

# New Synthesis – Plant Defense Signaling: New Opportunities for Studying Chemical Diversity

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Higher plants have evolved multilayered defense signaling systems that are based on the generation and perception of small molecules. These signaling pathways provide warning of incoming danger, triggering not only local resistance responses but also long-distance signals that lead to the protection of the whole plant against subsequent attack. This induced resistance against pathogens and herbivores often involves the production of alkaloids, terpenes, phenolics, and other small molecules with toxic and deterrent properties. However, although there are thousands of known plant metabolites with direct defensive functions, relatively few signaling molecules have been identified. Among these, salicylate, jasmonate, and related metabolites are the most extensively studied, and likely have universal functions as components of pathways leading to the induction of both local and systemic plant defense responses.

Salicylate and jasmonate-dependent signaling pathways in plants are presumed to have their evolutionary origins in the production of metabolites with a direct defensive function. Salicin, a metabolic precursor of salicylate, has a protective function in plants such as willows, and lipid intermediates in jasmonate biosynthesis also have been implicated in plant defense. For plants under attack, the induction of a local defense response is a reliable indicator of pests or pathogens that have the potential to spread more widely. Small molecules that are phloem mobile or even volatile, e.g., methyl salicylate and methyl jasmonate, provide an efficient means for propagating a systemic signal. Thus, by eliciting additional defenses and turning on signaling pathways, secondary metabolites (SMs) can contribute to a signal amplification loop that prepares otherwise naïve plant tissue for imminent attack.

Plant defense signaling does not occur through linear pathways, but rather is a complex network with numerous examples of crosstalk and an ever increasing number of known signaling molecules. In particular, the accumulation of certain SMs not only provides direct protection against disease and herbivory, but also serves as a trigger for further plant defense responses. For instance, our own work shows that 4-methoxyindol-3-ylmethylglucosinolate in *Arabidopsis thaliana* not only protects against pathogens and herbivores, but also elicits callose production as a secondary defense response. Azelaic acid is a phloem-mobile metabolite that can prime salicylate-dependent plant responses (Jung et al., 2009) and, as suggested by its use as a human acne treatment, also has antimicrobial properties. Production of reactive oxygen species has long

been implicated in plant resistance to disease and herbivory. More recently, hydrogen peroxide was reported as a key reactive oxygen signal in plant immune responses, acting downstream or independently of salicylate and jasmonate signaling pathways (Miller et al., 2009).

Just as the great diversity of plant SMs is required for defense against multiple threats, there is likely also natural selection for a diversity of defense signaling pathways. Species-specific pathways should be less susceptible to interference by herbivores and pathogens, either through the targeted degradation of plant-derived signals or by the insertion of interfering molecules, e.g., the jasmonate-isoleucine mimic coronatine, which promotes virulence of plant-pathogenic *Pseudomonas syringae* bacteria (Uppalapati et al., 2007). In this respect, defensive SMs may be particularly suitable as plant signaling molecules. These compounds exhibit great chemical diversity, generally are resistant to catabolism by non-specialist pathogens and herbivores, show increased local accumulation in response to infection or herbivory, and can spread through the plant vasculature to provide a systemic signal.

Given that the vast majority of plant SMs have been investigated primarily for their function as direct defenses, there are numerous opportunities for discovering as yet unidentified or incipient signaling pathways. New research tools, including metabolite profiling by mass spectrometry and analysis of gene expression by high-throughput sequencing, make it cost-effective to study global responses in non-model species. One approach would be an examination of plant responses to well-studied SMs, specifically to determine whether phloem and xylem-mobile toxins, e.g., nicotine, elicit additional systemic responses. New signaling molecules also may be discovered through systematic analysis of the countless unidentified plant metabolites that accumulate in response to pathogens and herbivores. Conducting such research with well-studied model species such as *A. thaliana*, rice, or tomato will make it possible to move beyond the identification of new signaling molecules to finding the genes and enzymes involved in their biosynthesis and response pathways.

## References

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