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INTRASPECIFIC FACILITATION THROUGH HOST PLANT QUALITY IMPROVEMENT? OBSERVATIONS ON THE AGGREGATION BEHAVIOUR AND POPULATION BIOLOGY OF THE SENESCENCE INDUCING PHLOEM FEEDER (*ISCHNODEMUS SABULETI*)

INTRASPECIFIKUS FACILITÁCIÓ A TÁPNÖVÉNYMINŐSÉG FELJAVÍTÁSA ÚTJÁN? MEGFIGYELÉSEK A SZENESZCENCIA INDUKÁLÓ KARCSÚ NÁDIBODOBÁCS *ISCHNODEMUS SABULETI* AGGREGÁCIÓIRÓL ÉS POPULÁCIÓBIOLÓGIÁJÁRÓL

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Abstract

The aggregation behaviour and the senescence inducing effect on its host plants (Glyceria spp.) of the European chinch bug (Ischnodemus sabuleti) is documented in several Hungarian high-density populations. The hypothesis of intraspecific facilitation through host plant quality improvement is formulated and discussed in detail. We suggest that drought stressed host plants improve the performance of I. sabuleti and facilitate the local population outbreaks. We suggest that the optimal host plant drought stress level is higher for senescence feeding herbivores than for the flush feeding herbivores.

Keywords: *Ischnodemus sabuleti, Heteroptera, Blissidae, Glyceria maxima, intraspecific facilitation, aggregation behaviour*

Összefoglalás

Megfigyeltük a közönséges karcsúbodobács (Ischnodemus sabuleti) aggregációképzését és szeneszcencia-kiváltó hatását a tápnövényen (Glyceria spp.) néhány nagy sűrűségű magyarországi populációjában. Megfogalmazzuk és részletesen tárgyaljuk a tápnövényminőség feljavítása révén megvalósuló intraspecifikus facilitáció hipotézisét. Feltételezzük, hogy a szárazságstressznek kitett tápnövény növeli az I. sabuleti életképességét és elősegíti a helyi gradációkat. Felvetjük, hogy, szemben a friss hajtásokra specializálódott növényevőkkel, a magas aszálystressznek kitett tápnövények előnyösebbek a szeneszcencia-kedvelő növényevők számára.

Kulcsszavak: *Ischnodemus sabuleti, Heteroptera, Blissidae, Glyceria maxima, intraspecifikus facilitáció, aggregáció*

Introduction

GIDÓ (2023 b) recently carried out systematic observations on the wing dimorphism of the European chinch bug species *Ischnodemus sabuleti* (Fallén, 1826). The results of this research will be published elsewhere. For these observations large, high-density populations of this species have been required. Although both *I. sabuleti* and its major foodplants, the mannagrass species (*Glyceria maxima* (Hartm.) and *fluitans* (L.)) are quite widespread and common in Hungary, large, continuous mannagrass stands holding abundant *I. sabuleti* populations are rather rare. Identifying and following up some of these populations (with the focus on wing dimorphism) inevitably led to some observations on the aggregation behaviour of this species, on its relationship with the host plant and on the fate of these "outbreak populations".

In this article we describe our -admittedly "anecdotal" - observations on the aggregation behaviour and host plant relations of *I. sabuleti*, and briefly reviewing the relevant literature on blissid bugs and other phloem-feeding heteropterans too. We draft some hypotheses which may generate ideas and may form a base of further, more focused research on the interaction of blissid bugs and their host plants and its consequences regarding the population structure and dynamics.

Chinch bugs, their aggregation behaviour and feeding mechanism.

Chinch bugs (Heteroptera: Blissidae) are a worldwide distributed true bug family. Almost 400 blissid species are recognised, which represent 56 genera. Most of the blissid species are tropical, but some species live in temperate regions (SLATER, 1976).

A remarkable feature of the family is the exclusive host plant specialisation to a few monocot families. The most important blissid host plant family is Poaceae, but members of Cyperaceae and of some smaller, related plant families are also utilised by blissids (SLATER, 1976). Some of the blissid species are serious agricultural pests like the Oriental Chinch Bug, *Cavelerius saccharivorus* (Okajima, 1922) on sugarcane in Eastern Asia (FUJISAKI, 1989) or *Blissus insularis* and *B. occidentalis* on different turf grass species in the USA (CHERRY et al.,2013; HENG-MOSS et al. 2004).

At least some of the blissid species are known to form crowded, often multi-generational (containing both different nymphal stages and adults of both sexes) aggregations on the living host plants. This is best documented at *Blissus insularis* Barber, 1918 (CHERRY, 2001; ADDESSO et al., 2012) and our own observations on the European species, *Ischnodemus sabuleti* reveal a very similar behaviour. PÉRICART (1998) cites PUTSCHKOV (1969) who reports aggregations consisted of over 100 *Dimorphopterus blissoides* nymphs inside the reed (*Phragmites australis* Linnaeus) leaf sheats. It is possible, that aggregations on the living host plants are quite widespread in this family, just this phenomenon is seldom documented at the economically insignificant, underresearched tropical species, which form the majority of blissid species. Aggregation of *B. insularis* is driven by aggregation pheromones, and its primary function cannot be sexual, as nymph are attracted by the pheromones, too (ADDESSO et al., 2012).

