We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,300

Open access books available

172,000

International authors and editors

190M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities

WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com

Aphid-Plant Interactions: Implications for Pest Management

Sarwan Kumar

Abstract

Aphids are important herbivores and important pest of many field and forest crops. They have specialized long and flexible stylets which are adapted to feeding on phloem sap. To establish successful feeding on host plant, they need to counter a range of both physical and chemical defenses. The defenses employed by plants can have direct effect on the aphid species through difficulty in establishing successful feeding due to the presence of trichomes, thick cell wall, etc. or effect on their biology with lethal consequences in extreme cases (direct defenses). In contrast to this, plants can attract natural enemies of aphids through the release of volatile compounds (the so-called “cry or call for help”) (indirect defense). The information on different defense strategies employed by plants can be utilized to enhance the level of resistance (R) to develop sustainable pest management strategies.

Keywords: Aphidoidea, insect-plant interactions, phloem feeding, plant defense, sieve elements

1. Introduction

Aphids constitute a major group of crop pests that limit productivity of many crops and cause serious damage to plants both by direct feeding and indirectly as vectors of many diseases. Despite being a relatively small insect group (about 5000 known species) compared to 10,000 species of grasshoppers, 12,000 species of geometrid moths, and 60,000 species of weevils, aphids are a serious problem for agriculture [1–3]. Of the 5000 known species in family Aphididae, 450 are endemic on crop plants, and 100 have successfully exploited the agricultural environment to the extent that they are of significant economic importance [3]. They are the specialized phloem sap feeders resulting in significant yield losses in many crops. It is their ability to rapidly exploit the ephemeral habitats that makes them serious pests, and this ability results from (i) their high reproductive potential, (ii) their dispersal capacities, and (iii) their adaptability to local survival [2]. Unlike majority of insects, aphids exhibit parthenogenetic viviparity—phenomenon that limits the need for males to fertilize females and eliminates egg stage from their life cycle. Thus, aphids reproduce clonally and give birth to young ones, and embryonic development of an aphid begins before its mother’s birth leading to telescoping of generations. All these traits allow aphids to exploit the periods of rapid plant growth, conserve energy, and allow for short generation times; nymphs of certain aphid species can reach maturity in as little as 5 days [4].

The well-known parthenogenesis exhibited by aphids sets them apart from other Hemiptera and has a great influence on their biology. In addition to parthenogenesis, many species of aphids also exhibit alternation of generations. The system of alternating one bisexual generation with a succession of parthenogenetic, all-female generation evolved as far back as the Triassic [3] which was later coupled with evolution of viviparity. All these led to reduction in their development period allowing them to multiply at a faster rate. Further, to conserve energy and to invest it in maximizing their reproduction and survival, aphid colonies exhibit wing dimorphism to produce highly fecund wingless morphs or less prolific winged progeny that can disperse to new host plant.

2. Aphid biology and behavior

Aphids are specialized phloem sap feeders and chemists *par excellence*. In most of cases, they exhibit passive feeding by high pressure within the sieve elements (SEs) and feed on virtually all plant families. While most of the species are specialists on a single host plant, some of them are generalists with relatively broad host range [5]. The aphid life cycles involve sexual and asexual morphs, and most of the species have relatively complicated life cycles with morphs that specialize in reproduction, dispersal, and survival under adverse conditions. Based on host utilization, aphids have two different types of life cycle: heteroecious or host alternating and monoecious/autoecious or nonhost alternating. Heteroecious species live on one plant species (primary host) in winter and migrate to another taxonomically unrelated plant species (secondary host) in summer and again migrate to primary host in autumn. While oviparity is exhibited on the primary host, on the secondary host, they reproduce parthenogenetically. These changes in sexual fate and reproductive mode are condition dependent and explain the extraordinary plasticity in development in response to environmental cues. Aphid species that interrupt parthenogenetic reproduction with sexual reproduction are termed as holocyclic. In contrast to host-alternating aphids, nonhost-alternating aphids remain either on the same or closely related host species throughout the year. They complete both sexual life cycle as well as parthenogenetic life cycle on the same host species. In contrast to this, there are species which do not produce eggs and are known as anholocyclic. Some species, particularly those having cosmopolitan distribution, exhibit both holocyclic and anholocyclic life, both at the same time in different geographical areas [6] but rarely both monoecy and heteroecy [7]. The presence of both biparental sexual and asexual life cycle ensures that aphids take advantage of both genetic recombination that help them to evolve and parthenogenesis (very convenient to exploit short-lived hosts).

3. Aphid mouthparts

The beak-like modification of mouthparts (labium, labrum, maxillae, and mandibles) is a distinct character of members of order Hemiptera. Generally the labium (and rarely labrum) is modified into rostrum, into the groove of which needlelike mandibular and maxillary stylets rest when not in use [8]. These needle-like mouthparts enable insects to penetrate the plant tissue and feed on the plant sap. Mandibles constitute the outer stylets and are important in physical penetration of cell walls, while maxillae form the inner ones [9] and form major role in selection of host plant [10]. Since the stylets can penetrate the individual cells due to their microstructure, this enables the aphids to puncture the symplast without wounding. This behavior is important for phloem-feeding insects which helps them

to inoculate viruses into vascular and nonvascular plant cells. Recently, Uzest et al. [11] reported the existence of distinct anatomical structure called “acrostyle” on the tips of maxillary stylets of aphids which is an expanded part of cuticle visible in the common duct of all aphid species.

The presence of four- or five-segmented rostrum (labium) is the characteristic of the family Aphididae [12], and five-segmented labium does not occur in the other groups of Hemiptera. The four-segmented labium has been confirmed in members of Aphidinae, e.g., *Aphis fabae* [13], *Myzus persicae* [14], and *Schizaphis graminum* [15], and the five-segmented labium is confirmed only in Lachninae, e.g., *Lachnus roboris* (L.), which has resulted from the secondary division of the apical segment [16]. However, Razaq et al. [17] observed another modification with only three-segmented labium in *Aphis citricola* van der Goot (Aphidinae). Labium exhibits variation in length, and in most of the species, it reaches the coxa of the third pair of legs. However, it can be exceptionally long (as long as the body) in species that feed on the trunk, branches, and roots of trees as in members of families Lachninae and Eriosomatinae.

