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Chemical and physiological changes caused by aphids feeding on their host plants*

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ABSTRACT. We present significant information about damage caused to plants by the feeding of piercing–sucking insects, based on the example of aphids. Research concerning the impact of aphids on their host plants was already being carried out in the 1950s in the 20th century, but it is still being undertaken as it is very important. Aphid feeding causes deformation of plant tissues, disorders in plant metabolism and changes in the amount of various compounds in plant tissues. Plant viruses are transmitted in aphid saliva.

KEY WORDS: aphid damage, aphid feeding, biochemistry and physiology of plant responses to aphids, piercing-sucking insects.

INTRODUCTION

Damage caused by insects with chewing mouthparts are often visible to the naked eye. These include biting out holes in plants, leaf mining, punctures in twigs, trunks, etc. The feeding of insects with piercing-sucking mouthparts is a highly complicated and often hidden process. This paper presents a review of the most important data concerning the

* The paper is dedicated to Prof. Wacław WOJCIECHOWSKI in recognition of his great contribution to the taxonomy and faunistics of Hemiptera.

negative effects of aphids feeding on plants and some other representatives of the Sternorrhyncha suborder.

THE FEEDING MECHANISM OF APHIDS

Aphids feed on phloem sap, which they draw using piercing-sucking mouthparts. The mouthparts of aphids have a quite complex structure (see MCLEAN & KINSEY 1984). The main components comprising this organ include the labium, two pairs of mandibular and maxillary stylets, the salivary pump, the cibarial pump and the taste organ. During food extraction the mandibular stylets adjoin one another closely, and the grooves that run along their sides form two canals – a food canal and a smaller salivary one. The food is extracted through the food canal and simultaneously, saliva is injected into the plant through the salivary canal. During the insertion of the stylets into the plant, the labium decreases in size, touching the surface of plant (TJALLINGII 1978). Feeding begins with the secretion of a drop of saliva onto the surface of the plant. Saliva is also secreted along the pathway of the stylets to ease their movements inside the plant. Most often the phloem sap is passively transferred into the mouthparts. However, sometimes the cibarial pump takes part in the active extraction and transfer of food into the stomach. With the aid of the salivary pump, saliva produced by four pairs of salivary glands is injected into the plant tissues (POLLARD 1973). Aphids produce two types of saliva – gel and watery (DAY & IRZYKIEWICZ 1954, WILL et al. 2007, WILL et al. 2012). Gel saliva forms a sheath around the stylets within which they can move freely (MILES 1987). But the lubrication function of the sheath is questioned by WILL & VILCINSKAS (2015). According to MITTLER (1957) aphid saliva creates a canal transporting liquid food into the body of the insect. Aphid gel saliva and the salivary sheath protect the stylets from damage. This salivary sheath remains in the plant as a remnant of stylet penetration. It also deactivates the protective substances secreted by the attacked plant (MILES 1987, WILL et al. 2012, WILL & VILCINSKAS 2015). Both saliva fractions mix in the salivary canal (MILES 1967, 1999). In insects we can observe adaptation of the salivary enzymes into the ingredients of the extracted food. The invariable components of Hemiptera saliva are hydrolases and polyphenol oxidase (NUORTEVA 1962).

AL-MOUSAWI et al. (1983) observed saliva lining the pathways of the stylets and detected streaky darkening of epidermal, bundle sheath and phloem cells. The walls of these cells were partially hydrolysed: nuclei, chloroplasts and mitochondria, as well as starch grains became degraded, whereas the protoplasts of the damaged cells, in the form of a bubbly mass, were transferred into the extracellular space. CICHOCKA (1984) observed darkening of the palisade and spongy parenchyma, damage to cell membranes and epidermal cells on both leaf sides in the galls of *Pemphigus bursarius* (LINNAEUS, 1758) on the petioles of cottonwood.

