FAs (TAs), the major polyunsaturated fatty acid species in the membrane lipids in plant cells, are involved in defense responses against pathogens, and mutant plants compromised in TA production are more susceptible to *Pseudomonas syringae* pv. *tomato* (*Pst*). In particular the most abundant TA, linolenic acid (18:3) is reported to directly activate NADPH-oxidase and, by extension, to

generate reactive oxygen intermediates after inoculation with *Pst* [22].

The eicosapolyenoic acids (EP), arachidonic acid (20:4) and eicosapentaenoic acid (20:5), common FAs in plant pathogenic oomycetes, and signals for immune responses and central nervous system development in mammals, function as conserved signaling molecules across eukaryotic kingdoms. EP released during infection of plants may serve as novel PAMPs that engage plant signaling networks to induce resistance to pathogens [23\*\*,24]. EP, which do not occur in higher plants, elicit a cascade of responses in plants, including an oxidative burst and the transcriptional activation of genes involved in phytoalexin synthesis, lignification, programmed cell death, and other responses typically associated with the hypersensitive response (HR) to pathogens [24]. Structure–activity studies with PUFAs implicate the action of a 9-lipoxygenase (9-LOX) in the initial signal generation from EP that leads to a postulated reactive intermediate(s) to trigger the specific responses observed [24]. The presence of foreign EP may perturb plant oxylipin metabolism to produce novel or uncommon oxylipins that alter the course of 18:2 and 18:3 peroxidative metabolism to provoke the intense plant response. In Arabidopsis, EP-induced activation of defense responses occurs in a JA-dependent manner indicating additional downstream regulation within the allene oxide synthase (AOS) pathway [23\*\*]. Thus, EP and other similar phylogenetically limited FAs enable plants to distinguish self from non-self-using FA-derived signals. Whether EP are recognized by pattern recognition receptors similar to bacterial PAMPs, such as flg22 and EF-Tu, is currently unknown [24].

### Oxylipins as cross kingdom communication signals

One of the key processes in early plant defense signaling is enhanced lipid peroxidation and production of a vast array of oxylipins through parallel and competing branches of the AOS and hydroperoxide lyase (HPL) pathways (Figure 1) [25]. The AOS pathway is responsible for stress-inducible production of jasmonates [jasmonic acid (JA), methyl jasmonate (MeJA) and their biosynthetic precursor, 12-oxophytodienoic acid (12-OPDA)]. The HPL pathway produces C<sub>6</sub>-aldehydes and corresponding derivatives [26,27]. The AOS and HPL pathways are both important for their production of signaling molecules in the elicitation of plant defense responses against biotic agents and in a broad array of other biological activities including intraplant and interplant communication [25,28,29\*\*].

The jasmonates, however, are the most intensively studied plant oxylipins, in part because of their role as phytohormones in various plant processes as well as their novel cyclopentanone ring structure that provokes

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