4. Compatible aphid-plant interactions

Aphids are specialized phloem sap feeders which insert their needle like stylets in the plant tissue avoiding/counteracting the different plant defenses and withdrawing large quantities of phloem sap while keeping the phloem cells alive. In contrast to the insects with biting and chewing mouthparts which tear the host tissues, aphids penetrate their stylets between epidermal and parenchymal cells to finally reach sieve tubes with slight physical damage to the plants, which is hardly perceived by the host plant [6]. The long and flexible stylets mainly move intercellular in the cell wall apoplasm [18], although stylets also make intracellular punctures to probe the internal chemistry of a cell. The high pressure within sieve tubes helps in passive feeding [6]. During the stylet penetration and feeding, aphids produce two types of saliva. The first type is dense and proteinaceous (including phenol oxidases, peroxidases, pectinases, β -glucosidases) that forms an intercellular-tunneled path around the stylet in the form of sheath [19]. In addition to proteins, this gelling saliva also contains phospholipids and conjugated carbohydrates [20–22]. This stylet sheath forms a physical barrier and protects the feeding site from plant's immune response. When the stylet comes in contact with active flow of phloem sap, the feeding aphid releases digestive enzymes in the vascular tissue in the form of second type of “watery” saliva. The injection of watery saliva (E1) prevents the coagulation of proteins in plant sieve tubes, and during feeding the watery (E2) saliva gets mixed with the ingested sap which prevents clogging of proteins inside the capillary food canal in the insect stylets [6]. Though the actual biochemical mode of action of inhibition of protein coagulation is unknown, the calcium-binding proteins of aphid saliva are reported to interact with the calcium of plant tissues resulting in suppression of calcium-dependent occlusion of sieve tubes and subsequent delayed plant response [23, 24]. This mechanism of feeding is more specialized and precise which avoids different allelochemicals and indigestible compounds abundant in other plant tissues [25]. In addition to this, aphid saliva also contains nonenzymatic-reducing compounds which in the presence of oxidizing enzymes inactivate different defense-related compounds produced by plants after insect attack [21].

The early response of plants to feeding by insects or infection by pathogens shares some common events such as protein phosphorylation, membrane depolarization, calcium influx, and release of reactive oxygen species (ROS, such as hydrogen peroxide) [26], which leads to the activation of

phytohormone-dependent pathways. In response to infestation/infection, different phytohormone-dependent pathways are activated. The ethylene (ET) and jasmonate (JA) pathways are activated by different necrotrophic pathogens [27] and grazing insects [28], while salicylate (SA)-dependent responses are activated by biotrophic pathogens [27]. These responses lead to the production of various defense-related proteins and secondary metabolites with antixenotic or antibiotic properties. In the case of infestation by aphids, a SA-dependent response appears to be activated, while the expression of JA-dependent genes is repressed [29–32]. All these responses lead to the manipulation of the plant metabolism to ensure compatible aphid-plant interactions.

5. Aphid endosymbionts

The plant phloem sap is a highly unbalanced diet composed principally of sugars and amino acids with high C:N content. To cope with excess of sugars in their diet, aphids have evolved modification in their intestinal tract and filter out excess of sugars and water in the form of honeydew [33]. The most of amino acids are present at very low concentrations. Despite their nutritionally poor diet, aphids exhibit high growth and reproduction rates. Since aphids directly feed on the sugars and amino acids, they need not spend extra energy to digest complex nutrients such as proteins which remarkably increases their assimilation efficiency. In addition to this, the essential amino acids required by their growth and development are synthesized by symbiotic bacteria present in their body. Generally two types of symbiotic bacteria are known to be present in aphids: the primary (obligate) symbionts and secondary (facultative) symbionts. *Buchnera aphidicola* (γ -proteobacteria: *Escherichia coli* is also a member of this group) is the most common vertically transmitted primary symbiont present in most aphid species [34]. Some species of aphids also bear other bacteria, i.e., “secondary symbionts.” These include several species of γ -proteobacteria such as *Serratia symbiotica*, *Regiella insecticola*, and *Hamiltonella defensa* [35–43]. *B. aphidicola* is a coccoid hosted in the cytoplasm of specialized cells called mycetocytes/bacteriocytes in the hemocoel of insect. These endosymbionts upgrade the aphid diet by converting nonessential amino acids to essential amino acids. The evolution of symbiotic relationship with endosymbionts has enabled aphids to exploit new ecological niches, i.e., to feed on the plant phloem sap which is otherwise the nutritionally poor diet.

6. Response of aphids to plant characters

The decision for suitability of the plant as a host is made in the very first phase of the host selection. *Alate* aphids use both visual [44] and chemical cues [45] to decide landing on a plant. Upon landing aphids encounter trichomes as the first line of defense. Trichomes can be either glandular or nonglandular. Regardless of their structure, trichome density has significant influence on aphid feeding [46]. Many crop wild relatives (CWRs) of cultivated plants and resistant varieties are resistant to aphid attack due to the presence of trichomes that affect aphid movement and stylet insertion [47]. For example, the presence of high density of trichomes (both simple and glandular) in wild tomato, *Lycopersicon pennellii* (Corr.) D’Arcy, imparts high level of resistance (R) to aphid attack. In addition, the glandular trichomes produce toxic exudates that trap aphids and kill them.

In addition to trichomes, plants possess other constitutive defenses such as thorns and thick cell walls that provide direct resistance to plants against aphid

feeding. Though these mechanical barriers are constitutive defenses, they can also be produced in response to aphid feeding (directly induced defenses).

In addition to these structural defenses, constitutive defenses can also be chemical. For example, glandular trichomes of *Solanum berthaultii* Hawkes produce (E)-farnesene—aphid alarm pheromone that triggers aphid dispersal and prevents colonization [48]. Such antixenotic defenses are of great significance and particularly effective against aphid species that act as vectors of plant pathogenic viruses. However, successful virus transmission can occur even on nonhost plants as stylet insertion is sufficient for some successful infection by quickly acquired viruses. Aphid salivation occurs on even resistant plants even if they do not feed on such resistant plants [23].

The depth of the sieve elements is an important factor determining successful feeding. The length of the aphid stylets must be compatible with the depth of sieve elements. In addition, thickness at the tip of stylets is also crucial for successful feeding [49]. The movement of stylets through plant tissue is mostly intercellular, and aphids probe all the cells that they encounter during probing. Sensorial structures located at the back of the mouth characterize the plant sap, and aphids recognize the substrate as host or nonhost. On nonhost plants, aphids retract the stylets and leaves in search of suitable host unless the plant produces toxins [50]. Many plant species possess toxic compounds that can be either constitutive or induced that have detrimental effect on insects. The well-known examples include plants in the family Brassicaceae and Solanaceae.

Brassica plants possess a well-studied class of sulfur-containing secondary metabolites—glucosinolates—that defend them from insects. However, during the course of evolution, some (though only a few) insects have been specialized to feed even on these plants. The examples include the turnip aphid, *Lipaphis erysimi* (Kaltenbach); cabbage aphid, *Brevicoryne brassicae* (L.); and cabbage white butterflies, *Pieris brassicae* and *P. rapae* [51]. These insects have evolved to use otherwise toxic compounds to their advantage—as cues for the identification of host plants and for development.

Similarly, members of family Solanaceae, e.g., potato and tomato, possess glycosidic alkaloids (tomatine, solanine) that defend them from not only insect pests but bacteria and fungi as well. However, some of the species have evolved to overcome this defense, for example, *Macrosiphum euphorbiae* (Thomas) and *Myzus persicae* (Sulzer). The well-known insecticidal compound, nicotine, found in *Nicotiana* spp. provides protection against feeding aphids. However, continuous selection pressure exerted by these compounds leads to the development of resistance in aphid populations to these compounds. The presence of both sexual (that includes a genetic variability) and asexual modes of reproduction (that leads to faster multiplication) aid in faster resistance development [52].

