Journal of Central European Green Innovation 12(3), 20–37. (2024) DOI: 10.33038/jcegi.6438

THE EFFECT OF THE NITROGEN FERTILISATION ON THE SAP-SUCKING HERBIVOROUS INSECTS (INSECTA, HEMIPTERA) AND ON THE HOST PLANT TOLERANCE – A REVIEW
I: CORRELATION AND EXPLANATIONS

A NITROGÉN TÁPANYAGUTÁNPÓTLÁS HATÁSA A SZIPÓKÁS FITOFÁG ROVAROKRA (INSECTA, HEMIPTERA) ÉS A GAZDANÖVÉNY TOLERANCIÁJÁRA – ÁTTEKINTÉS
I: KORRELÁCIÓ ÉS MAGYARÁZATOK

ZSOLT GIDÓ – ÉVA LEHOCZKY
gido.zsolt@uni-mate.hu

Abstract

In this article the available information on the effects of host plant's nitrogen fertilisation on the preference/performance of the sap-sucking insects (Hemiptera) and on host plants tolerance is reviewed. There is a very strong general tendency that nitrogen fertilisation increases the preference/performance of the sap sucking insects. Important exceptions are known, when the excessive nitrogen fertilisation decreases the preference/performance of the hemipteran herbivores. Host plant tolerance usually improves with nitrogen fertilisation: exceptions are known when the herbivore is very efficient in exploiting the host plants nitrogen content. Relationship is affected by the host plants and herbivore's genotype and by the type and the mode of application of the fertiliser. Direct underlining causes are complex and still not entirely known. Nitrogen fertilisation can affect the herbivore through changing the concentrations and ratios of the available nutrients in the plants and/or changing the concentrations of the host plant's defensive chemicals.

Keywords: *host plants, nutrients, tolerance, nitrogen fertilization, agriculture*

Összefoglalás

Írásunkban áttekintjük a nitrogén tápanyagutánpótlás hatását a fitofág szipókás rovarok (Hemiptera) preferenciájára/performanciájára és a gazdanövény toleranciájára a szakirodalmi források alapján. Az esetek döntő többségében erős pozitív korreláció állapítható meg a szipókás rovarok preferenciája/performanciája és a nitrogén tápanyagutánpótlás között. Ismertek fontos kivételek, amikor a szipókás rovarok preferenciája/performanciája csökken a nitrogén utánpótlás hatására. A gazdanövény toleranciája általában növekszik a nitrogén utánpótlás hatására: kivéve amikor a rovar nagyon hatékonyan hasznosítja a gazdanövény N-tartalmát. Az ok-okozati összefüggések összetettek és csak részben ismertek. A nitrogén tápanyag utánpótlás a növény tápanyag összetételének, valamint a rovar számára toxikus anyagok koncentrációjának a megváltoztatásával is befolyásolni tudja a fogyasztó rovar preferenciáját/performanciáját.

Kulcsszavak: *gazdanövények, tápanyagok, tolerancia, nitrogén műtrágyázás, mezőgazdaság*

Introduction

The extensive use of the concentrated inorganic fertilisers is an essential feature of intensive agricultural production. Despite the increasing availability of alternative nutrient replenishment technologies and soil-conserving farming methods to maintain and improve soil fertility the application of various mineral fertilisers is still a significant practice to ensure adequate food production. Unfortunately, extensive fertilisation has undesirable side effects (PRETTL et al., 2024). Apart from acidification and significant structural degradation of the soil one of the most significant is that promotes the reproduction of certain insect pests. For example, outbreaks of the brown planthopper (*Nilaparvata lugens*) in tropical Asia were first noted at the beginning of the Green Revolution (late 1960s–early 1970s) and had been associated with modern varieties of fertilizer and pesticides (BOTTRELL – SCHOENLY, 2012). *N. lugens* is one of the most serious pests of the rice (BOTTRELL – SCHOENLY, 2012).

This short review article summarises the known effects of nitrogen fertilisation on the preference/performance of the sap-sucking insects (Hemiptera) and on the tolerance of the host plants. In this first part the fact of the correlation is documented, and the underlining causes are briefly discussed. Interactions between nitrogen and the other plant macronutrients, tritrophic and community level effects and practical agricultural implications will be discussed in the second part of this article.

The mainstream: positive effects of the host plant's nitrogen fertilisation on the preference/performance of the heteropteran herbivores

Studies which found positive or neutral effects of the host plant's nitrogen fertilisation on the preference/performance of the heteropteran herbivores are summarised in Table 1. "Performance" of the insects has been characterised in numerous articles with different parameters: abundance, biomass, individual size, fertility, duration of the development, population growth, maximum reproductive rate (r_{max}), mortality and longevity. While usually these are strongly correlated, they are not equivalent, and they should be examined separately in a more detailed analysis. This distinction, however is beyond the scope of this short review, so here all the performance indicators are pooled together with the preference choices as "preference/performance".

Table 1: Studies which found positive (+) or neutral effect (0) of the host plant's nitrogen fertilisation on the preference/performance of the heteropteran herbivores

Insect species	Host plant	Effect	Reference(s)
Heteroptera			
Miridae			
Lygus lineolaris (Palisot de Beauvois, 1818)	*Artemisia ludoviciana* Nutt.	+	STRAUSS (1987)
Tingidae			
Stephanitis pyrioides (Scott, 1864)	*Rhododendron* spp.	0	CASEY & RAUPP (1999)
Auchenorrhyncha			
Cicadellidae			
Amrasca biguttula (Ishida, 1913)	*Abelmoschus esculentus* (L.)	+	BISWAS et al. (2009)
Empoasca decipiens Paoli, 1930	*Beta vulgaris* L. var. *saccharifera*	+	GHORBANI et al. (2010)

Delphacidae			
Peregrinus maidis (Ashmead, 1890)	*Zea mays* L.	+	WANG et. al. (2006)
Prokelsia marginata (Van Duzee, 1897)	*Sporobolus alternifolius* P.M. Peterson & Saarela	+	BOWDISH – STILLING (1998)
Sogatella furcifera (Horváth, 1998)	*Oryza sativa* L.	+	LI et al. (2021); HORGAN (2018); HORGAN et al. (2016, 2022, 2024) PENALVEZ-CRUZ & HORGAN (2022)
Nilaparvata lugens (Stål, 1854)	*Oryza sativa* L.	+	BOTTREL & SCHOENLY (2012); HORGAN (2018); HORGAN et al. (2022, 2024), LU et al. (2004, 2005, 2007); PRASAD et al. (2003); PREAP et al. (2001); RASHID et al. (2017 a,b); WANG et al. (2006)
Sternorrhyncha			
Psyllidae			
Cacopsylla pyricola (Foerster, 1848)	*Pyrus communis* L.	+	DAUGHERTY et al. (2007)
Aleyrodoidae			
Trialeurodes vaporarium Westwood, 1856	*Solanum lycopersicum* L. *Gerbera jamesonii* Bolus	+	JAUSET et al. (1998) ORTEGA-ARENAS et al. (2008)
Bemisia tabaci (Gennadius,1889)	*Gossypium hirsutum* L. *Euphorbia pulcherrima* Willd *Solanum lycopersicum* L.	+	BENTZ et al. (1995); BI et al. (2001, 2003); ISLAM et al. (2017); SALEH et al. (2016); BISWAS et al. (2009)
Pseudococcidae			
Saccharicoccus sacchari (Cockerell, 1895)	*Saccharum officinarum* L.	0/+	RAE & JONES (1992)
Planococcus citri Risso, 1813	*Theobroma cacao* L. *Coleus scutellaroides* (L.), *Vitis vinifera* L.	0/+	FENNAH (1959), HOGENDORP et al. (2006) COCCO et al. (2013)
Planococcus ficus (Signoret, 1875)	*Vitis vinifera L.*		COCCO et al. (2013, 2014)
Phenacoccus solenopsis Tinsley, 1898	*Zea mays* L.	+	BAKRY et al. (2023)
Phenacoccus manihoti Matile-Ferrero, 1977	*Manihot esculenta* Crantz	+	TRAN et al. (2020)
Ferrisia virgata (Cockerell, 1893)	*Gossypium hirsutum* L.	+	OLIVEIRA et al. (2014)

