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Authors: Louis, Joe, Singh, Vijay, and Shah, Jyoti

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Arabidopsis thaliana—Aphid Interaction

Joe Louis[a,b,1], Vijay Singh[a], and Jyoti Shah[a]

[a]Department of Biological Sciences, University of North Texas, Denton, TX 76203, USA
[b]Current address: Department of Entomology and Center for Chemical Ecology, The Pennsylvania State University, University Park, PA 16802, USA.
[1]Corresponding author: jml65@psu.edu

Aphids are important pests of plants that use their stylets to tap into the sieve elements to consume phloem sap. Besides the removal of photosynthates, aphid infestation also alters source-sink patterns. Most aphids also vector viral diseases. In this chapter, we will summarize on recent significant findings in plant-aphid interaction, and how studies involving *Arabidopsis thaliana* and *Myzus persicae* (Sülzer), more commonly known as the green peach aphid (GPA), are beginning to provide important insights into the molecular basis of plant defense and susceptibility to aphids. The recent demonstration that expression of dsRNA in Arabidopsis can be used to silence expression of genes in GPA has further expanded the utility of Arabidopsis for evaluating the contribution of the aphid genome-encoded proteins to this interaction.

INTRODUCTION

Over the past twenty five years, *Arabidopsis thaliana* has been utilized as a model plant to study plant growth, development and adaptation to the environment (Koornneef and Meinke, 2010). Arabidopsis has also provided valuable information on plant-insect interactions, including those involving insects in the orders Coleoptera, Diptera, Hemiptera, Lepidoptera and Thysanoptera. One of the early studies with Arabidopsis and the fungus gnat, *Bradysia impatiens*, shed light into the critical role of jasmonic acid signaling as a positive regulator of plant defense against dipteran insects (McConn *et al*., 1997). Since then several groups have successfully utilized Arabidopsis to gain important insights about genes and mechanisms that contribute to plant resistance and susceptibility to insects (Table 1).

Insects are broadly classified into two groups based on their feeding behavior – (i) the chewing insects, and (ii) the piercing-sucking group of insects. Chewing insects, for example, caterpillars and beetles, have very strong mandibles which allow them to chew on plant tissue and thus cause extensive physical damage to the plant (Karban and Baldwin, 1997; Kandoth *et al*., 2007). By contrast, insects with piercing-sucking mouthparts (for example aphids, whiteflies, leafhoppers, and thrips) feed on plant sap or cell contents by piercing plant tissue and extracting plant fluids (Walling, 2000). In comparison to chewing insects, feeding by piercing-sucking insects causes minimal physical damage to plant tissues (Walling, 2000). Many piercing-sucking insects have specialized to feed from the sieve elements, which are conduit for transport of phloem sap (Tjallingii and Hogen Esch, 1993; Prado and Tjallingii, 1994; Kehr, 2006). These phloem-feeding insects are adapted to consuming a diet that is rich in sugars and have evolved a variety of mechanisms to cope with the unbalanced and the high osmolarity diet, including oligomerization of sugars in the gut, expulsion of sugars in the form of honeydew, and diluting the gut content with water consumed from xylem (Spiller *et al*., 1990; Pompon *et al*., 2010).

APHIDS

Aphids (Hemiptera: Aphididae) constitute the major group of phloem-feeding insects that utilize their slender stylets, which are modified mouthparts (Figure 1a and 1b), to tap into the sieve elements (Pollard, 1973; Blackman and Eastop, 2000). On their way to the vascular tissue, the aphid stylet follows a predominantly intercellular route (Tjallingii, 1990; Walling, 2000), thus minimizing physical damage to the plant tissue. As discussed later, salivary components of aphids also help in minimizing physical damage. Occasionally, the aphid stylets also penetrate host cells, presumably sampling cell contents. Aphid infestation results in the creation of a strong sink in the aphid-infested organ which results in increased flow of nutrients to aphid-infested tissues thereby reducing the mass flow of nutrients to the primary growth zone of plants (Mittler and Sylvester, 1961; Dixon, 1998; Girousse *et al*., 2005). In addition, aphids have the capacity to achieve high population growth and importantly, many aphid species vector economically important viral diseases of plants (Kennedy *et al*., 1962; Matthews, 1991).

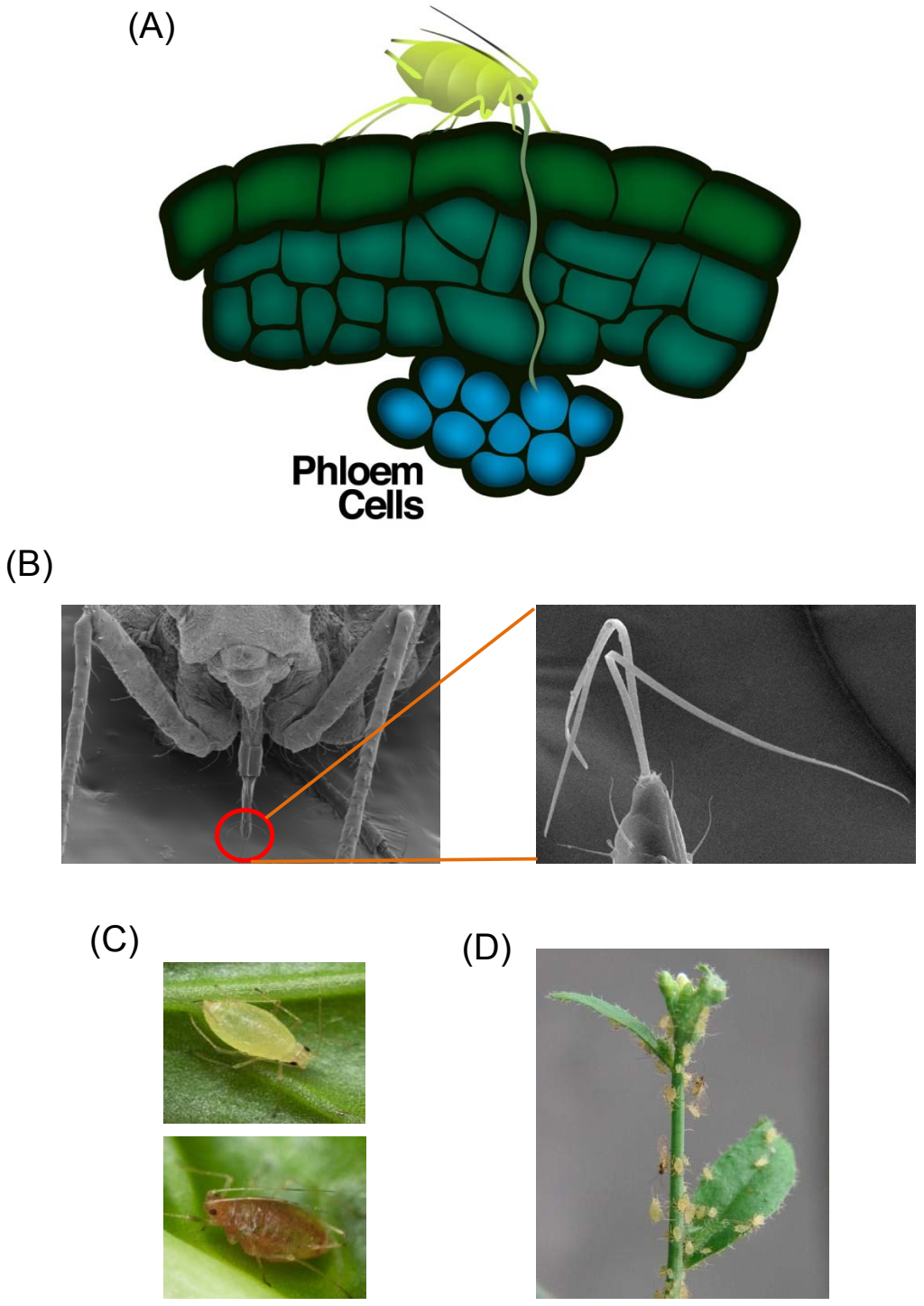

Figure 1.

(A) Aphid feeding track. Aphids use their slender stylets to penetrate between cells on their way to the phloem tissue to consume copious amount of phloem sap (Illustration by Nick Sloff).

(B) Scanning electron microscopy (SEM) images showing aphid mouthpart. Right panel shows the close-up image of aphid stylet. Images provided by John Diaz-Montano.

(C) Green and red morph of the green peach aphid (Images by Nick Sloff).

(D) Colonization by green peach aphid on the model plant *Arabidopsis thaliana*.