The resistance gene present in resistant plant provides protection against avirulent strains of insects. To date, one R gene (*Mi-1.2*) has been characterized at molecular level. Plants that possess *Mi-1.2* gene are resistant to potato aphid, two whitefly biotypes (silverleaf whitefly and biotype Q), syllid, and three nematode species [53–55]. Due to the high selection pressure on insect population, there are chances of resistance breakdown in plants due to the development of counter resistance to the *Mi-1.2* [56]. The other genes associated with aphid resistance include virus aphid transmission (*Vat*) resistance gene in melon that confers antixenotic resistance to melon aphid, *Aphis gossypii* Glover, and to virus transmission associated with this species [57] and recombination-activating gene (*Rag1*) in soybean that provides resistance to soybean aphid, *Aphis glycines* Matsumura [58].

The defense-signaling mechanism in plants after aphid attack is similar to incompatible responses in plant-pathogen interactions. Aphid feeding triggers SA-dependent response similar to that triggered by biotrophic pathogens and/or PR

gene RNAs in resistant than in susceptible plants [59–61], while there is downregulation of jasmonic acid-dependent genes [62]. From the very first stylet insertion in epidermal tissues to sustained feeding on sieve elements, aphids continuously inject saliva in the plant tissue which continuously interacts with plant cells to determine compatible/incompatible aphid-plant interactions. However, such interactions have been partially understood. Aphid saliva plays an important role in countering plant defense response and modifying the incompatible interaction to compatible one by modifying the plant metabolism. Aphid feeding may lead to alterations in host plants, including morphological changes, alteration in resource allocation and production of local, and systemic symptoms [32].

7. Response of host plants to aphid infestation

Plants respond in a variety of ways to attack by aphid herbivores. Simple feeding by aphids leads to withdrawal of large quantities of plant sap leading to local chlorosis, weakening of the plant, and increase in susceptibility to other insects or pathogens. The well-known examples include infestation of Brassica plants by *Lipaphis erysimi* and *Brevicoryne brassicae* [63] and of beans by *Aphis fabae* [64]. On the contrary, large aphid populations can also develop on host plant without manifestation of symptoms such as infestation of tomato plants by *Macrosiphum euphorbiae* [65]. The visible symptoms after aphid attack can vary from localized chlorosis at the feeding site or along the stylet path due to damage to the chloroplast [64]; localized tissue damage, e.g., *Dysaphis plantaginea* (Passerini) on apple fruits; curling of leaves, flower buds, and pods of mustard plants by *L. erysimi* [66]; leaf curling to cigar shape in peach by *Myzus persicae* Davidson; growth distortions on citrus by *Aphis spiraecola* Patch; to systemic effects caused by feeding of *Acyrtosiphon pisum* (Harris) and *Therioaphis trifolii* (Monell) on alfalfa [52]. All the manifestations are in part due to the toxic effect of saliva on host plant. Further, saliva may also have effect on the hormonal balance of plants leading to changes in normal cell division (hypertrophy) that can result in gall formation on host plant. The actual mechanism of gall formation is still not fully understood. Detailed studies on aphid saliva have found no evidence of any cecidogenic compound that can result in gall formation on host plant [67]. However, it has been postulated that galls contain higher concentration of nutrients than the uninfested plant part which may be of adaptive advantage to the insect that develops inside the gall. Koyama et al. [68] analyzed the concentration of amino acids in galled leaves of *Sorbus commixta* Hedl induced by *Rhopalosiphum insertum* (Walker) and found it to be five times higher than that in ungalled leaves without any difference in the composition. In addition to providing better nutrition, galls also provide conducive microclimate to the aphid species that develops within and protects it from its natural enemies as well as insecticides [69].

Unlike other herbivores that only cause direct feeding damage, aphids also cause indirect damage to plants. The honeydew drops deposited on the leaves act as magnifying lenses that may burn the leaf tissue beneath on sunny days. In addition, black sooty mold develops on the honeydew that interferes with normal photosynthetic activity and blocks the stomata which interferes with gas exchange leading to leaf fall. Some of the aphid species also act as vectors of phytopathogenic viruses, and the association is of advantage to both the aphid vector and the phytopathogenic virus. Aphids serve as an important mean of dispersion, and some species of viruses (replicative) even use aphids as favorable host for replication. Once inside the aphid body, both replicative and circulative viruses make aphids infective for the rest of its life. When aphid density increases on a virus-infected plant due to it being more nutritious than healthy plant, they produce *alate* forms that disperse

to new uninfected plants, which further aids in their dispersal [52]. In addition to being adaptive advantage to virus, this association is beneficial for aphids as well. The virus-infected plants become more nutritious to aphids than uninfected plants [52]. For example, the concentration of free amino acids is more in virus-infected plants. Virus infection also leads to downregulation of plant defenses, thus making the plant more suitable host for aphids. Further, virus-infected plants assume yellowish coloration making them more attractive to aphids.

8. Aphid-plant-natural enemy tritrophic interaction: the “cry or call for help”

In response to aphid feeding, plants release a number of volatile compounds which are perceived by aphid natural enemies. Since plants employ these natural enemies to defend themselves, the release of volatile compounds is analogous to “cry or call for help” by plants. This type of defense is referred to as indirect defense. A number of insects are associated with natural suppression of aphid population which includes predators such as ladybird beetles (e.g., *Coccinella* spp., *Brumus* sp., *Adalia bipunctata* L., *Menochilus* sp., etc.), green lacewing (*Chrysoperla carnea* Stephens), syrphids (*Episyrphus balteatus* De Geer), mirid bugs, and parasitoids (*Aphidius* spp., *Diaeretiella rapae* M’Intosh, *Praon* spp., etc.). However, these natural control agents are not efficient in suppressing aphid population, and there is a lack of synchrony in the peak activity of aphids and their natural enemies [63]. Aphid populations generally develop early in the season (mostly in spring) with delayed action of natural control agents. But once their action has started, there is sudden decline in aphid population as observed in oilseed Brassica [66] and organic crops [70].

The feeding by aphids triggers the release of volatile compounds from infested plants making them more attractive to parasitoids. For example, *Acyrtosiphon pisum*-infested broad bean plants are six times more attractive to *Aphidius ervi* Haliday than uninfested plants [71]. Similarly, *Brassica rapa* L. var. *rapifera* plants infested either by *L. erysimi* or *M. persicae* become more attractive to *D. rapae*. This increase in attractiveness has potential implications in aphid control, and researchers are working to find possible ways to elicit this attractiveness in uninfested plants. For example, exogenous application of (Z)-jasmone, a compound derived from jasmonic acid, results in increased attractiveness of uninfested broad bean plants to *A. ervi* similar to those infested by *A. pisum* [72].

