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Sources of specificity in plant damaged-self recognition

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Plants perceive injury and herbivore attack via the recognition of damage-associated molecular patterns (DAMPs) and herbivore-associated molecular patterns (HAMPs). Although HAMPs in particular are cues that can indicate the presence of a specific enemy, the application of pure DAMPs or HAMPs frequently activates general downstream responses: membrane depolarization, Ca^{2+} influxes, oxidative stress, MAPKinase activation and octadecanoid signaling at the molecular level, and the expression of digestion inhibitors, cell wall modifications and other general defenses at the phenotypic level. We discuss the relative benefits of perceiving the non-self versus the damaged-self and of specific versus non-specific responses and suggest that the perception of a complex mixture of DAMPs and HAMPs triggers fine-tuned plant responses. DAMPs such as extracellular ATP (eATP), cell wall fragments, signaling peptides, herbivore-induced volatile organic compounds (HI-VOCs) and eDNA hold the key for a more complete understanding of how plants perceive that and by whom they are attacked.

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Introduction

Plants share with other multicellular organisms the capacity to survive injury and infection. The necessity to activate wound sealing, immunity, and tissue repair, can be perceived via two major pathways. 'Damaged-self recognition' is mediated via the perception of damage-associated molecular patterns (DAMPs) [1], whereas 'non-self recognition' is mediated via the perception of herbivore-associated molecular patterns (HAMPs) in the case of herbivory, and by microbe-associated or pathogen-associated molecular patterns (MAMPs/PAMPs) in the case of infection [2]. Whereas DAMPs are endogenous molecules that stem from the damaged plant tissue itself, HAMPs are derived from the herbivore and thus, in principle, allow for a species-specific recognition of the attacking enemy. Research into damaged-self recognition has more than 20 years of history in the medical sciences [3••,4]. For plants, the concept was formalized only few years ago [1,5], because research into induced resistance to herbivores focused on non-self recognition. In this review, we present a short overview on DAMPs and HAMPs and discuss the relative advantages and disadvantages of damaged-self versus non-self recognition and of specific versus generalized responses in induced plant resistance.

Surprisingly, specificity on the side of enemy recognition seldom translates into specific phenotypic resistance responses. Although effects of herbivore-induced volatile organic compounds (HI-VOCs) on the third trophic level can very specifically depend on the type of the attacking herbivore [6], in other systems, damage inflicted by one type of herbivore caused resistance to other types of natural enemies. For example, *Solidago altissima* plants became more resistant to the chewing herbivore, *Trirhabda virgata*, after exposure to the sex pheromone of the gall-inducing fly, *Eurosta solidaginis* [7•]. The experimental application of purified HAMPs usually triggers conserved downstream signaling cascades that control a wide spectrum of resistance responses (Table 1), and transcriptional responses in Arabidopsis to insect chewing and bacterial infection showed a significant degree of overlap [8••]. Thus, the spectrum of enemies against which induced resistance acts is not necessarily restricted to the original attacker. What are, then, the benefits of the recognition of specific HAMPs, and why have plants evolved the capacity to recognize DAMPs as well? Here, we discuss four non-exclusive explanations: first, coping with injury and herbivory is mediated, at least in part, by general, non-specific phenotypic resistance traits; second, damaged-self recognition allows plants to maintain evolutionary control over their interactions with enemies; third, DAMPs prime plants for an enhanced sensitivity to enemy-derived cues; and fourth, it is the complex mixture of DAMPs and HAMPs, rather than single compounds, that carries specific information on the nature of the ongoing damage.

HAMPs frequently trigger general defense responses

The chemical cues that plants recognize as indicators of ongoing herbivory form a chemically diverse array of molecules (Figure 1). The earliest reported examples in this context include pectins, oligogalacturonides and other cell wall fragments [9,10]; systemin, inceptin, *At*Peps and other signaling peptides [11,12•]; and volicitin

Table 1

Cues that indicate acute or potential injury and the elicited responses

Cue	Source	Category	Herbivore	Plant	Response	Specificity of response	References
Systemin	Plant	DAMP	Colorado potato beetle or mechanical damage	*Lycopersicon* (*L.*) *esculentum*	Protease inhibitor (PI) 1 and 2	General	[33]
Inceptin (ATPase fragment)	Plant	DAMP	*Spodoptera frugiperda*	*Vigna unguiculata and Phaseolus* (*P.*) *vulgaris*	JA, SA, ET, VOCs and cystatin protease inhibitor gene	General	[31,55]
Volicitin (N-(17-Hydroxy linolenoyl)-l-Gln)	Plant + Insect	DAMP	*Spodoptera exigua*	*Zea* (*Z.*) *mays, Glycine max* and *Solanum* (*S.*) *melongena*	VOCs, JA and ET	General	[82]
18:3-Glu (*N*-linolenoyl-l-Glu)	Plant + Insect	DAMP	*Manduca sexta* and *Manduca quinquemaculata*	*Nicotiana* (*N.*) *attenuata*	JA, VOCs and defense-related mRNAs	General	[83]
18:3-Gln (N-linolenoyl-l-Gln)	Plant + Insect	DAMP	*Manduca sexta* and *Spodoptera exigua*	*Z. mays*	JA, ET, VOCs expression of allene oxide synthase and allene oxide cyclase	General	[53••,83]
18 OH-volicitin or 18-hydroxy-18:3-Gln (N-(18-Hydroxy linolenoyl)-l-Gln)	Plant + Insect	DAMP	*Manduca sexta*	*Z. mays*, *N. tabaccum* and *S. melongena*	VOCs	General	[84]
Caeliferins	Insect?	HAMP	*Schistocerca americana*	*Z. mays*	VOCs	General	[14]
β-Glucosidase	Insect	DAMP-producing enzyme	*Pieris brassicae*	*Brassica oleracea*	VOCs	General	[37]
Lipases	Insect	DAMP-producing enzyme	*Schistocerca gregaria*	*Arabidopsis*	Oxylipins, Ca^{2+}influx, MAPK signaling	General	[32••]
Pectinase	Insect	DAMP-producing enzyme	*Sitobion avenae*	*Triticum aestivum*	VOCs	General	[52]
Porin-like protein	Insect gut microbiome?	HAMP/PAMP	*Spodoptera littoralis*	*Arabidopsis*	Calmodulin-like genes and membrane channel formation	General	[85]
Ventral eversible gland (VEG) secretion (undefined)	Insect	HAMP	*Spodoptera exigua*	*S. lycopersicum*	VOCs and defense-related genes (peroxidase, polyphenol oxidase, and lipoxygenase)	General	[86]
Glucose oxidase (GOX)	Insect	DAMP-producing enzyme	*Helicoverpa zea*, *Spodoptera exigua* and *Heliothis virescens*	*S. lycopersicum*	JA, PI 2	General	[87]
			Spodoptera frugiperda	*Z. mays*	JA, defense-related genes (MPI, OPR2, RIP2)	General	[88]
			Ostrinia nubilalis	*Z. mays* and *S. lycopersicum*	PI 2 in S. *lycopersicum*, but no effect in *Z. mays*	General	[89]
Oligosaccharides (sucrose, raffinose, stachyose, and verbascose)	Insect and plant	DAMP	*Spodoptera littoralis* and *Autographa gamma*	*Tanacetum vulgare*	VOCs	General	[90]