Table 1. *Arabidopsis thaliana* as a model system to study different plant-insect interactions

Insect			
Common name	Scientific name	Order	Reference
Flea beetle	*Phyllotreta nemorum*	Coleoptera	Nielsen et al., 2001
Fungus gnat	*Bradysia impatiens*	Diptera	McConn et al., 1997
Drosophila	*Scaptomyza flava*	Diptera	Whiteman and Jander, 2010
Cabbage aphid	*Brevicoryne brassicae*	Hemiptera	Mewis et al., 2006; Kuśnierczyk et al., 2008
Green peach aphid	*Myzus persicae*	Hemiptera	Pegadaraju et al., 2005, 2007; De Vos et al., 2005; Mewis et al., 2005, 2006; Kim and Jander, 2007
Mustard aphid	*Lipaphis erysimi*	Hemiptera	Bruce et al., 2008
Silverleaf whitefly	*Bemisia tabaci*	Hemiptera	Kempema et al., 2007; Zarate et al., 2007
Leafhopper	*Colladonus montanus*	Hemiptera	Bressan and Purcell, 2005
Small cabbage white butterfly	*Pieris rapae*	Lepidoptera	De Vos et al., 2005, 2008; Little et al., 2007
Large white butterfly	*Pieris brassicae*	Lepidoptera	Little et al., 2007
Cabbage looper	*Trichoplusia ni*	Lepidoptera	Cui et al., 2005
Corn ear worm	*Helicoverpa zea*	Lepidoptera	Cardoza., 2011
Beet armyworm	*Spodoptera exigua*	Lepidoptera	Cipollini et al., 2004
Fall armyworm	*Spodoptera frugiperda*	Lepidoptera	Moreno et al., 2009
Egyptian cotton worm	*Spodoptera littoralis*	Lepidoptera	Stotz et al., 2000
Cotton leafworm	*Spodoptera litura*	Lepidoptera	Meur et al., 2008
Diamondback moth	*Plutella xylostella*	Lepidoptera	Stotz et al., 2000; Caputo et al., 2006
Western flower thrips	*Frankliniella occidentalis*	Thysanoptera	De Vos et al., 2005

Specialist v/s Generalist

Amongst the 4,000 aphid species that have been described, approximately 250 are considered a pest (Dixon, 1998; Blackman and Eastop, 2000). Based on their host range, aphids are classified as specialist or generalists. Specialist aphids feed only on a restricted set of related plant species (Lankau, 2007). For instance, mustard aphid (*Lipaphis erysimi*) and cabbage aphid (*Brevicoryne brassicae*) feed only on cruciferous plants (Blackman and Eastop, 2000). On the other hand, a generalist aphid, such as the green peach aphid (GPA; *Myzus persicae*) (Figure 1c and 1d) feeds on a wide array of plant species and is considered polyphagous (Lankau, 2007; Blackman and Eastop, 2000). It has been suggested that specialist aphids have the ability to locate their host plant based on the presence of unique secondary metabolite(s) that act as cues for host recognition, feeding and oviposition (Raybould and Moyes, 2001; Macel and Vrieling, 2003). By comparison, it has been suggested that generalist aphids cue in on a combination of plant primary and secondary metabolites to make their host selection (Powell *et al*., 2006).

Life Cycle

Aphids are capable of sexual and asexual reproduction. They have a heteroecious holocyclic life cycle, involving alternate hosts. For instance, peach (*Prunus persicae*) is the primary host for GPA. Other plants that can serve as primary hosts for GPA include black cherry, (*P. serotina*), canadian plum (*P. nigra*), dwarf Russian almond (*P. tenella*), and peach-almond hybrids (Blackman and Eastop, 2000). Secondary hosts for GPA include more than 50 families of plants that comprise, amongst others, vegetable crops like squash, cabbage, radish, mustard, celery, lettuce, tomato, potato and eggplant (Blackman and Eastop, 2000). Sexual reproduction, which occurs only during a portion of their life cycle, results in the production of female and male sexual morphs. The females lay their eggs on the primary host plant, where they can overwinter. In places where a primary host plant is absent or not available, and if climate permits the asexual stages to survive winter, GPA exhibits an anholocyclic life cycle and reproduces parthenogenically (offsprings produced without fertilization). In the lab, GPA exhibits an anholocylic life cycle under typical Arabidopsis growth conditions. However, in many GPA lineages, sexual reproduction can be induced in the laboratory by maintaining colonies at cool temperatures under short-day conditions (Blackman, 1974).

Feeding Patterns

Aphids display a variety of feeding patterns on plants. The electrical penetration graph (EPG) has provided a powerful technique to characterize the feeding patterns of phloem-feeding insects (Tjallingii, 1990; Tjallingii and Esch, 1993; Reese *et al*., 2000;

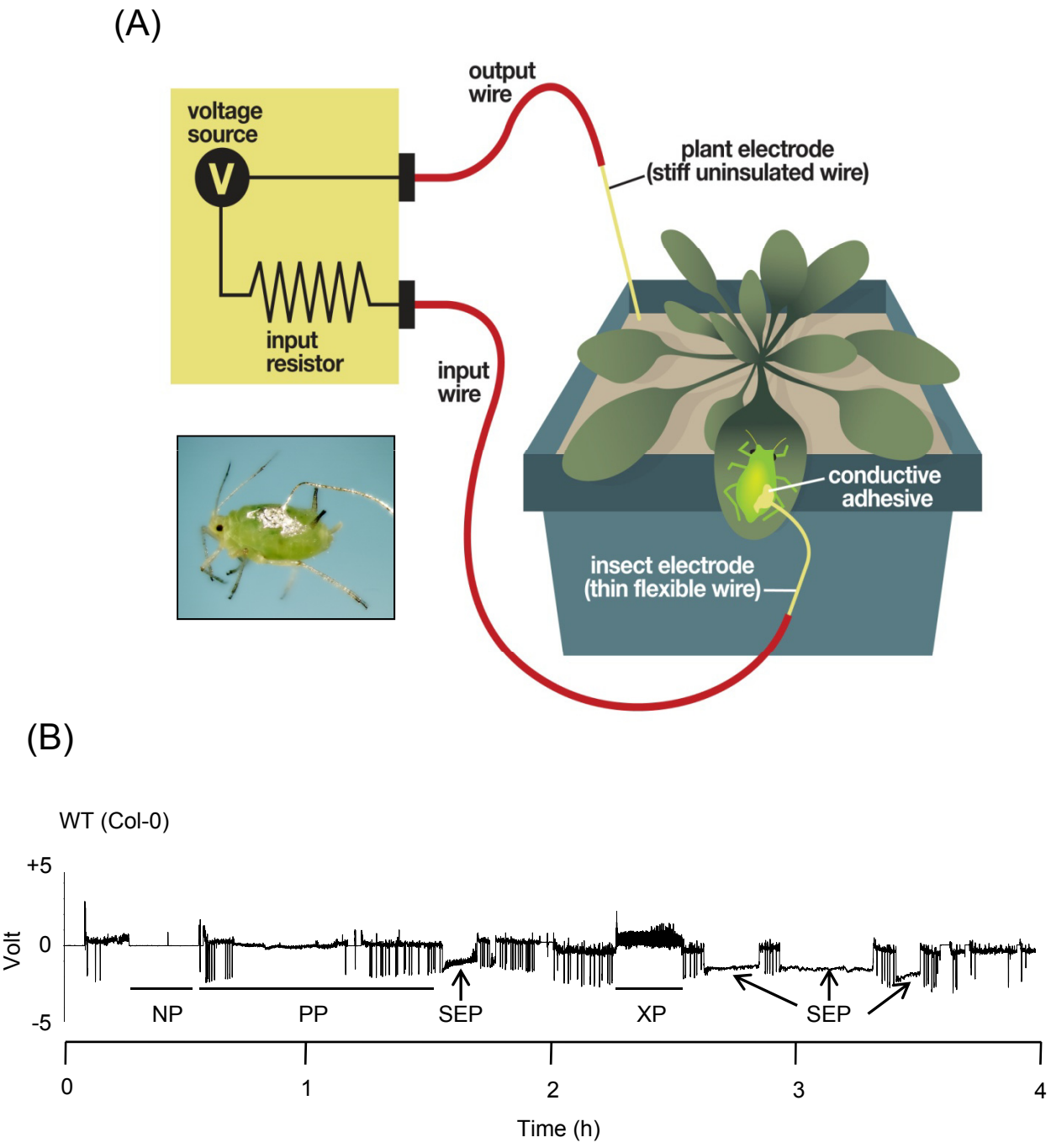

Figure 2. Electrical penetration graph (EPG) setup used for characterizing the feeding behavior of aphids on its host plant.

(A) Diagram depicting the components of EPG system (Illustration by Nick Sloff). The EPG set-up has two components –the insect and plant electrodes. A very thin, gold wire is glued to the dorsum of the aphid using a conductive silver paint. This thin wire (insect electrode), which helps in the free movement of the aphid on the plant surface is connected to the EPG probe. A stiff copper wire is inserted into the soil of the pot, in which the plant is rooted (plant electrode). It electrifies the plant with a low-voltage, low amperage current. As the stylet of the aphid comes into contact with the electrified plant, the circuit is closed and current flows through the insect and the different signals (waveforms) are thus produced. Inset shows an aphid wired with the thin gold wire using silver conductive paint (Picture provided by Gregory Zolnerowich, Kansas State University).

(B) A representative EPG waveform of GPA feeding on Arabidopsis wild type accession Columbia plant. The different waveform patterns shown here represent different phases of aphid probing of the plant. In the pathway phase (PP) the aphid stylet has penetrated the tissue but is outside the sieve elements and xylem. The pathway phase includes both the intercellular and/or intracellular stylet insertion or withdrawal during the brief sampling of cells. The non-probing (NP) phase represents a state when there is relatively no stylet movement (NP). The sieve element phase (SEP) and the xylem phase (XP) represent the stages when the stylet is in a sieve element or a xylem tissue, respectively.