The stylet pathways and the sites of sap extraction are different. The aphid stylets are inserted into the plant intercellularly, through cells, or even through trichomes (LESZCZYŃSKI 1996). POLLARD (1973) distinguished three groups in Sternorrhyncha: piercing intercellularly into the phloem (e.g. Aphididae), piercing intracellularly into the parenchyma (e.g. Lachnidae), and reaching the phloem intracellularly (e.g. Coccidae).

Aphids penetrate plant tissues intercellularly, but on their way they puncture the surrounding cells and then reach the phloem (POLLARD 1973, BOTHA & EVERT 1978, TJALLINGII & HOGEN ESCH 1993, HOGENHOUT & BOS 2011). Thanks to these punctures aphids can detect sieve tubes inside the plants. HEWER et al. (2010, 2011) showed that sucrose and pH are indicators of sieve tube recognition. Aphids normally feed on phloem sap, but if food resources are insufficient they will also feed on the parenchyma (POLLARD 1973). Sometimes aphids extract fluids from the xylem and bundle sheaths (SORIN 1966). They feed from the xylem in order to replenish their water supply (MONTLOR & TJALLINGII 1989). The manner in which aphids pierce plant tissues depends not only on the species (or even the biotype), but also on the stage of development, the host plant species and the type of tissue or organ (LOWE 1967, POLLARD 1973, CICHOCKA 1980). Aphids are also capable of piercing stomata (SORIN 1960, 1966, POLLARD 1971). Stylet insertion into the plant lasts between a few minutes and a few hours depending on the aphid species and host plant (CICHOCKA 1980). Aphid phloem feeding can last for up to 15 days (MONTLOR & TJALLINGII 1989).

SUBSTANCES INTRODUCED INTO PLANTS WITH APHID SALIVA AND THE DISORDERS THEY CAUSE

Phloem sap extraction, nutrient deprivation, the introduction of toxic saliva, and polluting plants with honeydew are examples of the direct harmfulness of piercing-sucking arthropods. On the other hand, plant virus transmission, which causes viral diseases, is indirectly harmful.

Aphid saliva has been found to contain mainly proteins and phospholipids, but also other compounds (MILES 1968, 1999, MADHUSUDHAN & MILES 1998, CHERQUI & TJALLINGII 2000, RAO et al. 2013). The saliva introduces into the plant enzymes that hydrolyse cell walls, partially digest nutrients, and detoxify plant allelochemicals in the food and in the surrounding tissues (MITTLER 1957). Aphid saliva also contains effector proteins that can be delivered into the host during feeding. These proteins are required for aphid feeding and they can modulate host cell processes (CHERQUI & TJALLINGII 2000,

TJALLINGII 2006, HOGENHOUT & BOS 2011, ELZINGA & JANDER 2013, RODRIGUEZ & BOS 2013, JAOUANNET et al. 2014). RODRIGUEZ & BOS (2013) suggest that aphid effectors interact with host plant proteins in order to suppress defences, for example. RAO et al. (2013) identified twelve proteins in the saliva of *Sitobion avenae* (FABRICIUS, 1775) and seven in that of *Metopolophium dirhodum* (WALKER, 1849). NICHOLSON & PUTERKA (2014) identified 32 salivary proteins in four *Schizaphis graminum* (RONDANI, 1852) biotypes, while CAROLAN et al. (2009) identified nine such proteins in *Acyrthosiphon pisum* (HARRIS, 1776). Aphid watery saliva contains sugars (FEIR & BECK 1961) and amino acids (SCHÄLLER 1963). NUORTEVA (1962) also detected gibberellic acid, whereas LINDNER et al. (1962) found phosphates. The watery saliva also contains proteins that prevent calcium–induced sieve tube occlusion (WILL et al. 2007, WILL et al. 2009, WILL & VAN BEL 2008, GIORDANENGO et al. 2010). The gel saliva of many aphid species contain the sheath protein (SHP), which is a major structural protein of the salivary sheath and is required for its hardening (WILL & VILCINSKAS 2015). WILL & VILCINSKAS (2015) also suggest that the salivary sheath prevents the influx of calcium from the apoplast.