Coccidae			
Coccus viridis (Green, 1889)	*Coffea arabica* L.	+	FERNANDES et al. (2012)
Diaspididae			
Lepidosaphes beckii (Newman, 1869)	*Citrus sinensis* L.	+	SALAMA et al. (1972)
Fiorinia externa Ferris, 1942	*Tsuga canadiensis* L.	+	MCCLURE (1980)
Rhizaspidiotus donacis (Leonardi, 1920)	*Arudo donax* L.	+	MORAN & GOOLSBY (2011)
Aphididae			
Aphis gossyphii Glover, 1877	*Gossyphium hirsutum* L. *Dendranthema grandiflora* (Tzvelev) *Chrysanthemum indicum* L. *Cucumis sativus* L.	+	CISNEROS & GODFREY (2001); CHAU et al. (2005); NEVO & COLL (2001); ROSTRAMI et al. (2012); SLOSSER et al. (1997); SALEH et al. (2016); PETITT et al. (1994); HOSSEINI et al. (2010)
Aphis nerii Fonscolombe, 1841	*Asclepias tuberosa* L.	+	ZEHNDER & HUNTER (2008)
Aphis glycines Matsamura, 1917	*Glycine max* (L.)	+	NOMA et al. (2010)
Schizolachnus pineti (Fabrizius, 1781)	*Pinus sylvestris* L.	+	KAINULAINEN et al. (1996)
Macrosiphum euphorbiae (Thomas, 1878)	*Petunia auxillaris hybrida* Villm.	+	JANSSON & EKBOM (2002)
Toxoptera aurantii (Boyer de Fonscolombe, 1841)	*Camellia sinensis* (L.)	+	POKHAREL et al. (2012)
Uroleucon tanaceti (Linnaeus, 1758)	*Tanacetum vulgare* L.	+	NOWAK & KOMOR (2010)
Macrosiphoniella tanacetaria (Kaltenbach, 1843)	*Tanacetum vulgare* L.	+	NOWAK & KOMOR (2010)
Myzus persicae (Sulzer, 1776)	*Capsicum annuum* L.	+	PETITT et. al. (1994)
Brevicoryne brassicae (Linnaeus, 1758)	*Brassica napus* L. *Brassica oleracea* L.	0/+	KOTLINSKI (2011); VAN EMDEN (1966); VAN EMDEN & BASHFORD (1971); ZARGHAMI et al., (2010);
Lipaphis erysimi (Kaltenbach, 1843)	*Sinapis alba* L. *Brassica campestris* L.	+	PANDEY, 2010; SINHA et al. (2018); RAM & GUPTA (2008);
Sipha flava (Forbes, 1885)	*Cenchrus clandestinus* (Hochst. ex Chiov.)	+	MIYASAKA et al. (2007)
Acyrthosiphon pisum	*Medicago truncatula*	0/+	GAO et al. (2018)

Harris, 1776	Gaertn.		
Hysteroneura setariae (Thomas, 1878)	*Oryza sativa* L.	+	JAHN et al. (2005)
Rhophalosiphum padi (Linnaeus, 1758)	*Hordeum vulgare* L.	+	PONDER et al. (2000); AQUEEL & LEATHER (2011)
Schizaphis graminum (Rodani, 1852)	*Triticum aestivum* L. *Hordeum spontane* C. Koch	0/+	ALASVAND ZARASVAND et al. (2013); ELBERSE et al. (2004);
Metopolophium dirhodum (Walker, 1849)	*Triticum aestivum* L.	+	DUFFIELD et al. (2008); HONEK (1991); GASH et al. (1996)
Sitobion avenae (Fabrizius,1781)	*Triticum aestivum* L. *Hordeum vulgare* L.	0/+	HONEK (1991); GASH et al. (1996); AQUEEL & LEATHER (2011)
Diuraphis noxia Kurdjamov, 1913	*Triticum aestivum* L.	0	MOON et al. (1995); ARCHER et al. (1995);
Capitophorus hippophaes (Walker, 1852)	*Polygonum pennsylvanicum* L.	0	MABRY et al. (1997)

As it clearly can be seen from Table 1. (especially, when compared with Table 2.) in the great majority of the cases a positive correlation has been found between the nitrogen fertilisation of the host plant and the preference/performance of the heteropteran herbivores**.** The relationship is affected by the host plant species and cultivar (KAZEMI & VAN EMDEN, 1992; BETHKE et al., 1998; PREAP et al., 2001; AQUEEL et al., 2011; HORGAN et al. 2016; 2021) by the insect species and genotype (GAO et al., 2018), by the fertiliser type and the mode of cultivation (KOTLINSKI, 2011). Moreover, even parental feeding on N-fertilised plants has been proven to positively influence the growth of aphid offspring (intergenerational effect, JAHN et al., 2005).

Sap-sucking insects are usually considered as nitrogen-limited due to the high C/N (sugar/amino-acid) ratios of the phloem sap (MATTSON, 1980). The most frequently applied explanation to the improved preference/performance of sap-sucking insects on N-fertilized plants is the increase of foliar N level/soluble protein level correlated with the increase of free amino acid and soluble protein concentration in the phloem sap available for the insects (WHITE, 1993; HOLOPAINEN et al., 1995; GAO et al., 2018, PETITT et al, 1994). Usually sap-sucking herbivores can also identify the plants with better nitrogen supply. For example, the amino-acid asparagine is known to be a phagostimulant for the brown planthopper (*Nilaparvata lugens*) (SOGAWA, 1974). The concentrations of asparagine and glutamine are known to increase in the phloem sap when the plants are well supplied with nitrogen (VAN EMDEN & BASHFORD, 1971). KAZEMI & VAN EMDEN (1992) found that the concentration of the amino acids' alanine histidine and threonine in different wheat cultivars accounted for over 95% of the variation of the aphid species *Rhopalosiphum padi*. However, as the authors underlined that doesn't necessarily mean causal relationship.

For some (rare but important) exceptions see the next chapter. The article of BI et al. (2003) holds special interest: although the silverleaf whitefly (*Bemiscia tabasci,* Hemiptera, Aleyrodidae) gave the usual positive numerical response to the nitrogen fertilisation of the cotton (*Gossyphium hirsutum*) plants, their reaction was not related to the total amino acid and soluble protein concentrations available in the phloem sap. The authors do not provide an explanation but suggest a more complex relation between the effect of nitrogen fertilization and sap-sucking insect's preference/performance.

Nitrogen fertilisation can also affect the sap-sucking insect's preference/performance by altering the concentrations of the plant's defensive compounds. It is generally held that because the phloem sap is usually poor in secondary metabolites, sap-feeding insects are less exposed to the host plants's secondary metabolites than members of the other feeding guilds (RAVEN, 1983; HUBERTY & DENNO, 2004). In reality there are some data indicating that they cannot always avoid ingesting some secondary metabolites. BRIDGES et al. (2002) showed that while the generalist aphid species *Myzus persicae* sequesters the glycosinolates into the honeydew when feeding on Brassicaceae, the specialist aphid species *Brevicornis brassicae* and *Lipaphis erysimi* accumulate the glucosinolates into their own tissues, which probably contribute to the alarm signaling to the insect in the case of injury. Another research found no significant difference between the performance of *Brevicornis brassicae* and *Myzus persicae* feeding on mustard (*Sinapis alba*) varieties with low and high glucosinolate levels. However, the specialist *B. brassicae* utilised the apical part of the mustard plants where both nutrient and glucosinolate levels are high, while the generalist *M. persicae* preferred the lower, older leaves with lower nutrient and glucosinolate levels (HOPKINS et al., 1998). In general, one can assume that while the glucosinolates are effective in preventing many generalist herbivores to feed on Brassicaceae, they are less effective against of the specialists and even against some well adapted polyphagous species (like *M. persicae*). Moreover, plant taxon specific secondary metabolites often act as phagostimulants for some of the specialist herbivores (e.g. glucosinolates for *B.brassicae)* (COLE, 1997).