Walker, 2000). This technique has been extensively utilized to investigate the details of plant resistance to aphids, whiteflies and leafhoppers (Diaz-Montano *et al*., 2007; Pegadaraju *et al*., 2007; Jiang *et al*., 2000; Stafford and Walker, 2009). In an EPG set up (Figure 2a), the insect on the plant is part of a low-voltage circuit. The patterns of electrical waveforms generated provide information on the feeding activity of the insect (van Helden and Tjallingii, 2000). In case of aphids, the three different phases that constitute the EPG waveforms include pathway phase, sieve element or phloem phase, and xylem phase (Reese *et al*., 2000; Tjallingii, 2006). During the pathway phase, the stylet is inserted in the tissue but outside the phloem and xylem. The pathway phase includes both the intercellular and/or intracellular stylet insertion or withdrawal during the brief sampling of cells (Tjallingii and Esch, 1993). The sieve element or phloem phase occurs when the stylet tips are in a phloem sieve element. EPG studies have indicated that during the sieve element phase, when the insect is ingesting phloem sap, it periodically resorts to intermittent salivation into the sieve elements. Xylem phase occurs when the insect is ingesting the xylem sap and is often thought to be related to water uptake (Spiller *et al*., 1990). Water uptake has been suggested as a means for the insect to dilute out the gut contents, and thus minimize dehydration (Pompon *et al*., 2010). A representative EPG waveform of a GPA feeding on wild type Arabidopsis accession Columbia plant is shown in Figure 2b. EPG has been used to study the impact of mutations in Arabidopsis genes on aphid feeding behavior and thus the contribution of individual genes and mechanisms to different aspects of Arabidopsis defense and susceptibility to aphids (Pegadaraju *et al*., 2007; Louis *et al*., 2010a, 2010b, 2012; Singh *et al*., 2011; Nalam *et al*., 2012).

Saliva

Salivary secretions of aphids have a vital role in plant-aphid interactions (Mutti *et al*., 2008; De Vos and Jander, 2009). The aphid stylet (Figure 1b) punctures the plant tissue and injects aphid salivary secretions into the host (Tjallingii, 1990). Two types of saliva are injected by aphids into the host plant - a gelling saliva and a watery saliva (Miles, 1999). The proteinaceous gelling saliva, which is secreted as the stylet penetrates the plant tissue, forms a supportive sheath around the stylet and a tight seal around the sites on the cell surface that may have been punctured by the stylet, thus further limiting wounding damage to the plant. Intracellular puncture by the stylet is followed by a rapid switch to secretion of non-gelling (watery) saliva and only this watery saliva is delivered into the penetrated cell or sieve elements (Cherqui and Tjallingii, 2000; Powell, 2005). The watery saliva is suggested to contain various enzymes, including pectinases, cellulases, polyphenol oxidases, peroxidases, and lipases (Campbell and Dreyer 1990; Miles, 1990, 1999). These enzymes may perform vital roles in insect feeding, including lubrication of the stylets, maintaining favorable oxidative-reduction (redox) conditions and detoxification of phenolics and other chemical factors (Miles and Oertli, 1993). Furthermore, once the aphid reaches the sieve elements of the plant, salivary secretions help to limit phloem sealing and callose deposition, which enables the aphid to feed continuously for many hours or even days from a single sieve element (Will and van Bel, 2006; Will *et al*., 2007, 2009). As discussed below, salivary components could potentially also function as effectors that modulate plant physiology, including defense responses.

APHID DIET

The aphid diet (phloem sap) is very rich in sugars but relatively poor in amino acids, which are essential nutrients for aphids and could thus limit aphid growth. In general, 10 amino acids are considered as essential nutrients for insects: arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine (Dadd, 1985). Insects cannot synthesize these amino acids and thus depend on their diet or endosymbiont bacteria to obtain adequate essential amino acids. Additionally, since tyrosine and cysteine, which are non-essential amino acids, are synthesized in the insect from phenylalanine and methionine, respectively, the availability of phenylalanine and methionine likely impact tyrosine and cysteine content as well (Dadd, 1985). Hence, aphids need to ingest large amounts of phloem sap in order to acquire sufficient amount of nitrogen. Mutation in Arabidopsis *AMINO ACID PERMEASE6* (*AAP6*; At5g49630) gene resulted in significant reduction of the essential and non-essential amino acid content in the sieve element and phloem sap of *aap6* mutant as compared to the wild type plant (Hunt *et al*., 2010). However, GPA proliferation and feeding behavior on the *aap6* mutant was comparable to the wild type plant (Hunt *et al*., 2010), suggesting that something other than amino acid availability is limiting aphid growth.

All phloem-feeding insects rely on endosymbiont bacteria to synthesize essential amino acids to complement the unbalanced nitrogen content of the phloem sap. In the case of aphids, an obligate bacterial endosymbiont, *Buchnera aphidicola*, which lives inside aphids in specialized cells called bacteriocytes, synthesize essential amino acids required by the aphids, but that are limiting in the phloem sap (Baumann, 2005; Douglas, 2006). Selective disruption of aphid symbionts with chlortetracycline severely affected aphid growth and development, suggesting that the bacterial symbionts are essential for supplementing nutrients required by aphids (Prosser and Douglas, 1991). In contrast to the aphid host, *Buchnera* spp. lack the non-essential amino acid biosynthetic pathways and thus depend on the host for these amino acids (Hansen and Moran, 2011).

REPROGRAMMING OF PLANT METABOLISM

Carbohydrate Metabolism

Aphid infestation alters source-sink patterns in the infested plant, leading to the generation of a strong sink in the aphid-infested organ and thus increasing flow of nutrients to the infested organ at the cost of nutrient flow to the natural sink tissues (Mittler and Sylvester, 1961; Dixon, 1998; Girousse *et al*., 2005). Indeed, expression of genes involved in sugar transport and metabolism were altered in GPA infested Arabidopsis (Moran and Thompson, 2001; Moran *et al*., 2002; Pegadaraju, 2005). The concentration of sucrose and starch increased in GPA-infested leaves of Arabi-

dopsis (Singh *et al*., 2011). Since sucrose has a large osmolyte effect, at first thought it would seem that this increase in sucrose and the corresponding increase in osmolarity of the phloem sap would be detrimental to the aphid, which expends lot of energy to counter the high osmolarity of the diet it consumes. However, Singh *et al*. (2011) demonstrated that GPA numbers were higher on the Arabidopsis *tps11* (At2g18700) mutant plant, which accumulates higher levels of sucrose and lower amounts of starch in response to GPA infestation, than in the wild type plant, suggesting that increased sucrose levels are unlikely to be a mechanism utilized by plant to control GPA infestation. Instead, Singh *et al*. (2011) proposed that the accumulation of starch, at the expense of sucrose, is a mechanism utilized by plants to counter the insect. They demonstrated that in comparison to the wild type plant, insect numbers were higher on the Arabidopsis *pgm1* (At5g51820) mutant plant, which is unable to synthesize starch. Similarly, in comparison to the wild type plant, the increment in starch content was lower in the *tps11* mutant on which the insect population was larger. It has been suggested that starch accumulation at the expense of sucrose results in a secondary intracellular sink that counters the ability of the insect to alter host physiology to make the plant more suitable for the insect (Singh *et al*., 2011).

Aphid infestation also impacts nitrogen metabolism in the plants. Pea aphid (*Acyrthosiphon pisum*) infestation on alfalfa (*Medicago sativa*) resulted in an evident shift from nitrogen sinks to nitrogen sources (Girousse *et al*., 2005). Furthermore, aphid settlement on the actively growing zones of stem resulted in a systemic reduction of C and N fluxes, especially at the apical zones of the stem (Girousse *et al*., 2005). Molecular studies have also indicated changes in expression and/or activity of genes/proteins involved in N metabolism. For example, GPA infestation resulted in increased nitrate reductase activity in cabbage (Wilson *et al*., 2011). Voelckel *et al*. (2004) showed that tobacco aphid (*Myzus nicotianae*) infestation resulted in the induction of glutamate synthase expression. Similarly expression of glutamine synthase was upregulated in GPA infested celery (Divol *et al*., 2005).

Premature Senescence

GPA infestation resulted in the up-regulation of a subset of *SENESCENCE ASSOCIATED GENES* (*SAG*) (Pegadaraju *et al*., 2005; De Vos *et al*., 2005), and the activation of cell death and senescence in Arabidopsis (Pegadaraju *et al*., 2005). Some of these *SAG* genes were also induced in leaves infiltrated with synthetic diet containing aphid saliva (De Vos and Jander, 2009), suggesting that aphid salivary components elicit cell death in Arabidopsis. Indeed, the putative salivary protein Mp10 from GPA when transiently overexpressed in *Nicotiana benthamiana* promoted chlorosis (Bos *et al*., 2010). When compared to wild type Arabidopsis, the hyper-senescent *ssi2* (At2g43710) and *cpr5* (At5g64930) mutants exhibited enhanced resistance to GPA, and insect population size was larger on the *pad4* (At3g52430) mutant, which exhibited delayed onset of senescence and expression of *SAG* genes in response to GPA infestation. Hence, it was suggested that premature senescence is a defense mechanism employed by the host to control GPA infestation (Pegadaraju *et al*., 2005). Senescence likely counters the efforts of the insect to increase sink nature of the infested tissues.