The salivary sheath has been found to contain polyphenol oxidase, which is said to accumulate indole-3-acetic acid in neighbouring cells. This acid can cause gall formation, which can also be enabled by the presence of gibberellins and cytokinins, as well as free amino acids in the saliva (CICHOCKA 2001). Both saliva fractions (watery and gel) have been found to contain numerous enzymes. These include polyphenol oxidase, peroxidase, polygalacturonase, cellulases, esterases, proteases, α-amylases, phosphatases, phosphorylases, β-glycosidase and pectin-esterases (LESZCZYŃSKI 1996, MADHUSUDHAN & MILES 1998, URBAŃSKA et al. 1998). Pectin polygalacturonase can cause hydrolysis of pectins in cell walls. Under the influence of aphid saliva, cell membranes are permeable not only to water, but also to sugars and low molecular weight proteins (CICHOCKA 2001). URBAŃSKA et al. (1994) found that the saliva of *Sitobion avenae* contains active peroxidases, polyphenol oxidase and β-glycosidases. These enzymes hydrolyse middle lamellas, cell walls, and even entire protoplasts, enabling the stylets to penetrate plant tissues (URBAŃSKA & NIRAZ 1990).

WHAT SUBSTANCES PRESENT IN A PLANT CAUSE IT TO BE ACCEPTABLE AS A HOST?

Whether a plant is acceptable as a host depends on basic metabolites such as monosaccharides, sucrose, peptides, as well as proteins and free amino acids (CIEPIELA 1990, SEMPRUCH 2010). Nitrogen can be found in plants in low concentrations of only 1-3%. Nonetheless, this element, being a constituent of amino acids, proteins, nucleotides, nucleic acids, plant pigments, vitamins and other compounds, is important for the growth and development of herbivores (CIEPIELA & SEMPRUCH 1993). To aphids the most important nutrients are nitrogen compounds such as free amino acids, low molecular weight amides, peptides, nucleotides and proteins (MORALES et al. 2001, SEMPRUCH 2010, CZERNIEWICZ et al. 2011). The main feeding stimulants for cereal aphids are sucrose, fructose, and the amino acids leucine, isoleucine and histidine. Plant sap extracted from the cutting mouthparts of aphids was found to contain 5-10% monosaccharides, as well as 0.2% amino acids and amides (AUCLAIR 1963). Only a fraction of sugars is utilized by aphids, the majority being excreted in the form of honeydew (AUCLAIR 1976). Phloem sap in sieve tubes contains a lower concentration of protein substances than cell sap in other tissues (CIEPIELA et al. 1991). Therefore, in order to satisfy their demand for protein compounds, aphids need to extract large amounts of sap. Aphids need about 20 amino acids in order to develop properly. Sugars are also important to these insects and the main feeding stimulator is sucrose (SRIVASTAVA & AUCLAIR 1975). Bartom, the broad bean cultivar preferred by *Aphis fabae* (SCOPOLI, 1763), was found to contain far more sugars, nitrogen, proteins and free amino acids than the less attractive Hangdom White cultivar (CICHOCKA & LESZCZYŃSKI 2000).