Aggregation behaviour is common in Heteroptera. It can take different forms and can have different functions. Perhaps the most known are the large aggregations of the diapausing bugs in suitable overwintering places, including human buildings. Overwintering aggregations are well known also among blissid, including the already mentioned *Dimorphopterus blissoides* (Baerenspreng, 1859) (KMENT et al., 2023). *Ischnodemus sabuleti* aggregations usually overwinter in leaf sheaths of different live or dry plants, usually on the host plant, but very often on other nearby plants which offer proper protection. The South African blissid species *Macchiademus diplopterus* (Distant, 1903) also leaves its host plants to overwinter on other plants suitable for gregarious hiding, which are often commercially marketed fruits (OKOSUN, 2012). Many adaptive functions have been proposed to explain the non-diapause aggregation behaviour present at the nymphs in many different heteropteran species: protection against desiccation, protection against predators/parasites, potential sharing of endosymbionts, development accelerated by crowding and better adherence to the substrate to prevent dislodging by wind or rain (LOCKWOOD and STORY, 1986; FUCARINO et al., 2004). When adults are also included, reproductive advantages of aggregation are also plausible.

It is quite possible, that some of the above listed, mutually not exclusive benefits contribute to the suspected adaptive role of the non-diapause aggregation behaviour of blissid bugs. However, in this case the short term and long-term effects of large aggregations (often several hundred chinch bugs/plant) on the host plant also have to be taken in consideration.

Unlike many other phytophagous true bugs (mostly members of the families of Tingidae and Miridae) blissids are salivary sheath feeders (BACKUS, 1988; BACKUS et al., 2013; RANGASAMY et al., 2015) which resemble the feeding strategy of many planthoppers (Auchenorrhyncha suborder) and of all of the members of Sternorrhyncha suborder (aphids, psyllids, whiteflies and scale insects). Some other families of phytophagous heteropterans are also salivary sheath feeders too, namely the pentatomids (BACKUS, 1988). Salivary sheath feeders are able to feed selectively from the chosen plant tissue (BACKUS, 1988). The feeding behaviour of the southern chinch bug (*Blissus insularis*) has been studied in detail with electrical penetration graph (EPG) method (RANGASAMY et al., 2015). *B. insularis* is proved to be predominantly a phloem feeder, although it also ingests some xylem sap as well. According to our knowledge, no such detailed experimental analysis has been carried out regarding the feeding mechanism of any other blissid species: however, it is widely held that most – if not all – blissids are phloem feeders.

Some known aspects of the biology of Ischnodemus sabuleti

Our focal species, *Ischnodemus sabuleti*, is a relatively well studied, wing dimorphic European chinch bug (TISCHLER, 1960, 1963). Like many other members of its family, it is an oligophagous herbivore. In Hungary its major foodplants are the mannagrasses (*Glyceria* spp.), but it is reported to feed on other Poaceae too, namely *Ammophila*, *Elymus*, *Phragmites* and *Phalaris* (TISCHLER, 1960). We occasionally have seen aggregations of late instar nymphs and young adults on *Typha* and even *Carex* sp., but it is not known, if the bugs were really feeding on these plants, which grew inside the *Glyceria* stands heavily infected with *I. sabuleti*. We never found any *I. sabuleti* away from *Glyceria* stands/spots, but, admittedly, large reed (*Phragmites australis*) and cattail (*Typha* sp.) stands were not systematically searched by us for *I. sabuleti*. As long as we know, *I. sabuleti* populations living on coastal sand dunes on *Ammophila* and *Elymus* spp. described from the Baltic and Atlantic region (TISCHLER, 1960) haven't been reported from inland Central Europe.

While TISCHLER (1960, 1963) presented a detailed analysis of the food plant use, life history, wing dimorphism and population dynamics of *I. sabuleti*, some aspects of its biology escaped his attention, and the general attention, too. The most striking, generally overlooked feature of this species is the late spring-early summer partial de-alation of the macropterous morph (GIDÓ, 2023b), which in this form – elimination of the membrane and serious damage of the hind wings – is not reported at any other hemipteran species. (Details on this topic will be published elsewhere.) Although TISCHLER (1960, 1963) discussed the population outbreaks and their relationship with the frequency of the macropterous morph, the spatial structure of the populations is not treated in his articles.

Material and methods

In the years 2021–2023 several "outbreak populations" (local populations with very high density) have been identified and regularly sampled for *I. sabuleti* to study wing dimorphism and partial de-alation. Samples usually were collected with sweep net, occasionally also manually from the host plants. As the goal of the sampling was to get the ratios of the different wing morphs (brachypterous/macropterous/de-alated macropterous) in 2021-2022 no attempts had been made to assess the population density (number bugs/ unit area and/or number of bugs/plant).

In 2023, when the bug – host plant relation raised our interest, we changed the collection method. Plastic bags were pulled on the *Glyceria* plants on the field, then the plant was pulled out, and sealed bags containing individual plants and the bugs on them were carried in the laboratory and frozen. Later, the dead bugs and nymphs were collected and counted from the plants in the bags. This method works fairly well with the nymphs, as they are usually less agile. Unfortunately, it is very hard to "single out" an individual plant from a dense *Glyceria* stand with the plastic bag, without alarming the active, adult *Ischnodemus* bugs, which often drop down themselves from the plant, so in the case of the adult bugs this method can yield serious underestimates.

