COMPLEXITY OF INSECT ORAL SECRETIONS: INTEGRATING ENZYMES, ELICITORS AND MICROBIAL INTERACTIONS IN PLANT IMMUNITY: A REVIEW

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Abstract. Insects cause damage to plants by feeding on plant tissues which subsequently release herbivore associated molecular patterns (HAMPs). In the course of devouring on plant parts, herbivores secrete oral secretions (OS) which contain a range of compounds that govern plants defense mechanism. Some of the OS constituents can trigger a defense reaction to fight insect attacks (elicitors), while others inhibit plant defenses (suppressors). The OS of insects contain salivary effectors like Glucose oxidase (GOX) and Fatty acid amino acid conjugates (FACs) and secretory proteins along with enzymes and fatty acids which specially help plants to elicit or suppress plant defense mechanism. Here we review the constituents of the OS of herbivores as well as the OS of different insect species which act both as elicitors and suppressors in induced plant defense. Some of the findings further indicated that certain insects dispose microorganisms in their OS on plants and can therefore be "falsely" recognised as microorganisms. As a result, the plants switch on the wrong signalling pathway and activate ineffective defense mechanisms. Furthermore, the composition of OS is highly flexible, influenced by temperature, diet, and ecological interactions like parasitism. These factors can modify salivary elicitors like GOX, thereby modifying plant defense responses. Recent advances in omics have permitted detailed characterization of OS variation across insect species.
Keywords: *herbivore associated molecular patterns, omics, plant defense, salivary gland, suppressors*

Abbreviations. Abscisic Acid (ABA), Damage Associated Molecular Patterns (DAMPs), Ethylene (ET), Fall armyworm (FAW), Fatty acid amino acid conjugates (FACs), Glucose oxidase (GOX), *Glutathione S-transferases* (GST), *Helicoverpa armigera* R-like proteins (HARPs), Herbivore associated molecular patterns (HAMPs), Hydrogen Peroxide (H_2O_2), Jasmonic acid (JA), JASMONATE ZIM-DOMAIN (JAZ), Laccase 1 (LAC1), Mitogen-Activated Protein Kinase (MAPK), Mucin-like protein (MLP), *Nilaparvata lugens'* mucin-like protein (NlMLP), oligogalacturonides (OGs), Oral secretions (OS), Polydnaviruses (PDVs), Polyphenol oxidase (PPO), Proteinase inhibitor (PTI), Reactive Oxygen Species (ROX), REPAT (REsponse to PAThogens), RNA interference (RNAi), Salicylic acid (SA), UDP-glycosyltransferases (UGT), Ventral Eversible Gland (VEG)

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Introduction

There has been an ongoing vigorous interaction between plants and insects for many millions of years (Mishra et al., 2015) both in beneficial way (pollinators) as well as in antagonistic way (herbivores). Insects are classified as generalists and specialists feeders based on the diversity of the host that they feed upon. The chewing insects possess strong and sharp mandibles for cutting and tearing plant parts. Sucking herbivores have needle-like stylet with which they suck out the contents of epidermal/xylem/phloem cells, thus weakening the plants. In any case, OS from herbivores are taken up by plants and might play a vital role in herbivore and plant interactions. Once they begin feeding on their host, insects emit "signal" which the host senses and utilizes to quickly trigger the defense mechanism in response to the attack. In addition to damage associated with munching (Maffei et al., 2006), plants distinguish as well as incorporate a whole range of herbivore signals. This begins as the herbivore first contact with the plant (Peiffer and Felton, 2009; Tooker et al., 2010), and through the insect attacking signals, which comprises of the secretion of elicitors for instance volicitin and terminating in the elimination of waste products (Howe and Jander, 2008). In addition to damage associated with munching (Maffei et al., 2006), plants distinguish as well as incorporate a whole range of herbivore signals. Most plants react to feeding damage with a sudden secretion of green leaf volatiles produced by the lipoxygenase pathway and with the upregulation of a further complex defense reaction to OS associated molecular patterns (Qi et al., 2018; Chen and Mao, 2020). Initial reactions to herbivore attack can begin with calcium fluxes, changes in plasma membrane potential, ROS assembly, and phosphorylation cascades (Zebelo and Maffei, 2015; Farmer et al., 2020), that may then give rise to systemic signals which affects plant tissue isolated from the injured region (Schilmiller and Howe, 2005). On recognising the chemicals, host expressess direct and indirect defense mechanism controlled chiefly by activities of phytohormonoes for instance jasmonic acid (JA), ethylene (ET) and/or salicylic acid (SA) (Diezel et al., 2009; Erb et al., 2012). JA (or ET) coordinate the downstream assembly of defense molecules active against lepidoptera and coleoptera (Erb et al., 2012), whereas SA has a crucial role in both local and systemic defenses against biotrophs (Felton et al., 2014). The JA/ET or SA signalling paths can interconnect and work together through an incompatible or compatible manner letting plants to establish defense responses to a particular insect or pathogen attack (Erb et al., 2012; Takatsuji and Jiang, 2014). There exist incompatible relations between JA and SA (Thaler, 2014), which microbes and insects can manipulate for their own advantage. In coyote tobacco, *Nicotiana attenuata*, impairment of ethylene signalling led to down regulation of basal as well as herbivore-induced nicotine levels, through overlapping with the JA pathway (von Dahl et al., 2007). Thus, the preparation of specific defenses occurs through signalling networks that modulate the heights of various kinases, transcription factors, plant hormones, specified metabolites and defense proteins that could affect host development.

