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Review article

Roles of herbivorous insects salivary proteins

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ABSTRACT

The intricate relationship between herbivorous insects and plants has evolved over millions of years, central to this dynamic interaction are salivary proteins (SPs), which mediate key processes ranging from nutrient acquisition to plant defense manipulation. SPs, sourced from salivary glands, intestinal regurgitation or acquired through horizontal gene transfer, exhibit remarkable functional versatility, influencing insect development, behavior, and adhesion mechanisms. Moreover, SPs play pivotal roles in modulating plant defenses, to induce or inhibit plant defenses as elicitors or effectors. In this review, we delve into the multifaceted roles of SPs in herbivorous insects, highlighting their diverse impacts on insect physiology and plant responses. Through a comprehensive exploration of SP functions, this review aims to deepen our understanding of plant-insect interactions and foster advancements in both fundamental research and practical applications in plant-insect interactions.

1. Introduction

Herbivorous insects primarily feed on plants and have been engaging in dynamic interactions with plants for over 350 million years, exhibiting a wide range of dietary preferences and feed on various plant parts, such as leaves, stems, flowers, and fruits, and some of them show specific selectivity towards certain plant species or families [1–4]. To obtain nutrients from their hosts, herbivorous insects actively select feeding sites and secrete saliva during feeding, aiding in nutrient acquisition from host plants [5–7]. Based on their mouthparts and feeding habits, herbivorous insects can be categorized into two main groups: chewing and piercing-sucking insects [8]. Chewing insects possess a complex mouthpart comprising the labrum, mandibles, first and second maxillae, hypopharynx, and epipharynx, allowing them to bite, chew, and ingest food [9,10]. Conversely, piercing-sucking herbivorous insects such as aphids and whiteflies utilize specialized mouthparts called stylets to extract sap from plants, primarily using the stylet for piercing and sucking phloem sap [11].

Within the realm of herbivorous insects, salivary proteins (SPs) emerge as a vital cohort nestled within insect oral secretions, encompassing a rich diversity of constituents ranging from digestive enzymes and immunomodulatory agents to other efficacious elements [12]. Some of these proteins undergo post-translational modifications (PTMs) following ribosomal translation, a process documented extensively in the literature [13,14]. Many of these modifications orchestrate exquisite modulation of protein function, structure, and stability. Examples include glycosylation, tyrosine sulfation, among others [15–17]. Traditionally sourced from insect salivary glands or via intestinal regurgitation, there are also documented instances of herbivorous insect SPs being acquired through

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horizontal gene transfer [12,18,19]. In chewing insects, SPs enter plants via oral secretions, comprised of regurgitant and saliva; while in piercing-sucking insects, SPs accompany the gelatinous and watery saliva secreted from salivary glands, penetrating into plants [18, 20,21]. These proteins facilitate digestion, digestion of secondary metabolites, detoxification, as well as activation and suppression of plant defenses and so on [12].

SPs are important for promoting efficient food uptake by the mouthparts of herbivorous insects [22]. And these proteins have implications beyond digestion, as they are involved in insect development, octopamine in saliva regulates the reproductive behavior of insects, and the damage of salivary gland derived secretion factor (Sgsf) in fruit flies can cause significant deceleration of body growth [23,24]. Moreover, insects produce a variety of adhesives, such as sporting, mating, ovipositing or pupae anchoring substrates. The glue is made up of SPs. These proteins exhibit repetitive motifs and glycosylation, which are common in adhesion proteins and are expected to spur innovation in bioinspired technology adhesives [15,16]. During feeding processes in both chewing and piercing-sucking insects, SPs are introduced into host plants alongside herbivorous insect oral secretions [25–27]. Recognized by host plants, these proteins subsequently trigger plant defenses, collectively referred to as herbivore-associated molecular patterns (HAMPs) [18,28]. Functionally categorized into two types, elicitors molecules induct plant defenses, while effectors inhibit them to facilitate successful infection [7,29–31].

This review expatiates the diverse roles of SPs in herbivorous insects, elucidating their profound impacts on insect physiology, host plants, and related phenomena. By unraveling the intricate interplay between SPs and various biological processes, this review seeks to provide a comprehensive understanding of their functions in digestion, lubrication, self-protection, insect growth and development, and plant defense mechanisms. Through this exploration, it uncovers complete insights into the multifaceted functions and applications of SPs, aim to foster advancements in both fundamental research and practical applications.