However, there are some indications, that plant's secondary metabolites still have a negative effect on some sap-sucking insect's performance. Gramine, an indol alkaloid known from barley (*Hordeum vulgare* L.) and some other grass species is known to have deterrent and toxic effect on aphids, when it is added to their artificial diets in concentrations comparable to those of the host plant tissues (CORCUERA, 1993; VELOZO et al., 1999). Gramine is absent in the phloem sap and the aphid species *Schizaphis graminum* and *Rophalosiphum padi* are known to avoid gramine ingestion by feeding exclusively from the phloem sap on the barley varieties with high gramine content (CORCUERA, 1993), but the susceptibility of different barley cultivars to the aphids is inversely correlated with their gramine content (VELOZO et al., 1999). Gramine most probably has a phagodeterrent effect on these aphids.

COLE (1977) pointed to that the host plant's glucosinolate profile has strong effect both on the performance of a specialist (*B. brassicae*) and a generalist (*Myzus persicae*) aphid species, affecting the host plant suitability in both intra-and interspecific levels.

One might expect that the concentration of the defensive phytochemicals – at least in the case of N-containing substances (alkaloids, glucosinolates, cyanogen glucosides, hydroxamic acids) - is positively correlated with N fertilisation. In some cases, like that of the gramine in barley seedlings (SALAS et al., 1990) it is so. However, more often the case is quite the opposite: nitrogen fertilisation decreases the concentration of the defensive phytochemicals (MATTSON, 1980; HOLOPAINEN et al.1995; KYTO et al., 1996; HERMS, 2002; FERNANDES et al. 2012). The most plausible explanation of this apparent paradox is the growth/differentiation balance hypothesis (HERMS & MATTSON, 1992). In nutrient poor environments the plants are unable to develop fast, so they are exposed for a long time to the herbivores, and they are unable to compensate the losses due to herbivory (low tolerance); therefore, they must invest in defensive allelochemicals (high resistance). Nitrogen fertilization shifts the balance towards high-tolerance and low resistance favouring rapid growth instead of the production of defensive allelochemicals. In other words: generally, the nitrogen fertilisation reduces host plant resistance and increases host plant tolerance to herbivorous insects (HORGAN et al., 2024). Further discussion on the host plant's tolerance is presented below. For the limits of the applicability of the growth/differentiation balance hypothesis see ELBERSE et al. (2004). POKHAREL et al. (2022) also present a more complex system, including aphid induced changes in the relationship between the nitrogen fertilization and secondary metabolite production of tea (*Camellia sinensis*) plants.

In conclusion: In most cases nitrogen fertilisation improves the nutritional quality of the host plants and at the same time it may decrease the level of the protective allelochemicals. Considering these synergistic effects, it is understandable why the great majority of the research articles found a positive correlation between nitrogen fertilisation and sap-sucking insect's performance.

In comparison to other herbivorous insects, hemipterans are considered to be more responsive to the host plants nitrogen fertilisation than the members of the other feeding guilds (BUTLER et al. 2012). However, the positive response is general among all the herbivorous insects and the differences between the feeding guilds are not large (CORNELISSEN - STILLING, 2006).

The exceptions: where the nitrogen fertilisation has negative or ambivalent effects on sap-sucking insect's preference/performance.

Studies which found negative or ambivalent effect of the host plant's nitrogen fertilisation on the preference/performance of the heteropteran herbivores are summarised in Table 2.

Table 2: Studies which found negative or ambivalent effect of the host plant's nitrogen fertilisation on the preference/performance of the heteropteran herbivores

Insect species	**Host plant**	**Reference(s)**
Diaspididae		
Aonidiella aurantii (Maskell, 1879)	*Citrus sinensis* L.	SALAMA et al. (1972)
Aphididae		
Aphis gossyphii Glover, 1877	*Dendranthema grandiflora* Tzvelev *Gossyphium hirsutum* L.	BETHKE et al. (1998); GUO et al. (2024)
Aphis nerii Fonscolombe, 1841	*Asclepias syriaca* L.	ZEHNDER & HUNTER (2009)
Myzus persicae (Sulzer, 1776)	*Brassica oleracea* L. *Solanum tuberosum* L. *Prunus persica* L.	VAN EMDEN (1966); VAN EMDEN & BASHFORD (1971); JANSSON & SMILOWITZ (2005); SAUGE et al. (2010);
Sitobion avenae (Fabrizius,1781)	*Triticum aestivum* L.	DUFFIELD et al. (2008)
Metopolophium dirhodum (Walker, 1849)	*Triticum aestivum* L.	GASH et al. (2012)
Schizaphis graminum (Rodani, 1852)	*Hordeum vulgare L.*	SALAS et al. (1990)

Considering the almost universal positive effect of the nitrogen fertilization on the sap-sucking herbivores, exceptions hold special interest. The few papers which found negative or ambivalent effect of nitrogen fertilisation to sap-sucking insects are summarised in Table 2.

None of these studies provides a confident explanation of their result, although most of them suggest some hypotheses. CASEY and RAUP (1999) found no effect of nitrogen fertilisation on Azalea lace bugs (*Stephanitis pyrioides*) (Table 1) and concluded that the mesophyll feeding species might be much less affected than the phloem feeders (hoppers, aphids, whiteflies, coccids).

Diuraphis noxia and *Schizaphis graminum* are very virulent, phytotoxic aphid species capable to enhance the host plant's nutritional quality due to their feeding (SANDSTÖRM et al. 2000), so they seem to be able to exploit very efficiently even the nitrogen deficient plants. None of the three research papers known by the authors (see Table 1.) found any effect of the nitrogen fertilization on *D. noxia*, while in the case of *S. graminum* positive, negative and zero effects all have been detected in the different studies. The possible negative effect of the gramine in the case of *S. graminum* feeding on barley seedlings has been already discussed. In this experiment the direct toxicity of the plant's high inorganic nitrate concentration has been also suggested by the authors (SALAS et al. 1990). As in this experiment the fertiliser was potassium nitrate, the effect of potassium fertilisation probably contributed to the negative effect. Potassium fertilisation of the host plants is widely known to reduce the preference/performance of the sap-sucking herbivores (see the review of SINGH & SOOD, 2017).

There are some data that the host plant's nutritive quality decreases with the excessive nitrogen overfertilization, which provides a good explanation, why the intermediate fertilization levels are most favourable in some cases to the sap-sucking insects. BETHKE et al. (1998) found that the cotton aphid (*Aphis gossyphii*) performed best on the chrysanthemum plants at the intermediate fertilisation level as these plants had the highest foliar amino acid and soluble protein levels. In contrast GUO et al. (2024) found that the population growth of the same species was the slowest on the cotton plants which received intermediate N fertilisation, and at the same time these plants showed the highest soluble sugar content. Excess of the sugar or rather the unfavourable C/N (sugar/amino acid) ratio might be indeed unfavourable to sap sucking insects (see also below) and the authors suggest direct causal connection between the two facts. However, caution is needed, as no measurement has been performed on amino acid concentration or profile in this experiment.

The elevated leaf nitrogen content is not always beneficial for the sap-sucking insects (MABRY et al. 1997). The most interesting question which certainly merits further research is, if the extremely low C/N (sugar/amino acid) ratios in the phloem sap can be directly disadvantageous to the sap sucking insects. Usually the sap-sucking insects face the opposite problem: they need to cope with the too high C/N ratio of the phloem sap (see above). N-limitation is very common among the herbivorous animals (WHITE, 1993) but it is by no means universal. LE GALL et al. (2020) found that the low C/N ratio of the food is disadvantageous for the female locusts. The question remains open whether this also occurs at some hemipteran insects. For example, if the food uptake of the sap-sucking insect is determined by the amount of the ingested amino acids, then the insect might stop feeding before the ingestion of the proper amount of carbohydrates. High carbohydrate/amino acid ratios are required for the animals which consume much energy (like large, flying locusts): this is certainly not the case of the aphids (apart for the alates), mealybugs and coccids. Nevertheless, some studies (JANSSON & SMILOWITZ, 1986; ZEHNDER & HUNTER, 2009; SAUGE et al., 2010; GASH, 2012) found that the preference/performance of some aphid species initially increased with the nitrogen fertilisation and plant nitrogen levels but declined after reaching the optimal level (which is usually a high value). Some of these authors (ZEHNDER & HUNTER, 2009; GASH, 2012) suggest that this might be the consequence of the unbalanced diet (too low C/N ratio) at high fertilisation level.

