Understanding the Plant Aphid Interaction: A Review

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ABSTRACT

The interaction between plant-aphid is phenomenal and complex. Aphids possess efficient mouthparts which feed on plant sap intensively. Adaptation to host plants and successful feeding is achieved through the strategic ability of aphids to reproduce sexually and asexually (parthenogenesis). Aphid infestation damages the plant in diverse ways and induces plant defense. Though plant elicit direct and indirect defense to resist aphid feeding, the effectiveness of plant resistance depends largely on the aphid infestation rate and quality of the host plant. To control aphid infestation and plant damage, dependency on insecticides is undesirable due to insecticidal resistance of aphids and environmental pollution. The approach towards the development of the genetically engineered crops which are aphid resistant can be the considerable potential to aphid control.

Keywords: host selection, feeding injury, plant-aphid interaction, plant defense.

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I. INTRODUCTION

Aphids are major group of herbivores which belong to order Hemiptera and superfamily Aphiditae. As a crop pest aphids affect the agro economy by excessive feeding on plant phloem and serving as the vectors of various plant diseases. There are almost 4000-5000 aphid species are described, among them 250 are important agricultural pest which vary with their host plants (Blackman & Eastop, 1994; Blackman & Eastop, 2000; Kumar, 2019). The extent of being adapted to tropical environment to subtropical environment make them widely distributed throughout the world and impact badly on agro economy (Poirié & Coustau, 2011). This extent of wide range of availability, agricultural conditions, diversity of crops, variations in population size and in the crop areas damage make researchers difficult to give a precise assessment of total global economic loss (Dedryver *et al.*, 2020). The reason of being able to limit the productivity lies in the amazing biological features and population strategies. These phytophagous insects possess long slender mouthparts which pierce a tender plant and suck plant sap which ferries sugar and other nutrients. This specific habit of feeding is highly supported by the high reproductive potential. Aphids undergo parthenogenesis and viviparity showing the maximum intrinsic rate. Conserving the energy in reproduction, possession of needle-like structure of stylet capable of piercing plant cell walls and acting as a vector to deliver viruses into host cell (Ng & Perry, 2004) make them enough to exploit agricultural environment. Aphid feeding on plants and reaction of the plant as defense make the complex processes involved in plant aphid interaction. This review understands and summarizes this co evolutionary relation

between plant and aphids (Fig. 1).

II. HOST SELECTION BY APHIDS

The interaction of aphid with the plant starts with the host selection process. The host selection is a complex process involving various steps like host location, host acceptance, feeding of phloem or with rejection (Ernesto, 1997). Aphids are highly selective insects in their selection of plants as host plants. Sensory and behavioral mechanisms help aphids in decisions of host selection process comprise of vision, olfaction, mechano-sensation, and gustation (Verdugo *et al.*, 2106; Powell *et al.*, 2006). Sensory cues start playing the role with the process of host location. Aphids get attracted towards yellow and green colored leaves other than autumnal red leaves (Döring *et al.*, 2009). Here, though aphids are poor flyers but they locate the plant for landing using visual cues but at the short distance, here plant volatiles play a role (Döring, 2014; Bernays, 2001). The selection of landing on a specific plant occurs due to visual and olfactory cues. As aphids land after locating the host, they assess the initial plant contact and surface cues before stylet penetration. After landing, antennal movement of aphids judges the physical appearance of the plant surface. Chemosensory and mechano receptors of antennal hair detect the color, wax, trichome, texture of the plant surface, thickness of leaf (Mandal *et al.*, 2020). After dealing with the plant surface, probing i.e., plant penetration process is initiated with insertion of long stylet. Stylet is made of two long mandibles and two inner maxillae which form food and salivary canal (Giordanengo *et al.*, 2010) (Pettersson *et al.*, 2018; Uzest *et al.*, 2010). Stylet penetrates beyond epidermis sampling the sap for gustatory discrimination. The longer Sieve elements sucking may

represent the host acceptance. Aphids utilize the surface cues present on the plant to decide whether to feed and or oviposit (Walling, 2008). In phloem phase after sap sampling aphid may reject the plant depending on upon its quality. Level of nitrogen, water content, defensive components, trace

elements, carbon comprise the quality of a host plant (Mandal *et al.*, 2020). The acceptance leads to sustain feeding which ultimately starts damaging the plant.

Fig. 1 shows the plant insect interaction starting with the host selection process followed by feeding. Aphids show feeding injury which is symptomatic and asymptomatic. This process of integration may end on plant defense and aphid counter defense of counter adaptations depending upon the quality of the host plant and aphid infestation rate.