2. Roles of SPs of herbivorous insects

2.1. Effects of SPs on herbivorous insects

SPs are extremely important to the herbivorous insects themselves, and when feeding, acting as lubricants and digestives [22]. Moreover, SPs influence various aspects of insect physiology, including growth, development, mating, and spawning [23,24]. Additionally, they contribute to the formation of protective glues for insect eggs, while CarEs (carboxylesterases) play a detoxification role [15,16,32] (Fig. 1).

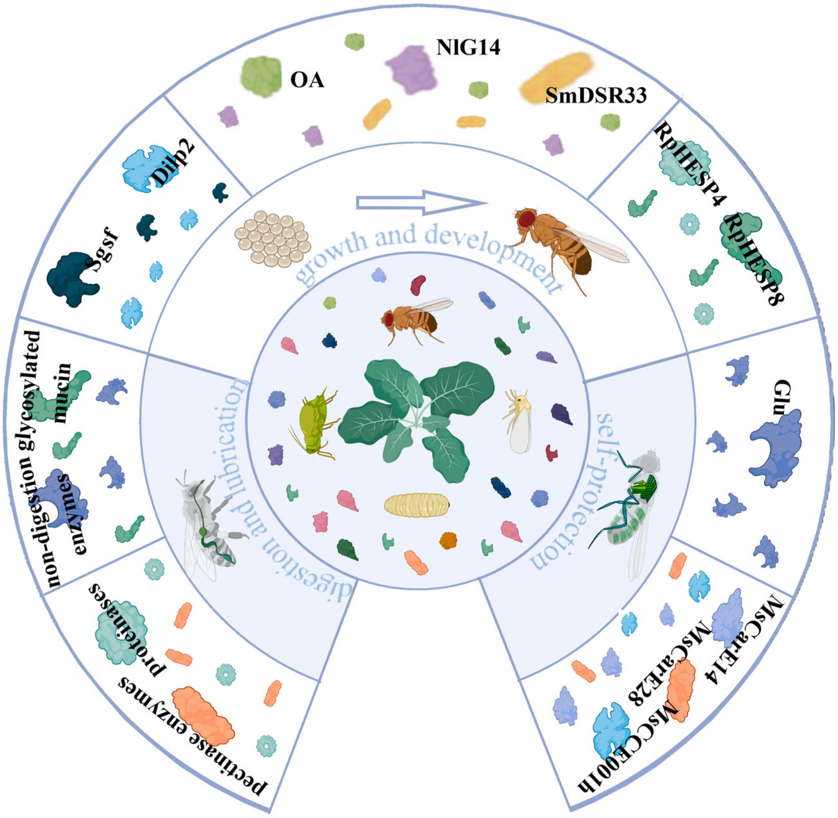

Fig. 1. Schematic diagram of bioactive molecules of salivary proteins acting on themselves by insects.

2.2. *Insect digestion and lubrication*

During the feeding process of herbivorous insects, SPs are instrumental in digestion and lubrication. Previous studies have identified numerous salivary proteins crucial for digestion in hosts [33]. For instance, in *Subpsaltria yangi* (Hemiptera, Cicadidae), comparative transcriptome analysis revealed two putative proteinases essential for breaking down proteins into free amino acids, thus rendering them nutritionally valuable [33,34]. Insects' salivary complexes, consisting of watery saliva rich in lipids, carbohydrates, and enzymes, contribute significantly to extra-oral digestion [35,36]. This process begins with saliva injection into the plant, followed by the suction of liquified food [37,38]. Additionally, salivary glands in phytophagous insects produce pectinase enzymes to rupture the cell wall and aid in ingestion [39–41].

SPs in herbivorous insects also serve a lubricating function, facilitating smooth food consumption during feeding events [22]. During feeding, SPs are selectively deposited onto the mouthpart surface, reducing friction between the mouthparts and the food surface [42–44]. Glycosylated mucin or non-digestive enzymes secreted by salivary glands during the larval stage play a critical role in lubricating food, enabling smooth nutrient intake during this developmental phase [45–47]. In *Drosophila melanogaster* (Diptera, Drosophilidae) larvae, non-digestive enzyme synthesis dominates for most of their life cycle, aiding efficient food lubrication in the intestine [48].