Plant Hormones

Plants produce a variety of hormones including auxins, gibberellins, abscisic acid, cytokinins, salicylic acid, jasmonic acid, ethylene, brassinosteroids and peptide hormones. Of these, salicylic acid (SA) and jasmonic acid (JA) are more widely studied for their signaling role in plant defense against various biotic stresses (Shah, 2003; Lorenzo and Solano, 2005; Broekaert *et al*., 2006; Bari and Jones, 2009; Pieterse *et al*., 2009). Several studies have shown that aphid feeding on host plant activates SA and JA-mediated defense pathways (Moran and Thompson, 2001; Mewis *et al*., 2005). GPA feeding on Arabidopsis activates genes that are involved in SA biosynthesis and signaling (Moran and Thompson, 2001; Pegadaraju, 2005). However, GPA population size on the SA biosynthesis mutant *sid2* (*salicylic acid-induction deficient2;* At1g74710), the SA insensitive mutant *npr1* (*non-expressor of PR-1*; At1g64280) and a SA deficient NahG transgenic plant that expresses a SA-degrading salicylate hydroxylase, were comparable to that on wild type plants, suggesting that SA is not a key player in Arabidopsis defense against GPA (Moran and Thompson, 2001; Pegadaraju *et al*., 2005). Quite to the contrary, Mewis *et al*., (2005) showed that both the GPA and cabbage aphid populations on the *npr1* mutant and the NahG plant were smaller as compared to the wild type plant, suggesting that lack of NPR1 function and SA accumulation resulted in increased resistance. However, the role of SA may differ depending on the plant and insect involved. In contrast to the studies in Arabidopsis, in tomato, it was shown that hyperaccumulation of SA due to knockdown of *FAD7* activity resulted in enhanced resistance to potato aphid (*Macrosiphum euphorbiae*) (Avila *et al*., 2012).

Since SA signaling is known to attenuate the activation of JA signaling, Mewis *et al*., (2005) suggested that the higher level of resistance against GPA observed in the *npr1* mutant and NahG plants could possibly result from the stronger activation of the JA signaling pathway in these plants. Similarly, in the case of another sap-sucking insect, silverleaf whitefly (*Bemisia tabaci*), larval growth was reduced on *npr1* and NahG plants, whereas the growth was higher on SA-overexpressing *cim10* plants as compared to the wild type plants (Zarate *et al*., 2007). Zarate *et al*., (2007) suggested a 'decoy' hypothesis in which the insect evades host defenses by tricking the host plant into inappropriately activating SA signaling and thus depressing the activation of JA signaling. Indeed, other studies also have shown that resistance against aphids is mediated through the JA pathway (Ellis *et al*., 2002; Zhu-Salzman *et al*., 2004; Gao *et al*., 2007). For example, the GPA population was smaller on the Arabidopsis *cev1* (At5g05170) mutant, which has high JA content (Ellis *et al*., 2002). In contrast, GPA numbers were higher on JA-insensitive mutant *coi1* (At2g39940) mutant compared to the wild type plant (Ellis *et al*., 2002). JA has also been suggested to have an important role in defense against aphids in other plant species. For example, methyl jasmonate (MeJA) treatment of sorghum (*Sorghum bicolor*) seedlings resulted in fewer numbers of greenbug aphids (*Schizaphis graminum*) as compared to the untreated control plants (Zhu-Salzman *et al*., 2004). However, JA-responsive genes were only weakly induced in greenbug-infested sorghum leaves. By comparison, SA responsive genes were strongly induced in greenbug-infested sorghum (Zhu-Salzman *et al*., 2004).

It is likely that, as in the case of whitefly infestation of Arabidopsis, greenbug tricks sorghum plants to induce SA signaling to prevent the timely activation of JA signaling. Similarly, the JA pathway is also required for *AKR* (*Acyrthosiphon kondoi Resistance*) mediated resistance against the blue green aphid (*Acyrthosiphon kondoi*) in *Medicago truncatula* (Gao *et al*., 2007).

JA also contributes to basal resistance against cabbage aphid in Arabidopsis. Cabbage aphid populations were smaller on the Arabidopsis *cev1* and *fou2* (Arabidopsis *fatty acid oxygenation up-regulated2*; At4g03560) mutants, respectively, both of which have high JA content (Kuśnierczyk *et al*., 2011). However, EPG studies revealed that the *fou2* allele does not limit cabbage aphid feeding from sieve elements, thus suggesting that mechanisms other than feeding deterrence contribute to *fou2* and JA-determined resistance against cabbage aphid. In addition to elevated levels of JA, Arabidopsis *fou2* mutants also had higher levels of the JA precursor, oxo-phytodienoic acid (OPDA) and the related dinor oxo-phytodienoic acid (dnOPDA) (Bonaventure *et al*., 2007; Kuśnierczyk *et al*., 2011). Hence, further experiments are required to tease apart the contributions of JA and/or OPDA to *fou2*-determined heightened resistance against cabbage aphid. Besides JA, OPDA is also known to function as a signal molecule in Arabidopsis (Taki *et al*., 2005).

PERCEPTION OF APHIDS

During the last 20 years immense progress has been made in understanding the molecular mechanism underlying plant recognition of microbes. Several membrane spanning as well as intracellular *Resistance* (*R*) genes facilitate plant recognition of specific pathogen-derived molecules and plant-derived factors that are produced in response to infection (Chisholm *et al*., 2006; Jones and Dangl, 2006). For instance, a bacterial flagellin protein-derived Pathogen Associated Molecular Pattern (PAMP) - is recognized by Pattern Reception Receptors (PPR) in the plant resulting in the activation of PAMP-triggered immunity (PTI) (Chisholm *et al*., 2006; Schwessinger and Zipfel, 2008). However, over the years, pathogens have evolved effector molecules that can suppress the PTI. In comparison, plants have evolved additional *R* genes that recognize these effector molecules leading to the activation of effector-triggered immunity (ETI) (Chisholm *et al*., 2006). How aphids are perceived by plants has not been elucidated. As described below, in recent years a few *R* genes involved in recognizing aphids have been identified and some progress has been made in identifying effector molecules that either stimulate plant defense or promote insect infestation by manipulating plant metabolism/physiology.

Effectors

Oral secretions from caterpillars contain elicitors of plant defenses (e.g. volicitin, caeliferins and inceptins) (Alborn *et al*., 1997, 2007; Schmelz *et al*., 2006). Aphids also intermittently inject into sieve elements a watery saliva that contains proteins and other metabolites. One or more of these salivary components could elicit and/or modulate plant responses. For example, aphid saliva contains oxidases (e.g. glucose oxidase) (Harmel *et al*., 2008) that could potentially produce hydrogen peroxide (H_2O_2), a key modulator of plant defense (Bede *et al*., 2006; Maffei *et al*., 2006), similar to that observed with glucose oxidase from corn earworm (*Helicoverpa zea*) (Musser *et al*., 2002). Although the exact function of glucose oxidase in aphid saliva is not known, recently it was shown that the Arabidopsis *RBOHD* (*RESPIRATORY BURST OXIDASE HOMOLOG D*; At5g47910) gene, which is responsible for accumulation of reactive oxygen species (ROS), including local accumulation of H_2O_2, at the wound/injury site, modulates defense against GPA (Miller *et al*., 2009). GPA proliferation was higher on *rbohD* mutant plants than the wild type plant. These results suggest that any changes in the ROS status in the sieve elements could influence plant resistance/susceptibility to aphids. Further, evidence indicating a potential role for aphid salivary components in modulating plant response against aphids was provided by experiments with Arabidopsis leaves infiltrated with an artificial diet on which GPA had fed and thus contained aphid salivary secretions. Infiltration of diet containing aphid saliva resulted in differential expression of Arabidopsis genes related to signal transduction, response to stress and secondary metabolite biosynthesis (e.g. glucosinolate), and genes encoding various stress associated transcription factors (De Vos and Jander, 2009).

RNAi experiments with pea aphid provided the first evidence of importance of salivary components in facilitating aphid infestation on plants. Silencing expression of the pea aphid gene encoding the C002 protein, which is normally expressed in the salivary glands, adversely impacted the ability of the C002-silenced aphids to feed from the host plant (Mutti *et al*., 2008), thus suggesting that C002 is critical for aphids to continuously feed from the host plant (Mutti *et al*., 2008). Similarly, silencing expression of the C002 homolog of GPA by expression of dsRNA in transgenic Arabidopsis resulted in the production of less progeny by the C002-silenced GPA (Pitino *et al*., 2011). By contrast, agroinfiltration mediated overexpression of the GPA C002 protein in *Nicotiana benthamiana* enhanced GPA fecundity as compared to the vector control (Bos *et al*., 2010). These results suggest that C002 facilitates aphid infestation, most likely due to its action in the host plant. By contrast to C002, the Mp10 and MP42 proteins from GPA, which are encoded by genes expressed in the salivary glands of the aphid, when overexpressed in *N. benthamiana* resulted in reduced fecundity of GPA. Mp10 overexpression in *N. benthamiana* also resulted in chlorosis and attenuated ROS production in response to treatment with flg22, a bacterial effector peptide (Bos *et al*., 2010), suggesting that Mp10 impacts plant responses. Although, whether plants perceive the presence of aphids by recognizing these effectors is not known, the above studies suggest that aphid salivary components can elicit plant responses that likely impact the interaction between the host plant and aphid.