In 2021 a single large *Glyceria maxima* stand with an "outbreak" *I. sabuleti* population had been discovered and sampled regularly with sweep net near Darány village (South-West Hungary). As this population collapsed due to the local elimination of *G. maxima* in the late autumn of 2021, attempts were made during the following winter and early spring to find new "outbreak populations". Three other "outbreak" populations had been chosen for regular sampling in 2022: a *Glyceria maxima* stand on the dried-out edge of an old oxbow-lake at Felsőszentmárton (South-West Hungary), a very large, heterogenous *Glyceria maxima* stand on the floodplain of the Rába river at Csörötnek (West Hungary) and a section the *Glyceria* (probably *fluitans*) belt of the Fekete-víz brook right at the margin of Baranyahidvég village (South Hungary). The populations at Baranyahidvég and Csörötnek have been sampled regularly during the year 2022; the Felsőszentmárton population has been regularly sampled during the spring, but it collapsed in the early summer of 2022 with the local extinction of the *Glyceria*. In the winter of 2022, the unusually high-water level of the Fekete-víz brook eliminated the overwintering population at Baranyahidvég. So, in 2023 plastic bag samples had been taken from the Csörötnek population, and from two, newly identified "outbreak populations". Both of them are large *Glyceria maxima* stands; one is located on the Danube floodplain near to Kölked village (South Hungary), the another grows on the dried-out bottom of a former fishpond at Darány, and it is located several hundred meters away from the extinct population sampled in 2021. During the autumn of 2023 regular sweep-net samples has been carried out from the above-mentioned populations at Kölked and Darány and from a third "outbreak population" found at Nagynyárád village (S Hungary) on the *Glyceria* belt of a small brook. The main scope of these samplings was the collection of nymphs for an ongoing rearing experiment.

So, the following, admittedly not standardised field observations are mostly the "by-products" of a research directed on wing dimorphism and de-alation of *I. sabuleti*; however, we think they are worthy for mention and further consideration of planning focused observations, samplings and experiments.

Results

The phenology of Glyceria maxima – Ischnodemus sabuleti relationship in Hungary

The general model described below is based on the above-described observations from 2021–2023. Phenology is strongly dependent of the weather conditions of the actual year, sometimes also from the local weather conditions, and frequent catastrophic events (floods, devastation of the host plant etc.) can disrupt or modify the duration of the developmental phases. Food plant quality and the direct effect of population might affect the phenology, too.

As no systematic samplings directed on the larval phenology has been carried out, our data is somewhat sporadic and further, directed sampling is needed to complete and confirm our findings.

The majority of the *I. sabuleti* population overwinters as adults, but usually several percentages of the population overwinter as late-stage nymphs, mixed in-between adults. Aggregations of the *I. sabuleti* overwinter on or nearby the overwintering vegetative *Glyceria* shots, which developed during the previous autumn. After the end of the diapause, *I. sabuleti* adults and nymphs start feeding on the growing vegetative shots. The spring and the early summer are the main seasons for reproduction. Old adults might persist until mid-July (2021, Darány), in this case there is a generational overlap between the early instar nymphs and the remaining adults. On occasion (documented in 2022 at Darány, June 12.) young, freshly moulted adults appear in June: these probably develop from the last overwintered nymphs.

Young nymphs appear in June: their mass appearance more or less coincides with the flowering period of the *Glyceria maxima*. The ripening of the *G. maxima* seeds and the senescence of the generative shots in late July–early August precedes the mass appearance of the new adult *Ischnodemus* generation in late August–September. Older nymphs and young adults aggregate both on the senescent generative shots and on the newly growing fresh shots. The bulk of the *I. sabuleti* population develops to adults in August–September; a small percentage of nymphs transforms during October while another small percentage overwinters as nymphs and transforms to adults during the next spring or even early summer. It has to be clarified yet, if any oviposition occurs in the autumn period.

This phenology is in a good accordance with the observations of TISCHLER (1960, 1963) from Northern Germany, but under the warmer Hungarian climate the nymphs and the adults appear appr. a month earlier.

Aggregation behaviour of Ischnodemus sabuleti

All developmental stages of *I. sabuleti* tend to form large aggregations on the host plants (Fig.1), which behaviour is most conspicuous at high but not very high population densities. (At smaller population densities the aggregations are small – up to appr. ten bugs/plant - and may be confined to individual plants. At very high densities all the plants are “flooded” with the bugs, so the former aggregation spots “melt together” and the whole *Glyceria* stand transforms a to a single aggregation spot. In the typical case, the aggregations form well identifiable spots with the diameter of several meters. Inside in an aggregation spot all (or almost all) *Glyceria* plants are heavily infected (up to 500–600 bugs/plant in the case of nymphs during the late summer, and up to 100 (but more often 10–30) bugs/plant of feeding adults on the much smaller *Glyceria* shots during the spring). Outside the aggregation spot – just a few meters away – the density of *I. sabuleti* is considerably lower: most of the plants are free of the bugs, while some hold several individuals. These aggregations are most conspicuous visually during the late summer–early autumn, when the pale coloration of the heavily infested new *Glyceria* shoots markedly differs from the healthy green of the uninfected shoots outside the aggregations (Fig. 3 top).

Figure 1: Aggregation of late instar nymphs of *Ischnodemus sabuleti* on *Glyceria maxima* plants on 3rd and 25th August 2023 (Darány, SW Hungary). Photos by Zs. Gidó

When different developmental stages overlap (late summer, autumn, winter and early spring) the different nymphal stages and the adults form mixed aggregations.

It is very important to emphasize that very large numbers (up to 600–700 bugs/plant) of *I. sabuleti* nymphs and adults can aggregate on dead, totally dry *Glyceria* or *Phragmites* plants, which are obviously not suitable as food. Considering this fact, and the observed mobility of *I. sabuleti* nymphs and adults, it is certain, that in some cases the bugs aggregate on individual plants suitable only for shelter and visit the nearby suitable plants to feed. It is unclear, however, that how often do this in that case when they aggregate on seemingly suitable, living host plant.