The effect of the fertilisation on the plant's protective secondary metabolites and their possible effect on sap sucking insects also need to be taken into consideration (see above).

In conclusion: Although they don't invalidate the very strong general tendency these exceptions reveal the complex nature of the effects of the nitrogen fertilization on sap sucking insects and hopefully inspire further research for deeper and more thorough understanding these processes.

Compensation/tolerance

Tolerance of the plants to herbivores can be defined as the ability of the plant to "reduce the negative effects of herbivory on plant fitness after herbivory has occurred, all the while maintaining insect populations similar to those seen on susceptible plants" (KOCH et al., 2016). Tolerance is often mentioned in the literature as "compensation". Five basic insect induced plant compensatory mechanisms are known: increased photosynthetic activity, increased net growth, increased branching or tillering, pre-existing nutrient storages inaccessible to the insect and the ability of nutrient allocation (STRAUSS & AGRAWAL, 1999; KOCH et al., 2016). One might wonder if some plants might be able to increase the nutrient uptake level from the soil as a compensatory response to herbivory, but the sporadic empirical research on this topic suggests quite the contrary (KATAYAMA et al., 2014; WU et al., 2013). In the case of sap-sucking hemipterans the following compensatory responses have been documented: the increased photosynthetic activity and the up-regulation of detoxification mechanisms (references in KOCH et al., 2016), tillering and resource allocation. RUBIA-SANCHEZ et al. (1999) reported that the presence of tillers reduces the deleterious effects of the brown planthopper (*Nilaparvata lugens*) on the main shoot of the rice plants by allocation of the assimilates from the tiller to the main shoot. According to the field observations of the present authors, the shoot senescence induced by the mass feeding of the blissid bug *Ischnodemus sabuleti* (Heteroptera, Blissidae) probably induces increased tillering on the mannagrass (*Glyceria maxima*), however this still needs confirmation with quantitative data (GIDÓ & LEHOCZKY, unpublished).

Compensation responses of the plants are usually nutrient limited. When nutrients are scarce, plants are unable to compensate for the losses caused by herbivory, but when nutrients are abundant not only total compensation, but even overcompensation (greater primary production in the presence of the herbivory) frequently occurs (MASCHINSKI & WHITHAM, 1989).

HORGAN et al. (2016) measured the tolerance of the rice plants to insect herbivores in insect biomass/plant biomass ("biomass density", mg insect/g plant dry weights). Nitrogen fertilization decreased the biomass density of the less exploitative white backed planthopper (*Sogattella furcifera*), while increased the biomass density of the much more virulent brown planthopper (*Nilaparvata lugens*). Moreover, nitrogen fertilisation decreased the mortality of the young rice plants infested with *S.furcifera*, but increased the mortality induced by *N. lugens*. In the same research nitrogen fertilisation has been found to increase the grain yield tolerance of some rice cultivars to *S. furcifera*, but no such effect was detected on hybrid rice lineages (HORGAN et al., 2016). The different tolerance responses to nitrogen fertilisation of the rice infested with the different planthopper species are probably related to the much higher nitrogen utilization efficiency of *N. lugens* (higher increase of growth and reproduction speed as a response of improved food quality). In a recent article it was demonstrated by the same research group that in the less susceptible rice cultivars nitrogen fertilization also increased the rice plant's tolerance to *N. lugens* (HORGAN et al., 2021). While the performance (and thus the "pressure") of *N. lugens* increased with nitrogen fertilisation also on these tolerant cultivars, at higher nitrogen availability these plants were simply large and fast growing enough to overcome the effects of *N. lugens* feeding.

In practical agriculture host plant tolerance meant that nitrogen fertilization still increases the net crop yield, despite the increased insect pest damage. This is a common case, although exceptions do occur. This topic will be discussed in detail in the second part of this article.

Conclusions

Nitrogen fertilisation usually increases both the host plants' susceptibility and tolerance to their sap-sucker insect herbivores. As discussed in this review, there are some important exceptions from this broadly applicable generalisation. In some cases, higher than optimal nitrogen fertiliser doses can reduce the sap-sucker insect's performance. When the herbivore exploits the host plant's nitrogen very efficiently, like the brown planthopper (*Nilaparvata lugens*) than nitrogen fertilisation can reduce the host plant's tolerance. The underlying causes of these correlations are only partially known, and further research on this topic, including also the "omics" methodology is important both for theoretical and practical (agricultural) reasons.

References

AI, T.C. – LIU, Z.Y. – LI, C.R. – LUO, P. – ZHU, J.Q. (2011): Impact of fertilization on cotton aphid population in Bt. cotton production system. *Ecological Complexity*, 8, 9-14. https://doi.org/10.1016/j.ecocom.2010.08.002

ALASVAND ZARASVAND, A. - ALLAHYARI, H. - FATTAH-HOSSEINI, S. (2013). Effect of nitrogen fertilisation on biology, life table parameters and population abundance of greenbug; *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae). Archives of *Phytopathology and Plant Protection*, 46, 882-889. https://doi.org/10.1080/03235408.2012.749700.

ANUSHA, S. – PRASADA RAO, G.M.V. – SAI RAN KUMAR, D.V. (2017): Effect of different nitrogen doses on sucking pests and yield in Bt cotton under unprotected and protected conditions. *Journal of Entomology and Zoology Studies*, www.entomoljournal.com

AQEEL, M. A. - LEATHER, S. R. (2011): Effect of nitrogen fertilizer on the growth and survival of *Rhopalosiphum padi* (L.) and *Sitobion avenae* (F.) (Homoptera: Aphididae) on different wheat cultivars. *Crop Protection*, 30, 216-221. https://doi.org/10.1016/j.cropro.2010.09.013.

ARCHER, T. - BYNUM, E. - ONKEN, A. - WENDT, C. (1995): Influence of water and nitrogen fertilizer on biology of the Russian wheat aphid (Homoptera: Aphididae) on wheat. *Crop Protection*, 14, 165-169. https://doi.org/10.1016/0261-2194(95)92872-K

BAKRY, M. - MAHARANI, Y. - AL-HOSHANI, N. - El, R. A. (2023): Influence of maize planting methods and nitrogen fertilization rates on mealybug infestations, growth characteristics and eventual yield of maize. *International Journal of Agriculture and Biology*, 29. https://doi.org/401-409. 10.17957/IJAB/15.2046.

BENTZ, J.A. - REEVES, J. – BARBOSA, P. - FRANCIS, B. (1995): Effect of nitrogen fertilizer source and level on ovipositional choice of *Poinsettia* by *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Journal of Economical Entomology*, 88, 1388-1392. https://doi.org/10.1093/jee/88.5.1388

BETHKE, J.A. - REDAK, R.A. - SCHUCH, U.K. (1998): Melon aphid performance on chrysanthemum as mediated by cultivar, and differential levels of fertilization and irrigation. *Entomologia Experimentalis et Applicata*, 88, 41-47. https://doi.org/10.1046/j.1570-7458.1998.00344.x

BI, J.L. - BALLMER, G.R. - HENDRIX, D.L. - HENNEBERRY, T.J. - TOSCANO, N.C., (2001): Effect of cotton nitrogen fertilization on *Bemisia argentifolii* populations and honeydew production. *Entomologia Experimentalis et Applicata*, 99, 25-36. https://doi.org/10.1046/j.1570-7458.2001.00798.x

BI, J.L. - TOSCANO, N.C. & MADORE, M.A. (2003): Effect of urea fertilizer application on soluble protein and free amino acid content of cotton petioles in relation to silverleaf whitefly (*Bemisia argentifolii*) populations. *Journal of Chemical Ecology,* 29, 747-761. https://doi.org/10.1023/A:1022880905834

BISWAS, S. -MAHATO, B. - PANDA, P. - GUHA, S. (2009): Effect of different doses of nitrogen on insect pest attack and yield potentiality of okra, *Abelmonschus esculentus* (L.). *Journal of Entomological Research*, 33, 219-222.