Resistance genes

The Arabidopsis-GPA and Arabidopsis-cabbage aphid systems have been successfully utilized by several groups to identify a number of plant genes (Table 2 and 3) and mechanisms that contribute to plant defense against aphids. However, to date, *R* gene type resistance against aphids in Arabidopsis has not been

reported. Only very few examples of gene-for-gene resistance in plant-aphid interactions are known. For example, the *Mi-1.2* gene in tomato (*Solanum lycopersicum*) and the *Vat* gene in melon are involved in providing protection against certain isolates of potato aphid and melon aphid (*Aphis gossypii*), respectively (Rossi *et al*., 1998; Dogimont *et al*., 2007). *Mi-1.2* was the first aphid resistance gene to be cloned. Both *Mi-1.2* and *Vat* genes are members of plant *R* genes consisting of nucleotide binding site (NBS) and leucine-rich-repeat (LRR) motifs (Milligan *et al*., 1998, Dogimont *et al*., 2007). In addition to potato aphids, *Mi-1.2* also confers resistance against certain isolates of root-knot nematodes and biotypes of whitefly (*B. tabaci*), and the tomato psyllid (*Bactericera cockerelli*) (Nombela *et al*., 2003; Casteel *et al*., 2006). *Mi-1.2* mediated resistance against root-knot nematodes functions through the activation of hypersensitive response (HR), which is associated with cell death at the feeding site, which results in the blockage of nematode feeding (Dropkin *et al*., 1969; Roberts and Thomason, 1986). In contrast, the *Mi-1.2*-mediated resistance to potato aphid is independent of HR (de Illarduya *et al*., 2003). Presence of *Mi-1.2* confers resistance to potato aphid by limiting the insect's ability to feed continuously from the phloem sap (Kaloshian *et al*., 2000; Palliparambil *et al*., 2010). The bluegreen aphid resistance gene, *AKR*, identified in *M. truncatula*, also maps to a region containing NBS-LRR class of genes (Klingler *et al*., 2005). In addition, *Nr* in lettuce, *Sd1* in apple, *RAG1* and *RAG2* in soybean, and *RAP1* in *M. truncatula* have also been reported in conferring resistance against lettuce aphid, rosy-leaf curling aphid, soybean aphid and pea aphid, respectively (Helden *et al*., 1993; Roche *et al*., 1997; Hill *et al*., 2006; Stewart *et al*., 2009, Kim *et al*., 2010). Several loci conferring biotype-specific resistance, including *Aph* in maize, and *Gby* and *Dn* in wheat, have also been reported in providing resistance against corn leaf aphid, greenbug and Russian wheat aphid, respectively (Marais and Du Toit, 1993; Boyko *et al*., 2004; Castro *et al*., 2005; So *et al*., 2010).

CATEGORIES OF PLANT RESISTANCE

In the early 1950's, Dr. R.H. Painter, a well renowned entomologist at Kansas State University, introduced, three categories of plant resistance mechanisms to aphids: non-preference, antibiosis and tolerance (Painter, 1951). The term non-preference was then replaced to 'antixenosis' by Kogan and Ortman (1978). Antixenosis is a resistance mechanism, in which a plant either fails to serve as a host for the insect pest, or the insects prefer an alternate host plant (Smith, 2005). Strong antixenosis may result in starvation even when no alternative host is available. In other cases, antixenosis adversely impacts insect behavior, for example its ability to find sieve elements, thus deterring infestation. Antibiosis

Table 2. Arabidopsis mutants and transgenic plants exhibiting altered resistance to green peach aphid

AtG #	Gene	Name (Function)	Reference
At1g10550	*xth33*	*xyloglucan:xyloglucosyl transferase33* (endoxyloglucan transferase)	Divol et al., 2007
At1g64280	*npr1*	*non-expresser of PR genes1* (transcription regulator)	Mewis et al., 2005
At1g66340	*etr1*	*ethylene response1* (ethylene receptor)	Mewis et al., 2006
At2g18700	*tps11*	*trehalose-6-phosphate synthase11*	Singh et al., 2011
At2g39940	*coi1*	*coronatine-insensitive1* (JA-Ile perception)	Ellis et al., 2002
At2g43710	*ssi2*	*stearoyl-ACP desaturase*	Pegadaraju et al., 2005
At3g09710	*iqd1*	IQ-Domain1 (calmodulin-binding nuclear protein)	Levy et al., 2005
At3g11170	*fad7*	*fatty acid desaturase7*	Avila et al., 2012
At3g22400	*lox5*	*lipoxygenase 5* (9-lipoxygenase)	Nalam et al., 2012
At3g52430	*pad4*	*phytoalexin deficient4* (putative acyl hydrolase/lipase)	Pegadaraju et al., 2005, 2007; Louis et al., 2012
At4g19840	*pp2-A1*	*phloem protein 2A1*	Zhang et al., 2011
At5g05170	*cev1*	*constitutive expression of VSP1* (cellulose synthase)	Ellis et al., 2002
At5g14180	*mpl1*	*Myzus persicae-induced lipase1* (lipase/esterase)	Louis et al., 2010a
At5g47910	*rbohd*	*respiratory burst oxidase homolog D*	Miller et al., 2009
At5g51820	*pgm1*	*phosphoglucomutase1* (starch biosynthesis)	Singh et al., 2011
At5g57220	*cyp81F2*	Cytochrome P450 monooxygenase (glucosinolate metabolism)	Pfalz et al., 2009 De Vos and Jander, 2009
At5g60890	*atr1D*	*altered tryptophan regulation1* (indole glucosinolate metabolism)	Kim et al., 2008
At5g64930	*cpr5*	*constitutive expression of PR genes5*	Pegadaraju et al., 2005
Transgene	35S:*EBF*	Overexpression of (*E*)-β-farnesene synthase	Beale et al., 2006
Transgene	*NahG*	Salicylate hydroxylase	Mewis et al., 2005; Pegadaraju et al., 2005

Table 3. Arabidopsis mutants and transgenic plants exhibiting altered resistance to the cabbage aphid

AtG #	Gene	Name (Function)	Reference
At1g64280	*npr1*	*non-expresser of PR genes1* (transcription regulator)	Mewis et al., 2006
At1g66340	*etr1*	*ethylene response1* (ethylene receptor)	Mewis et al., 2006
At2g39940	*coi1*	*coronatine-insensitive1* (JA-Ile perception)	Mewis et al., 2006
At3g26830	*pad3*	*phytoalexin deficient3* (camalexin biosynthesis)	Kuśnierczyk et al., 2008
At4g03560	*fou2*	*fatty acid oxygenation up-regulated2*	Kuśnierczyk et al., 2011
At5g02310	*cer3*	Wax biosynthesis	Rashotte, 1999
Transgene	*NahG*	Salicylate hydroxylase	Mewis et al., 2005

is the category in which aphid physiology is affected, resulting in adverse impact on the growth, development and/or, reproduction or survival of the insect (Smith, 2005). Antibiosis may result from chemical and physical defenses of the plant. It could also result from the absence of sufficient nutrients in the plant (Pedigo, 1999; Smith, 2005). The third resistance category, tolerance, is the ability of the plant to withstand and/or recover from damage caused by the insect at a scale that is comparable to that on a plant without any resistant characteristics (Pegido, 1999). In many cases, tolerance is considered as the most durable kind of resistance against insects, because of the reduced selection pressure for new insect biotypes and also less deleterious effects on natural enemies (Flinn *et al*., 2001). Both constitutive (preformed physical and chemical factors) and inducible defenses involving small metabolites and macromolecules contribute to overall plant resistance to aphids by impacting insect behavior and physiology (Chen, 2008).

Besides the above categories of resistance, plants also attract predatory insects to control aphid infestation. Plant volatiles produced in response to aphid infestation attract several natural enemies of aphids including lacewings, hoverflies, parasitoid wasps and coccinellid beetles (Francis *et al*., 2004; Zhu *et al*., 2005; Hatano *et al*., 2008). For instance, methyl salicylate (MeSA), a soybean aphid-induced plant volatile, attracts its predatory beetle, *Coccinella septempunctata*, to the aphid-infested plant and this predatory insect helps to curtail the aphid population (Zhu and Park, 2005). Volatiles produced by aphids also contribute to tritrophic interactions. For example, (*E*)-β-Farnesene (EBF), which is a key component of the aphid alarm pheromone (Pickett *et al*., 1992), was shown to attract predatory insects. Plants overexpressing EBF provided enhanced resistance by deterring aphids and also by attracting the aphid parasitoid, *Diaeretiella rapae*, to the infested plant which resulted in the reduction of aphid settlement on host plants (Gibson and Pickett, 1983; Beale *et al*., 2006; De Vos *et al*., 2010). Whether plant volatiles that mimic alarm pheromones could be targeted for durable resistance, remains to be determined. In Arabidopsis, it has been shown that EBF overexpression leads to habituation in three successive GPA generations (De Vos *et al*., 2010). Although Arabidopsis constitutive EBF-emitting transgenic plants supported higher proliferation of EBF-habituated GPA as compared to EBF-non-habituated GPA, these transgenic plants also recruited increased predators of attacking aphids (De Vos *et al*., 2010), suggesting that aphid alarm pheromone production could be engineered to promote indirect defense mechanism in plants.

CONTROLLING INFESTATION AT PLANT SURFACE

Insects utilize surface cues present on the plant to make decisions on feeding and/or oviposition (Walling, 2008). Thus, the leaf surface, in particular the waxy cuticle, could influence the ability of the aphid to colonize a plant and act as one of the first layers of defense against aphids. Indeed, cabbage aphid population size was adversely impacted on the Arabidopsis wax mutant, *cer3* (At5g02310), which accumulates elevated levels of the C30 alcohol, triacontanol (Rashotte, 1999). However, the GPA population size on *cer3* mutant was comparable to that of wild type plants (Rashotte, 1999), thus suggesting that the detrimental impact of C30 alcohol is aphid species specific.

