



## Shared weapons of blood- and plant-feeding insects: Surprising commonalities for manipulating hosts



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### ABSTRACT

Insects that reprogram host plants during colonization remind us that the insect side of plant–insect story is just as interesting as the plant side. Insect effectors secreted by the salivary glands play an important role in plant reprogramming. Recent discoveries point to large numbers of salivary effectors being produced by a single herbivore species. Since genetic and functional characterization of effectors is an arduous task, narrowing the field of candidates is useful. We present ideas about types and functions of effectors from research on blood-feeding parasites and their mammalian hosts. Because of their importance for human health, blood-feeding parasites have more tools from genomics and other – omics than plant-feeding parasites. Four themes have emerged: (1) mechanical damage resulting from attack by blood-feeding parasites triggers “early danger signals” in mammalian hosts, which are mediated by eATP, calcium, and hydrogen peroxide, (2) mammalian hosts need to modulate their immune responses to the three “early danger signals” and use apyrases, calreticulins, and peroxiredoxins, respectively, to achieve this, (3) blood-feeding parasites, like their mammalian hosts, rely on some of the same “early danger signals” and modulate their immune responses using the same proteins, and (4) blood-feeding parasites deploy apyrases, calreticulins, and peroxiredoxins in their saliva to manipulate the “danger signals” of their mammalian hosts. We review emerging evidence that plant-feeding insects also interfere with “early danger signals” of their hosts by deploying apyrases, calreticulins and peroxiredoxins in saliva. Given emerging links between these molecules, and plant growth and defense, we propose that these effectors interfere with phytohormone signaling, and therefore have a special importance for gall-inducing and leaf-mining insects, which manipulate host-plants to create better food and shelter.

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### 1. Introduction

To colonize and exploit plants, parasites must defeat a multi-layered defense system. The earlier the plant's “danger signaling” is defeated, the better it is for the parasite. Research on plant pathogens has produced a four-part model of plant defense and parasite adaptation (Dangl et al., 2013). The first layer of plant defense involves plants recognizing ‘non-self’ molecules belonging to the invading organism, which are known as microbe- or herbivore-associated molecular patterns (MAMPs or HAMPs, respectively) (Erb et al., 2012; Heil, 2009; Acevado et al., 2015).

This layer of defense also recognizes ‘self’ molecules arising from damage to plant cells, which are known as damage-associated molecular patterns (DAMPs) (Erb et al., 2012; Heil, 2009; Acevado et al., 2015). Only few DAMPs have been extensively studied in plant-insect interactions and their recognition and associated signaling mechanisms remain unclear (Tanaka et al., 2014). Detection of MAMPs, HAMPs, and DAMPs occurs by pattern recognition receptors (PRRs) located in the plasma membrane. Detection triggers a set of broad-spectrum downstream defense responses, known as pattern-triggered immunity (PTI) (Zipfel, 2014). To counter this first layer of defense, plant parasites have evolved secreted effector proteins, which act in the plant apoplast or cytosol (Dangl et al., 2013). The plant's second layer of defense takes advantage of these effectors by having surveillance systems that detect a specific

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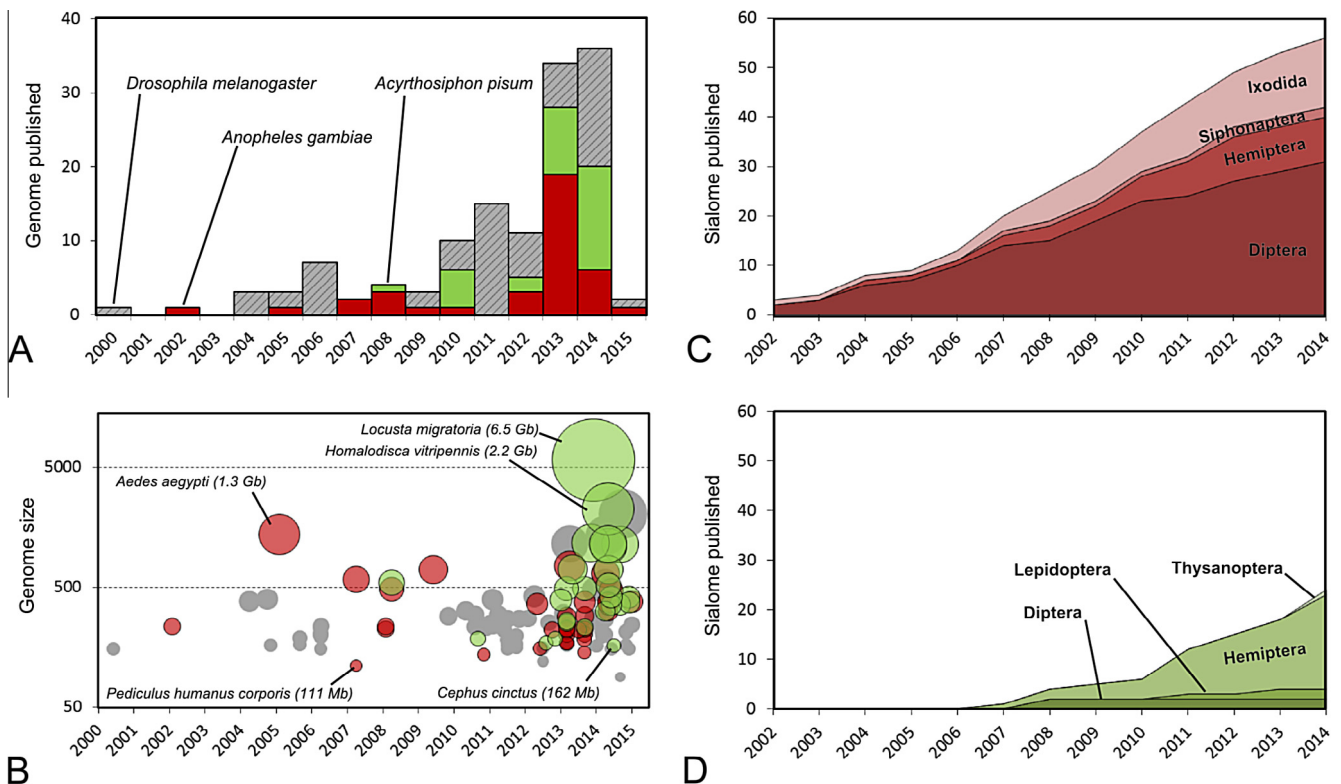
parasite effector, referred to as an *Avirulence* (*Avr*) effector because it renders the parasite avirulent rather than virulent. The surveillance system relies on plant *Resistance* (*R*) proteins encoded by plant *Resistance* genes. Detection by the second layer of defense activates effector-triggered immunity (ETI), which is generally seen as more harmful to the parasite than PTI. To counter this second layer of defense, parasites modify the *Avirulence* effector so that detection by the *R* protein-mediated surveillance system is no longer possible.