BOTTRELL, D. - SCHOENLY, K. (2012). Resurrecting the ghost of green revolutions past: The brown planthopper as a recurring threat to high-yielding rice production in tropical Asia. *Journal of Asia-Pacific Entomology*, 15, 122–140. https://doi.org/10.1016/j.aspen.2011.09.004.

BOWDISH, T I. - STILLING, P. (1998): The influence of salt and nitrogen on herbivore abundance: direct and indirect effects. *Oecologia*, 113, 400-405. https://doi.org/10.1007/s004420050392

BRIDGES, M. – JONES, A.M. – BONES, A.M. – HODGSON, C. – COLE, R. – BARTLET, E. – WALLSGROVE, R. – KARAPAPA, V.K. – WATTS, N. – ROSSITER, J.T. (2002): Spatial organization of the glucosinolate-myrosinase system in brassica specialist aphids is similar to that of the host plant. *Proceedings of the Royal society B: Biological Sciences* 22, 187-91. https://doi.org/10.1098/rspb.2001.

BUTLER, J. - GARRATT, M.P.D. - LEATHER, S.R. (2012): Fertilisers and insect herbivores: a meta-analysis. *Annals of Applied Biology*, 161, 223-233. https://doi.org/10.1111/j.1744-7348.2012.00567.x

CASEY, C. A. – RAUPP, M. J. (1999): Supplemental nitrogen fertilization of containerized azalea does not affect performance of *Azalea* lace bug. *Environmental Entomology*, 28, 998-1003. https://doi.org/10.1093/ee/28.6.998

CHAU A. - HEINZ K. M. - DAVIES, F. T. (2005): Influences of fertilization on *Aphis gossypii* and insecticide usage. *Journal of Applied Entomology*, 129, 89-97. https://doi.org/10.1111/j.1439-0418.2005.00943.x

CISNEROS, J. J. – GODFREY, L D. (2001): Midseason pest status of the cotton aphid in California cotton: Is nitrogen a key factor? *Environmental Entomology*, 30, 501-510. https://doi.org/10.1603/0046-225X-30.3.501

COCCO, A. - MARRAS, P. - NUVOLI, M. - MAMELI, M. - LENTINI, A. (2013): Preliminary results on the influence of nitrogen fertilization on the development of *Planococcus* citri and *Planococcus ficus* on grapevine. IOBC-WPRS Bulletin. 85. 19-24.

COCCO, A. -MARRAS, P. - MUSCAS, E. -MURA, A. - LENTINI, A. (2014). Variation of life-history parameters of *Planococcus ficus* (Hemiptera: Pseudococcidae) in response to grapevine nitrogen fertilization. *Journal of Applied Entomology*, 139. https://doi.org/10.1111/jen.12192.

COLE, R.A. (1997): The relative importance of glucosinolates and aminoacids to the development of two aphid pests *Brevicoryne brassicae* and *Myzus persicae* on wild and cultivated brassica species. *Entomologia Experimentalis et Applicata*, 85: 121133. https://doi.org/10.1046/j.1570-7458.1997.00242.x

CORCUERA, L.J. (1993): Biochemical basis for the resistance of barley to aphids. *Phytochemistry,* 33, 741–747. https://doi.org/10.1016/0031-9422(93)85267-U

CORNELISSEN, T. – STILING, P. (2006): Responses of different herbivore guilds to nutrient addition and natural enemy exclusion. *Ecoscience*, 13, 66-74. https://doi.org/10.2980/1195-6860(2006)13[66:RODHGT]2.0.CO;2

DAUGHERTY, M.P. - BRIGGS, C.J. - WELTER, S.C. (2007): Bottom-up and top-down control of pear psylla (*Cacopsylla pyricola*): fertilization, plant quality, and the efficacy of the predator *Anthocoris nemoralis*. *Biological Control*, 43, 257-264. https://doi.org/10.1016/j.biocontrol.2007.09.001

DUFFIELD, S.J. - BRYSON, R.J. - YOUNG, J.E.B. - SYLVESTER-BRADLEY, R. -SCOTT, R.K. (1997), The influence of nitrogen fertiliser on the population development of the cereal aphids *Sitobion avenae* (F.) and *Metopolophium dirhodum* (Wlk.) on field grown winter wheat. *Annals of Applied Biology*, 130, 13-26. https://doi.org/10.1111/j.1744-7348.1997.tb05779.x

ELBERSE, I - TURIN, H. & WACKERS, F. - DAMME, J. - TIENDEREN, P. (2004). The relationship between relative growth rate and susceptibility to aphids in wild barley under different nutrient levels. *Oecologia*, 137, 564-71. https://doi.org/10.1007/s00442-003-1383-4.

FENNAH, R.T. (1959): Nutritional factors associated with the development of mealybugs in cacao. *Reports of the Cacao Research Institute Trinidad,* 1957–1958, 18-28.

FERNANDES, F. L. - PICANCO, M. C. - FERNANDES, M.E.S.- QUIEROZ, R. - XAVIER, V. - PRIETO, M. (2012). The effects of nutrients and secondary compounds of *Coffea arabica* on the behaviour and development of *Coccus viridis*. *Environmental Entomology*, 41, 333-41. https://doi.org/10.1603/EN11003.

FLUEGEL, S.M. - JOHNSON, J.B. (2001). The effect of soil nitrogen levels and wheat resistance on the Russian wheat aphid, *Diuraphis noxia* (Homoptera: Aphididae). *Journal of the Kansas Entomological Society*, 74, 49-55.

GAO, J. - GUO, H. - SUN, Y. - GE, F. (2018): Differential accumulation of leucine and methionine in red and green pea aphids leads to different fecundity in response to nitrogen fertilization. *Pest Management Science*, 74, 1779-1789. https://doi.org/10.1002/ps.4875

GASH, A.F. - CARTER, N. - BALE, J.S. (1996): The influence of nitrogen fertiliser applications on the cereal aphids *Metopolophium dirhodum* and *Sitobion avenae.* In *Proceeding of the Brighton Crop Protection Conference, Brighton, UK, 18–21 November 1996; BCPC: Farnham, Surrey, UK, 1996;* pp. 209-214.

GASH, A. (2012). Wheat nitrogen fertilisation effects on the performance of the cereal aphid *Metopolophium dirhodum*. *Agronomy*, 2, 1-13. https://doi.org/10.3390/agronomy2010001.

GHORBANI., R. - MOUSAVI, S.K. - NAZARI, S. - HATAMI, B. (2010) Study of the effect of irrigation and nitrogen fertilizer on sugar beet growth and population dynamism of *Empoasca decipiens* (Hom: Cicadellidae) and *Thrips tabaci* (Thys: Thripidae). *Applied Entomology and Phytopathology* 78, 61-80.

GUO L. – NIU, L. – ZHU, X. – WANG, L. – ZHANG, K. – LI, D. – ELUMALAI, P. – GAO, X. – JI, J. – CUI, J. -LUO, J. (2024): Moderate nitrogen application facilitates Bt cotton growth and suppresses population expansion of aphids (*Aphis gossypii*) by altering plant physiological characteristics. *Frontiers in Plant Science*, 15, 1328759. https://doi.org/10.3389/fpls.2024.1328759

HERMS, D. A. (2002): Effects of fertilization on insect resistance of woody ornamental plants: reassessing an entrenched paradigm. *Environmental Entomology*, 31, 923-933. https://doi.org/10.1603/0046-225X-31.6.923

HERMS, D. A - MATTSON, W.J. (1992): The dilemma of plants: to grow or defend. *Quarterly Review of Biology,* 67, 283-335. https://doi.org/10.1086/417659

HOGENDORP, B. – CLOYD, R.A. – SWIADER, J.M. (2006) Effect of nitrogen fertility on reproduction and development of citrus mealybug, *Planococcus citri* Risso (Homoptera: Pseudococcidae), feeding on two colors of coleus, *Solenostemon scutellarioides* L. Codd. *Environmental Entomology*, 35, 201-211. https://doi.org/10.1603/0046-225X-35.2.201.