2.3. *Insect growth and development*

Octopamine (OA) signaling plays a pivotal role in regulating essential reproductive processes, including oogenesis, ovulation, sperm storage, and other reproductive behaviors. These regulatory mechanisms are highly sensitive to both internal states and external conditions of the female [49–53]. Studies have demonstrated that injections of OA can stimulate egg laying in species such as *Plutella xylostella* (Lepidoptera, Plutellidae) and *Trigonotylus caelestialium* (Hemiptera, Miridae) [54]. Interestingly, the opposite effect is observed in the western tarnished plant bug, *Lygus Hesperus* (Hemiptera, Miridae), where injection of OA suppresses egg laying [55,56]. Furthermore, knocking down NlG14, a salivary gland-specific gene in *Nilaparvata lugens* (BPH) (Hemiptera, Delphacidae), disrupts ovulation in BPH females, resulting in the accumulation of mature eggs in the ovary and reduced egg laying [57]. Similarly, decreased SmDSR33 expression levels significantly reduce fecundity, survival, and reproduction in *Sitobion miscanthi* (Hemiptera, Aphididae) [58].

In *Drosophila*, insulin-like peptide 2 (Dilp2) assumes a crucial role as a master regulator of systemic growth, originating from the

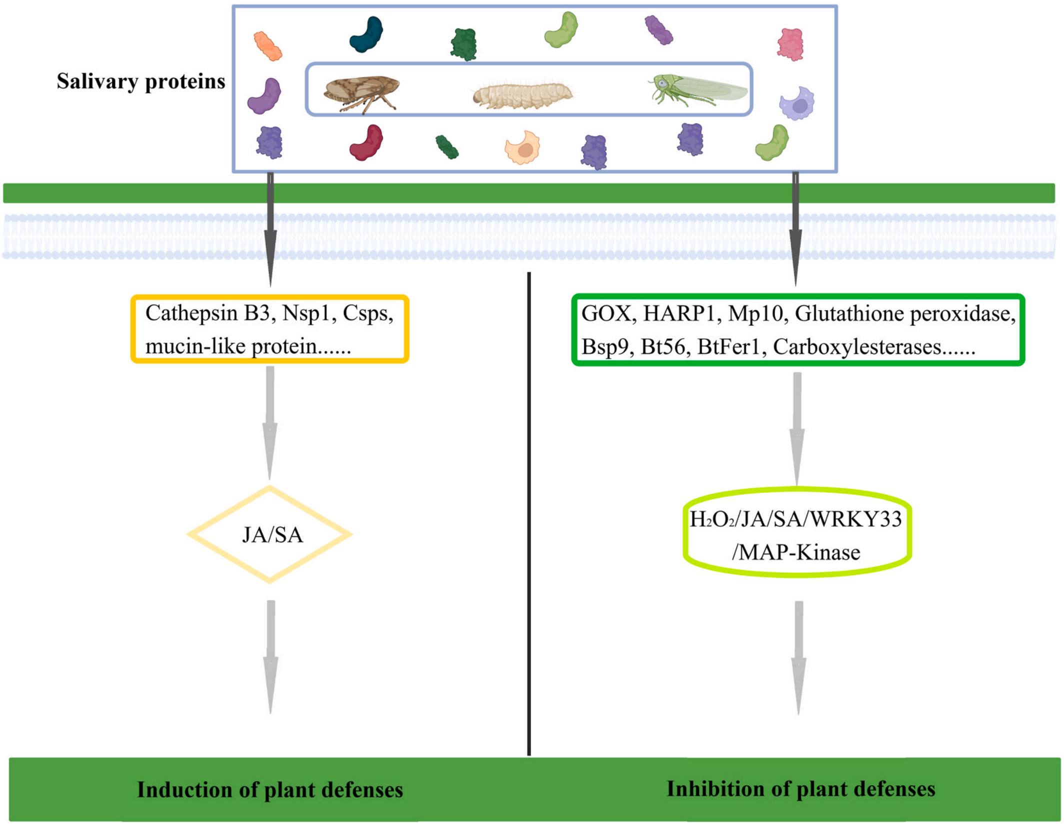

Fig. 2. Schematic diagram of bioactive molecules of insect salivary proteins interacting with plants.

insulin-producing cells (IPCs) located in the larval brain [24,59–61]. Remarkably, a salivary gland-derived secreted factor (Sgsf) in *Drosophila* is released into the hemolymph. Through meticulous investigations involving Sgsf knockout and signal peptide deletion experiments, its indispensable role in regulating Dilp2 secretion is highlighted, with Sgsf knockout mirroring the effects of salivary gland ablation. Impairment of Sgsf leads to a noticeable deceleration of systemic growth by suppressing Dilp2 secretion in brain IPCs and downregulating mTOR signaling in the fat body [23]. In *Riptortus pedestris* (Hemiptera, Alydidae), two salivary proteins derived from horizontal gene transfer, RpHESP4 and RpHESP8, play crucial roles in salivary sheath formation [19].