The Herbivore Associated Molecular Patterns (HAMPs) are invariable crucial components of insects and induces the first line of plant defenses. They include modified lipids such as FACs, GOX, b-glucosidase and inceptins from lepidopterans (Schmelz et al., 2007), and sulfur-containing fatty acid caeliferins from a grasshopper (Alborn et al., 2007) (*Figure 1*). The HAMPs, for instance some compounds in herbivore OS can be identified by crops and trigger definite defense response. The OS of insects include regurgitant and salivary secretions having different origins and chemical constitution. Regurgitants initiate from the fore gut and mid gut of insects, whereas salivary secretions

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are restricted to the labial gland through the spinneret (Peiffer and Felton, 2005). Constituents of OS may either elicit or subdue plant defenses which are referred as elicitors and suppressors (Alborn and Schmelz, 2008; Louis et al., 2013) (*Figure 2*). The production and role of OS constituents could rely on the hosts or the feeding tissue. It is known that a different plant diet influences the components of the OS of herbivores and thus also the defense responses of the plants. The fatty acid parts of fatty acid amides are straightly linked to the food which can influence the food choice of insects. Thus, as part of herbivore's diet, plant defense proteins and metabolites from host plants can guide the composition of the OS (Acevedo et al., 2015). As HAMPs, the best categorized OS constituents are proteins for example, GOX, various aphid protein (ApC002, MpC002, Bsp9, Me10, Me23, Bt56), protease, lipase and *Helicoverpa armigera* R-like proteins (HARPs). Some of the minor molecules includes FACs, peptides, oligosaccharides, amino acids, fatty acids, sugars, etc. (Kallure et al., 2022).

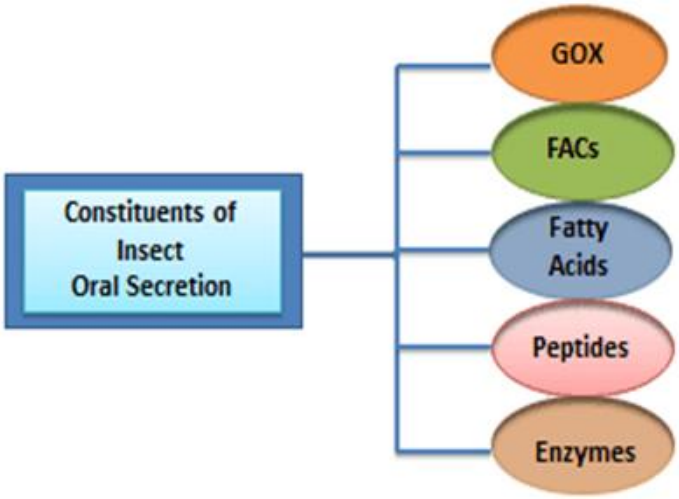

Figure 1. *The constituents of OS of different insects*

The review outlines the major components of insect OS comprising of enzymes, elicitors, and other bioactive molecules that directly interact with plant tissues. The role of microbial symbionts and their metabolites highlights how these associated microbes expand the functional repertoire of OS. It further depicts the HAMPs and effectors across different insect taxa, underscoring their dual capacity to either activate or suppress plant defense signaling. We also contemplate various environmental and dietary factors that shape OS composition, and how tri-trophic interactions with natural enemies influence plant responses. Moreover, we focus the technological advances driving this field, presenting insect OS as a multifaceted mediator of plant–insect–microbe interactions with implications for research and sustainable pest management.

Components of OS of insects

The OS of insects are diverse and may include enzymes such as GOX and b-glucosidase (Eichenseer et al., 1999), different types of lipids [fatty acid and amino acid conjugates and sulfur-containing fatty acids (caeliferins)] (Alborn et al., 2007), cell-wall fragments (pectins and oligogalacturonides) (Bergey et al., 1999), peptides from digested

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plant proteins (Schmelz et al., 2006), or organisms (microbes, fungi, viruses, and parasites), and/or organism derived proteins (Hughes et al., 2012) that disrupt with the consequence of the plant–insect interaction.