While it is certain, that the bugs (including even the less mobile young nymphs) often move from plant to plant, it is unlikely that they regularly leave the area of the large aggregation spots to feed on the healthy plants of nearby areas, and then return to the aggregation area for resting.

In some cases, the flood conditions might explain the position of the aggregation spots. At Csörötnek, a large aggregation spot (which has been persistent for at least in two subsequent years) is less often flooded than the other parts of that large *Glyceria* stand, and the frequently flooded parts are almost *Ischnodemus*-free (Fig. 2). In the case of the *Glyceria* stands growing at brook margins, *I. sabuleti* usually aggregates on the – usually underdeveloped - *Glyceria* plants growing farthest from the water, which are reached only by the larger floods, while the inner plants permanently standing in the water are usually avoided.

Figure 2: Parts of the same, continuous large stand of *Glyceria maxima* at Csörötnek (floodplain of the Rába river, West Hungary) on 30th July 2023. (Photos by Zs. Gidó) Top: a frequently flooded area, with very low densities of *Ischnodemus sabuleti*. Bottom: A more elevated area, less frequently flooded, holding a large aggregation of *I. sabuleti*. Average chinch bug nymphal density exceeds one hundred/per plant.

Fig. 3: Top: a large *Glyceria maxima* stand on the dried-out bottom of a former artificial fishpond at Darány (SW Hungary) on 25th August 2023. The chlorotic/necrotic colour of the *Glyceria* plants on the left, holding a dense aggregation of *I. sabuleti* nymphs is clearly recognisable, especially when compared with the fresh green colour of the healthy plants on the right, which are hardly infested with the chich bugs.
Bottom: *Glyceria* spp. (probably *fluitans*) growing along a small brook at Nagynyárád (Southern Hungary) on 27th August 2023, heavily infested with *I. sabuleti*. Plants on the upper half of the photo have been already destroyed by the bugs, and even the plants on the bottom show recognisable chlorosis. (Photos by Zs. Gidó)

Unsurprisingly, *I. sabuleti* has some behavioural adaptations to cope with smaller floods. *I. sabuleti* bugs can walk shorter distances on the surface film of the water and can avoid submersion by climbing up to the top parts of the high *Glyceria* plants. However, we have some indirect, *post situ* observations at Csörötnek and Baranyahidvég which suggest that *I. sabuleti* populations are often seriously decimated or even eliminated by larger floods, which pull down even the tallest *Glyceria* plants. In winter, diapausing *I. sabuleti* bugs might be vulnerable even to less severe but persistent floods.

However, well defined aggregation spots of *I. sabuleti* are clearly recognisable even in visually more or less homogenous *Glyceria* stands unaffected by severe floods as it has been documented at Darány, in 2023. (Fig. 3, top).

Interactions of Ischnodemus sabuleti with the host plant

Persistent, large *I. sabuleti* aggregations have detrimental effect on the host plants. Heavily infested plants during the spring period may be prevented in flowering. The habitat spot in Csörötnek, which held a large *I. sabuleti* aggregation at least for two subsequent years failed to develop flowerheads in 2013 (Fig 2., bottom). We suspect that *G. maxima* might compensate more successfully the detrimental effects of the *I. sabuleti* infection before and during the flowering period than after, in late summer and autumn. In 2021 a heavily infested *Glyceria* stand in Darány has been able to develop flowerheads and seeds, but the young vegetative shots had been eliminated during the autumn. However, this hypothesis needs further confirmation. The *Ischnodemus* populations have a numerical peak in summer when the new generation appears, but the feeding impact of the bugs might be the strongest in late summer -early autumn, as the larger nymphs and adults probably consume more phloem sap than the smaller early instars. Typical *I. sabuleti* aggregations have an average density of 10-30 adult bugs/plant in spring and over a hundred of nymphs/plant in the late summer: this fact alone might explain the suspected greater vulnerability of the autumn shoots.

Heavily infested shoots turn chlorotic (Fig. 3., top) and after several weeks or months of persistence, they often die. The visually apparent changes of the infested plants resemble the natural senescence.

A remarkable fact is, that *I. sabuleti* aggregations (nymphs and adults) persist for many weeks on dying shoots: both on the naturally senescent generative shoots after the seed ripening, and on the sick young shoots overexploited by themselves. This is most apparent in late-summer early autumn, when often there is new, healthy, fresh growth available right near the aggregation spot (Fig. 3, top). The bugs are spreading out from the aggregation spot to the adjacent, less infested plants, but this happens only slowly, and usually it is finished only during the next spring. Dry leaves of the killed plants offer superior overwintering places for the *Ischnodemus* bugs. It has to be clarified, how much the late instar nymphs and the young adults feed in autumn.

The preliminary food preference experiments carried out in our laboratory did not give any conclusive results; however, it can be stated that the older nymphs (IVth -Vth stage) used in the trials did not show a clear preference of young, fresh leaves over the chlorotic, senescent leaves.

The role of the plant water stress in the Glyceria – Ischnodemus relationship

There are some observations which may suggest that drought stressed *Glyceria* plants are preferred by *I. sabuleti* over the *Glyceria* plants standing in the water. In the case of larger *Glyceria maxima* stands no outbreak populations have been found in the stands standing in the water for a long time. The direct effect of the floods is discussed above, however, in-water *Glyceria* stands are usually avoided even if the absence of heavy floods, in standing water bodies. The reduced physical accessibility of the in-water *Glyceria* plants might be the part of the explanation, however, the food plant quality of the in-water vs. drought stressed *Glyceria* is a question worthy for further investigations.