Aphids also encounter trichomes on plant surface, which provide a physical barrier to insect movement on the plant. Trichomes in some plant species have glands at their base, which contain secondary metabolites (Wagner *et al*., 2004). Damage to these trichomes, as a result of insect activity, results in the exudation of glandular contents. The sugar esters present in these exudates from tobacco are known to adversely impact GPA population size (Wang *et al*., 2004; Jin *et al*., 2011), thus indicating that trichomes also contribute to chemical defenses in plants. Trichomes present in Arabidopsis are non-glandular, and so far there are no reports in Arabidopsis of trichomes providing defense against aphids.

Both cabbage aphid and GPA infestation on Arabidopsis induce changes in expression of genes involved in cell wall metabolism and remodeling (Divol *et al*., 2007; Kuśnierczyk *et al*., 2008). For example, aphid feeding on Arabidopsis altered expression of *XTH33* (At5g02310), which encodes a xyloglucan endotransglycosylase/ hydrolase that is involved in cell wall remodeling (Divol *et al*., 2005, 2007; Kuśnierczyk *et al*., 2008). GPA preferred to settle on the *xth33* mutant as compared to the wild type plant, suggesting that *XTH33* is involved in providing cell wall mediated defense against GPA (Divol *et al*., 2007). However, tissue specific expression of *XTH33* in the companion cells did not provide enhanced resistance against GPA than the wild type plant (Divol

et al., 2007), suggesting that *XTH33*-mediated resistance against GPA is exerted at a step outside of vascular tissues. Alternatively, *XTH33* might work in conjunction with another gene(s) in Arabidopsis to control aphid infestation.

DEFENSE IN THE PHLOEM

When the aphids are feeding on a non-host or a resistant plant, they ingest phloem sap initially at normal rates, but will subsequently stop feeding, withdraw their stylet and leave the plant (Kloft, 1977), suggesting that aphids tend to move away from the plant possibly because the phloem sap is nutritionally unfavorable. Studies with Arabidopsis indicate that the sap contains a factor(s) that is detrimental to the insect. Petiole exudates, which are enriched in phloem sap, collected from leaves of wild type Arabidopsis, when added to a synthetic diet had a detrimental effect on GPA population (Louis *et al*., 2010a, 2010b). As mentioned later, the *pad4* and the *mpl1* mutant, both of which are deficient in this antibiotic activity, exhibited lowered resistance to GPA (Louis *et al*., 2010a, 2010b). By contrast, insect populations were smaller on mutant plants that constitutively accumulate high levels of this activity, for example the *ssi2* (*suppressor of SA-insensitivity2*) mutant, than on the wild type plant (Louis *et al*., 2010b). However, despite the presence of this detrimental activity in petiole exudates of wild type plants, GPA manages to successfully colonize Arabidopsis, suggesting that over time it can overcome this detrimental factor(s), presumably by either detoxifying it *in planta*, and/or suppressing its production by the host plant, or activating mechanisms that inactivate this factor in the insect body. Previous studies have indicated that aphid infestation results in alterations in the composition of phloem sap (Sandström *et al*., 2000). Indeed, petiole exudates collected from GPA-infested leaves of wild type Arabidopsis lacked this inhibitory activity (Nalam *et al*., 2012). Quite to the contrary, these exudates now contained an activity that promoted GPA proliferation on an artificial diet, thus suggesting that aphids infestation results in the destruction or suppression of this inhibitory activity.

Several stress and defense associated proteins are present in the sap of plants (Walz *et al*., 2004; Gaupels *et al*., 2008). The PP2-A1 (Phloem Protein2-A1; At4g19840) in Arabidopsis, which is associated with the sieve elements (Beneteau *et al*., 2010), possesses lectin activity (Dinant *et al*., 2003; Beneteau *et al*., 2010). Lectins are proteins that have an affinity for carbohydrates and have insecticidal activities, presumably due to interference with processes in the aphid gut (Carlini and Grossi-de-Sa, 2002; Vasconcelos and Oliveira, 2004). This insecticidal effect of lectins has been successfully used to engineer plants with enhanced resistance against several aphids. For example, potato plants engineered to express high levels of snowdrop lectin were more resistant to GPA (Gatehouse *et al*., 1996). Recombinant PP2-A1 protein when added to a synthetic diet, also exhibited inhibitory activity against GPA (Beneteau *et al*., 2010). Furthermore, GPA had difficulty feeding from sieve elements of transgenic Arabidopsis plants that overexpressed PP2-A1 (Zhang *et al*., 2011), thus indicating that *in planta* produced PP2-A1 is also detrimental to GPA.

Phloem proteins are also involved in occlusion of sieve elements upon wounding. Plants also deposit callose in sieve elements penetrated by stylets, thereby preventing the prolonged feeding of phloem-feeding insects. In plants, callose synthesis is Ca^{2+}-dependent (King and Zeevaart, 1974). It has been shown that sieve tube occlusion upon wounding in legumes involves the dispersion of spindle like proteins (forisomes) with the aid of Ca^{2+} influx to the injury site (Knoblauch *et al*., 2001; Thorpe *et al*., 2010). Occlusion of sieve elements by forisome plugging resulted in a change in feeding behavior of aphids on *Vicia faba* (Will *et al*., 2007). As a counter-mechanism, the Ca^{2+}-binding proteins present in the aphid saliva have been suggested to participate in reverse phloem occlusion, which allows the aphids to feed continuously from the phloem sap (Will *et al*., 2007). In Arabidopsis, cabbage aphid infestation upregulated the expression of *CALLOSE SYNTHASE* (*CALS1*; At1g05570) gene (Kuśnierczyk *et al*., 2008), thus suggesting that aphid infestation induces the synthesis of callose by stimulating expression of plant genes involved in callose biosynthesis. Similarly, infestation by sliverleaf whitefly (*B. tabaci*) and brown leafhopper (*Nilaparvata lugens*), on Arabidopsis and rice, respectively, induced the accumulation of callose near the vascular tissues (Kempema *et al*., 2007; Hao *et al*., 2008).

Phloem sap also contains defensive compounds, such as gluconiolates and non-protein amino acids that impact Arabidopsis interaction with aphid. These are discussed in more detail below.

Glucosinolates—a *Brassicaceae*-specific Chemical Defense

Plants in the *Brassicaceae* family, which includes *Arabidopsis thaliana*, accumulate glucosinolates, a family of secondary metabolites that are sources of thioacyanates and other breakdown products that are toxic to some aphids (Rask *et al*., 2000; Halkier and Gershenzon, 2006). Levy *et al*., (2005) showed that the expression level of the *IQD1* (At3g09710) gene, which encodes a transcription factor that is responsible for glucosinolate accumulation, impacts host plant choice by GPA. Another study showed that the fecundity of both generalist (GPA) and specialist aphid (cabbage aphid) were higher on Arabidopsis *coi1* mutant that contained lower amount of glucosinolates than the wild type plant (Mewis *et al*., 2005). Differences have been observed in the profile of glucosinolates in aphid-infested compared to uninfested Arabidopsis. For example, although the total glucosinolate content does not change in GPA-infested (Kim and Jander, 2007, Louis *et al*., 2010a), compared to uninfested plants, the GPA-infested plants contain higher levels of indole glucosinolates. Kim *et al*., (2008) reported that GPA population size was smaller on the Arabidopsis *atr1D* (At5g60890) mutant plant, which accumulates elevated levels of indole glusocinolates, thus suggesting that indole glucosinolates are detrimental to GPA (Kim *et al*., 2008).

Glucosinolates themselves are not insecticidal. However, when acted upon by myrosinases, glucosinolates produce toxic thiocyanates and other breakdown products that act as defensive compounds against insects (Chew, 1988; Louda and Mole 1991; Rask *et al*., 2000). In Arabidopsis, β-thioglucoside glucohydrolases encoded by *TGG1* and *TGG2* (At5g25980 and At5g26000)

contribute to the majority of the myrosinase activity (Barth and Jander, 2006). However, both GPA and cabbage aphid populations were unaffected on Arabidopsis *tgg1* and *tgg2* single and the *ttg1 ttg2* double mutant plants, compared to the wild type plant, suggesting that aphids evade the production of toxic thiocyanates or modulate the activity of enzymes that synthesize these thiocyanates (Barth and Jander, 2006). Instead, Kim *et al*., (2008) showed that the adverse effect of glucosinolates on aphid performance correlated with the accumulation of indole glucosinolate breakdown products in the insect body, indicating that aphids consume glucosinolates produced by the host plant. In particular, diindolylmethylcysteines and other amino acid conjugates, which form after indole glucosinolate breakdown during aphid feeding from Arabidopsis, reduce aphid reproduction on artificial diets (Kim *et al*., 2008). Further studies identified the indol-3-ylmethyl glucosinolate -derived 4-methoxyindol-3-ylmethyl glucosinolate and 1-methoxyindol-3-yl-methyl glucosinolate as strong deterrents of GPA proliferation (Kim and Jander, 2007; Pfalz *et al*., 2009). GPA reproduction was improved on *cyp81F2* (At5g57220) mutants, which are defective in the production of 4-methoxyindol-3-ylmethyl glucosinolate (Pfalz *et al*., 2009; De Vos and Jander, 2009). Unlike in the generalist GPA, the effect of glucosinolate breakdown products against the specialist cabbage aphids have not been reported. It is possible that the specialist aphids are able to evade, suppress and/or adapt to these glucosinolate breakdown products as opposed to the generalist aphids. Readers are directed to some excellent reviews that have summarized glucosinolate biosynthesis and metabolism, and its role in plant defense (Bednarek *et al*., 2009; Wittstock and Burow, 2010).