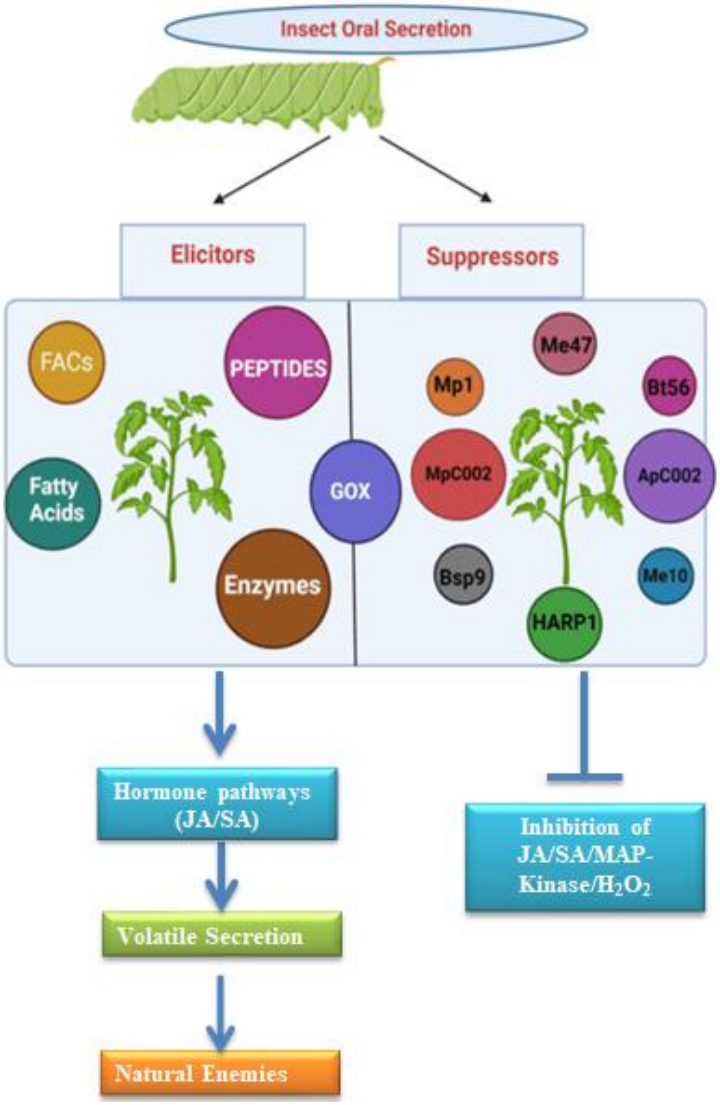

Figure 2. *Schematic representation of the constituents of OS of insects which are involved in eliciting and suppressing plant defense*

In the OS of insects, a well-characterized salivary enzyme is GOX, largely observed in caterpillars like corn earworm *Helicoverpa zea*, which modulates plant defenses in various ways depending on the host plant species. Studies have shown that GOX suppresses JA and ET pathways while triggering SA signaling, thus dampening plant resistance in *Nicotiana* but inducing defense in tomato (Tian et al., 2012; Lin et al., 2021). Its function is subjective of larval nutrition, salivary quantity, and host specificity, indicating that GOX is a crucial effector moulded by ecological interactions (Yang et al., 2017). Another class of herbivore-associated molecular patterns (HAMPs), FACs like volicitin and N-linolenoyl-L-glutamine, which induces MAPK and JA-dependent signalling, resulting in the production of volatiles and secondary metabolites across

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diverse plant taxa (Yoshinaga, 2016). Variation in FAC structures adds to species-specific responses, and in certain solanaceous crops, these elicitors fail to induce any defense responses, proposing evolutionary loss of responsiveness (Grissett et al., 2020). Sulfoxy fatty acids such as caeliferins, identified from the OS of grasshoppers, elicit terpenoid-based responses and trigger JA-ET pathways, escalating the diversity of elicitor molecules (O'Doherty et al., 2011). In addition to chemical cues, numerous secretory proteins have been associated in defense modulation. While suppressor proteins like HARP1 from gram pod borer, *H. armigera* block JA signaling by stabilizing JAZ repressors, elicitory proteins like spider mite tetranins and *Nilaparvata lugens'* mucin-like protein (NlMLP) increase SA and JA pathways (Chen et al., 2019; Iida et al., 2019). Numerous salivary effectors in piercing-sucking insects, including white fly *Bemisia tabaci*, pea aphid *Acyrthosiphon pisum*, and green peach aphid *Myzus persicae*, have been discovered using high-throughput proteomic-transcriptomic techniques; some of these effectors inhibit SA defenses or lower host fertility (Xu et al., 2019). These results point to possible targets for creating pest-resistant crops by highlighting the evolutionary complexity of insect salivary secretions and their crucial roles in defeating plant defences.

