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Aphid-Plant Interactions: Implications for Pest Management

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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.

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