In the case of the brookside *Glyceria* belts, in-water plants are often heavily infected too, but the core of these aggregations are usually the plants standing farthest from the brook. The bugs spread out from these “refugia” to the in-water plants during the population outbreaks. However, this might be entirely explained by the flood dynamic (see above).

Discussion

“Senescence feeders”, “nutritional enhancement” and “senescence inducing” insects. Ischnodemus sabuleti and Blissus sp. as senescence inducing insects.

The term “senescence feeder” has been introduced and propagated by WHITE (2015). While most herbivores (arthropods and vertebrates as well) prefer young fresh plant growth (they are called “flush feeders” by WHITE, 2015), there are some species, which deliberately prefer old, senescent leaves over the young, fresh ones. Senescence feeders occur in all major arthropod herbivore guilds except the gall-forming insects; there are senescence feeders among chewers, sap feeders and leaf miners (WHITE, 2015). Here only the phloem feeders will be further discussed.

In general, the quality of the food for an herbivore is determined by two groups of factors: it has to get the essential nutrients in sufficient quantity/concentration and has to avoid the toxic secondary metabolites produced by the plants. (The topic of the actual host plant choice is a more complex issue, as the insects’ host plant preference and performance on the selected host plant often, but not always meet (GRIPENBERG et al., 2010). However, this topic is not discussed here.) It is widely held, that the phloem feeding insects are usually less influenced by the plant’s secondary metabolites than leaf chewers, as the phloem sap is relatively poor in secondary metabolites and the phloem feeders avoid feeding from the mesophyll cells (HUBERTY and DENNO, 2004). On the other hand, phloem feeders need to cope with a dilute food, containing a lot of sugar (usually sucrose), but poor in N-sources – mostly free amino-acids (HUBERTY and DENNO, 2004).

There is some evidence that senescing plant parts provide an improved food for the phloem feeders. The plant mobilises the resources – especially N-containing molecules – and redirects them to the surviving parts, which causes temporally elevated amino-acid concentrations in the phloem (WHITE, 2015). Moreover, many of those phloem-feeding insects, which choose to feed on mature leaves or plants, actively accelerate the senescence of the plant. Evidence is available on some aphid, psyllid and scale insect species feeding on the mature leaves on coniferous (HOPMANS et al., 2008; PARRY, 1979;) and deciduous trees (COCKFIELD et al., 1987; COTTREL et al., 2009; MORATH et al., 2006) or on herbaceous crops (DILLWITH et al., 1991; REAGAN et al., 2011) that these insects cause senescence-like visual symptoms (chlorosis) on the leaves they feed upon, and increase the foliar N-content and/or the amino-acid concentration of the phloem sap. Regarding our topic the most interesting examples are those senescence-inducing phloem feeders which infest plants of the Poaceae family. For example, the wheat aphid, *Schizaphis graminum* (Rondani,1852) feeds on mature leaves, causing ultrastructural and visible tissue damage and discolouration, and significantly raising the concentration of essential amino acids in the phloem sap it ingests (SANDSTRÖM et al. 2000). The cereal aphid, *Sipha flava* (Forbes,1885), colonizes older leaves of sorghum where it produces a red spot at its feeding site that spreads to cover the entire leaf as chloroplasts in the mesophyll cells are degraded. This accelerated senescence enhances the flow of nutrients, especially nitrogen, in the phloem resulting in faster growth and increased survival of the aphid

(GONZALES et al. 2002). *Rhopalosiphum maidis* (Fitch, 1856). also attacks sorghum, causing similar red discolouration of the leaf, enhanced quality of the aphids' food, and increased aphid reproduction (WHITE, 2015).

It is very important to note, that not all sap feeding insects cause senescence-like symptoms on their host plants. STEINBAUER et. al (2014) deliberately use the term "senescence inducing herbivores" as a subgroup. Other authors like ZHANG et. al. (2019) classifies the aphids as "phytotoxic" and "non-phytotoxic", the former corresponds to the "senescence inducing". Of course, in the case of the agricultural pests this distinction has an enormous economic significance, as if the transmission of viruses or other plant pathogens is not involved, then the phytotoxic species cause far worse damage to the host plants. TELANG et al. (1999) report that the aphid species *Diuraphis noxia* Kurdjumov,1913 is able to induce serious tissue damage on some wheat varieties but not on a resistant wheat variety. *D. noxia* is able to survive on the resistant wheat, but – unlike in the case of the susceptible genotypes – it is not able to benefit from the phloem sap enriched in essential amino acids, which accompanies the tissue damage. Therefore *D. noxia* performs poorer on the resistant variety.

Phytotoxic (or senescence inducing) sap-feeders can enhance the nutritional quality of the host plant not only for themselves but also for their conspecifics or for other species too. A phytotoxic variant (biotype) of the already mentioned, wheat aphid, *S. graminum*, is able to perform well on a certain resistant wheat variety (DORSCHNER et al., 1987). The other aphid biotype is not phytotoxic and performs poorly on the resistant wheat. However, the non-phytotoxic biotype performs very well on the resistant wheat previously infected by the phytotoxic biotype. The authors (DORSCHNER et al., 1987) contribute these results to the increased amino-acid levels of the phloem sap of the wheat damaged by the phytotoxic variety. Such cases of intra- and/or interspecific facilitation due to the nutritional enhancement of the host plant have been reported at several other phloem feeding insect species as well (CAO et al., 2016; FISCHER, 1987; KAPLAN and DENNO, 2007; SANDSTRÖM et al., 2000; SRINIVASAN et al., 2016; VARENHORST et al., 2015).