2.4. Insect self-protection

In the late larval stage of *Drosophila*, the fruit fly secretes a glue from its salivary glands, composed of SPs with repetitive motifs and glycosylation, facilitating attachment to substrates during pupation. This phenomenon of pupal attachment holds great significance for insect survival, serving several essential purposes such as preventing displacement by predators, enhancing resilience against environmental factors like wind or rain, and facilitating the emergence of adults from pupae during metamorphosis [15,16,62]. Additionally, the knockdown of MsCarE14, MsCarE28, and MsCCE001h in *Mythimna separata* (Lepidoptera, Noctuidae) resulted in reduced susceptibility to CGA (Chlorogenic acid), a potential botanical insecticide metabolite naturally occurring in various plants, underscoring the crucial roles of these three CarEs in CGA detoxification [63].

3. Effects of SPs on host plants

Elicitor-induced defenses comprise a range of responses, including depolarization of plasma membrane potential, activation of JA and SA pathways, ROS burst, callose deposition, Ca^{2+} influx, MAPK activation etc [29,30,64]. Conversely, effectors attenuate plant defense responses [31,65–67], with those suppressing plant responses often recognized by corresponding resistance proteins, thereby initiating a secondary layer of defense, known as effector-triggered immunity (ETI) [68,69] (Fig. 2).

3.1. Induction of plant defense

Two SPs, Sm10 and SmC002, derived from the grain aphid *Sitobion miscanthi* (Hemiptera, Aphididae), have been identified to increase the expression of SA-associated defense genes and elevate wheat SA levels, thus enhancing host plant susceptibility. During *S. miscanthi* feeding, the application of Sm10 or SmC002 into wheat plants significantly inhibits callose deposition and alters the transcript levels of callose synthase genes [70]. Additionally, SmCSP4, secreted into wheat plants during *S. miscanthi* feeding, activates the SA-mediated defense pathway; silencing the SmCSP4 gene diminishes the aphids' ability to activate the SA defense pathway [71]. The salivary protein Cathepsin B3 from *Myzus persicae* (Diptera, Culicidae) elicits a recognition response in *Nicotiana tabacum* plants, resulting in the suppression of aphid feeding through the accumulation of reactive oxygen species (ROS) [72]. The salivary protein 1 from BPH (Nsp1) induces cell death, H_2O_2 accumulation, expression of defense-related genes, and callose deposition when transiently expressed in *Nicotiana benthamiana* leaves or rice protoplasts, highlighting its role in BPH-induced plant defense mechanisms [73]. Moreover, caterpillars produce SPs (Csps) that induce the expression of late-responding defense genes, such as proteinase inhibitor 2 (Pin2) [74].

3.2. Inhibition of plant defenses

The herbivorous insect, *Helicoverpa zea* (Lepidoptera, Noctuidae), first identified the effector protein glucose oxidase (GOX), which inhibits nicotine accumulation and defense responses in tobacco [75]. BtFer1 from *Bemisia tabaci* (Hemiptera, Aleyrodidae) exhibits Fe^{2+} binding ability and ferroxidase activity, suppressing H_2O_2-generated oxidative signals in *Solanum lycopersicum* [76]. Aphid carboxylesterases (ACEs) play a pivotal role in hydrolyzing systemin or other signal molecules that induce plant immune reactions, effectively inhibiting plant defense responses, simultaneous knockdown of ACE1 and ACE2 leads to an enhancement in aphid feeding [77]. Additionally, the effector glutathione peroxidase from *Apolygus lucorum* (Hemiptera, Miridae) has been found to inhibit ROS, inducing cell death and consequently increasing plant susceptibility [78].