HOLOPAINEN, J. K. - RIKALA, R - KAINULAINEN, P. - OKSANEN, J. (1995): Resource partitioning to growth, storage and de fence in nitrogen-fertilized Scots pine and susceptibility of the seedlings to the tarnished plant bug *Lygus rugulipennis*. *New Phytologist*, 131, 521-532. https://doi.org/10.1111/j.1469-8137.1995.tb03088.x

HONEK, A. (1991): Nitrogen fertilization and abundance of the cereal aphids *Metopolophium dirhodum* and *Sitobion avenae* (Homoptera, Aphididae). *Zeitschrift für Pfanzenkrankheiten und Pflanzenschutz*, 98:655-60.

HOPKINS, R.J. - EKBOM, B. - HENKOW, L. (1998): Glucosinolate content and susceptibility for insect attack of three populations of *Sinapis alba*. *Journal of Chemical Ecology,* 24, 1203-1216. https://doi.org/10.1023/A:1022498903175

HORGAN, F. (2018): Integrating gene deployment and crop management for improved rice resistance to Asian planthoppers. *Crop Protection,* 110, 21-33. https://doi.org/10.1016/j.cropro.2018.03.013.

HORGAN, F. - CRISOL-MARTÍNEZ, E. - ALMAZAN, M. L. - ROMENA, A. - RAMAL, A. - FERRATER, J. - BERNAL, C. (2016). Susceptibility and tolerance in hybrid and pure-line rice varieties to herbivore attack: biomass partitioning and resource-based compensation in response to damage: Herbivory on hybrid and pure-line rice. *Annals of Applied Biology*, 169. https://doi.org/10.1111/aab.12296.

HORGAN, F.G. - CRISOL-MARTÍNEZ, E. - STUART, A.M. - VILLEGAS, J.M. - PENALVER-CRUZ, A. - MUNDACA, E.A. - PEREZ, M.O. - BERNAL, C.C. - ALMAZAN, M.L.P. - RAMAL, A.F. (2022): Direct and indirect effects of planting density, nitrogenous fertilizer and host plant resistance on rice herbivores and their natural enemies. *Agriculture,* 12, 2053. https://doi.org/10.3390/agriculture12122053

HORGAN, F.G. - CRUZ, A.P. - BERNAL, C.C. - RAMAL, A.F. - ALMAZAN, M.L. - WILBY, A. (2017): Resistance and tolerance to the brown planthopper, *Nilaparvata lugens* (Stål), in rice infested at different growth stages across a gradient of nitrogen applications. Field Crops Research, 217, 53-65. https://doi.org/10.1016/j.fcr.2017.12.008

HORGAN, F.G. - DE FREITAS, T.F.S. - CRISOL-MARTÍNEZ, E. - MUNDACA, E.A. - BERNAL, C.C. (2021): Nitrogenous fertilizer reduces resistance but enhances tolerance to the brown planthopper in fast-growing, moderately resistant rice. *Insects*, 12, 989. https://doi.org/10.3390/insects12110989.

HOSSEINI, M. - ASHOURI, A. - ENKEGAARD, A. - GOLDANSAZ, S. H. – NASSIRI-MAHALATI, M. – HOSSEININAVEH, V. (2010): Performance and population growth rate of the cotton aphid and associated yield losses in cucumber, under different nitrogen fertilization regimes. *International Journal of Pest Management*, 56, 127-135. https://doi.org/10.1080/09670870903248827

HUBERTY, A.F. -DENNO, R.F. (2004): Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology*, 85, 1383-1398. DOI: https://doi.org/10.1890/03-0352

ISLAM, M.N. – HASSANUZAMAN, A.T. – ZHANG, Z.F. – ZHANG, Y. – LIU, T.X. (2017): High level of nitrogen makes tomato plants releasing less volatiles and attracting more *Bemisia tabaci* (Hemiptera: Aleyrodidae). *Frontiers in Plant Science*, 31, 8, 1-14. https://doi.org/10.3389/fpls.2017.00466.

JAHN, G. C. – ALMAZAN, L. P. – PACIA, J. B. (2005): Effect of nitrogen fertilizer on the intrinsic rate of increase of *Hysteroneura setariae* (Thomas) (Hom. Aphididae) on rice (Oryza sativa L.). *Environmental Entomology*, 34, 938-943. https://doi.org/10.1603/0046-225X-34.4.938

JANSSON, J. - EKBOM, B. (2002): The effect of different plant nutrient regimes on the aphid *Macrosiphum euphorbiae* growing on petunia. *Entomologia Experimentalis et Applicata*, 104, 109-116. https://doi.org/10.1046/j.1570-7458.2002.00997.x

JANSSON, R.K. - SMILOWITZ, Z. (1986): Influence of nitrogen on population parameters of potato insects: abundance, population growth, and within-plant distribution of the green peach aphid, *Myzus persicae*. *Environmental Entomology*, 15, 49-55. https://doi.org/10.1093/ee/15.1.49

JAUSET, A.M. - SARASUA, M. – AVILLA, J. - ALBAJES, R. (1998): The impact of nitrogen fertilization of tomato on feeding site selection and oviposition by *Trialeurodes vaporariorum*. *Entomologia Experimentalis et Applicata.* 86, 175-182. https://doi.org/10.1023/A:1003145813704.

KAINULAINEN, P. – HOLOPAINEN, J. – PALOMAKI, V. – HOLOPAINEN, T (1996): Effects of nitrogen fertilization on secondary chemistry and ectomycorrhizal state of Scots pine seedlings and on growth of grey pine aphid. *Journal of Chemical Ecology*, 22, 617-636. https://doi.org/10.1007/BF02033574

KATAYAMA, N. - SILVA, A.O. - KISHIDA, O. - USHIO, M. - KITA, S. - OHGUSHI, T. (2014): Herbivorous insect decreases plant nutrient uptake: the role of soil nutrient availability and association of below-ground symbionts. *Ecological Entomology*, 39, 511-518. https://doi.org/10.1111/een.12125

KAZEMI, M.H. -VAN EMDEN, H.E. (1992): Partial antibiosis to *Rhopalosiphum padi* in wheat and some phytochemical correlations. *Annals of Applied Biology*, 121, 1-9. https://doi.org/10.1111/een.1212510.1111/j.1744-7348.1992.tb03981.x

KOCH, K.G. – CHAPMAN, K. – LOUIS, J. - HENG-MOSS, T. – SARATH, G. (2016): Plant tolerance: a unique approach to control hemipteran pests. *Frontiers in Plant Science*, 7. https://doi.org/10.3389/fpls.2016.01363

KOTLINSKI, S. (2011): Influence of nitrogen fertilization of cabbage grown in mulches of winter cover crops on reducing the population of the cabbage aphid (*Brevicoryne brassicae* L.). *Journal of Fruit and Ornamental Plant Research*, 74, 87-96. https://doi.org/10.2478/v10032-011-0007-5

KYTO, M. - NIEMELA, P. - LARSSON, S. (1996): Insects on trees: population and individual response to fertilization. *Oikos*, 75, 148-159. https://doi.org/10.2307/3546238

LE GALL, M. – WORD, M.L. – THOMPSON, N. – BEYE, A. – CEASE, A.J. (2020): Nitrogen fertilizer decreases survival and reproduction of female locusts by increasing plant protein to carbohydrate ratio. *Journal of Animal Ecology,* 89, 2214-2221. https://doi.org/10.1111/1365-2656.13288

LI, Z. - XU, B.- DU, T - MA, Y.- TIAN, X. - WANG, F. - WANG, W. (2021): Excessive nitrogen fertilization favors the colonization, survival, and development of *Sogatella furcifera* via bottom-up effects. *Plants*, 10, 875. https://doi.org/10.3390/ plants10050875

LU, Z. - HEONG, K.L. - YU, X. - HU, C. (2004): Effects of plant nitrogen on ecological fitness of the brown planthopper, *Nilaparvata lugens* Stal. in Rice. *Jourmal of Asian Pacific Entomology*, 7, 97-104. https://doi.org/10.1016/S1226-8615(08)60204-6.

LU, Z. - HEONG, K.L. - YU, X. - HU, C. (2005): Effects of nitrogen on the tolerance of brown planthopper, *Nilaparvata lugens*, to adverse environmental factors. Insect Science. 12, 121-128. https://doi.org/10.1111/j.1744-7917.2005.00014.x.