The chlorotic-necrotic spots induced by *Blissus insularis* aggregations in St. Augustinegrass (*Stenotaphrum secundatum* (Walt.)) are very similar to what has been described above for the *I. sabuleti* in *Glyceria* stands, but they are even more apparent (CHERRY et al., 2013).

Relatively little is known about the plant-physiological mechanisms involved in the senescence induced by insect phloem feeders. Available information suggests that the induced senescence is different in some respects from the natural senescence. CRAWFORD and WILKENS (1996) report that the senescence induced by the psyllid species *Cardiaspina retator* Taylor, 1962 on *Eucalyptus* leaves involves the disintegration of the chloroplast membranes, which is not characteristic to the natural senescence. STEINBAUER et al. (2014) report that senescent leaf tissues induced by *Cardiaspina* do not become dehydrated and necrotic until the psyllid nymphs keep feeding upon them. On the other hand, natural and induced senescence have many common features: disintegration of the mesophyll tissues, degradation of the chlorophyll (chlorosis), mobilization of the nutrients (free amino acids, soluble proteins and sugars) and in many cases anthocyanin-synthesis (visible as reddish-purple discoloration of the leaf). It cannot be assumed that all the changes induced by the phytotoxic herbivores are beneficial for the feeding insect; some of them are in fact the resistance mechanisms of the host plant (PEGADARAJU et al, 2005). Resistant and susceptible plant genotypes often give different responses to the feeding of the phytotoxic insect (TELANG et al, 1999; NI et al., 2009). This topic has enormous economic importance, and unsurprisingly attracts considerable research attention (a blissid example: REINERT et al., 2011)

Causative mechanisms of the herbivore induced senescence are not entirely known and can be different even in the case of the closely related phloem feeding species. In the case of the phloem-feeders, especially salivary sheath feeders, the mechanical damage caused by the feeding insect is negligible if compared with the impact of the chewing defoliators. However, the production of callose which blocks the sieve elements of the phloem is the part of the plant's resistance response to the phloem-feeders, and it can disrupt the local nutrient flow which may lead to further metabolic changes (NALAM et al., 2019). Phloem feeders are infamous virus vectors, and it is documented that viral or endophytic fungal infection can enhance the food plant susceptibility for the phloem feeding insect (CLIFTON et al., 1998; HE et al., 2012; LIU et al., 2019). In other cases, endophytic fungi contribute to the plant resistance against the insect, as it is reported in the case the *Lolium perenne* L. – *Blissus leucopterus hirtus* Montadon, 1893 relationship (RICHMOND and SHETLAR, 2000). Facultative mutualistic relationships between viral and fungal pathogens and their herbivore insect vectors, involving host plant food quality improvement might be quite widespread. This topic undoubtedly merits much further research.

However, in the case of the phloem feeders, effector molecules injected into the plant with the insect's saliva are likely the most important causative agents of the induced senescence (ELZINGA and JANDER, 2013). Despite the recent great research interest and activity on this topic, including the proteome analysis of the salivary gland of *Blissus occiduus (Barber, 1918s* (RAMM et al. 2015), details remain mostly unknown. Hydrolases found in the *Blissus* saliva certainly contribute to the local tissue degradation, while the role of oxido-reductases is mainly to supress the so-called "reactive oxygen species" produced by the plant as a defensive reaction (HENG-MOSS et al., 2004; RAMM et. al, 2015). The suspected more sophisticated molecular agents and mechanisms which modify the plant's hormonal signalling pathways to the benefit of the phytotoxic insects are still poorly known.

The inorganic nutrient depletion of the plants heavily infested by chinch bugs (CHERRY et al., 2013) can be attributed to the overexploitation of the plant and/or to the reduced photosynthesis and nutrient uptake of the infested plants.

As conclusion we emphasize that *Ischnodemus sabuleti, Ischnodemus variegatus* (Signoret, 1857) (OVERHOLT et al., 2004), the mentioned *Blissus* spp. and supposedly many more blissid species are senescence inducing insects, and suggest, that the induced senescence of the host plant improves the nutritional value of the phloem sap for the chinch bug.

Aggregation behaviour and intra-specific facilitation through the host plant quality improvement

Individual chinch bugs cause negligible damage to the host plant. (Therefore, we suggest, that the senescence inducing effect of the chinch bugs is related to salivary effector molecules and/or to sieve tube occlusion and/or to nutrient depletion rather than to the transmission of a pathogen). The observed phytotoxic effects are achieved by the joint effort of a chinch bug aggregation.

Unlike in some other gregarious insects, the chinch bugs aggregations are not the by-products of the low mobility of the insects sometimes amplified by huge egg clusters deposited by a single female. Although they spent most of their time hiding inside the leaf sheathts of the host plant, or sometimes in any suitable hiding place close to the host plant, *I. sabuleti* bugs often are seen actively walking on the plants and on the ground, especially in warm weather. Even the less mobile early instar nymphs could easily walk several meters to find a new host plant (although probably they rarely do so). The egg clusters deposited by *I. sabuleti* are not large: TISCHLER (1960) reports 12eggs/cluster on average. The 5-600 nymphs often sharing a single *Glyceria* shoot are certainly not the offspring of a single female; rather adult females live aggregated on the food plants (together with the males and the nymphs) and oviposit on the food plants where they live. It is highly probable, that *I. sabuleti* aggregations are initiated and maintained with the help of an aggregation pheromone, as it has been already proven at *Blissus insularis* (ADESSO et al., 2012).