HARP1, a significant effector found in the oral secretions of *Helicoverpa armigera* (Lepidoptera, Noctuidae), downregulates global wound and jasmonic acid (JA) responsive genes in *Arabidopsis*, thereby increasing susceptibility to insect feeding by interfering with JA signaling transduction. This inhibitory action of HARP1 is attributed to its direct interaction with JASMONATE-ZIM-domain (JAZ) repressors, effectively impeding COI1-mediated JAZ degradation and consequently obstructing JA signaling transduction [79]. Rp614, originating from *Riptortus pedestris* (Hemiptera, Alydidae), serves as a pivotal inducer of cell death in nonhost *Nicotiana benthamiana* leaves, involving NbSGT1 and NbNDR1. Concurrently, it suppresses the soybean immune response during *R. pedestris* infestation by influencing the expression of hormonal defense genes, particularly those associated with SA and JA pathways [80]. Salivary proteins Bsp9 and Bt56 from *B. tabaci* modulate plant defense differently, with Bsp9 enhancing feeding on tomato plants by suppressing WRKY33 and MAP-kinase interactions, while Bt56 influences SA signaling in tobacco through the regulation of a KNOTTED1-like transcription factor [81,82].

The saliva effector Mp10, injected into plant cytoplasm during aphid probing, binds specifically to the acrostyles—cuticular organs located at the tip of maxillary stylets—of *Acyrthosiphon pisum* (Hemiptera, Aphididae) and *M. persicae*. Through interaction with Stylin-03, Mp10 effectively evades the activation of plant defense systems, ensuring continuous feeding by the aphids [83]. BISP from BPH secreted into rice targets OsRLCK185, suppressing basal defenses in susceptible plants [84]. BtFTSP1, originating from a horizontal gene transfer event from fungi in *B. tabaci*, targets a defensive protein, NtFD1, disrupting NtFD1-NtFD1 interaction in *Nicotiana tabacum*, ultimately leading to NtFD1 degradation [85].

In *Laodelphax striatellus* (Hemiptera, Delphacidae), nymphs treated with dsLsSP1-treated had lower rice plants intake than those treated with dsGFP-treated ones, indicating that LsSP1 in *L. striatellus* inhibited rice defense [86].

4. SPs with multiple functions

Transcriptomic and proteomic analysis have revealed the presence of a mucin-like protein (NlMLP) secreted by BPH. Inhibition of NlMLP expression in BPH disrupts the formation of salivary sheaths. NlMLP induces cell death, expression of defense-related genes, and callose deposition. These defense responses are associated with calcium mobilization, MEK2 MAP kinase, and JA signaling pathways [7]. NlDNAJB9, a highly expressed DNAJ protein in BPH salivary glands, when knocked down, results in increased BPH fecundity and honeydew excretion. Conversely, overexpression of NlDNAJB9 induces plant cell death and triggers defense mechanisms such as calcium signaling, MAPK cascades, ROS accumulation, JA hormone signaling, and callose deposition [87] (Fig. 3).

BtE3 is a newly identified salivary effector in the whitefly *B. tabaci*, specifically expressed in the head and secreted into host plants during feeding. Silencing of BtE3 reduces *B. tabaci*'s ability to feed continuously on phloem sap, leading to decreased survival and fecundity. Overexpression of BtE3 in *B. tabaci* up-regulates the SA pathway while simultaneously suppressing JA-mediated defenses in plants [88] (Fig. 3).

The enzyme (3Z):(2E)-hexenal isomerase (Hi-1) in *Manduca sexta*'s (Lepidoptera, Sphingidae) oral secretions catalyzes the conversion of the green leaf volatiles (GLVs) from Z-3-hexenal to E−2-hexenal. This volatile signal serves to attract natural enemies of the insect. Hi-1 mutants raised on a GLV-free diet exhibited developmental disorders, indicating that Hi-1 likely metabolizes other substrates crucial for the insect's development [89] (Fig. 3).