Non-protein Amino Acids

Plants produce several non-protein amino acids that serve as intermediates in the synthesis of primary metabolites. In addition, these compounds are also reported to have defense related functions against insects (Rosenthal, 1991). For instance, L-canavanine, an L-arginine analog, is a major storage compound in legumes and also has insecticidal allelochemical properties (Rosenthal, 2001). N^{δ}-acetylornithine has been identified as a new class of defense related compound in Arabidopsis (Adio *et al*., 2011). This non-protein amino acid has been identified in phloem sap collected from methyl jasmonate-treated Arabidopsis. The Arabidopsis *NATA1* gene (At2g39030), which encodes a protein with N-acetyltransferase activity, is involved in the biosynthesis of N^{δ}-acetylornithine and is expressed in the phloem-associated tissues. Expression of the *NATA1* gene was induced and N^{δ}-acetylornithine content was higher in GPA infested Arabidopsis compared to uninfested plants. Furthermore, GPA population on aphid diet containing N^{δ}-acetylornithine was significantly reduced, suggesting that this compound has a direct toxic and/or deterrent effect on GPA (Adio *et al*., 2011). Transient expression of *NATA1* in tobacco significantly reduced GPA population size as compared to the vector control plants (Adio *et al*., 2011). Resistance in these experiments correlated with the level of N^{δ}-acetylornithine. Whether N^{δ}-acetylornithine has any effect on specialist cabbage aphids, is not known. However, by contrast to aphids, although *NATA1* expression and N^{δ}-acetylornithine accumulation were also induced in response to infestation by chewing herbivores, the *nata1-1* mutation did not affect *Pieris rapae* (white cabbage butterfly) and *Plutella xylostella* (diamondback moth) caterpillar growth, suggesting that N^{δ}-acetylornithine accumulation is either not important or not sufficient to deter chewing insects. A recent review by Huang *et al*. (2011) summarizes the role of non-protein amino acids in plant defense against various insect pests.

CONTRIBUTION OF HOST LIPIDS TO *ARABIDOPSIS*-APHID INTERACTION

Lipids are considered as vital structural components of biological membranes (Somerville *et al*., 2000). In addition, lipids also function as signaling molecules in plant growth, development and stress response (Wang 2004; Shah, 2005; Upchurch, 2008; Scherer, 2010). Fatty acids serve as substrates for enzymes that produce lipid-based signaling molecules, for instance, several oxylipins. Oxylipins are oxidized fatty acids and their synthesis in plants is initiated by the action of lipoxygenases (LOXs). LOXs are classified as 9- or 13-LOXs based on their ability to add oxygen at the 9- or 13-C position of the fatty acids to yield the corresponding fatty acid hydroperoxides. JA is derived from the 13-LOX pathway. As mentioned above, JA promotes host defense against a variety of aphids in several plants (Ellis *et al*., 2002; Zhu-Salzman *et al*., 2004; Gao *et al*., 2007).

9-LOX-derived oxylipins

Recently, it was shown that 9-LOX-derived oxylipins contribute to host susceptibility to aphids (Nalam *et al*., 2012). In Arabidopsis, GPA infestation resulted in an increase in the level of 9-LOX-derived oxylipins in the petiole exudates (Nalam *et al*., 2012). Genetic and physiological evidence indicates that GPA cues in on 9-LOX pathway derived oxylipins in Arabidopsis to facilitate infestation (Nalam *et al*., 2012). GPA population was significantly reduced on Arabidopsis *lox5* (At3g22400) mutants, in which the accumulation of 9-LOX-derived oxylipins is attenuated, as compared to the wild type plants. EPG studies indicated that insects on the *lox5* mutant had difficulty feeding from sieve elements and xylem tissues. This reduction in feeding activity of GPA on the *lox5* mutant also resulted in a reduction in water content in the aphids. Application of the 9-LOX-derived 9-hydroxyoctadecadienoic acid (9-HOD) restored water content and insect population size on the *lox5* mutant, thus confirming that 9-LOX products have an important contribution in facilitating insect feeding. 9-HOD and 9-hydroperoxyoctadecadienoic acid (9-HPOD) when added to an artificial diet enhanced GPA population size, suggesting that 9-LOX-derived oxylipins are susceptibility factors that facilitate colonization of GPA on Arabidopsis. Micro-grafting experiments (wild type *LOX* scions and *lox5* mutant rootstock, and vice-versa) demonstrated that the oxylipins that promote GPA susceptibility in Arabidopsis leaves are root-derived (Nalam *et al*., 2012). GPA infestation of Arabidopsis foliage was found to induce expression of *LOX5* and promote accumulation of 9-LOX products in roots from where they are likely transported to shoots via the vasculature. Experiments in potato plants (*Solanum tuberosum*) have

also indicated that accumulation of 9-LOX products is increased in GPA infested plants (Gosset *et al*., 2009).

MPL1

In Arabidopsis a lipase encoded by the *MPL1* (*MYZUS PERSICAE INDUCED LIPASE1*; At5g14180) gene, is required for the accumulation of an activity in petiole exudates that is detrimental to GPA (Louis *et al*., 2010a). Loss of this antibiosis activity in the petiole exudates of the *mpl1* mutant was accompanied by larger population size of GPA on the *mpl1* mutant compared to wild type Arabidopsis plants. Loss of *MPL1* function in the *mpl1* mutant did not impact insect feeding behavior. *MPL1* expression is induced in GPA-infested plants and is constitutively elevated in the *ssi2* mutant, which exhibits enhanced resistance to GPA (Louis *et al*., 2010a, 2010b). Indeed, MPL1 function was required for the *ssi2*-determined resistance against GPA and accumulation of antibiosis activity in petiole exudates. Furthermore, constitutive overexpression of *MPL1* from the *Cauliflower mosaic virus 35S* promoter resulted in enhanced resistance against GPA, suggesting that the induction of *MPL1* expression is important for controlling GPA infestation (Louis *et al*., 2010a). Constitutive overexpression of *PAD4* (described later) and *MPL1* in *mpl1* and *pad4* plants, respectively, rescued the antibiosis deficiency of the *mpl1* and *pad4* mutants, suggesting that *MPL1* and *PAD4* contribute to two parallel antibiosis mechanisms and the elevated levels of one component/mechanism, can overcome the deficiency of the other.

Fatty Acid Desaturases

The stearoyl-ACP desaturase activity encoded by the Arabidopsis *SSI2* gene catalyzes the desaturation of stearic acid to oleic acid (Shah *et al*., 2001; Kachroo *et al*., 2001) and thus contributes to Arabidopsis membrane lipid composition (Nandi *et al*., 2003). The *ssi2* mutant plants constitutively accumulate high levels of SA, which is responsible for the heightened resistance of the *ssi2* mutant to some pathogens (Shah *et al*., 2001; Kachroo *et al*., 2001). In comparison to the wild type plant, GPA reproduction was lower on the Arabidopsis *ssi2* mutant plant as compared to its wild type plant (Pegadaraju *et al*., 2005). However, GPA growth was comparable on the *ssi2* single mutant and the *ssi2 nahG* (SA-deficient) plant, suggesting that the high levels of SA present in the *ssi2* plants do not contribute to the *ssi2*-conferred resistance to GPA. In addition, GPA counts on the *suppressor of npr1-1*, *constitutive 1* (*snc1*; At4g16890) mutant, which accumulates high levels of SA (Zhang *et al*., 2003), was comparable to those on the wild type plant (Pegadaraju *et al*., 2005). These results suggested that some factor(s) other than SA contributes to the *ssi2*-conferred hyper-resistance against GPA. Petiole exudates collected from uninfested *ssi2* mutant contain elevated levels of antibiosis activity against GPA, than similar exudates collected from the wild type plant. Whether this antibiosis factor is a lipid is not known. However, the *ssi2*-determined enhanced antibiosis and resistance to GPA was attenuated in the absence of MPL1 activity in the *ssi2 mpl1* double mutant (Louis *et al*., 2010b). Phloem sap contains lipids (Madey *et al*., 2002; Nalam *et al*., 2012), and the salivary glands of phloem-feeding insects contain putative lipases (Shukle *et al*., 2009), thus suggesting that these insects likely encounter lipids in their diet, one or more of which could be detrimental to GPA.

More recently, loss of *FAD7* and *FAD8* (At3g11170 and At5g05580)-encoded fatty acid desaturases in Arabidopsis and the LeFAD7 activity in tomato (*Solanum lycopersicum*) were also shown to result in enhanced resistance against GPA and potato aphid (*Macrosiphum euphorbiae*), respectively (Avila *et al*., 2012). In Arabidopsis, FAD7 and FAD8 catalyze the desaturation of dienoic acyl chains in plastid galactolipids to yield lipids with trienoic fatty acyl chains. FAD7/FAD8 synthesized trienoic acyl chains are substrates for the synthesis of signaling oxylipids like OPDA and JA. The tomato *fad7* plants are deficient in JA, yet they are more resistant to potato aphid. Similarly, the Arabidopsis *fad7 fad8* mutant was more resistant to GPA. These results suggest that the impact of *fad7* on aphid colonization is independent of *fad7*'s effect on JA. Indeed, potato aphid numbers were comparable on wild type plants and in tomato mutants impaired in JA synthesis (*acx1*) or perception (*jai1-1*) (Avila *et al*., 2012), thus further supporting the suggestion that the impact of *fad7* mutation on aphids is unrelated to FAD7's role in JA accumulation. In tomato, loss of *FAD7* function resulted in increased antibiotic and antixenotic resistance to potato aphids, which was dependent on the accumulation of elevated SA levels in the *fad7* tomato plants as evident from experiments with *fad7 NahG* plants in which attenuation of SA accumulation by expression of the *NahG*-encoded salicylate hydroxylase, resulted in suppression of *fad7*-conferred enhanced resistance to potato aphid. Whether, *fad7 fad8* determined enhanced resistance against GPA in Arabidopsis is similarly dependent on SA remains to be determined, although as mentioned above, in Arabidopsis SA is not required for basal resistance against GPA (Moran and Thompson, 2001; Pegadaraju *et al*., 2005).