9. Potential applications for aphid management

The current understanding of these interactions can help find ways to improve plant resistance to aphids. Since aphids cause serious damage to many agricultural crops, there is a need to find sustainable solution for the management as an effective alternative strategy to synthetic insecticides. There are accelerated global research efforts to search for source(s) of aphid resistance especially in crop wild relatives (CWRs) [4, 73–75]. There is a growing body of literature that suggests that almost all the variations necessary for crop improvement can be found in their CWRs that were lost over the course of domestication [76–80]. The use of CWRs is continuously increasing over the years for a range of beneficial traits including pest and disease resistance [81–83]. In a comprehensive survey by Hajjar and Hodgkin [83] about the use of CWRs in crop improvement for the period 1986–2005, over 80% of the beneficial traits involved pest and disease resistance. The present knowledge of genomics and availability of tools of biotechnology have erased the boundaries of crossing the

species from different gene pools, and there has been a significant increase in the number of wild species in gene banks. Despite this, the use of CWRs in their contributions in providing useful genes for improvement of crop plants has been less than expected. In addition to this, the external application of analogues of jasmonic acid and salicylic acid can also be used to further enhance the level of resistance in crop plants [84].

In recent years, there has been an increase in the knowledge on resistance genes, but only a few *R* genes that confer resistance against hemipteran insects have been identified. Some of them include *Vat* that confers resistance to *Aphis gossypii* in melon [85], *Bph 14* and *Bph 26* genes in rice that confer resistance to *Nilaparvata lugens*, and *Mi-12*. gene in tomato that confers resistance to *Macrosiphum euphorbiae* [32]. The *Vat* gene in melon enhances SE wound healing and thus confers resistance to *A. gossypii* [86]. The cloning of *Mi-1.2* gene has been a milestone in plant resistance to aphids [54, 55, 86–88], and it has distinct resistance mechanisms against different pests. Against root-knot nematode, *M. incognita*, plants exhibit hypersensitive response, and this response is not manifested upon aphid infestation. The resistance to aphids is antibiotic and phloem based, while it is antixenotic to psyllids. On the other hand, *Mi-1.2*-mediated resistance to whiteflies deters insect settling. However, if the insect establishes a feeding site, it can develop even on the *Mi-1.2* plants. The resistant plants exhibit distinct mechanism of resistance against members of four different animal taxa; however, the biochemical basis of such resistance is not yet known.

The attractiveness of the crop plants to aphids and subsequently to their parasitoids can also be augmented to increase effectiveness of parasitoids/natural enemies provided aphids do not act as vector of the phytopathogenic virus. This strategy is especially important as it does not exert any ecological pressure on the aphids. Germplasm screening can be targeted for genotypes that are good at defending themselves from aphid attack and simultaneously attractive to aphid natural enemies. For example, *Eruca sativa* genotypes are particularly attractive to coccinellid beetles in *Brassica* systems compared to *B. juncea*, *B. napus*, *B. carinata*, or *B. rapa*.

Another area of potential application in aphid control is the development of transgenic plants expressing resistance against aphids. Modern breeding techniques can be of great help in transferring target trait to the cultivated plant compared to traditional breeding methods. The commercial insect-resistant GM crops that express *Bt* toxins are particularly effective against Lepidoptera and Coleoptera [89] with no efficacy against phloem feeders including aphids [90]. This accelerated the work on finding alternate strategies such as protease inhibitors, RNAi, antimicrobial peptides (AMPs), etc. Protease inhibitors which may be small peptides or protein molecules inhibit the activity of proteases, thus disrupting the normal protein digestion and consequent amino acid assimilation vital for insect growth. These are already present in plant storage organs and are induced upon insect feeding. Significantly high activity of PI was reported in barley infested with *Schizaphis graminum* with minor effect on its survival, while survival of *Rhopalosiphum padi* was significantly affected [91]. Oryzacystatin-I in transgenic rapeseed [92] and egg plants [93] and cysteine in *Arabidopsis thaliana* [94] from barley are known to provide protection against aphid infestation with their effect on aphid survival, growth, and reproduction. Thus, the use of PIs in aphid management has a good promise as an alternate control strategy [92–94].

Another potential area in aphid management is the exploitation of RNAi technology, which is posttranslational RNA-mediated gene silencing. Plants can be genetically engineered to produce dsRNA to provide protection against a target pest. Transgenic maize plants that produce dsRNA significantly reduced feeding damage by Western corn rootworm, *Diabrotica virgifera* larvae [95]. In the case of aphids, different workers have achieved RNAi-mediated gene silencing either by injecting the siRNA (short-interfering RNA) [96, 97] or dsRNA into insect hemolymph or

feeding the insect with dsRNA [98, 99]. A temporary mRNA inhibition of about 30–40% in aphids was observed by single dose of dsRNA [96]. Similarly, 50% reduction in salivary gland protein expression was observed by Mutti et al. [97].

All the organisms synthesize small 12–50 amino acid long peptides which have antibiotic activity and are termed antimicrobial peptides. They are generally synthesized ribosomally but are also produced enzymatically in fungi and bacteria. They are known to possess antibiotic activity against both gram-positive and gram-negative bacteria and provide immunity against microbial infection. Many insect species are known to produce AMPs [100, 101]. On the contrary aphids do not produce AMPs [95] as they have mutual relationship with endosymbiotic bacteria such as *Buchnera aphidicola*, *Hamiltonella*, *Serratia*, *Rickettsia*, and *Regiella* spp. [102] which play an important role of converting nonessential amino acids in phloem sap to essential ones [103]. Thus, aphid bacterial endosymbionts can be a useful target for AMPs. Any adverse effect on aphid endosymbionts can adversely affect aphid fecundity and can prolong development period [104, 105]. So far, there is only one report on the effect of AMP (indolicidin) on aphids, ingestion of which reduces the number of bacteriocytes and number of bacteria in *M. persicae*, which have significant negative effect on aphid survival, development, and fecundity [106]. This suggests that AMPs expressed in GM plants offer a promising approach for aphid control.

Production of volatile compounds by plants is another area that can be explored. Aphids respond to plant volatiles and use them for long-range orientation as recorded in *Aphis fabae*, *A. pisum*, *Brevicoryne brassicae*, and *M. persicae* [107–110]. Many plants synthesize E- β -farnesene (E β f), a well-known alarm pheromone of aphids, as aphid repellent such as wild potato species [48]. Choice experiments by these authors indicated that aphids remain at a distance of 1–3 mm from leaf surface. Apart from general avoidance, aphids also responded to E β f by producing higher proportion of *alate* (migratory) individuals on treated plants under controlled conditions [111] as well in the field [112]. Thus, plants are exposed to reduced number of apterous (feeding) forms and high proportion of *alates* (migratory forms) that have greater tendency to leave the plant [111]. Besides a repellent effect on aphids, E β f is also known to attract natural enemies of aphids such as ladybirds *Coccinella septempunctata* and *Harmonia axyridis*, parasitoids *Aphidius uzbekistanicus* and *A. ervi*, and syrphid fly *Episyrphus balteatus* [113–117]. Thus, production of transgenic plants expressing E β f can have dual effect on aphids and can increase the benefits of E β f production.