III. APHID REPRODUCTIVE STRATEGY

Higher reproductive abilities make aphids causing maximum loss in plants. Aphids start reproducing during host acceptance process as, parturition cues are mostly detected early in the stylet pathway (Powell *et al.*, 2006). Aphids reproduce parthenogenetically followed by viviparity (Miura *et al.*, 2003), phenomenon of telescopic generation where newly born offspring is already pregnant allows rapid parturition on the selected host plant and start sucking the plant sap and grow rapidly (Powell *et al.*, 2006). This is the mostly adopted method of reproduction while colonizing on new plant (Giordanengo *et al.*, 2010). Reproduction without male increases the intrinsic rate (r_m) of the population. The reproduction in aphids is season specific. In autumn sexual reproduction takes place, where oviparous female opulate with male aphid and lay eggs. Whereas in spring and summer parthenogenetic female gives birth to larvae (Murano *et al.*, 2018; Ogawa & Miiura, 2014). On the basis of utilization of host plants, reproductive strategy of aphids varies. Host altering i.e., heterocious reproduce sexually on primary host by laying eggs. These eggs hatch in spring giving birth to fundatrices or stem mother, wingless morphs which further gives birth to fundatrigenia generation. Later reproduction of spring migrants, winged morphs fly to secondary host where they reproduce parthenogenetically. Here several generations are produced of winged male and gynoparae are produced then they migrate to primary host (Kumar, 2019; Hardie, 2018). In other hands non host altering species i.e., monoceous species remain on the same plant throughout the year showing winged or wingless polyphenism in summer. Whereas in autumn male and oviparae are produced by same mother (Thomas *et al.*, 2012). Depending on the breadth of their host range aphids have been classified as monophagous, oligophagous, polyphagous, pantophagous aphids (Eastop, 1973). The reproductive strategies are mostly factor dependent. These alternations of reproductive modes make them worst impacting badly on their feeding behavior and thus on plant health.

IV. APHID FEEDING BEHAVIOR

Sustained ingestion after host acceptance determines the rate of infestation and further causes significant changes in plants. Host acceptance further leads to utilization of cell contents or phloem and or xylem sap with their piercing mouthparts. The modified mouthparts are able to probe into plant tissue and feed from sieve element. While feeding from SE aphid secrete gelling saliva which hardens to form a sheath (Nalam *et al.*, 2018; Miles, 1999; Cherqui & Tjallingii, 2000; Will *et al.*, 2013). This tactic facilitates the smooth movement of the stylet in intracellular spaces and also lowers the threat of wounding response by the host plant and prevents the induction of defense responses (Kumar, 2019; Will & Van Bel, 2006). Along with gelling saliva aphid produces watery saliva. The gelling saliva is viscous, dense, and proteinaceous (Guerrieri & Digilio, 2008) and contains complex carbohydrates, phospholipids and protein sap that appear to be consistently represented in the sheath saliva in number of aphid species (Miles, 1999) (Cherqui & Tjallingii, 2000). The watery saliva, which is secreted intracellularly, either when the stylets briefly puncture cells during probing or

immediately and during sap ingestion (Will *et al.*, 2013). Aphids take help from gustatory cues to make decision to continue feeding on plant or not. This happens when aphids put stylet into contents of epidermal and mesophyll cells while entering into SE through intracellular spaces (Nalam *et al.*, 2018). This release triggers the plants first line of defense. Plant surface characteristics such as hairiness and the structure of epicuticular wax may reject aphid walking. Presence of trichomes hampers the movement of aphids, which affects the stylet insertion, indirectly the host selection process (Guerrieri & Digilio, 2008). Still some aphids manipulate this defense such as *M. mentzeliae* is capable of feeding on *M. Pumila* manages to avoid entrapment by trichomes by walking slowly which does and by having tipped legs it is able to somehow to tiptoe through the thorns (Eisner *et al.*, 1998). Further phloem feeding may lead to dehydration of the insect due to presence of large concentration of carbohydrates in the sap which created an osmotic pressure (Walling, 2018). Continuous feeding on phloem makes plant weak and lead to alteration of plant hormone along with induction of defense mechanism. Nonetheless, along with secretion of saliva aphids also secrete waste products of phloem ingestion onto plants in the form of honeydew. This honeydew secretion can also modulate host defense and also have lethal effects on plant. Continuous feeding on plant leads to feeding injuries.