If the above hypothesis is correct (that the senescence induced by the feeding of the *I. sabuleti* aggregation enhances the host plant's food value), then the communal host plant quality enhancement may be the main functional role of the aggregation behaviour of *I. sabuleti*, and the same applies to *Blissus* sp. Other potential benefits of the aggregation (see Introduction) cannot be excluded *a priori*, but in this case none of them is likely to have a great effect. (In our opinion, any predator or parasitoid can find much easier the large *Ischnodemus* aggregations on damaged plants using either visual and/or olfactory cues, then the widely dispersed individuals inside the healthy vegetation. So, we suspect, that aggregation in this case cannot be a defensive adaptation against predators/parasitoids).

Host plant drought stress and the preference/performance of Ischnodemus sabuleti

The effect of the plant's drought stress on the insect herbivores' preference/performance has been a hot topic long time ago, and its significance is amplified by the ongoing climate change. While lot of individual research has targeted this topic during the past decades, it is not easy to find the general patterns within the mass of the often (seemingly?) contradicting data. Here we discuss only very briefly the most relevant information available on phloem feeders.

In their, otherwise excellent review GELY et al. (2020) propagate the "intermediate water stress hypothesis" also for the phloem feeders. According to that, an intermediate water stress is beneficial for the phloem feeders, as increases the concentration of the free amino acids in the phloem, but the severe drought stress is disadvantageous, as the low turgor pressure and/or high viscosity of the phloem sap rises to that level, that the sucking insect cannot consume it.

Although there is no doubt that the intermediate stress hypothesis holds in many documented cases for phloem-feeding insects (KHAN et al., 2011; TARIQ et al. 2012), there are too many exceptions (MODY et al., 2009; KANSMAN et al. 2022, HALE et al., 2003) to get away with this elegant oversimplification. Some of the contradictions may be only delusory arising for the ill-defined terms of "intermediary" and "severe" water-stress, but some results suggest that there are more species-specific subtilities in the herbivore reactions to the plant water stress (BANFIELD-ZANIN and LEATHER, 2015). Plants adapted to different ecological conditions respond to the water stress in different ways. Highly revealing are the findings of KAMPS and POLEMAN (2023) about three *Rorippa* species and their common aphid pestss (two species). The performance of both aphid species increased all of the times when the host plant got stressed, but "water stress" meant very different things for the three related plant species. *R. amphibia* L. which is a semi-aquatic species, unsurprisingly remained unaffected by the waterlogging, but got stressed by dry conditions. *R. sylvestris* L., a terrestrial species suffered greater stress when waterlogged than when was exposed to drought, while *R. palustris* L., a floodplain species remained indifferent both to the waterlogging and to the drought level applied in the experiment.

We suggest that optimal level of host plant drought stress from the perspective of the phloem feeding insect is lower for the flush feeders than for the senescence feeders. Flush feeders are adapted to the succulent young growth containing a sap with high turgor pressure and moderate osmotic pressure, while senescence feeders – including the senescence inducing species – are better adapted to feed on saps of high osmotic and low turgor pressure. Severe drought stress accelerates or induces the senescence of old leaves, or of the whole plant which is beneficial for the senescence feeder. We formulate the hypothesis, that typical flush feeders react to the drought stressed host plants according the "intermediate stress hypothesis", while the performance of the typical senescence feeders should monotonously grow with the magnitude of the host plants drought stress, at least up until the point when the plant dies.

HUBERTY and DENNO (2004) formulated the "pulsed water stress hypothesis" suggesting that moderate intermittent drought might offer periods of nutrient availability with turgor recovery, allowing phloem-feeders, such as aphids, to take advantage of stress-induced increases in nitrogen availability. Following the same argumentation as above, we suggest, that the "pulsed water stress hypothesis" is better applicable to the "flush feeders", while senescence feeders might benefit even from longer, continuous drought events.

I. sabuleti is not an obligate senescence feeder as it is able to feed and grow on healthy, growing *Glyceria* plants. During the spring and early summer and especially when the population density is too low to form effective aggregations, *I. sabuleti* bugs often simply don't have any other choice. However, it's senescence inducing ability and its reluctance to leave the chlorotic, overexploited *Glyceria* shots for the fresh ones in the autumn suggest, that senescent *Glyceria* might be its preferred food. Very likely the same applies to *Blissus* sp.

RANGASAMY et. al. (2015) reports that *Blissus occiduus* ingests some xylem sap as well. Xylem sap is probably a water source for the bugs feeding on the very concentrated phloem sap of the senescent plants. We suggest that *I. sabuleti* and many other piercing-sucking senescence feeders probably also obtain water from the xylem sap.

As drought stress induces the senescence of the plants (at least those of the old leaves), so we suggest that *I. sabuleti* performs better on drought stressed *Glyceria*. This hypothesis is in accord with our (anecdotal) observations, that the large local *I. sabuleti* population outbreaks are initiated on presumably drought stressed *Glyceria* plants growing in the dried-out beds of ponds and oxbow lakes or on the outermost plants of the brookside *Glyceria* belts.