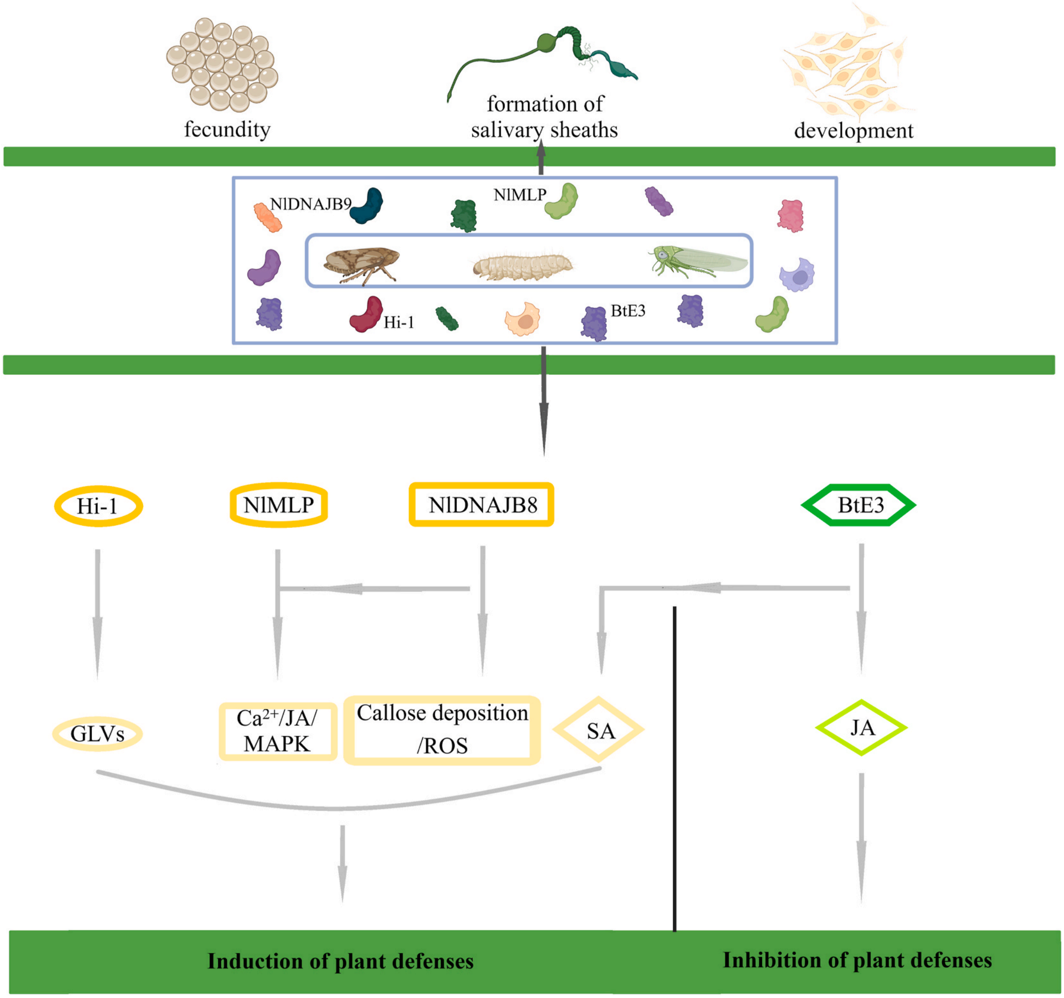

Fig. 3. Schematic diagram of bioactive molecules of insect salivary proteins with multiple functions.

5. Applications of SPs

Natural adhesives play a paramount role in biology and serve as crucial inspirations for the development of bio-inspired adhesives. In insects, the diversity of bioadhesives is notably vast [90,91]. Prior to pupation, *D. melanogaster* [92] and other *Drosophila* species, including *D. virilis* [93], *D. natusa*, and *D. gibberosa* [94], secrete a gel from their salivary glands [95], composed of SPs. These proteins exhibit repetitive motifs and glycosylation, common characteristics of adhesion proteins [15,91]. This glue enables the flies to firmly attach to external surfaces for several days until the emergence of adult flies from the pupa shell, which remains attached to the substrate [95].

In the wild, *Drosophila* pupae display diverse adhesion capabilities, adhering to various substrates such as fruits and beer bottles [96]. They have been observed to attach to wood, wet and decaying parts of fruits, deep within the soil, and even to one another [97–99]. A recent study focusing on the adhesive produced by *D. melanogaster* for pupa adhesion reported remarkable findings, with the glue capable of supporting approximately 15,500 times the weight of a pupa and exhibiting an impressive adhesion strength ranging from 137 to 244 kPa. Notably, the pull-off forces were found to be independent of the contact area, presenting a surprising aspect of this adhesive mechanism [16].