V. APHID FEEDING INJURY

Consumption of phloem sap by piercing mouthparts affects plant physiology in diverse ways. The phases of feeding including stylet probing, salivation, and ingestion of sap damage the plant diversely. Plant damage depends on aphid infestation rate, developmental stage of the plant of the plant when infested and the sensitivity of each stage to sieve diversion (Dedryver *et al.*, 2020). Stylet penetration and withdrawal injure the plant. The sieve diversion causes extensive apparent symptoms where some damages are asymptomatic (Quisenberry & NI, 2007). These symptomatic and asymptomatic damages reduce the growth and development of the plant and eventually death. Moreover, intracellular penetration causes more ultrastructural damage to plant tissue than does intercellular penetration (Goggin *et al.*, 2018). Plant response to aphid damage is sometimes asymptomatic i.e., plant does not show any aberrations while symptomatic is apparent visible damage. Symptomatic damage varies from desistance (Chlorosis, necrosis, stunting, and leaf curling) to neoplasm (abnormal structures) (Goggin *et al.*, 2018). The Black Pecan aphid causes chlorotic feeding damage to pecan foliage which encourages aphid settling and nymphal growth (Cottrell *et al.*, 2009). Neoplasm deforms the new growth, strongly disturbs the cell multiplication around the feeding point and proliferate the plant tissue into abnormal structure (Dedryver *et al.*, 2020). Gall formation is the unique group of interaction between aphids and host plants where it is species specific and induced by aphid with a different shape, size, and galling sites (Kmiec *et al.*, 2014) and can be formed on only young plant organs (Wool, 2004). The biological complexity of galls with aphids promises the protection from natural enemies and insecticide (Guerrieri & Digilio, 2008).

TABLE I: APHIDS ATTACKING CROPS, FEEDING INJURIES AND APHID TRANSMITTED VIRUSES

Sr. no.	Aphid	Host plant	Feeding injury	Virus
1.	<i>Dysaphis plantaginea</i> (Parsserini)	Apple fruits	Leaf/ fruit deformation, localized tissue damage	D. Plantaginea virus
2.	<i>L. erysini</i>	Mustard plant	Curling of leaves, flower and pods	Common mosaic virus
3.	<i>Myzus varians</i> (Davidson)	Peach	Leaf curling to cigar shape	Plum pox virus
4.	Russian wheat aphid (<i>Diuraphis noxia</i>)	Wheat Barley	Leaf rolling Whitish, yellow and red leaf markings, leaf decoloration	Barley yellow dwarf virus
5.	Oat aphid (<i>Rhopalosiphum padi</i>)	Oats Wheat Barley	Reduced tillering Stunting	Barley yellow dwarf virus
6.	Green peach aphid (<i>Myzus persicae</i>)	Canola Lupin Pulses Tobacco Pepper	Leaf distortion, wilting of cotyledons, leaf senescence, seedling death	Beet western yellow virus Cucumber mosaic virus Pea seed borne mosaic virus
7.	Cabbage aphid (<i>brevioryne brassicae</i>)	Canola Crutiferous forage crops	Reducing pod set, pod fill, reduced grain quality, late flowering	Beet western yellow virus Cucumber mosaic virus
8.	Turnip aphid (<i>Lipaphis pseudo brassicae</i>)	Canola Crutiferous forage crops	Reducing pod set, pod fill, reduced grain quality, late flowering	Turnip mosaic virus Cucumber mosaic virus
9.	Blue green aphid	Lupins Lucerne	Wilting, stunted growth, leaf curling, leaf drop	Beet western yellow virus Cucumber mosaic virus
10.	Cow pea aphid (<i>Aphis craccivora</i>)	Legume Faba beans Lentils	Yellowing/ whitening of leaf veins, wilting of leaves and plant death, leaf bunching, stem twisting	Alfalfa mosaic virus Alfalfa leaf curl virus Beet western yellow virus Cucumber mosaic virus
11.	Pea aphid (<i>Acyrtosiphon pisum</i>)	Faba beans, Lucerne, chickpea	Leaf deformation, wilting, yellowing, stunting, leaf curling, leaf drop, reduced dry matter	Beet western yellow virus Cucumber mosaic virus Pea seed borne mosaic virus Alfalfa mosaic virus

Ryckebusch *et al.*, 2020; Gálvez, 1990; Aphid-transmitted viruses in vegetable crops; Contingency Plan, 2011; Gildow, 1983; Halbert *et al.*, 1994; Adachi *et al.*, 2018; Ghosh *et al.*, 2017; Katis *et al.*, 2007; Aphids on Cruciferous Crops Identification and Management; Goggin *et al.*, 2018; Dedryver *et al.*, 2020; Kumar, 2015; Eisner *et al.*, 1998.