Microbial symbionts and their metabolites

Herbivorous insects are known to harbor a diverse community of microbial symbionts that significantly influence plant–insect interactions by manipulating host plant defenses. These microbes, often residing in the insect gut or OS, not only provide essential nutrients or protection from predators and parasites (Oliver et al., 2010), but also play a pivotal role in suppressing or eliciting plant immune responses (Barr et al., 2010). Notably, several studies have revealed that during herbivory, gut-associated or salivary bacteria are introduced onto plant tissues through OS or frass, thereby altering the plant's signaling pathways. For instance, in the Colorado potato beetle (*Leptinotarsa decemlineata*), Chung et al. (2013) demonstrated that salivary-associated bacteria such as *Pseudomonas*, *Stenotrophomonas*, and *Enterobacter* can suppress JA mediated defenses in tomato by activating the antagonistic (SA) signaling pathway. Similarly, in tobacco cutworm *Spodoptera litura*, the presence of *Staphylococcus epidermidis* in OS enhanced SA pathway activation and suppressed JA responses in *Arabidopsis*, thus facilitating herbivore performance (Yamasaki et al., 2021). Flagellin from *Pseudomonas* was also implicated in the suppression of JA-related defenses through SA pathway activation (Chung et al., 2013). In contrast, certain gut bacteria may elicit plant defenses: *H. zea*'s gut symbiont *Enterobacter ludwigii* was shown to induce polyphenol oxidase and JA-responsive genes while repressing SA-related genes in tomato, potentially benefiting plant fitness (Wang et al., 2017). Interestingly, the influence of a specific bacterium can vary by host plant; for example, *Pantoea* isolated from maize fall armyworm (FAW) *S. frugiperda* OS elicited defensive responses in maize but suppressed them in tomato (Acevedo et al., 2017). Such plant-dependent effects underscore the complexity of tripartite interactions between plants, herbivores, and their associated microbes (Mason et al., 2019). Furthermore, studies in *Phenacoccus solenopsis* have indicated that its salivary bacteria enhance SA responses and inhibit JA-mediated defenses, with feeding performance restored after antibiotic treatment followed by reinoculation with *Enterobacteriaceae* or *Stenotrophomonas*, highlighting the bacteria's essential role in suppressing plant immunity (Zhao et al., 2023). Beyond bacteria, fungal symbionts in insect OS have also been shown to modulate plant defenses. In black cutworm *Agrotis*

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ipsilon, fungi such as *Fusarium subglutinans* and *Mucor circinelloides f. lusitanicus* isolated from the OS induced robust plant defenses that negatively impacted caterpillar performance, suggesting that fungi may also play a dual role depending on the plant host context (Chen et al., 2020). In another example of a microbial component activating plant immunity, Chaudhary et al. (2014) found that chaperonin GroEL, secreted by the endosymbiont *Buchnera aphidicola* in aphids, triggered resistance in *Arabidopsis*, demonstrating the immunogenic potential of microbial effectors associated with insect herbivores. These findings collectively demonstrate that microbial symbionts in herbivore OS act as key modulators of plant defense signaling, particularly by skewing the JA-SA antagonistic pathways to the insect's advantage or sometimes inadvertently aiding the plant depending on microbial identity and host plant species.

HAMPs and effectors in different insect species

Piercing and sucking herbivores

Aphids

The protein found in saliva (C002) was the foremost recognized supressor in aphid which helped in consuming and reproducing of pea aphid (Mutti et al., 2008). Later several effector proteins has been identified *viz* Armet (Cui et al., 2019), Mp1 (Wang et al., 2021), Mp2, Mp10 (Bos et al., 2010), Me47 (Atamian et al., 2013), Me10, Me 23 (Atamian et al., 2013). Fewer studies have also showed that the aphid effectors act in response to host (Rodriguez et al., 2017). For example, there was increased breeding of green peach aphid on genetically engineered *Arabidopsis* which expresses the green peach aphid effectors C002, Mp1 and Mp2, however the reproduction of green peach aphid on *Arabidopsis* which expresses the *A. pisum* orthologs of protein did not show any increased fecundity (Pitino and Hogenhout, 2013). Additionally, one investigation stated that suppressors from aphids are both aphid-specific and host-specific. The breeding of potato aphid, *Macrosiphum euphorbiae* has been augmented on *N. benthamiana* with Me23, but on tomato expressing Me23 there was increase in fecundity (Atamian et al., 2013). These results suggested that host specialisation of an aphid may be due to varying expression of suppressors between diverse biotypes. In a current research, a minimum of four effectors were identified in the *Medicago sativa* biotype but not in the pea biotype of pea aphid (Boulain et al*.,* 2019). The triggering of defense responses in *Triticum* spp may be due to presence of salivary enzymes in grain aphid *Sitobion avenae*. The pectinase enzyme found in the saliva stimulated the release of volatiles sulcatol and sulcaton, that were recorded only in pectinase-treated plants and aphid attacked hosts (Liu et al., 2009). Polyphenol oxidase (PPO) present in the salivary secretions of cereal aphid was shown to induce a defensive reaction in wheat via the JA signalling mechanism (Ma et al., 2010). Tobacco plants are able to identify an elicitor protein CathB3 in the saliva of *M. persicae* which suppresses aphid feeding by activating ROS accumulation in the phloem (Guo et al., 2020). PPO in the saliva of aphids is assumed to be involved in the detoxification of phenols (Urbanska et al., 1998).

Whiteflies

The constituents of saliva permit *B. tabaci* to control the host's defensive pathway, thus elevating the host’s vulnerability and improving *B. tabaci* activity (Walling, 2008). Nevertheless, plants react to whitefly by prompting various hormone regulated defensive

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mechanisms. Some of the most prevelant and invasive *B. tabaci* species are thought to be the Mediterranean (MED, previously known as the Q biotype) and the Middle-East-Asia Minor 1 (MEAM1, previously called as the B biotype or *Bemisia argentifolii*) (Boykin et al., 2013). The MEAM1 nymphs of *B. tabaci* trigger the SA mediated metabolic pathway which either suppress or have no measurable effect on the expression of JA and ET regulated genes in *Arabidopsis thaliana* (Zarate et al., 2007). Adult MED whiteflies upsurge SA content and simultaneously reduce JA content in tomato leaves (Shi et al., 2014).