10. Conclusion

The aphid-plant coevolution is a continuous arms race that helps to improve defense strategies employed by plants to ward off aphids and counter defense mechanisms employed by aphid herbivores. For a compatible aphid-plant interaction, aphids not only need to alter local and systemic events but also need to modify resource allocation to suit phloem sap to their requirements. Generally, the JA-mediated defenses are employed by plants to control aphids. But aphids through the use of specific effectors are able to modify the JA-mediated defense response of plant and are able to establish successful feeding. Plants, on the other hand, have evolved to use aphid salivary components as elicitors of defense response. The phloem sealing mechanism is one such response observed in resistant plants. In addition, plants have also evolved a plethora of plant secondary metabolites (PSMs) that have defensive functions. But some specialist aphids have learned to use these compounds to their own advantage and use them as cues for feeding and colonization and even sequester them for their advantage.

The current knowledge on aphid-plant interactions is still in its infancy. But the recent studies have provided insights into such interactions which will have far-reaching implications at different levels including development of novel aphid management strategies.

Conflict of interest

The author declares that he has no conflict of interest.

Author details

Sarwan Kumar
Department of Plant Breeding and Genetics, Punjab Agricultural University,
Ludhiana, India

*Address all correspondence to: sarwanent@pau.edu

IntechOpen

© 2019 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/3.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

References

- [1] Remaudiere G, Remaudiere M. Catalogue des Aphididae du Monde. Paris: INRA; 1997. 473 p
- [2] Dedryver CA, Le Ralec A, Fabre F. The conflicting relationship between aphids and men: A review of aphid damages and of their control strategies. *Comptes Rendus Biologies*. 2010;**333**:539-553
- [3] Blackman RL, Eastop VF. Taxonomic issues. In: van Emden HF, Harrington R, editors. *Aphids as Crop Pests*. 2nd ed. UK: CAB International; 2017. pp. 1-36
- [4] Goggin FL. Plant-aphid interactions: Molecular and ecological perspectives. *Current Opinion in Plant Biology*. 2007;**10**:399-408
- [5] Peccoud J, Simon JC, von Dohlen C, Coeur d'acier A, Plantegenest M, Vanlerberghe-Masutti F, et al. Evolutionary history of aphid-plant associations and their role in aphid diversification. *Comptes Rendus Biologies*. 2010;**333**:474-487. DOI: 10.1016/j.crv.2010.03.004
- [6] Bhatia V, Uniyal PL, Bhattacharya R. Aphid resistance in Brassica crops: Challenges, biotechnological progress and emerging possibilities. *Biotechnology Advances*. 2011;**29**:879-888
- [7] Williams IS, Dixon AFG. Life cycles and polymorphism. In: van Emden HF, Harrington R, editors. *Aphids as Crop Pests*. 1st ed. UK: CAB International; 2007. pp. 69-85
- [8] Capinera JL. Green peach aphid, *Myzus persicae* (Sulzer) (Insecta: Hemiptera: Aphididae). In: Capinera JL, editor. *Encyclopedia of Entomology*. Dordrecht, The Netherlands: Springer; 2008. pp. 1727-1730
- [9] Forbes AR. The mouthparts and feeding mechanism of aphids. In: Harris K, Maramorosch K, editors. *Aphids as Virus Vectors*. New York: Academic Press; 1977. pp. 83-103
- [10] Powell G, Tosh CR, Hardie J. Host plant selection by aphids: Behavioral, evolutionary, and applied perspectives. *Annual Review of Entomology*. 2006;**51**:309-330
- [11] Uzeš M, Gargani D, Dombrovsky A, Cazevieuille C, Cot D, Blanc S. The "acrostyle": A newly described anatomical structure in aphid stylets. *Arthropod Structure and Function*. 2010;**39**:221-229
- [12] Guyton TL. A taxonomy, ecologic and economic study of Ohio Aphididae. *The Ohio Journal of Science*. 1924;**26**:1-26
- [13] Skelett WH. Muskulatur und Darm der Schwarzen Blattlaus *Aphis fabae* SCOP. *Zoologica*. 1928;**76**:1-120
- [14] Forbes AR. The stylets of the green peach aphid, *Myzus persicae* (Homoptera: Aphididae). *The Canadian Entomologist*. 1969;**101**:31-41
- [15] Saxena PX, Chada HL. The greenbug, *Schizaphis graminum*. Mouthparts and feeding habits. *Annals of the Entomological Society of America*. 1971;**64**:897-904. DOI: 10.1093/aesa/64.4.897
- [16] Wojciechowski W. Studies on the systematic system of aphids (Homoptera: Aphidinea). Katowice: Uniwersytet Slaski; 1992
- [17] Razaq A, Toshio K, Pear M, Masaya S. SEM observations on the citrus green aphid, *Aphis citricola* van der Goot (Homoptera: Aphididae). *Pakistan Journal of Biological Sciences*. 2000;**3**:949-952. DOI: 10.3923/pjbs.2000.949.952

- [18] Giordanengo P, Brunissen L, Rusterucci C, Vincent C, van Bel A, Dinant S, et al. Compatible plant-aphid interactions: How aphids manipulate plant response. *Comptes Rendus Biologies*. 2010;**333**:516-523. DOI: 10.1016/j.crvi.2010.03.007
- [19] Felton GW, Eichenseer H. Herbivore saliva and induction of resistance to herbivores and pathogens. In: Agrawal AA, Tuzun S, Bent E, editors. *Induced Plant Defenses Against Pathogens and Herbivores: Biochemistry, Ecology, and Agriculture*. St. Paul, MN: APS Press; 1999. pp. 19-36
- [20] Urbanska A, Tjallingii WF, Dixon AFG, Leszczynski B. Phenol oxidizing enzymes in the grain aphid's saliva. *Entomologia Experimentalis et Applicata*. 1998;**86**:197-203
- [21] Miles PW. Aphid saliva. *Biological Reviews*. 1999;**74**:41-85
- [22] Cherqui A, Tjallingii WF. Salivary proteins of aphids, a pilot study on identification, separation and immunolocalisation. *Journal of Insect Physiology*. 2000;**46**:1177-1186
- [23] Will T, Tjallingii WF, Thonnessen A, van Bel AJE. Molecular sabotage of plant defense by aphid saliva. *Proceedings of the National Academy of Sciences of the United States of America*. 2007;**104**:10536-10541
- [24] Will T, Kornemann SR, Furch ACU, Tjallingii WF, van Bel AJE. Aphid watery saliva counteracts sieve-tube occlusion: A universal phenomenon? *Journal of Experimental Biology*. 2009;**212**:3305-3312
- [25] Schoonhoven LM, van Loon JJA, Dicke M. *Insect-Plant Biology*. Oxford: Oxford University, Press; 2005. 421 p
- [26] Garcia-Brugger A, Lamotte O, Vandelle E, Bourque S, Lecourieux D, Poinssot B, et al. Early signaling events induced by elicitors of plant defenses. *Molecular Plant-Microbe Interactions*. 2006;**19**:711-724
- [27] Thomma BPHJ, Penninckx IAMA, Cammue BPA, Broekaert WF. The complexity of disease signaling in *Arabidopsis*. *Current Opinion in Immunology*. 2001;**13**:63-68
- [28] Maffei ME, Mithofer A, Boland W. Before gene expression: Early events in plant-insect interaction. *Trends in Plant Science*. 2007;**12**:310-316
- [29] Zhu-Salzman K, Salzman RA, Ahn JE, Koiwa H. Transcriptional regulation of sorghum defense determinants against a phloem-feeding aphid. *Plant Physiology*. 2004;**134**:420-431
- [30] Thompson GA, Goggin FL. Transcriptomics and functional genomics of plant defence induction by phloem-feeding insects. *Journal of Experimental Botany*. 2006;**57**:755-766
- [31] Gao LL, Anderson JP, Klingler JP, Nair RM, Edwards OR, Singh KB. Involvement of the octadecanoid pathway in bluegreen aphid resistance in *Medicago truncatula*. *Molecular Plant-Microbe Interactions*. 2007;**20**:82-93
- [32] Walling LL. Avoiding effective defenses: Strategies employed by phloem-feeding insects. *Plant Physiology*. 2008;**146**:859-866
- [33] Dixon AFG. *Aphid Ecology: An Optimization Approach*. 2nd ed. London: Chapman and Hall; 1998. 300 p
- [34] Munson MA, Baumann P, Kinsey MG. *Buchnera* gen. nov. and *Buchnera aphidicola* sp. nov., a taxon consisting of the mycetocyte-associated, primary endosymbionts of aphids. *International Journal of Systematic Bacteriology*. 1991;**41**:566-568
- [35] Loudit SMB, Bauwens J, Francis F. Cowpea aphid-plant interactions:

Endosymbionts and related salivary protein patterns. *Entomological Experimentalis et Applicata*. 2018;**166**:460-473. DOI: 10.1111/eea.12687

[36] Chen DQ, Purcell AH. Occurrence and transmission of facultative endosymbionts in aphids. *Current Microbiology*. 1997;**34**:220-225

[37] Fukatsu T, Nikoh N, Kawai R, Koga R. The secondary endosymbiotic bacterium of the pea aphid *Acyrtosiphon pisum* (Insecta: Homoptera). *Applied and Environmental Microbiology*. 2000;**66**:2748-2758

[38] Fukatsu T, Tsuchida T, Nikoh N, Koga R. *Spiroplasma* symbiont of the pea aphid *Acyrtosiphon pisum* (Insecta: Homoptera). *Applied and Environmental Microbiology*. 2001;**67**:1284-1291

[39] Darby AC, Birkle LM, Turner SL, Douglas AE. An aphid-borne bacterium allied to the secondary symbionts of whitefly. *FEMS Microbiology Ecology*. 2001;**36**:43-50

[40] Sandstrom JP, Russell JA, White JP, Moran NA. Independent origins and horizontal transfer of bacterial symbionts of aphids. *Molecular Ecology*. 2001;**10**:217-228

[41] Haynes S, Darby AC, Daniell TJ, Webster G, van Veen FJF, Godfray HCJ, et al. Diversity of bacteria associated with natural aphid populations. 2003;**69**:7216-7223

[42] Russell JA, Latorre A, Sabater-Munoz B, Moya A, Moran NA. Independent origins and horizontal transfer of bacterial symbionts of aphids. *Molecular Ecology*. 2003;**12**:1061-1075

[43] Moran NA, Russell JA, Koga R, Fukatsu T. Evolutionary relationships of three new species of enterobacteriaceae

living as symbionts of aphids and other insects. *Applied and Environmental Microbiology*. 2005;**71**:3302-3310

[44] Doring TF, Chittka L. Visual ecology of aphids: A critical review on the role of colours in host finding. *Arthropod-Plant Interactions*. 2007;**1**:3-16

[45] Pickett JA, Birkett MA, Bruce TJA, Chamberlain K, Gordon-Weeks R, Matthes MC, et al. Developments in aspects of ecological phytochemistry: The role of cis-jasmone in inducible defence systems in plants. *Phytochemistry*. 2007;**68**:2937-2945

[46] Musetti L, Neal JJ. Resistance to the pink potato aphid, *Macrosiphum euphorbiae*, in two accessions of *Lycopersicon hirsutum* f. *glabratum*. *Entomologia Experimentalis et Applicata*. 1997;**84**:137-146

[47] Bin F. Influenza dei peli glandolari sugli insetti in *Lycopersicon* spp. *Frust Entomology*. 1979;**15**:271-283

[48] Gibson RV, Pickett JA. Wild potato repels aphids by release of aphid alarm pheromone. *Nature*. 1983;**302**:608-609

[49] Will T, van Bel AJE. Physical and chemical interactions between aphids and plants. *Journal of Experimental Botany*. 2006;**57**:729-737

[50] Martinez CE, Leybourne DJ, Bos JIB. Non-host and poor host resistance against aphids may reside in different plant cell layers depending on the plant species-aphid species interaction. *BioRxiv*. 2018. DOI: 10.1101/372839

[51] Hopkins RJ, van Dam NM, van Loon JJA. Role of glucosinolates in insect plant relationships and multitrophic interactions. *Annual Review of Entomology*. 2009;**54**:57-83

[52] Guerrieri E, Digilio MC. Aphid-plant interactions: A review. *Journal of Plant Interactions*. 2008;**3**:223-232