Feeding requirements in aphids depend not only on the quantity, but also the quality, or even the ratio between individual ingredients found in the food matter. What is more, the requirements change with the growth and development of the given species (LESZCZYŃSKI et al. 2000). Proper growth and development of herbivores depends on proteins and amino acids. Plant cell sap contains around 0.2% protein amino acids, whereas phloem sap contains even less (KRZYWIEC 1968, SEMPRUCH 2010). The presence of particular amino acids in the plant influences fertility, growth and development of females and also plant resistance (CIEPIELA et al. 2002, SEMPRUCH & CIEPIELA 2002, SPRAWKA et al. 2002, WILKINSON & DOUGLAS 2003, SEMPRUCH & CIEPIELA 2004). Equally important are vitamins, as well as macro- and microelements. Also vital is the presence of saponins, which are harmful to aphids (SZYNKARCZYK et al. 2001). *Acyrtosiphon pisum* did not develop well on burclover with a high level of these substances. Covering leaves with wax is another factor that influences the acceptability of a plant as a host (WÓJCICKA et al. 2001). Cultivars of winter triticale heavily coated with wax were not widely accepted by *Sitobion avenae*. The number of aphids on plants is also limited by phenol compounds (CICHOCKA et al. 2000, CHRZANOWSKI et al. 2002). Higher levels of these substances lowered the feeding preferences of *A. fabae* in the case of broad beans, and could enhance resistance of winter triticale against *S. avenae* (CIEPIELA et al. 2000). GOLAN (2013) studied the influence of *Coccus heperidum* LINNAEUS 1758 on three host plants – *Citrus limon* (LINNAEUS, 1753) BURMAN, 1768, *Ficus benjamina* LINNAEUS, 1767, and *Nephrolepis biserrata* (SWARTZ, 1800) SCHOTT, 1834. *Coccus heperidum* was the most abundant on

Citrus limon, but in the free-choice test *Ficus benjamina* was chosen by mobile individuals of *Coccus heperidum* as a host plant. Leaves of *Ficus benjamina* contained the highest amounts of sugars and protein nitrogen, while *Nephrolepis biserrata* contained the highest levels of essential and non-essential amino acids.

Virus infections that induce physiological changes in wheat tissues can increase the nutritional value of plants, thus increasing the number of aphids (FERERES et al. 1990, CIEPIELA et al. 1998). Pesticides (herbicides and insecticides) that can change the quality of proteins or influence the metabolism of the host plants may aid the development of the cereal aphid population (ROOT & SKELSEY 1969, SLOSSER 1989, CIEPIELA et al. 2001, 2004). More intense application of nitrogenous fertilizers increased the abundance of whitefly (*Bemisia argentifolii* BELLOWS & PERRING, 1994) on cotton (BI et al. 2001).

THE INFLUENCE OF APHID FEEDING ON PLANT GROWTH AND DEVELOPMENT

The saliva of aphids can block the transfer of sap in sieves and that of water in vessels. Plant cells and nuclei increase in size. Around the stylets one can observe an increase in the number of cells and nucleic acid. Chloroplasts degenerate, and starch is broken down to monosaccharides. It has also been observed that the leaf blade becomes smaller and deformed. Saliva that permeates xylem causes disorders in its differentiation (CICHOCKA 1980). Moreover, aphid saliva contains viruses that can cause viral diseases in plants, including those they do not inhabit. This is possible because in order to find the right host plant winged morphs pierce numerous plants; in doing so they extract viruses and transmit them to other plants. Some aphids can transmit numerous viruses. For instance, *Myzus persicae* (SULZER, 1776) transmits over 100 viruses (CICHOCKA 1980, KATIS et al. 2007).