REGULATION OF PLANT DEFENSES

PAD4

In Arabidopsis, the *PAD4* (*PHYTOALEXIN DEFICIENT4*) gene modulates antibiotic and antixenotic defense against GPA (Pegadaraju *et al*., 2005, 2007). In addition, *PAD4* promotes premature leaf senescence and *SAG13*, *SAG21* and *SAG27* (At2g29350, At4g02380, and At4g44300) expression in GPA-infested plants (Pegadaraju *et al*., 2005). *PAD4* was required for deterring insect settling on plants (Pegadaraju *et al*., 2007) and the accumulation of a factor in petiole exudates of uninfested plants that was detrimental to GPA (Louis *et al*., 2010b, 2012). In addition, EPG analysis indicated that *PAD4* controls insect feeding from sieve elements (Pegadaraju *et al*., 2007). *PAD4* is also involved in plant defense against a subset of pathogens, where it modulates the synthesis of SA and the phytoalexin, camalexin (Glazebrook *et al*., 1997; Zhou *et al*., 1998; Jirage *et al*., 1999). However, genetic studies have suggested that the involvement of *PAD4* in plant defense against GPA is not due to its involvement in SA and camalexin metabolism (Pegadaraju *et al*., 2005). The N-terminal half of PAD4 shares homology with α/β-fold acyl hydrolases that include lipases and esterases (Zhou *et a*l., 1998; Jirage *et al*., 1999).

Although, the biochemical function of PAD4 is not known, at the molecular level PAD4 protein interacts with its signaling partner EDS1 (ENHANCED DISEASE SUSCEPTIBILITY1; At3g48090) thereby promoting defense against pathogens (Falk *et al*., 1999; Feys *et al*., 2005). EDS1, like PAD4, has homology to lipases/acylhydrolases, and like *PAD4*, *EDS1* expression is also induced in GPA-infested leaves (Feys *et al*., 2005; Pegadaraju *et al*., 2007). However, *PAD4*-mediated defense against GPA does not require *EDS1* (Pegadaraju *et al*., 2007; Louis *et al*., 2012), suggesting that PAD4s involvement in Arabidopsis defense against aphids is distinct from its involvement in defense against pathogens.

Mutational analysis of PAD4 indicated that Ser118, which is a catalytic residue in α/β fold acyl hydrolases, although not required for PAD4's involvement in defense against pathogens, is required for a subset of PAD4 activities in defense against GPA (Louis *et al*., 2012). It was essential for limiting insect feeding from sieve elements and for accumulation of the antibiosis factor in petiole exudates of uninfested plants (Louis *et al*., 2012). However, Ser118 is not required for controlling insect settling and premature senescence in GPA-infested plants. These results suggest that distinct molecular activities of PAD4 modulate different functions in Arabidopsis defense against GPA.

In Arabidopsis, *PAD4* also modulates accumulation of camalexin (Tsuji *et al*., 1992; Rogers *et al*., 1996). Camalexin levels increase in GPA-infested Arabidopsis leaves. However, there was no significant difference in camalexin content in GPA infested leaves of *pad4* mutant and wild type plants (J Louis, J Keerantweep and J Shah, unpublished data), suggesting that *PAD4* is not required for camalexin accumulation in GPA-infested Arabidopsis. Camalexin synthesis also requires the *PAD3* (At3g26830) gene, which encodes an enzyme that catalyzes the terminal step in the synthesis of camalexin (Schuhegger *et al*., 2006). *PAD3* expression is induced in GPA-infested plants (Pegadaraju *et al*., 2005). However, GPA population size on the *pad3* mutant was comparable to that on the wild type plant (Pegadaraju *et al*., 2005), thus indicating that *PAD3* and camalexin are not essential for controlling GPA infestation on Arabidopsis. Cabbage aphid infestation also results in an increase in camalexin accumulation (Kuśnierczyk *et al*., 2008). *PAD3* expression was induced in response to cabbage aphid infestation (Kuśnierczyk *et al*., 2008). Furthermore, fecundity of cabbage aphid was significantly higher on the *pad3* mutant than on the wild type plant (Kuśnierczyk *et al*., 2008), thus indicating that unlike GPA infestation, camalexin accumulation has a role in controlling cabbage aphid infestation on Arabidopsis. Comparative analysis of EST sequences from the GPA with the whole genome sequence of the specialist pea aphid revealed that a generalist aphid like GPA has more detoxification enzymes, including cytochrome P450 monooxygenases, glutathione *S*-transferases, and carboxy/cholinesterases, likely because GPA encounters more diverse host plant species (Ramsey *et al*., 2010). Presence of these detoxification mechanisms could explain the lack of any obvious effect of camalexin on GPA.

TPS11 and Trehalose

Trehalose is a non-reducing disaccharide composed of two molecules of glucose. It is present in a wide spectrum of living organisms, as varying as bacteria, fungi, insects and angiosperms. Singh and co-workers (2011) recently demonstrated that transient accumulation of trehalose, dependent on the *TPS11*-encoded trehalose-6-phosphate synthase, modulates Arabidopsis defense against GPA. *TPS11* was required for the timely induction of *PAD4* in GPA-infested leaves. In addition, *TPS11* was required for promoting starch accumulation at the expense of sucrose in GPA-infested leaves. As mentioned earlier, genetic studies have indicated that starch accumulation in Arabidopsis contributes to controlling GPA infestation. Petiole exudates of the *tps11* mutant lacked the antibiosis activity that was present in petiole exudates of wild type plants. In addition, EPG analysis indicated that GPA spent more time in sieve element phase on the *tps11* mutant, and given a choice the insects preferred to settle on the *tps11* mutant than the wild type plant. Trehalose application restored wild type level of resistance against GPA in the *tps11* mutant, indicating that the *tps11* mutant phenotypes are due to its inability to accumulate elevated levels of trehalose in response to GPA infestation. The role of trehalose in defense against GPA is further evident from experiments with the trehalose hyper-accumulating *tre1* (At4g24040) mutant, which contains a T-DNA insertion in the trehalase encoding *TRE1* gene. GPA population was smaller on the *tre1* mutant, compared to the wild type plant. Similarly, GPA population was also smaller on transgenic plants expressing the bacterial *otsB* gene, which encodes a trehalose-6-phosphate phosphatase involved in trehalose synthesis. Singh *et al*. (2011) suggested that *TPS11* provides a threshold level of 'signaling' trehalose that is essential for regulating Arabidopsis defense against GPA, including the up-regulation of *PAD4* expression and full extent of starch accumulation. Trehalose application promotes starch accumulation in Arabidopsis leaves (Wingler *et al*., 2000; Kolbe *et al*., 2005; Singh *et al*., 2011). As shown in other studies, the ability of trehalose to promote starch accumulation in GPA-infested plants could be due to the inhibition of starch turnover (Ramon *et al*., 2007) and/or the redox activation of AGPase, a key enzyme in starch synthesis, by trehalose-6-phosphate (Paul *et al*., 2008).

FINAL REMARKS

In the last decade, the use of Arabidopsis as a model plant system has helped us to better understand the genetic, biochemical and molecular aspects of plant interaction with aphids. Undoubtedly, applying the basic information gained from *Arabidopsi*s to economically important crop plants will be a big step forward in improving our understanding of defense signaling in economically important crop species. In the future, the availability of new molecular tools and progress of genome sequences of several phloem-feeding insects will enable exploring Arabidopsis—phloem-feeding insect interactions from the perspective of both the plant and the insect. These tools will allow determining how alterations in activity of Arabidopsis genes and mechanisms involved in defense and susceptibility impact gene expression in the insect, and thus provide clues on how insect physiology is impacted on these Arabidopsis mutant and transgenic plants. The ability to silence expression of aphid genes by expressing dsRNA in Arabidopsis will permit in identifying and characterizing aphid-derived effectors and elicitors of plant defenses, and in assessing the function

of aphid genes and the impact of these genes to the interaction with varied Arabidopsis genotypes.

Aphids also vector many economically important plant pathogenic viruses. Aphid settlement, growth and development are impacted on virus-infected plants (Colvin *et al*., 2006; Mauck *et al*., 2010). However, the molecular and biochemical mechanisms that contribute to this effect of viral infection on aphid performance are poorly understood. Recently, it was shown that microRNA (miRNA) profiles of resistant and susceptible melons are altered upon aphid herbivory (Sattar *et al*., 2012). However, the role of phloem-specific miRNAs in plant-aphid interaction is not characterized. Likewise, the role of phloem proteins and phloem-translocated small molecules in plant-aphid interaction is also poorly understood. Arabidopsis provides an excellent model system to characterize the role of these small and macromolecules, and the molecular and physiological impact of viral infection on plant-aphid interaction.

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