- [53] Nombela G, Williamson VM, Muniz M. The rootknot nematode resistance gene Mi-1.2 of tomato is responsible for resistance against the whitefly *Bemisia tabaci*. *Molecular Plant-Microbe Interactions*. 2003;**16**:645-649
- [54] Kaloshian I, Walling LL. Hemipterans as plant pathogens. *Annual Review of Phytopathology*. 2005;**3**:491-521
- [55] Casteel C, Walling LL, Paine T. Behavior and biology of the tomato psyllid, *Bactericera cockerelli*, in response to the Mi-1.2 gene. *Entomologia Experimentalis et Applicata*. 2006;**121**:67-72
- [56] Goggin FL, Williamson VM, Ullman DE. Variability in the response of *Macrosiphum euphorbiae* and *Myzus persicae* (Hemiptera: Aphididae) to the tomato resistance gene Mi. *Environmental Entomology*. 2001;**30**:101-106
- [57] Chen JQ, Rahbe' Y, Delobel B, Sauvion N, Guillaud J, Febvay G. Melon resistance to the aphid *Aphis gossypii*: Behavioral analysis and chemical correlations with nitrogenous compounds. *Entomologia Experimentalis et Applicata*. 1997;**85**:33-44
- [58] Li Y, Hill C, Carlson S, Diers B, Hartman G. Soybean aphid resistance genes in the soybean cultivars Dowling and Jackson map to linkage group M. *Molecular Breeding*. 2007;**19**:25-34
- [59] Forslund K, Pettersson J, Bryngelsson T, Jonsson L. Aphid infestation induces PR proteins differently in barley susceptible or resistant to the bird cherry-oat aphid (*Rhopalosiphum padi*). *Physiologia Plantarum*. 2000;**110**:496-502
- [60] Mohase L, van der Westhuizen AJ. Salicylic acid is involved in resistance responses in the Russian wheat aphid-wheat interaction. *Journal of Plant Physiology*. 2002;**159**:585-590
- [61] Martinez de Ilarduya O, Xie QG, Kaloshian I. Aphid-induced defense responses in *Mi-1*-mediated compatible and incompatible tomato interactions. *Molecular Plant-Microbe Interactions*. 2003;**16**:699-708
- [62] Zarate SI, Kempema LA, Walling LL. Silverleaf whitefly induces salicylic acid defenses and suppresses effectual jasmonic acid defenses. *Plant Physiology*. 2007;**143**:866-875
- [63] Kumar S, Singh YP. Insect pests. In: Kumar A, Banga SS, Meena PD, Kumar PR, editors. *Brassica Oilseeds: Breeding and Management*. Wallingford, UK: CABI Publishing; 2015. pp. 193-232
- [64] Miles PW. Specific responses and damage caused by Aphidoidea: Principles. In: Minks AK, Harrewijn P, editors. *Aphids: Their Biology, Natural Enemies and Control*. New York: Elsevier; 1989. pp. 23-47
- [65] Guerrieri E. Afidone verde del pomodoro e della patata *Macrosiphum euphorbiae*. Lavoro pubblicato dalla Regione Campania nell'ambito dei finanziamenti UE Obiettivo 1 _ Quadro comunitario di sostegno; 2001. pp. 94-99. Regg. Ce 2052/88, 2081/93 _ POM
- [66] Kumar S. Relative abundance of turnip aphid and the associated natural enemies on oilseed *brassica* genotypes. *Journal of Agricultural Science and Technology*. 2015;**17**:1209-1222
- [67] Otha S, Kajino N, Hashimoto H, Hirata T. Isolation and identification of cell hypertrophy-inducing substances in the gall forming aphid *Colopha moriokaensis*. *Insect Biochemistry and Molecular Biology*. 2000;**30**:947-952
- [68] Koyama Y, Yao I, Akimoto SI. Aphid galls accumulate high concentrations of amino acids: A support for the

nutrition hypothesis for gall formation. *Entomologia Experimentalis et Applicata*. 2004;**113**:135-144

[69] Wool D. Gallling aphids: Specialization, biological complexity and variation. *Annual Review of Entomology*. 2004;**49**:75-192

[70] Trembley E. Possibilities for utilization of *Aphidius matricariae* Hal. (Hymenoptera Ichneumonidae) against *Myzus persicae* (Sulz.) (Homoptera Aphidoidea) in small glasshouses. *Journal of Plant Diseases and Protection*. 1974;**81**:612-619

[71] Guerrieri E, Pennacchio F, Tremblay E. Flight behaviour of the aphid parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae) in response to plant and host volatiles. *European Journal of Entomology*. 1993;**90**:415-421

[72] Birkett MA, Campbell CAM, Chamberlain K, Guerrieri E, Hick AJ, Martin JL, et al. New roles for cis-jasmone as an insect semiochemical and in plant defence. *Proceedings of the National Academy of Sciences of the United States of America*. 2000;**97**:9329-9334

[73] Dosdall LM, Kott L. Introgression of resistance to cabbage seed pod weevil to canola from yellow mustard. *Crop Science*. 2006;**46**:2437-2445. DOI: 10.2135/cropsci2006.02.0132

[74] Gos R, Wagenaar R, Bukovinszky T, van Dam NM, Dicke M, Bullock JM, et al. Genetic variation in defense chemistry in wild cabbages affects herbivores and their endoparasitoids. *Ecology*. 2008;**89**:1616-1626

[75] Edwards D, Henry RJ, Edwards KJ. Advances in DNA sequencing accelerating plant biotechnology. *Plant Biotechnology Journal*. 2012;**10**:621-622. DOI: 10.1111/j.1467-7652.2012.00724.x

[76] Tanksley SD, McCouch SR. Seed banks and molecular banks: Unlocking genetic potential from the wild. *Science*. 1997;**277**:1063-1066. DOI: 10.1126/science.277.5329.1063

[77] Fernie AR, Tadmor Y, Zamir D. Natural genetic variation for improving crop quality. *Current Opinion in Plant Biology*. 2006;**9**:196-202. DOI: 10.1016/j.pbi.2006.01.010

[78] Vaughan DA, Balazs E, Heslop-Harrison JS. From crop domestication to super domestication. *Annals of Botany*. 2007;**100**:893-901. DOI: 10.1093/aob/mcm224

[79] Burger JC, Chapman MA, Burke JM. Molecular insights into the evolution of crop plants. *American Journal of Botany*. 2008;**95**:113-122

[80] Pelgrom K, Broekgaarden C, Voorrips RE, Vosman BJ. Successful use of crop wild relatives in breeding: Easier said than done. In: *International Conference on Enhanced Gene Pool Utilization-Capturing Wild Relative and Landrace Diversity for Crop Improvement*. Vol. 10. University of Birmingham; 2015. 15 p

[81] Prescott-Allen C, Prescott-Allen R. *The First Resource: Wild Species in the North American Economy*. New Haven: Yale University; 1986

[82] Prescott-Allen C, Prescott-Allen R. *Genes from the Wild: Using Wild Genetic Resources for Food and Raw materials*. London: International Institute for Environment and Development; 1988

[83] Hajjar R, Hodgkin T. The use of wild relatives in crop improvement: A survey of developments over the last 20 years. *Euphytica*. 2007;**156**:1-13. DOI: 10.1007/s10681-007-9363-0

[84] Cooper WC, Jia L, Goggin FL. Acquired and R-gene-mediated

resistance against the potato aphid in tomato. *Journal of Chemical Ecology*. 2004;**30**:2527-2542

[85] Martin B, Rahbe Y, Fereres A. Blockage of stylet tips as the mechanism of resistance to virus transmission by *Aphis gossypii* in melon lines bearing the Vat gene. *The Annals of Applied Biology*. 2003;**142**:245-250

[86] Kaloshian I, Kinsey DE, Ullman DE, Williamson VM. The impact of *Meu1*-mediated resistance in tomato on longevity, fecundity, and behavior of the potato aphid, *Macrosiphum euphorbiae*. *Entomologia Experimentalis et Applicata*. 1997;**83**:181-187

[87] Rossi M, Goggin FL, Milligan SB, Kaloshian I, Ullman DE, Williamson VM. The nematode resistance gene *Mi* of tomato confers resistance against the potato aphid. *Proceedings of the National Academy of Sciences of the United States of America*. 1998;**95**:9750-9754

[88] Vos P, Simons G, Jesse T, Wijbrandi J, Heinen L, Hogers R, et al. The tomato *Mi-1* gene confers resistance to both root-knot nematodes and potato aphids. *Nature Biotechnology*. 1998;**16**:1365-1369

[89] Kumar S, Chandra A, Pandey KC. *Bacillus thuringiensis* (Bt) transgenic crop: An environment friendly insect-pest management strategy. *Journal of Environmental Biology*. 2008;**29**:641-653

[90] Raps A, Kehr J, Gugerli P, Moar WJ, Bigler F, Hilbeck A. Immunological analysis of phloem sap of *Bacillus thuringiensis* corn and of the non-target herbivore *Rhopalosiphum padi* (Homoptera: Aphididae) for the presence of Cry1Ab. *Molecular Ecology*. 2001;**10**:525-533

[91] Ryan JD, Morgham AT, Richardson PE, Johnson RC, Mort AJ, Eikenbary R.