LU, Z. - YU, X. - HEONG, K.L. - HU, C. (2007): Effect of nitrogen fertilizer on herbivores and its stimulation to major insect pests in rice. *Rice Science*, 14, 56-66. https://doi.org/10.1016/S1672-6308(07)60009-2.

MABRY, C.M. – JASIENSKI, M. – COLEMAN, J.S. – BAZZAZ, F.A. (1997): Genotypic variation in *Polygonum pensylvanicum:* nutrient effects on plant growth and aphid infestation. *Canadian Journal of Botany*, 75, 546-551. https://doi.org/10.1139/b97-060

MASCHINSKI, J. - WHITHAM, T. (1989): The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *The American Naturalist*, 134, 1-19. https://doi.org/10.1086/284962.

MATTSON, W.J. (1980): Herbivory in relation to plant nitrogen-content. *Annual Review of Ecology and Systematics*, 11, 119 – 161. https://doi.org/10.1146/annurev.es.11.110180.001003

MCCLURE, M.S. (1980): Foliar nitrogen: a basis for host suitability for elongate hemlock scale, *Fiorinia externa* (Homoptera: Diaspididae). *Ecology*, 61, 72-79. https://doi.org/10.2307/1937157

MEYER, G.A. - ROOT, R.B. (1996), Influence of feeding guild on insect response to host plant fertilization. Ecological Entomology, 21, 270-278. https://doi.org/10.1111/j.1365-2311.1996.tb01244.x

MIYASAKA, S.C. -HANSEN, J.D. - MCDONALD, T.G. - FUKOMOTO, G.K. (2007): Effects of nitrogen and potassium in kikuyu grass on feeding by yellow sugarcane aphid. *Crop Protection*, 26, 511-517. https://doi.org/10.1016/j.cropro.2006.04.023

MOON, C. E. – LEWIS, B. E. – MURRAY, L. – SANDERSON, S. M. (1995): Russian wheat aphid (Hom. Aphididae) development, reproduction, and longevity on hydroponically grown wheat with varying nitrogen rates. *Environmental Entomology*, 24, 367-371. https://doi.org/10.1093/ee/24.2.367

MORAN, P.J. – GOOLSBY, J.A. (2011): Effect of nitrogen addition on population establishment of the arundo armored scale *Rhizaspidiotus donacis*. *XIII International Symposium on Biological Control of Weeds – 2011.*

NEVO, E. - COLL, M. (2001): Effect of nitrogen fertilization on *Aphis gossypii* (Homoptera: Aphididae): variation in size, color and reproduction. *Journal of Economic Entomology*, 94: 27 – 32. https://doi.org/10.1603/0022-0493-94.1.27

NOMA, T. - GRATTON, C. - COLUNGA-GARCIA, M. - BREWER, M.J. - MUELLER, E.E. - WYCKHUYS, K.A. - O'NEAL, M.E. (2010): Relationship of soybean aphid (Hemiptera: Aphididae) to soybean plant nutrients, land scape structure, and natural enemies. *Environmental Entomology*, 39, 31-41. https://doi.org/39. 31-41. 10.1603/EN09073.

NOWAK, H. -KOMOR, E. (2010): How aphids decide what is good for them: Experiments to test aphid feeding behaviour on *Tanacetum vulgare* (l.) using different nitrogen regimes. *Oecologia* 163, 973-984. https://doi.org/10.1007/s00442-010-1652-y

OLIVEIRA, M. - BARBOSA, P. - SILVA-TORRES, C. & SILVA, R. - BARROS, E. (2014): Reproductive performance of striped mealybug *Ferrisia virgata* Cockerell (Hemiptera: Pseudococcidae) on water-stressed cotton plants subjected to nitrogen fertilization. *Arthropod-Plant Interactions*, 8, 461-468. https://doi.org/10.1007/s11829-014-9320-5.

ORTEGA, L. - MIRANDA, D. - SANDOVAL-VILLA, M. (2008): Greenhouse whitefly eggs and nymphs' density on *Gerbera jamesonii* under different nitrogenous fertilizer regimes. *Journal of Insect Science*, 8, 37-37.

PANDEY, A. K. (2010): Effect of nitrogen, phosphorus and potash on mustard aphid and yield attributing characters of mustard in cold arid region (Ladakh). *Indian Journal of Entomology*, 72, 117-121.

PENALVER-CRUZ, A. – HORGAN, F.G. (2022): Interactions between rice resistance to planthoppers and honeydew-related egg parasitism under varying levels of nitrogenous fertilizer. *Insects*. 13, 251. https://doi.org/10.3390/insects13030251

PETITT, F.L. - LOADER, C.A. - SCHON, M.K. (1994): Reduction of nitrogen concentration in the hydroponic solution on population growth rate of the aphids *(Homoptera*: Aphididae) *Aphis gossypii* on cucumber and *Myzus persicae* on pepper. *Environmental Entomology*, 23, 930-936. https://doi.org/10.1093/ee/23.4.930

POKHAREL, S.S. – ZHONG, Y. – CHANGNING, L. – SHEN, F. – LIKUN, L. – PARAJULEE, M.N. – FANG, W. – CHEN, F. (2022): Influence of reduced N-fertilizer application on foliar chemicals and functional qualities of tea plants under *Toxoptera aurantii* infestation. *BMC Plant Biology*, 22, 166. https://doi.org/10.1186/s12870-022-03533-9.

PONDER, K.L. - PRITCHARD, J. - HARRINGTON, R. - BALE, J.S. (2000): Difficulties in location and acceptance of phloem sap in addition to reduced amino acid concentration explain lowered performance of the aphid *Rhopalosiphum padi* on nitrogen deficient barley (*Hordeum* *vulgare*) seedlings. *Entomologia Experimentalis et Applicata,* 97, 203-210. https://doi.org/10.1046/j.1570-7458.2000.00731.x

PRASAD, B.R.- PASALU, I. - RAJU, N. - VERMA, N. (2003): Influence of nitrogen and rice varieties on population build-up of brown planthopper, *Nilaparvata lugens* (Stal.). *Journal of Entomological Research*, 27, 167-170.

PREAP, V. - ZALUCKI, M.P. - NESBITT, H.J. - JAHN, G.C. (2001): Effects of fertilizer, pesticide treatment, and plant variety on the realized fecundity and survival rates of brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae) gener ating outbreaks in Cambodia. *Journal of Asia-Pacific Entomology,* 4, 75-84. https://doi.org/10.1016/S1226-8615(08)60107-7

PRETTL, N. - BIRÓ, B. - NUGROHO, P.A. - KOTROCZÓ, ZS. - SUNDOSS, K. - KOVÁCS, F. - PAPDI, E. - JUHOS, K. (2024): Limited effect of mycorrhizal inoculation depending on soil type and fertilization level in a central European field trial. *Plant Growth Regulation,* 1-13. https://doi.org/10.1007/s10725-024-01251-w

RAE, D.J. - JONES, R.E. (1992): Infuence of host nitrogen levels on development, survival, size and population dynamics of sugar cane mealybug, *Saccharicoccus saccari* (Cockerell) (Homoptera: Pseudococcidae). *Australian Journal of Zoology,* 40, 327-342, https://doi.org/10.1071/ZO9920327

RAM, S. - GUPTA, M. (2008): Effect of nitrogen, phosphorus and potassium on the population of insect pests of fodder mustard (*Brassica campestris* L.) and its seed yield in India. *Tropical Pest Management,* 34, 435-437. https://doi.org/10.1080/09670878809371296.

RASHID, M. D. - JAHAN, M. – ISLAM, K.S. (2016): Impact of nitrogen, phosphorus and potassium on brown planthopper and tolerance of its host rice plants. *Rice Science*, 23, 119-131, https://doi.org/10.1016/j.rsci.2016.04.001.

RASHID, M.D. - JAHAN, M. - ISLAM, K. (2017a). Effects of nitrogen, phosphorous and potassium on host-choice behavior of brown planthopper, *Nilaparvata lugens* (Stål) on rice cultivar. *Journal of Insect Behavior*, 30, 1-15. https://10.1007/s10905-016-9594-9

RASHID, M.D. – JAHAN, M. - ISLAM, K. S. – LATIF, A (2017b): Ecological fitness of brown planthopper, *Nilaparvata lugens* (Stål), to rice nutrient management. *Ecological Processes,* 6, https://doi.org/10.1186/s13717-017-0080-x.

