

Aggregation and survival of *Neophilaenus albipennis* (Hemiptera: Cercopidae) spittlebug nymphs

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Abstract. The nymphs of spittlebugs (Hemiptera, Cercopidae) are xylem-feeders and live on herbs, grasses or woody plants within their self-produced spittle masses. Nymphs of the spittlebug *Neophilaenus albipennis* live aggregated in these spittle masses on their host plant *Brachypodium pinnatum*, a common grass in dry grassland. The objective of this study was to estimate nymphal mortality rates and to examine what role aggregation and vegetation structure play in the mortality of the nymphs. The aggregation and mortality were measured using two different methods, direct monitoring and caging of nymphs. The nymphs passively aggregated with up to 4 nymphs per spittle and aggregation decreased with instar. The aggregation of the nymphs resulted in a reduced mortality in all instars. Although it has already been argued that aggregation may be an advantage, this study is the first direct evidence (i.e. direct measurement of single individuals) for the benefit of aggregation to individual spittlebug nymphs. Despite a clumped distribution of *N. albipennis* nymphs in tall vegetation, nymphal mortality was not correlated with vegetation height.

INTRODUCTION

Aggregation of insects in the immature stage has been frequently documented in various taxonomic groups. The aggregation of sometimes large numbers of immatures may occur through passive aggregation due to clumped egg-laying (e.g. Atkinson & Shorrocks, 1984) or active crowding (e.g. Bales & Furniss, 1984), which may be driven by aggregation pheromones (Sauphanor & Sureau, 1993). Particularly in phytophagous insects, aggregation may benefit the individual through enhanced exploitation of food resources (Tsubaki & Shiotsu, 1982; Peterson, 1987), lower predation risk (Cappuccino, 1987; Turchin & Kareiva, 1989; Lawrence, 1990), improved thermo-regulation (Seymour, 1974) or faster development (Lawrence, 1990; Denno & Benrey, 1997). On the other hand, aggregation may entail costs such as intra-specific competition (Faeth, 1990) or higher infection rates through, for instance, viruses (Hochberg, 1991). The balance of these advantages or disadvantages of aggregation will affect mortality of the immatures and thus may have a strong influence on the population dynamics of species.

The nymphs of spittlebugs (Hemiptera, Cercopidae) are xylem-feeders and live on herbs, grasses or woody plants within their self-produced spittle masses. The spittle consists of the excretion of surplus water originating from the large amount of ingested xylem sap, which may be enriched with mucopolysaccharides and proteins from the Malpighian tubules (Marshall, 1966; Mello et al., 1987). The spittle is thought to give shelter to the nymphs, protecting them from predation and providing a suitable microclimate (Whittaker, 1970). Within these spittle masses aggregation of the nymphs has been found in many species (e.g. Whittaker, 1965b; Mangan & Wutz, 1983; Akiyama & Matsumoto, 1986; Martin et al., 1995; Peck, 1998) and even aggregations of different species in

one spittle mass have been documented (Halkka et al., 1977). Despite the ubiquity of aggregations in spittlebugs, there is little information on the role of the aggregation for nymphal survival. Is there reduced mortality in aggregated spittlebug nymphs? How does the aggregation come about?

To answer these questions, the nymphal biology of the spittlebug *Neophilaenus albipennis* was studied in detail. Nymphs of this species aggregate on the host plant *Brachypodium pinnatum*. The objectives of this study were to (1) measure the mortality rates of aggregated and non-aggregated nymphs, (2) assess the effect of vegetation structure on nymphal mortality, and (3) shed light on the mechanism of aggregation of spittlebug nymphs. Nymphal mortality was measured by direct observations of individuals in the field and caging nymphs. The mortality rates were compared between aggregated and non-aggregated nymphs. If there is a benefit of aggregation, a lower mortality would be expected in aggregated nymphs. The distribution on the host plant and the instar composition of the nymphs within spittle masses were used to elucidate the mechanism of the aggregation, i.e. to answer the question whether there is an active or passive aggregation.

MATERIALS AND METHODS

Study system

The spittlebug *Neophilaenus albipennis* (Fabricius, 1798) (Hemiptera, Cercopidae) is univoltine and hibernates in the egg stage. The nymphs hatch in April and live in self-produced spittle masses. The species exhibits five instars. In the study area the first adults occurred in June and were found until September. The density of older nymphs was up to 5.0 nymphs per 0.25 m² (n = 6, S.D. = 4.3). The nymphs live on the stems of the grass *Brachypodium pinnatum* (L.) P.B., a clonal plant not building distinct tufts but its erect stems being relatively sepa-

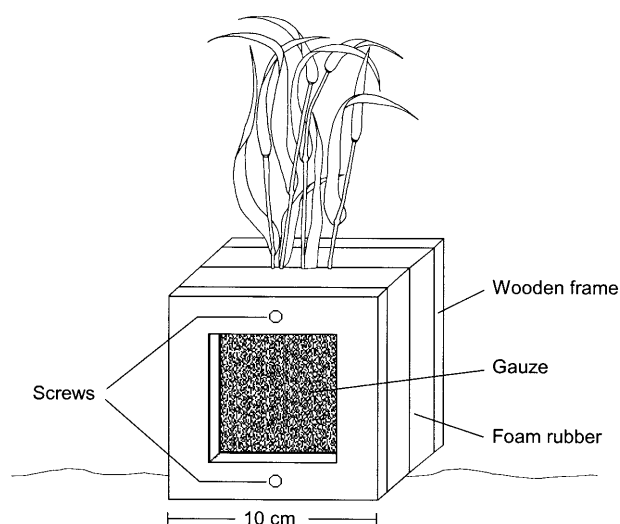


Fig. 1. Mini-cage used for measuring the mortality of the nymphs of *Neophilaenus albipennis* by exclusion of predators.