Oral secretions of insect herbivores are important recognition cues that can be used by plants to mediate induced defenses (i.e., elicitors). Oral secretions also have important functions for herbivores (i.e., effectors) as some components are instrumental for interfering with plant defense-signaling pathways, altering plant development to modify or create new habitats, and manipulating plant resources (Chung et al., 2013; Consoles et al., 2011; Giron and Glevarec, 2014; Nabity et al., 2013). We view elicitors and effectors as overlapping subsets of HAMPs. Salivary effectors may be especially important for organisms that reprogram host plants during colonization, including the leaf-mining insects and gall-inducing insects that are the subjects of many of the papers in this Special Issue. However, in contrast to effectors of plant pathogens, understanding of effectors of plant-feeding insects is in its infancy (Harris et al., 2015). Insights will come from genome sequencing. The first genome sequence of a plant-manipulating insect was published recently for the Hessian fly, *Mayetiola destructor* (Diptera: Cecidomyiidae), (Zhao et al., 2015), which provided evidence for hundreds of transcripts encoding candidate effectors. The four Hessian fly candidate *Avirulence* effector genes that have been identified through genome sequencing and map-based cloning (Aggarwal et al., 2014; Zhao et al., 2015, 2016) exhibit gene-for-gene interactions with four grass *Resistance* genes *H6*, *H9*, *H13*

and *H24*. Suppression of the first layer of defense, i.e., PTI, is expected to be an important function of Hessian fly *Avirulence* effectors. Functional studies of the four *Avr* effector candidates are now underway.

Clearly it is an arduous task to clone and functionally characterize even a single effector gene. If plant-manipulating insects produce many effectors, scientists need information to narrow the field of candidates. Where can this information be found? We propose interactions between blood-feeding parasites and their mammalian hosts. Because of their importance for human health, blood-feeding parasites have been studied for a longer time than plant-feeding parasites and have more tools from genomics and related-omics (Fig. 1). Whereas the first genome of a blood-feeding insect was published in 2002, it took more 6 years to publish the genome of the first plant-feeding insect (Fig. 1A). Differences in the chronology of genome sequencing may also be related to genome size, average genome size being smaller for sequenced species of blood-feeding versus plant-feeding insects (Fig. 1B). Sequencing of salivary gland proteomes or transcriptomes (hereafter referred to as sialomes) occurred 5 years earlier for blood-feeding insects (Fig. 1C) than for plant-feeding insects (Fig. 1D).

A number of recent discoveries have shifted attention to DAMPs involved in the earliest events that occur during plant attack by herbivorous insects (Maffei et al., 2007; Zebelo and Maffei, 2015). These include the plant's perception of specific physiological alterations that occur at the attack site, including the release of extracellular ATP (eATP), the elevation of cytosolic calcium concentration ( $[Ca^{2+}]_{cyt}$ ), and the production of reactive oxygen (ROS) and nitrogen (RNS) species (Zebelo and Maffei, 2015). These responses originate at the plant cell plasma membrane, and are triggered by physical damage caused by insect herbivores. These



**Fig. 1.** Comparison of omics studies between blood- and plant-feeding insects. Insect genomes are compared in terms of (A) year of publication and (B) size. Cumulative number of salivary gland proteomes or transcriptomes (here referred to as sialome) published for (C) blood-feeding insects and (D) plant-feeding insects (sources: NCBI and Web of Science). Plant-feeding insects are shown in green, blood-feeding insects in red, and other insects in grey.

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