Table 1. *Elicitors and effectors in OS of some other hemipterans*

Insects	Plant Species	Compound	Defense Response	Mechanism	Reference
Smaller brown planthopper, *Laodelphax striatellus*	Rice, *Oryza sativa*	Ca2+ -binding proteins and LsDNase II	(-)	Suppressed planthopper-elicited H_2O_2 accumulation	Ye et al. 2017; Tian et al. 2021
Mirid bug, *Apolygus lucorum*	Wild tobacco, *N. benthamiana*	Glutathione peroxidase	(-)	Suppressed the ROS signalling mechanism	Dong et al. 2020
Smaller brown planthopper *L. striatellus*, SBPH)	Rice, *O. sativa*	Nutritious protein, vitellogenin	(-)	Hindered H_2O_2 accumulation and promoted insect activity.	Ji et al. 2021
Tarnished Plant Bug (*Lygus lineolaris*)	Cotton, *Gossypium spp.*	Polygalacturonases	(+)	Break down pectin, Cell wall degradation, Release of oligogalacturonides (OGs) which act as Damage Associated Molecular Patterns (DAMPs)	Zhu et al. 2016
Planthopper (*N. lugens*)	Rice, *O. sativa*	NlSEF1 and endo β 1–4 endoglucanase	(-)	Suppressed the increase in cytosolic Ca^{2+} induced by plant defences	Ji et al. 2017
Planthopper (*N. lugens*)	Rice, *O. sativa*	mucin-like protein (NlMLP)	(+)	Cell death, expressed pathogen-response genes and callose deposited.	Shangguan et al. 2018, Huang et al. 2016
Planthopper (*N. lugens*)	Rice, *O. sativa*	EF-hang calcium binding protein	(+)	Cell death, expressed pathogen-response genes and callose deposited.	Ye et al. 2017
Planthopper (*N. lugens*)	Rice, *O. sativa*	Salivary Protein 1	(+)	Cell death, H_2O_2 accumulate, defense-related gene expressed, and callose deposited.	Huang et al. 2020
(WBPH), *Sogatella furcifera*	Rice, *O. sativa*	Mucin like protein (SFMLP)	(+)	Increased levels of JA, jasmonoyl-isoleucine, and H_2O_2	Wang et al. 2020, Liu et al. 2022
Halyomorpha halys, *Nezara viridula*, *Euschistus conspersus*, *Thyanta pallidovirens*, *Chlorochroa ligata*	-	Serine proteases, lipases	(+)	Mechanical and enzymatic tissue injury, Release of DAMPs, Triggers JA and SA signaling pathways	Marshall et al. 2023

(+) sign indicates the elicitors and (-) sign indicated the suppressors

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The foremost evidence about whiteflies actually secreting particles into tissues of plants was provided by van Kleeff and coworkers (2016). This research illustrated that small RNAs (sRNAs) derived from whitefly exist in phloem exudations of tomato plants attacked by whiteflies. It suggests that these sRNAs behave as effectors by disrupting gene expression in host cells (Van Kleeff et al., 2016). Laccase 1 (LAC1), present in the transcriptome of the salivary gland of *B. tabaci* (MED), was the first whitefly effector whose mode of action was studied (Yang et al., 2017). The three Cu oxidase domains that LAC1 has are characteristic of the blue copper-containing polyphenol oxidase family and are conserved in a number of laccases from other insect species (Yang et al., 2017). These domains are believed to be vital for the metabolism of metal ions, the digestion of lignocellulose, and the detoxification of specific plant metabolites (Dittmer et al., 2004; Yang et al., 2017). The LAC1 protein is secreted by *B. tabaci*, as evidenced by the detection of LAC1 enzyme activity in artificial food. Although in all the developmental stages including eggs LAC1 is expressed, the highest expression of LAC1 is observed in the adult salivary glands, but expression can also be spotted in the midgut (Yang et al., 2017). The expression of LAC1 is predisposed by the host and is higher when *B. tabaci* is nursed with tomato plants compared to its artificial diet. Reduced expression of LAC1 by RNA interference (RNAi) drops the survival rate of adult *B. tabaci* feeding on tomato plants but not with artificial diet. Furthermore, the expression of LAC1 upsurges in both the salivary glands and midgut when the whiteflies feed on JA-treated plants compared to control plants. Together with the evidence of LAC1 secretion upon artificial feeding, this proposes that LAC1 helps *B. tabaci* to overcome plant defense responses and possibly acts as an effector in the plant cell (Yang et al., 2017). The elicitors and effectors in the OS of some other hemipterans are listed in *Table 1*.

Chewing herbivores

Lepidoptera

Most investigation on OS of lepidopteran larvae led to the documentation of HAMPs, though much lesser amount is known about suppressors. Most HAMPs from lepidoptera was recognised in regurgitant with contents from the digestive system.