In addition to these injuries, honeydew causes indirect feeding damage to plants from physical level to chemical level. Honeydew secretion in aphids causes development of Black sooty mold on leaf that interferes with normal photosynthetic activity (Dedryver *et al.*, 2020). That not only blocks stomata, interfering the gaseous exchange but also leads to leaf fall (Kumar, 2019). Honeydew also creates a mutualism in ants, parasitoid wasp with aphids (Tena *et al.*, 2018). The secretion of honeydew creates a symbiotic relationship between aphids and ants, which further protects aphids from their natural enemies (Mandal *et al.*, 2020). The black bean aphid *A. fabae* is regularly tended by honeydew collecting ants and benefits then from mutualism; in return ants defend the aphid from natural enemy (Fischer *et al.*, 2005). Furthermore, it suppresses the jasmonic acid to reduce plant defense activity (Schwartzberg & Tumlinson, 2014). One of the factors that affect the feeding injury is aphids acting as a vector for plant viruses. During feeding aphid simultaneously ingest sap contents and infect saliva which can contain viruses if the aphid has fed previously on virus infected plant (Stevens & Lacomme, 2018). This virus transmission takes down the plant machinery by manipulating and suppressing the plant defense showing various symptomatic and asymptomatic damages (Table I).

VI. PLANT DEFENSE

Aphid feeding causes alterations in their host plant and eventually death. To fight against aphid attack plants have developed a defensive mechanism which is elicited during sap sampling itself. Plant characteristics such as thickness of cuticle, presence, or absence of waxy layer above the leaf surface, trichomes and nutritional status of plants greatly influence aphid species to select their suitable host (Mandal *et al.*, 2020). This defensive system is guided by various forms: antixenosis, antibiosis and tolerance. Where antixenosis and antibiosis are fall under resistance category in which plant uses chemical and physical mechanisms to reduce herbivory (Verdugo *et al.*, 2016). Antixenosis can be the important mode of resistance by reducing the host selection machinery of the aphid (Ogawa & Miiura, 2014).

Disturbing the host selection process adversely impacting insect behavior to find sieve element deters infestation (Pettersson *et al.*, 2018). Antibiosis i.e., chemical, and physical defense of the plant affect the growth, development and or reproduction of the insect. Constitutive presence of trichomes, thorns, epidermal wax, cell wall thickness, color prevents the feeding activity (Guerrieri & Digilio, 2008). Epicuticular wax from plant act as aphicide against grain aphids (Wójcicka, 2015). Trichomes resemble hair like structures that have possibility to consist of different types: non glandular, glandular, curly, straight, unicellular, multicellular, hooked and simple (Werker, 2000), (Pritchard, 2017). High density of glandular trichomes show high

resistance to green peach aphid (Antonio da Silva *et al.*, 2019). These trichomes also contribute to chemical defense along with acting as a physical barrier to aphid movement on the plant (Louis *et al.*, 2012). Likewise, in solanum berthault Hawkes whose glandular hairs produce (E) Farnesene the aphid alarm hormone that prevents the colonization by inducing dispersal behavior in winged aphids (Guerrieri & Digilio, 2008).

There are probably different factors other than physical barriers that cause induced resistance such as changing in quality of amino acid, jasmonic acid and salicylic acid which hinders the feeding mechanism (Amiri *et al.*, 2017) by contributing to signaling associated with plant defense (Nalam *et al.*, 2018). Volatiles including alkaloids, phenols, terpenoids inhibits the oviposition and attract natural enemy (Sánchez-Sánchez & Morquecho-Contreras, 2017). Amino acids and other secondary metabolites influence the ability of survive and reproduction of melon aphid (Daryanto *et al.*, 2017). Apart from antixenosis and antibiosis, tolerance minimizes the plant damage and recover the plant (Louis *et al.*, 2012), (Nalam *et al.*, 2018). In order to tolerate the aphid infestation, plants reduce photosynthetic activity by decreasing total chlorophyll and carotenoid content (Koch *et al.*, 2016). This defensive system depends upon the quality of the host plant and infestation rate.

VII. FUTURE ASPECT OF PLANT APHID INTERACTION

Plant aphid interaction is the co-evolutionary process where both are biotic and abiotic factor dependent. There are many ways to control aphids including chemical pesticides along with IPM. Though chemical insecticides are found lethal against aphids they have their own limits as they also have harmful effects on environment. It is also necessary to overcome the limits of traditional management ways. To lower the feeding injury many researchers are studying plant defense system to have genetic control on aphids. Testing genetically engineered varieties against aphids provides new insights in aphid management. The innovative genetic strategies, study of interaction between bio pesticides and plants can offer the possibility of the development in an appealing avenue of future aphid plant interaction research.

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