In order to assess the harmfulness of aphids it is important to determine their impact on plant assimilation and respiration, as well as the components of the dry matter (VICKERMAN & WRATTEN 1979). The substances present in aphid saliva impact on growth and basic life processes, such as photosynthesis, respiration, transpiration and nitrogen metabolism (RABBINGE et al. 1990, KORNATOWSKA & PIETKIEWICZ 1991, SEMPRUCH & CIEPIELA 2001, GOGGIN 2007). CICHOCKA et al. (1992) studied the influence of seven aphid species on the photosynthesis, respiration and transpiration of their host plants. They came to the conclusion that these responses depended on the aphid and plant species. After longer feeding periods the rate of photosynthesis always decreased, whereas respiration decreased in some plants and increased in others. The same was observed in relation to transpiration. As a result of aphid feeding, cereal ears receive fewer photosynthesis products, which affects the yield and quality of the plants (RABBINGE et al. 1990). The number of seeds in an ear and their mass were both found to decrease. The majority of the examined types of wheat showed lower levels of germination energy and force in seeds originating from plants inhabited by aphids (KORNATOWSKA 1994). The feeding of *Sitobion avenae* causes an increase in nitrogen transfer into the ears, where it is extracted by aphids (JAHN & MERBACH 1984). In the seeds of wheat infested by *S. avenae* the amounts of amino acids such as aspartic and glutamic acids, methionine and arginine were lower than in the control sample (ZWOLIŃSKA-ŚNIATAŁOWA et al. 1989). SPRAWKA et al. (2003) showed that the feeding of *S. avenae* on the ears of spring triticale caused a decrease in the content of essential amino acids.

Indirect harmfulness includes the excretion of large amounts of honeydew by Sternorrhyncha. This was found to contain glucose, sucrose, fructose, maltose, trehalose, mannitol, arabinose, as well as dextrins and small amounts of amino acids (WOOL et al. 2006, GOLAN & NAJDA 2011). The amount of excreted honeydew depends on the aphid species and the quality of extracted food matter (AUCLAIR 1984). *Therioaphis trifolii* (MONELL, 1882) produces more honeydew on susceptible plants, than on resistant ones (CICHOCKA & GOSZCZYŃSKI 1986). Differences in the quantity of excreted honeydew and its chemical ingredients in the case of *Sitobion avenae* feeding on various types of winter triticale are also described by CIEPIELA & SEMPRUCH (2000). Honeydew covers the leaves and shoots; assimilation by these organs is thus impaired, especially if saprophytic fungi develop on the honeydew. This also makes it harder for the plant to respire and can cause chlorosis and physiological changes in leaves. Leaves covered in honeydew fall early (CICHOCKA 1984, RABBINGE et al. 1990, ROSSING & VAN DE WIELL 1990, CICHOCKA 2001). Large amounts of honeydew are excreted by *Eucallipterus tiliae* (LINNAEUS, 1758) on lime trees in the years of its large-scale occurrence (CICHOCKA 2001, MACKOŚ-IWASZKO & LUBIARZ 2014). Large amounts of honeydew are also excreted by *Trialeurodes vaporariorum* (WESTWOOD, 1856) on its host plants. However, GOSZCZYŃSKI (1988) claims that the coating of plants by honeydew is just one of the many reasons for the harmfulness of this whitefly species in greenhouse cultivation in Poland.