FACs has a major role in N_2 absorption in caterpillar as the FACs which contains glutamine plays a vital role in N_2 breakdown (Yoshinaga et al., 2008). OS from *Loreyi* leafworm prompts a greater secretion of volatiles by paddy saplings compared to that from *Parnara guttata* (Sobhy et al., 2017). OS of fall armyworm, *Spodoptera frugiperda*, cotton leafworm *S. littoralis* and beet armyworm *S. exigua* also elicits various levels of volatiles from maize, presumably due to different levels of insect elicitors (De Lange et al., 2020). Although numerous elicitors were recognized in Lepidopterans, very limited information is available about the chemistry of the recognized volatiles and their inter-relationship with the volatiles secreted from the crops. Insect OSs and saliva are found to contain a mixture of various compounds, most of which are not identified (Acevedo et al., 2019). In FAW larvae apart from GOX, ATPases, and PLC which act as elicitors in plant defense the saliva is also reported to contain certain heat resistant molecules that help in induction of plant defense (Acevedo et al., 2018). Certain non-protein plant defense elicitors were also reported from FAW larvae. The saliva of FAW comprises of benzoic acid and plant hormones such as JA, SA, and ABA at lower concentrations. When maize plants were treated with the phytohormones extracted from the saliva of fall armyworm, it boosted the expression of the maize proteinase inhibitor (PI) gene whereas

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when applied in tomato, it downregulated the expression of late herbivore-induced defense (Acevedo et al., 2019). Gokila et al. (2021) tested the OS of rice leaf folder, *Cnaphalocrocis medinalis* and among the different elicitors tested, methyl salicylate at 10 mM concentration recorded the lowest per cent leaf damage in rice.

Adenosma or Ventral Eversible Gland (VEG) is a large sac like gland present adjacent to the thorax of caterpillar is also another known source of HAMPs. The secretions of adenosma are settled down into the food material with the OS (Zebelo and Maffei, 2012). The activity of adenosma in plant-insect communications is still uncertain. The emissions from VEG of *S. littoralis* larvae are found to trigger early defense signalling events with increased levels of H_2O_2 concentration as well as higher levels of cytosolic calcium levels in *Arabidopsis thaliana* (Zebelo and Maffei, 2012). VEG of *S. exigua* acts as elicitors and trigger late plant defense responses by triggering terpene synthase genes and additional defense genes (Zebelo et al., 2014). The REPAT38 effector in tomato leafminer *Phthorimaea absoluta* suppresses tomato defenses by inducing early stomatal closure and obstructing key plant hormones (JA, ET, ABA) and defense-related genes (Wang et al., 2024). Another recent study identified a salivary protein, SfPDI, in FAW which enhances insect growth and alters plant defense by suppressing JA pathways and triggering cell death in host plants (Cai et al., 2025).

Coleoptera

Coleoptera (beetles and weevils) represent the most species-rich herbivores, but the starring role of their OS in facilitating plant defense mechanisms has acknowledged surprisingly little though (Chung and Felton, 2011). Unlike lepidopteran insects, coleopterans lack functional mandibles, so their regurgitant may act as source of OS. OSs covers the regurgitant from the fore gut and mid gut of grub and mature beetles as well as the saliva secreted from the labial gland (Kallure et al., 2022). In cotton, Cotton Boll Weevil OS stimulated GhMPK3 and GhMPK6 and triggered the PTI marker gene FRK1. Moreover, the marker gene for ETI WRKY46 in *Arabidopsis* reporter lines, signifying the HAMPs present in OS from *L. decemlineata* can trigger plant defense responses in cotton and *Arabidopsis* (de Moura et al., 2022). Use of OS from *L. decemlineata* larvae to mechanical injured foliage was found to suppress induced defense in tomato and potato when compared with wounded and water-treated plants.

The OS are primarily secreted by hemipterans, lepidopterans and to some lesser extent by the coleopteran insects which help the plants to induce or to suppress plant defense. Apart from the above mentioned orders, the OS of the insect orders Orthoptera and Diptera are also reported to induce plant defense in insects. In orthoptera, HAMPs were first recorded in the grasshopper *Schistocerca americana* (Bonaventure, 2014). Transitory express of secretion enzyme, disulfide isomerase from brown locust *L. striatellus* prompts JA indicating and callose discharge in *N. benthamiana* (Fu et al., 2021).

In dipterans FACs were reported in fruitfly (*Drosophila melanogaster*) (Yoshinaga et al., 2007). The hessian fly, *Mayetiola destructor* feeding on *Triticum spp.* injects saliva proteins in plant tissues, where the saliva helps in induction of hypersensitive reactions responsible for chemical and physical defense which is ultimately responsible for the death of larvae (Kosma et al., 2010).

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Influence of external factors on defense signalling