Elicitors can activate plant defense-related signaling pathways or enhance sensitivity to trigger defense responses, thereby boosting plants' resistance to herbivorous insects [100]. Some elicitors have shown promising results in field applications. For instance, field spraying of methyl jasmonate has been demonstrated to effectively reduce the population density of aphids and thrips [101]. External application of high concentrations of *cis*-jasmone can induce wheat (*Triticum aestivum*) to release (Z)-3-hexenyl acetate, thereby repelling wheat stem sawflies [102]. Application of β-1,3-glucan laminarin can activate the MAPK signaling cascade and transcription factors WRKYs in tea plants (*Camellia sinensis*), increasing the levels of signaling molecules such as H_2O_2, SA, abscisic acid (ABA), and defense chemicals including chitinase, phenylalanine ammonia lyase, polyphenol oxidase, flavonol synthase, and volatile compounds. Field application of laminarin enhances tea plants' direct and indirect resistance to the tea green leafhopper (*Empoasca onukii* Matsuda) [103]. Treatment with flonicamid and knockdown of Nl16 and Nl32 genes (salivary protein genes) significantly reduced the feeding activity of *N. lugens* in the phloem and also decreased honeydew excretion and fecundity. These results suggest that the inhibition of flonicamid on the feeding behavior in *N. lugens* might be partially attributed to its effect on the expression of salivary protein genes [104].

By leveraging the interaction between SPs and plants, along with modern genetic modification techniques like gene editing and transgenesis, it becomes feasible to develop insect-resistant varieties [105]. For instance, generating stable transgenic wheat lines expressing dsRNA for targeted silencing of SmDSR33 in grain aphids through plant-mediated RNAi has shown promising results. After feeding on transgenic wheat plants expressing SmDSR33-dsRNA, aphids exhibited attenuated expression levels of SmDSR33 compared to aphids feeding on wild-type plants. The decreased SmDSR33 expression levels consequently led to significantly reduced fecundity, survival, and reproduction of aphids [58]. Similarly, generating 35S:BtE3-RNAi plants that systematically synthesize double-stranded RNA targeting BtE3 transcripts in tobacco plants has demonstrated efficacy in controlling *B. tabaci*. These transgenic plants prevented *B. tabaci* from continuously ingesting phloem sap, resulting in reduced survival and fecundity of *B. tabaci* individuals [88].

5.1. Future perspectives

In this review, we have explored the multifaceted roles of salivary proteins (SPs) in herbivorous insects, spanning their impacts on insect physiology, host plants, and ecological dynamics. While progress has been made, several key areas merit further investigation.

1 Complexity of Salivary Proteins: Herbivore saliva contains a diverse array of proteins, enzymes, and compounds, necessitating advanced analytical methods for comprehensive characterization.
2 Species-Specific Variation: Different insect species exhibit distinct feeding behaviors and salivary compositions, emphasizing the need for species-specific studies to fully understand the roles of SPs.
3 Lack of Functional Annotations: Many salivary proteins lack well-defined functional annotations, underscoring the importance of elucidating their molecular functions and ecological significance.
4 Limited Understanding of Plant Responses: Despite some progress, gaps remain in understanding the specific plant responses triggered by insect herbivore salivary proteins.

Prospects.

1 Biopesticide Development: SPs that modulate plant defenses hold promise for biopesticide development, offering potential insights into novel defense mechanisms and signaling pathways.
2 Crop Protection: Targeted manipulation of interactions between insect SPs and plants could lead to effective crop protection strategies.
3 Ecological Insights: Further exploration of SP roles provides valuable insights into insect ecology and plant-insect interactions.
4 Functional Genomics: Advances in genomics and proteomics offer opportunities to elucidate the functions of SPs with greater precision.
5 Natural Adhesives: Study of biological adhesives in insect saliva inspires the development of bio-inspired adhesives for various applications.

In conclusion, while challenges remain in understanding the complexity of insect herbivore SPs, the prospects for biopesticide development, crop protection, and ecological insights make this area of research highly promising. Continued efforts are essential to fully harness the potential of SPs for practical applications in managing plant-insect interactions.

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Ethics declarations

Review and/or approval by an ethics committee was not needed for this study because this is a review article that all the content we use has been published.

Data availability statement

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

CRediT authorship contribution statement

Xinyi Ma: Writing – review & editing, Writing – original draft. **Zhiyong Yin:** Writing – review & editing, Writing – original draft. **Haiyin Li:** Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Jianjun Guo:** Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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