One might think, that the *Glyceria* plants standing in permanent water are not stressed, because *Glyceria* is a semi-aquatic plant, and these plants are tall, green and have an overall healthy appearance. However, leaves of the in-water *Glyceria* often have a purplish colour (most apparent on the leaf sheets) which is not common in the *Glyceria* plants growing overland during the warm season. Anthocyanin production in vegetative organs is a common stress signal in the plants (CHALKER-SCOTT, 1999), and young *Glyceria* shots are usually purplish during the early spring due to the cold stress. The possible physiological/biochemical changes of *G. maxima* plants induced by the permanent water logging are not clarified yet, and neither their possible role in the seemingly low attractiveness of in-water plants to *I. sabuleti*.

Intraspecific facilitation and the turbulent population dynamic of Ischnodemus sabuleti and of the ecologically similar species

The supposed intraspecific facilitation through the host plant quality improvement meant that the growth rate of the local *I. sabuleti* populations has a strong positive density dependence (also called inverse density dependence) up until a very high population density. That meant, that the population number is regulated by positive feedback, which meant instability (COURCHAMP et al., 1999). According to this hypothesis it is not easy for the local small, low-density *I. sabuleti* populations to grow, instead they frequently get extinct. However, after reaching a certain population density, the population will show accelerated growth – even faster than the exponential growth predicted by the simplest, density independent model of population growth. The resulted local population outbreak is followed by a rapid collapse, which in the case of the *I. sabuleti* is caused by the local elimination of the food plants.

If we take into the account the aggregation behaviour of *I. sabuleti*, the picture becomes more complex, more interesting, and more realistic. Due to the aggregation behaviour the intraspecific facilitation may be realised even in the case of low population densities, as the bugs can form sporadic aggregations restricted to individual plants and therefore can be still able to induce senescence of the host plants, supposedly improving their reproduction rate. That may reduce the extinction rate of the low-density populations and allows the spontaneous emergence of small, local outbreak centres, which hold the potential to expand rapidly causing a larger scale population outbreak. Of course, is very unlikely that most of the small aggregations confined to several plants will ever expand to a local outbreak, as they easily got eliminated by chance events or predators/parasites, or simply got "dissolved" by emigration, however some of them will succeed, with a probability determined mainly by extrinsic factors (weather, parasitoid pressure etc.). Drought stress might increase the frequency of the population outbreaks, even if it is confined to smaller parts of the *Glyceria* stands, as improves the food plant quality even in the absence of the intraspecific facilitation. The initially low-density populations can quickly grow on the drought stressed plants to the density which allows the efficient intraspecific facilitation and the subsequent mass colonisation of the healthy plants.

The above drafted scenario is admittedly hypothetical. Its basic assumption is that there is a significant intraspecific facilitation through the host plant quality improvement at *I. sabuleti* and at many other, ecologically similar species. According to our knowledge this hypothesis is formulated here for the first time for any blissid species. This assumption has to be tested rigorously by conducting standardised nymphal rearing experiments.

The most speculative part of this scenario is the aggregation level of *I. sabuleti* in low-density populations, as it came to our focus only very recently. Direct field observations of the spatial structure of low- and high-density *I. sabuleti* populations should be carried out, and a predictive mathematical model should be constructed to test our assumptions.

The high population density is known to induce a greater percentage of macropters able to long term dispersal in *Cavelerius saccharivorus*, another wing dimorphic blissid species (FUJISAKI, 1989). Although experimentally never tested, very likely this is the case at *I. sabuleti* as well. This type of wing dimorphism, very common in Blissidae family, is probably an adaptation to the above drafted population dynamics. Emigration from aggregations might be strongly disadvantageous at low population density, as it disrupts the intraspecific facilitation, while emigration becomes a necessity after the destruction of the host plants. In the wing dimorphic brown rice planthopper (Nilaparvata lugens, Delphacidae) also the macropter inducing effect of the host plant senescence has been demonstrated (LIN et. al., 2018). For further discussion of this topic see GIDÓ (2022, 2023 a,b).

Finally, we suggest, that in the case of the intraspecific facilitation of phytophagous insects, aggregation pheromones are more likely to evolve in species living on host plants which grow in large, homogenous stands than in those species whose host plants grow in small, isolated patches. In the latter case, the aggregation is forced on the insect simply due to the spatial distribution of the resource, even in the absence of any pheromones. Blissid species adapted to grasses clearly represent the first group.

Conclusions

We conclude the following facts:

I. *I. sabuleti* tends to form large, multi-generational aggregations on the host plant (alike some other blissid species).
II. *I. sabuleti* aggregations cause senescence-like symptoms on the infested host plants (alike some other blissid species).
III. *I. sabuleti* often produces “local outbreaks”, which usually collapse due to the local elimination of the host plants.

We formulate the following testable hypotheses regarding the *Glyceria maxima – Ischnodemus sabuleti* relationship:

I. *I. sabuleti* (alike some other blissid species) is a facultative senescence feeder, it performs better when feeding upon senescent host plants.
II. The aggregation behaviour is advantageous for *I. sabuleti* due to the intraspecific facilitation through the host plant quality improvement.

III. Drought stress improves the host plant quality for *I. sabuleti*.
IV. The aggregation behaviour and the intraspecific facilitation have a crucial effect on the population dynamics of the *I. sabuleti*.

We also suggest a more general hypothesis:

The optimal host plant drought stress level is higher for the senescence feeder herbivores than for the flush feeder species. The "intermediate drought stress hypothesis" and the "pulsed water stress hypothesis" is well applicable for most of the flush feeders, while the performance of the senescence feeders increases monotonously with the host plant's drought stress level, up until the point when the plant dies.

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