Temperature plays a vital role as an abiotic factor persuading both herbivorous insects and their host plants. It has been shown to modulate the effectiveness of plant defense induction by caterpillars through its impact on the salivary enzyme GOX, a known elicitor of plant defenses (Paudel et al., 2020). Furthermore, variations in the dietary intake of insects can lead to changes in the amount of salivary compounds such as GOX (Hu et al., 2008). Insects are tended to experience changes in the expression and secretion of salivary enzymes depending on the nutritional quality of their diet (Das et al., 2010). This dietary influence on salivary composition is not limited to caterpillars; for instance, the saliva of the Russian wheat aphid, *Diuraphis noxia*, is also diet-dependent (Cooper et al., 2010). GOX performs by catalyzing glucose oxidation, and its action is known to rise in caterpillars feeding on diets rich in carbohydrates. This proposes that GOX might act as a pre-ingestive tool to regulate sugar consumption, which is critical since excessive carbohydrate intake can have a negative impact on mortality in these insects (Babic et al., 2008). Salivary proteomes of *S. exigua* caterpillars remain largely diet-invariant, but nutrient-poor diets trigger stress-related and vesicular-secretion proteins (e.g., PPIase, GRP94), whereas a protein-rich diet induces developmental proteins like arylphorin (Afshar et al., 2013). In another study, hundreds of proteins, primarily digestive enzymes, whose content varies depending on food (artificial vs. pepper/tomato leaves), were identified from the OS of *S. exigua* and *S. littoralis*. The salivary composition of FAW caterpillar varies according to their food; when given tomato as opposed to maize or Bermuda grass, more proteins are differentially expressed (Acevedo et al., 2017). Another study identified hundreds of proteins in the OS of *S. exigua* and *S. littoralis* involved in digestion, with diet-dependent variation in their abundance. Feeding on pepper and tomato leaves changed the expression of several proteins such as lipases, peptidases, and REPATs (Response to Pathogens) (Gao et al., 2024). REPATs are a large gene family of small proteins. Important proteins, such as lipases and β-1,3-glucan binding protein, rose in response to plant feeding, while other proteins varied depending on the plant and species, demonstrating the adaptability and evolutionary flexibility of OS to various host plants (García-Marín et al., 2025). Altogether, these studies show that plastic variations in the biochemical composition and secretion of insect saliva are linked with nutrition.

Tri-trophic interactions (How natural enemies regulate OS in insects)

Plants can defend themselves from herbivore attacks in a variety of ways. Among these, mechanical damage to herbivores and their OS specifically cause induced defense reactions (Lin and Felton, 2020). Consequently, changes in herbivore behaviour or salivary content may change how plants react to herbivores. This type of herbivore modification usually occurs when parasitoid that target herbivorous insects parasitize them (Forbes et al., 2018). Plants can recognize herbivore cues like touch, wounding, oviposition, and the feeding cues from OS (Acevedo et al., 2015). Certain parasitoid species have obligate mutualistic polydnaviruses (PDVs), that are often transported to their caterpillar hosts at the time when parasite deposits their eggs within their hosts (Strand and Burke, 2014). PDVs are categorized into two genera: Bracoviruses and Ichnoviruses that are found in parasitoids from the Braconidae and Ichneumonidae families, respectively (Strand and Burke, 2015). They are essentially symbionts of certain parasitoid wasps like braconid wasp *Microplitis croceipes* which not only suppress the caterpillar *H. zea* immunity but also regulate caterpillar salivary enzymes such as GOX,

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thus modifying plant defense responses and enhancing parasitoid success (Tan et al., 2018). Several evidences also demonstrated that plants diminish their defences when attacked by caterpillars carrying PDVs associated parasitoids (Cusumano et al., 2018; Tan et al., 2018). Besides bracoviruses, other groups of parasitoid viruses may also influence plant-insect interaction, since herbivory by parasitized caterpillars induces specific plant responses and parasitoid identity often has a stronger effect than the insect pest (Cusumano et al., 2019). GOX levels were also found to be decreased in *S. frugiperda* caterpillars parasitized with ichnoviruses infected Ichneumnid wasp *Hyposoter didymator*. While the GOX levels declined in the parasitized caterpillars, apyrase levels increased. Apyrase, an ATP-hydrolyzing enzyme has been associated in the salivary secretions of *H. zea* (Wu et al., 2012) and *S. frugiperda* (Acevedo et al., 2017). It is anticipated that the observed rise in apyrase levels in the salivary glands of *S. frugiperda* infected with HdIV will contribute to the reduction in plant defenses brought on by insect feeding (Cusumano et al., 2021). In *S. frugiperda* larvae, parasitism by *Cotesia marginiventris* dramatically changes the gut microbiota, decreasing *Enterococcus* and boosting *Pseudomonas*, as well as lowering reactive oxygen species levels. Reduced salivary gland GOX activity is correlated with these microbiome changes, which weakens the induction of defense in maize plants. According to the study, parasitic infection has a cascading effect on herbivore–microbe–plant interactions at all trophic levels (Wang et al., 2021).