Greenbugs and wheat: A model system for the study of phytotoxic Homoptera. In: Campbell RK, Eikenbary RD, editors. *Aphid-Plant Genotype Interactions*. Amsterdam: Elsevier; 1990

[92] Rhabé Y, Deraison C, Bonadé-Bottino M, Girard C, Nardon C, Jouanin L. Effects of the cysteine protease inhibitor oryzacystatin (OC-I) of different aphids and reduced performance of *Myzus persicae* on OC-I expressing transgenic oilseed rape. *Plant Science*. 2003;**164**:441-450

[93] Ribeiro APO, Pereira EJG, Galvan TL, Picanco MC, Picoli EAT, da Silva DJH, et al. Effect of eggplant transformed with oryzacystatin gene on *Myzus persicae* and *Macrosiphum euphorbiae*. *Journal of Applied Entomology*. 2006;**130**:84-90

[94] Carrillo L, Martinez M, Álvarez-Alfageme F, Castanera P, Smagghe G, Diaz I, et al. A barley cysteine-proteinase inhibitor reduces the performance of two aphid species in artificial diets and transgenic *Arabidopsis* plants. *Transgenic Research*. 2011;**20**:305-319

[95] Baum JA, Bogaert T, Clinton W, Heck GR, Feldmann P, Ilagan O, et al. Control of coleopteran insect pests through RNA interference. *Nature Biotechnology*. 2007;**25**:1322-1326

[96] Jaubert-Possamai S, Trionnair GL, Bonhomme J, Christophides GK, Rispe C, Tagu D. Gene knockdown by RNAi in the pea aphid *Acyrtosiphon pisum*. *BMC Biotechnology*. 2007;**7**:63

[97] Mutti NS, Park Y, Reese JC, Reek GR. RNAi knockdown of a salivary transcript leading to lethality in the pea aphid *Acyrtosiphon pisum*. *Journal of Insect Science*. 2006;**6**:38

[98] Whyard S, Singh AD, Wong S. Ingested double-stranded RNAs can act

as species specific insecticides. *Insect Biochemistry and Molecular Biology*. 2009;**39**:824-832

[99] Shakesby AJ, Wallace LS, Isaacs HV, Pritchard J, Roberts DM, Douglas AE. A water-specific aquaporin involved in aphid osmoregulation. *Insect Biochemistry and Molecular Biology*. 2009;**39**:1-10

[100] Bulet P, Stöcklin R. Insect antimicrobial peptides: Structures, properties and gene regulation. *Protein and Peptide Letters*. 2005;**12**:3-11

[101] Vilcinskis A. Evolutionary plasticity of insect immunity. *Journal of Insect Physiology*. 2013;**59**:123-129

[102] Moran NA, Russell JA, Koga R, Fukatsu T. Evolutionary relationship of three new species of enterobacteriaceae living as symbionts of aphids and other insects. *Applied Environmental Biology*. 2005;**71**:3302-3310

[103] The International Aphid Genomics Consortium. Genome sequence of the pea aphid *Acyrtosiphon pisum*. *PLoS Biology*. 2010;**8**(2):e1000313. DOI: 10.1371/journal.pbio.1000313

[104] Keymanesh K, Soltani S, Sardari S. Application of antimicrobial peptides in agriculture and food industry. *World Journal of Biotechnology and Biotechnology*. 2009;**25**:933-944

[105] Koga R, Tsuchida T, Sakurai M, Fikatsu T. Selective elimination of aphid endosymbionts: Effects of antibiotic dose and host genotype, and fitness consequences. *FEMS Microbiology Ecology*. 2007;**60**:229-239

[106] Le-Feuvre RR, Ramirez CC, Olea N, Meza-Basso L. Effect of the antimicrobial peptide indolicidin on the green peach aphid *Myzus persicae* (Sulzer). *Journal of Applied Entomology*. 2007;**131**:71-75

[107] Hardie J, Visser JH, Piron PGM. Peripheral odour perception by adult aphid forms with the same genotype but different host-plant preferences. *Journal of Insect Physiology*. 1995;**41**:91-97

[108] van Giessen WA, Fescemyer HW, Burrows PM, Peterson JK, Barnett OW. Quantification of electroantennogram responses of the primary rhinaria of *Acyrtosiphon pisum* (Harris) to C4–C8 primary alcohols and aldehydes. *Journal of Chemical Ecology*. 1994;**20**:909-927

[109] Visser JH, Piron PGM, Hardie J. The aphid's peripheral perception of plant volatiles. *Entomologia Experimentalis et Applicata*. 1996;**80**:35-38

[110] Wang Q, Zhou JJ, Liu JT, Huang GZ, Xu WY, Zhang Q, et al. Integrative transcriptomic and genomic analysis of odorant binding proteins and chemosensory proteins in aphids. *Insect Molecular Biology*. 2019;**28**:1-22. DOI: 10.1111/imb.12513

[111] Kunert G, Otto S, Röse USR, Gershenzon J, Weisser WW. Alarm pheromone mediates production of winged dispersal morphs in aphids. *Ecology Letters*. 2005;**8**:596-603

[112] Hatano E, Kunert G, Weisser WW. Aphid wing induction and ecological costs of alarm pheromone emission under field conditions. *PLoS One*. 2010;**5**(6):e11188. DOI: 10.1371/journal.pone.0011188

[113] Abassi A, Birkett S, Petterson MA, Pickett JA, Wadhams LJ, Woodcock CM. Response of the seven-spot ladybird to an aphid alarm pheromone and an alarm pheromone inhibitor is mediated by paired olfactory cells. *Journal of Chemical Ecology*. 2000;**26**:1765-1771

[114] Zhu JW, Cosse AA, Obrychi JJ, Boo KS, Baker TC. Olfactory reactions of the

twelve-spotted lady beetle, *Coleomegilla maculata* and the green lacewing, *Chrysoperla carnea* to semiochemicals released from their prey and host plant: Electroantennogram and behavioral responses. *Journal of Chemical Ecology*. 1999;25:1163-1177

[115] Micha SG, Wyss U. Aphid alarm pheromone (E)- β -farnesene: A host finding kairomone for the aphid primary parasitoid *Aphidius uzbekistanicus* (Hymenoptera: Aphidiinae). *Chemoecology*. 1996;7:132-139

[116] Du YJ, Poppy GM, Powell W, Pickett JA, Wadhams LJ, Woodcock CM. Identification of semiochemicals released during aphid feeding that attract parasitoid *Aphidius ervi*. *Journal of Chemical Ecology*. 1998;24:1355-1368

[117] Verheggen FJ, Haubruge E, De Moraes CM, Mescher MC. Social environment influences aphid production of alarm pheromone. *Behavioral Ecology*. 2009;20:283-288