RAVEN, J. A. (1983): Phytophages of xylem and phloem: a comparison of animal and plant sapfeeders. *Advances in Ecological Research*, 13, 135-234. https://doi.org/10.1016/S0065-2504(08)60109-9

ROSTAMI, M. - ZAMANI, A.A. - GOLDASTEH, S. - SHOUSTARI, R.V. - KHERADMAND, K. (2012): Influence of nitrogen fertilization on biology of *Aphis gossypii* (Hemiptera: Aphididae) reared on *Chrysanthemum indicum* (Asteraceae). *Journal of Plant Protection Research*, 52, 118-121. https://doi.org/10.2478/v10045-012-0019-2.

RUBIA-SANCHEZ, E. - SUZUKI, Y. - ARIMURA, K. - MIYAMOTO, K. - MATSUMURA, M. -WATANABE, T. (2003): Comparing *Nilaparvata lugens* (Stal) and *Sogatella furcifera* (Horvath) (Homoptera: Delphacidae) feeding effects on rice plant growth processes at the vegetative stage. *Crop. Protection,* 22, 967-974.

SALAS, M.L. - CORCUERA, L.J. - ARGANDONA, V.H. (1990): Effect of potassium nitrate on gramine content and resistance of barley against the aphid *Schizaphis graminum*. *Phytochemistry*, 29, 3789 -3791. https://doi.org/10.1016/0031-9422(90)85332-A

SALAMA, H.S. - AMIN, A.H. - HAWASH, M. (1972): Effect of nutrients supplied to *Citrus* seedlings on their susceptibility to infestation with the scale insects *Aonidiella aurantii* (Maskell) and *Lepidosaphes beckii* (Newman) (Coccoidea). *Zeitschrift für Angewandte Entomologie*, 71, 395-405. https://doi.org/10.1111/j.1439-0418.1972.tb01766.x

SALEH, A.A. – El-GOHARY, L.R. – HAMED, A.M. – BAZ, R.I. (2016): Effect of nitrogen fertilisation doses of cotton crop insects and their certain associated predators. *Journal of Plant Protection and Pathology*, Mansoura University, 7, 183-191.

SANDSTÖRM, J.P., TELANG, A., MORAN, N.A. (2000): Nutritional enhancement of host plants by aphids – a comparison of three aphid species on grasses. *Journal of Insect Physiology*, 46, 33-40. https://doi.org/10.1016/S0022-1910(99)00098-0

SAUGE, M.H. - GRECHI, I. - POESSEL, J.L. (2010): Nitrogen fertilization effects on *Myzus persicae* aphid dynamics on peach: Vegetative growth allocation or chemical defence? *Entomologia Experimentalis et Applicata* 136, 123-133. https://doi.org/10.1111/j.1570-7458.2010.01008.x

SINGH, V. – SOOD, A.K. (2017): Plant nutrition: a tool for the management of hemipteran insect-pests. A review. *Agricultural Reviews*. 38, 260-270. https://doi.org/10.18805/ag.R-1637

SINHA, R. - SINGH, B - RAI, P.K. - KUMAR, A. - JAMWAL, S. - SINHA, B.K. (2018): Soil fertility management and its impact on mustard aphid, *Lipaphis erysimi* (Kaltenbach) (Hemiptera: Aphididae). *Cogent Food & Agriculture*, 4, 1450941. https://doi.org/10.1080/23311932.2018.1450941

SLOSSER, J.E. - MONTANDON, R. - PINCHAK, W.E. - RUMMEL, D.R. (1997): Cotton aphid response to nitrogen fertility in dryland cotton. *Southwestern Entomologist*. 22, 1e10.

SOGAWA, K. (1974): Studies on the feeding habits of the brown planthopper, *Nilaparvata lugens* (STÅL) (Hemiptera : Delphacidae) : IV. Probing Stimulant. *Applied Entomology and Zoology*, 9, 204-214. https://doi.org/10.1303/aez.9.204

STRAUSS, S.Y. (1987): Direct and indirect effects of host-plant fertilization on an insect community. *Ecology*, 68, 1670–1678. https://doi.org/10.2307/1939859

STRAUSS, S. Y. - AGRAWAL, A. A. (1999): The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution*, 14, 179-185. https://doi.org/10.1016/s0169 5347(98)01576-6

TRAN, D.H. - NGUYEN, T. G. - HOANG, T. N. - TINH, H. - KHAC, P. - NGUYEN, H. L. - HOANG, H. L. - PHUONGH, T. (2020): Effects of nitrogen fertilization on the biology of the cassava pink mealybug *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae). 5, 162 - 166. *International Journal of Entomology Research*, 5, 162-166.

VAN EMDEN, H.F. (1966): Studies on the relations of insect and host plant. III. A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae* (Hemiptera: Aphididae) on Brussels sprout plants supplied with different rates of nitrogen and potassium. *Entomologia Experimentalis et Applicata*, 9, 444-460. https://doi.org/10.1111/j.1570-7458.1966.tb01005.x

VAN EMDEN, H.F. – BASHFORD, M.A. (1971): The performance of *Brevicoryne brassicae* and *Myzus persicae* in relation to plant age and leaf amino acids. *Entomologia Experimentalis et Applicata*, 14, 349-360. https://doi.org/10.1111/j.1570-7458. 1971.tb00172.x

VELOZO, J.A. – ALVAREZ, R.I. – WACHTER, G.A. – TIMMERMANN, B.N. – CORCUERA, L.J. (1999) Increase in gramine content in barley infested by the aphid *Schizaphis graminum*. *Phytochemistry*, 52, 1059-1061. https://doi.org/10.1016/S0031-9422(99)00358-1

WANG, J.-J - TSAI, J. - BROSCHAT, T. (2006): Effect of nitrogen fertilization of corn on the development, survivorship, fecundity and body weight of *Peregrinus maidis* (Hom., Delphacidae). *Journal of Applied Entomology*, 130, 20-25. https://doi.org/10.1111/j.1439-0418.2005.01030.x

WANG, P. - WU, J.C. - XUE, S. - WANG, F. - LIU, J.L. - YU, Y.S. - GU, H. (2006): Responses in nutrient uptake in rice roots to infestation of brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). *International Journal of Pest Management*, 52, 97-107. https://doi.org/10.1080/09670870600619809

WHITE, T.C.R. (1993): The inadequate environment: nitrogen and the abundance of animals. Springer-Verlag, New York.

WU, J.-C. - QIU, H.-M. – YANG, G.-Q. - DONG, B. - GU, H. (2003): Nutrient uptake of rice roots in response to infestation of *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). *Journal of Economical Entomology*, 96, 1798-1804. https://doi.org/10.1093/jee/96.6.1798

ZARGHAMI, S. - ALLAHYARI, H. - BAGHERI, M. R. - SABOORI, A. (2010): Effect of nitrogen fertilization on life table parameters and population growth of *Brevicoryne brassicae*. *Bulletin of Insectology*, 63, 39-43.

ZEHNDER, C.B. - HUNTER, M.D. (2008): Effects of nitrogen deposition on the interaction between an aphid and its host plant. *Ecological Entomology*, 33, 24-30. https://doi.org/10.1111/j.1365-2311.2007.00945.x

ZEHNDER, C.B. – HUNTER, M.D. (2009): More is not necessarily better: The impact of limiting and excessive nutrients on herbivore population growth rates. *Ecological Entomology*, 34, 535-543. https://doi.org/10.1111/j.1365-2311.2009.01101.x

Authors

Dr. Zsolt Gidó, PhD
assistant professor
Department of Environmental Sustainability
Institute of Environmental Sciences
Hungarian University of Agriculture and Life Sciences, Georgikon Faculty
H-8360, Keszthely, Deák Ferenc utca 16., Hungary
Gido.Zsolt@uni-mate.hu

Prof. Dr. Éva Lehoczky, DSc
professor
Department of Environmental Sustainability
Institute of Environmental Sciences
Hungarian University of Agriculture and Life Sciences, Georgikon Faculty
H-8360, Keszthely, Deák Ferenc utca 16., Hungary
Lehoczky.Eva@uni-mate.hu