During spring *Dysaphis crataegi* (KALTENBACH, 1843) causes red protuberances on hawthorn leaves. The assimilation of these leaves was found to be weaker than that of control leaves; the chlorophyll content was lower as well (GOSZCZYŃSKI 1994). CICHOCKA (1984) reports that *Pemphigus bursarius* caused a threefold decrease in the intensity of photosynthesis in the leaves of cottonwood. This species decreased the mass of lettuce heads in direct proportion to the number of aphids on the plant's roots (CICHOCKA & GOSZCZYŃSKI 1992). The dry matter content of the leaves of this lettuce also decreased, with a consequent reduction in sugars and vitamin C, and an increase in nitrogen, protein and chlorophyll contents. The tap roots of carrots infested by *Pemphigus phenax* (BÖRNER & BLUNK 1916) exhibited a decrease in reducing sugars, as well as an increase in the amount of proteins and β-carotene. The leaves of cottonwood that had galls of both these *Pemphigus* HARTIG, 1839 species, displayed the greatest decrease in chlorophyll content (CICHOCKA & GOSZCZYŃSKI 1992). *Cavariella aegopodii* (SCOPOLI, 1763) feeding on dill reduced the rate of photosynthesis by about 40%, while simultaneously increasing the rate of respiration (CICHOCKA 1992). The feeding of *Macrosiphoniella sanborni* (GILLETTE, 1908) decreased the rate of photosynthesis in only some chrysanthemum cultivars, but respiration neither increased nor decreased. The chlorophyll content in some varieties was lower, some did not react to aphid feeding while in others the content was slightly higher (CICHOCKA 1992). SYTYKIEWICZ et al. (2013) demonstrated loss of chlorophyll in maize seedlings infested by *Rhopalosiphum padi* (LINNAEUS, 1758) and *Sitobion avenae*. The feeding of *Coccus heperidum* caused an increase in the sugar concentration of leaves of *Citris limon*, *Ficus benjamina* and *Nephrolepis biserrata*, and a decrease in the contents of other primary metabolites (GOLAN 2013). GOSZCZYŃSKI (1988, 1992) studied the influence of *Trialeurodes vaporariorum* on tomatoes and cucumbers, the latter proving to be more susceptible than the former. Ingredients of whitefly saliva caused physiological changes to photosynthesis and respiration, as well as to the amounts of some substances in leaves. TOMCZYK & GOSZCZYŃSKI (1996) observed a negative influence of *Hyperomyzus lactucae* (LINNAEUS, 1758) on photosynthesis, growth and yield in blackcurrants, and there were higher amounts of reducing sugars and phenol compounds in the leaves and fruit of this plant.

Aphid feeding influences the activity of enzymes (SEMPRUCH & CIEPIELA 2001, CHRZANOWSKI et al. 2003, CIEPIELA et al. 2005, SEMPRUCH et al. 2009). *Rhopalosiphum padi* feeding increases the activity of chlorophyllase and Mg-dechelatase in the leaves of bird cherry. In the places where aphids were numerous the leaves were discoloured yellow or light green (CIEPIELA et al. 2005). *Sitobion avenae* feeding induced fluctuations of tyrosine decarboxylase in the winter triticale Tornado cv. Furthermore, changes in this enzyme’s activity were of a systemic character (SEMPRUCH et al. 2009). The feeding of *S. avenae* also reduced polyphenoloxidase activity in the ears of spring wheat and triticale (CHRZANOWSKI et al. 2003). SEMPRUCH et al. (2008a, 2008b) demonstrated the influence of grain aphid feeding on the activity of ornithine decarboxylase and arginase in two cultivars of winter triticale.

CONCLUSIONS

Mutual interactions between piercing–sucking insects and their host plants are a vast subject, so this paper has focused only on some of the most important issues. The manner in which aphids penetrate plant tissues, as well as the influence on host plants of the saliva they produce are discussed. Other issues addressed include the changes (mainly decreases) in the quality of plants infested by aphids and other representatives of the Sternorrhyncha suborder. To conclude, the most important consequences of aphid feeding include:

1. deformation of tissues, which the aphid mouthparts pierce during feeding,
2. disorders of plant metabolism:
   – impaired plant growth,
   – disorders in plant development, evidenced by weaker blooming, or weaker germination energy in seeds that originated from plants infested by aphids,
   – decreases in the rate of photosynthesis and respiration of infested plants,
   – blocked sap transfer in sieves, and water transfer in vessels,
3. by coating plant organs, the honeydew excreted by piercing-sucking insects also affects the metabolism and development of the infested plants,
4. changes (increase or decrease) in the amounts of various substances (e.g. sugars, amino acids, proteins, phenol compounds) in plant tissues caused by aphid feeding,
5. introduction of viruses with aphid saliva into plants, which can cause viral diseases in them.

Therefore, the most important consequence of aphid feeding is decreased yield quality. The feeding of piercing-sucking insects leads to dieback of entire herbaceous plants or some parts (organs) in the case of trees and shrubs. This, in turn, causes yield losses during the time when numerous colonies of aphids attack herbs as wells as cultivated and decorative plants. This also leads to financial losses.

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