Technological and experimental approaches

By affecting plant defense signals and metabolism, insect OS play a crucial role as mediators in plant–insect interactions. The intricacy and functional dynamics of OS in a variety of herbivorous insects have been better understood because of integrated transcriptome and metabolomic investigations. Shotgun proteomics in *N. lugens* identified 107 proteins in watery saliva, including binding proteins (such as ATP- and DNA-binding proteins) and enzymes (such as oxidoreductases, peptidases, and hydrolases), many of which are believed to reduce rice defenses to facilitate feeding (Liu et al., 2016). In maize, OS of paddy armyworm *Mythimna separata* encouraged wide and more persistent changes across transcriptome, proteome, and metabolome in comparison to mechanical wounding alone, linking hundreds of transcription factors and specific metabolites, highlighting the specific role of OS as elicitor (Qi et al., 2016). Applying OS to infested cotton leaves caused over 12,000 genes to express differently in chewing insects such as *H. armigera* and *S. litura*. This comprised of considerable inhibition of genes associated to SA and increased activation of the JA pathway (Si et al., 2020) (*Figure 3*). Another study investigated the salivary proteome of *B.tabaci* to understand its role in countering plant defences using transcriptomics and mass spectrometry. In the study, 698 salivary gland-enriched genes and 171 salivary proteins were recognised revealing conserved functions like binding, hydrolysis, and redox activity, alongside 34 species-specific proteins. 13 proteins have differential expression across host plants, which may indicate their functions in modifying defense and host adaptation (Huang et al., 2021). Comparative proteomic analyses of planthoppers (*N. lugens*, *S. furcifera*, *L. striatellus*) revealed that although several proteins such as serine proteases, aminopeptidases, and carbonic anhydrases are conserved across insect species, many salivary proteins are exclusive to planthoppers, signifying host-specific adaptations (Huang et al., 2018). In Asian citrus psyllid *Diaphorina citri*, vector of citrus greening

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disease, more than 200 salivary proteins were recorded, and candidate effectors residing within salivary glands indicate their function in pathogen transmission (Wu et al., 2021). Furthermore, *H. armigera*, under stress due to gossypol and tannins demonstrated upregulation of detoxification genes (e.g., cytochrome P450s, GSTs, UGTs) in salivary glands and significant change in OS protein profile, indicating an adaptive approach towards abrogating plant defense (Zheng et al., 2022). These studies together confirm that OS is not a passive secretion but an active molecular cocktail engaged in regulating host defense, propelled by transcriptomic reprogramming and metabolomics realignment.

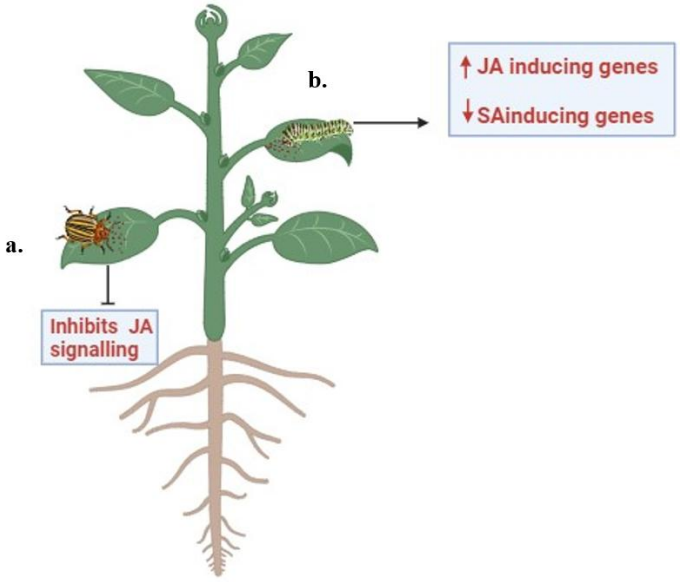

Figure 3. *Insect OS can a. inhibit JA signalling by triggering the SA pathway by suppressing the JA pathway and b. insect OS can help in expressing JA inducing genes and suppressing SA inducing genes*

Conclusion

The intricate relationship between plants and insects has developed over millions of years influencing ecosystems and manipulating the strategies of both the parties involved. This interaction encompasses a range of dynamics from beneficial relationships like pollination to conflicting encounters where insects behave as herbivores triggering complex defense mechanisms in plants. At the core of these interactions are the secretions released by insects during feeding which serve as signals perceived by plants, igniting a chain reaction of defense responses.

Plant further displays adaptability in their response to signals from herbivores employing mechanisms that go beyond physical damage. Early indicators include calcium fluxes changes, plasma membrane potential and the making of reactive oxygen species. Coordination of defense responses primarily involves three hormones- JA, ET and SA. These hormones regulate the production of defense compounds that effectively combat types of herbivores. This creates a network of signaling pathways. The composition of herbivore secretions plays a role in how plants respond. Within the species different herbivores can produce secretions, with unique compositions, which impact plant defense reactions. Notable components like volicitin and various peptides contribute

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to the complexity of the signalling network affecting how plants tune their defense strategies.

Recent research has shed light on the role of effector proteins found in insect saliva. These proteins can enhance plant defense mechanisms, demonstrating the sophisticated tactics insects employ to manipulate plant responses for their own advantage. Moreover, some external factors like temperature and diet are also found to influence the expression and activity of OS enzymes GOX. Furthermore, tritrophic interactions, particularly parasitoid-induced modulation of OS via PDVs, depict how parasitoids can reshape plant responses by changing herbivore salivary physiology. Looking into the future understanding the intricacies of interactions between insects and plants carries implications for agriculture, ecology and our comprehension of ecosystem dynamics. Further research should focus on disentanglement of the mechanisms that trigger these interactions. This exploration could lead to targeted strategies in pest management and sustainable agriculture practices. Moreover, by understanding how plants have evolved to perceive and respond to signals from herbivores innovative approaches can be developed to enhance crop resilience while reducing reliance on pesticides. The ongoing communication between plants and insects continues to reveal insights about coevolution, an area for scientific exploration with practical applications, in ecological sustainability.

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