rated (see Fig. 1). In the study area *B. pinnatum* grows in dense and homogenous stands. In Central Europe *N. albipennis* occurs in dry grassland sites. This study was conducted in the porphyry landscape north of Halle in Sachsen-Anhalt, Germany. A description of the study area is given by Bliss et al. (1996). Within the study area 506 host plant patches were identified and mapped (Biedermann, 2000). Two large patches, Br2 (area: 390 m²) and Br498 (1293 m²), were chosen for the detailed study of the nymphal aggregation and survival.

Phenology, aggregation and distribution

The instar composition during the development of the nymphs was measured using the quadrat sampling method. This method has been frequently used to quantify the density of spittlebug nymphs (e.g. Whittaker, 1965a; Martin et al., 1995; Whittaker & Tribe, 1998). At each of the two patches, Br2 and Br498, spittle masses were examined in plots of 0.5 × 0.5 m. In the two patches on each sampling date six plots were chosen randomly. The nymphs were counted and their instar was determined using Vilbaste (1982). Additionally, some nymphs were reared to adults in the laboratory to confirm their species. Samples were taken every 3 to 7 days. For the measurement of aggregation, additional randomly chosen spittle masses were examined outside these plots (n = 124). The degree of aggregation was calculated for each instar as the proportion of nymphs that lived in nymphal aggregation (one to four nymphs).

The nymphs of *N. albipennis* live fairly sessile on their host plants. In patch Br2 the position above ground of the nymphs on their individual host plant stem (marked by labels, see below) was recorded during nymphal development. In order to characterise the locations where nymphs live, the height of the vegetation layer was documented by simply measuring the height of the surface of the dense and homogenous grass layer (predominated by the host plant *B. pinnatum*), peaks formed by single taller plants were disregarded. The vegetation height was measured both at locations where nymphs were found and at random samples within the patch.

Mortality

Two parallel methods were used to estimate nymphal mortality. (1) The patches Br2 and Br498 were searched for spittle masses of *N. albipennis*, nymphs were identified to instar, and the corresponding stem of the host plant was marked by a label (n = 76). The host plant *B. pinnatum* is not a tufted grass, thus

single stems are distinct from each other and can be clearly relocated using the attached labels. The nymphs seldom moved to other individual host plants. Frequently the exuviae of preceding moultings could be found in the spittle masses. Thus it was possible to relocate the spittle masses individually. The degree of aggregation with other nymphs, the development and the mortality were recorded for each nymph over time. The status (dead or alive) of the nymphs was recorded every 2 to 4 days from early May to late June 1995. From these data the mortality rate of each instar was calculated. (2) Mini-cages, 15 in Br2 and 5 in Br498, were attached to the host plants. Those cages have been successfully used in the study of the development of spittlebug nymphs (Halkka et al., 1967; Whittaker, 1968, 1971; Halkka & Mikkola, 1977). The cages prevent the escape of the nymphs and the access of predators. The cages used in this study consisted of two frames of foam rubber covered by two wooden frames that are held together with two screws (Fig. 1). The wooden frames were covered by gauze. Resting on the ground, the cages were attached to host plants with one spittle mass containing up to three nymphs. The stems were clamped between the two frames of foam rubber (see Fig. 1), so that growth and photosynthesis of most parts of the host plants would be little affected. The development and mortality of the nymphs was measured every 5 to 10 days. Additionally the cages were used to determine the mortality of nymphs of instar V, which is not possible with the technique of individual marking of the stems where the nymphs live. The moulting adults live outside the spittle and would disappear from the marked stems.

In both approaches, a spatula was used to lift the spittle from the nymphs in order to follow the fate of the nymphs in the spittle masses. After the examination the nymphs were manually covered with spittle again.

At the locations of the nymphs the vegetation height was measured. A logistic regression analysis (using SPSS 10.0, SPSS Inc., Chicago, Illinois) was performed in order to test the influence of vegetation height on the survival of the nymphs. Due to continued growth of the vegetation during nymphal development, the values of vegetation height were standardised within each instar and the samples were pooled.

RESULTS

Phenology

In patch Br2, after hibernation of the eggs, first instars were detected at the end of April to the beginning of May (Fig. 2a). Instars II to IV occurred in May, while instar V peaked early June. In patch Br498, the nymphal stages were delayed by about 10 days compared to Br2 (Fig. 2b). The duration of nymphal development, however, was not prolonged (Fig. 2). In both patches the development from instar I to the adult took 6 to 7 weeks. No obvious differences in stadia were detected; each took 8 to 10 days.

Distribution

The nymphs of *N. albipennis* were found at the base of the stems of their host plant. The mean position of nymphs at instar I was 1.5 cm above ground (Table 1). With successive instars the position on the stem increased up until instar V with a mean of 4.8 cm. The variation in the position at the stem also increased with instar. Mean stem length increased from 15.9 to 29.4 cm over the period of nymphal development. In spite of this consider-

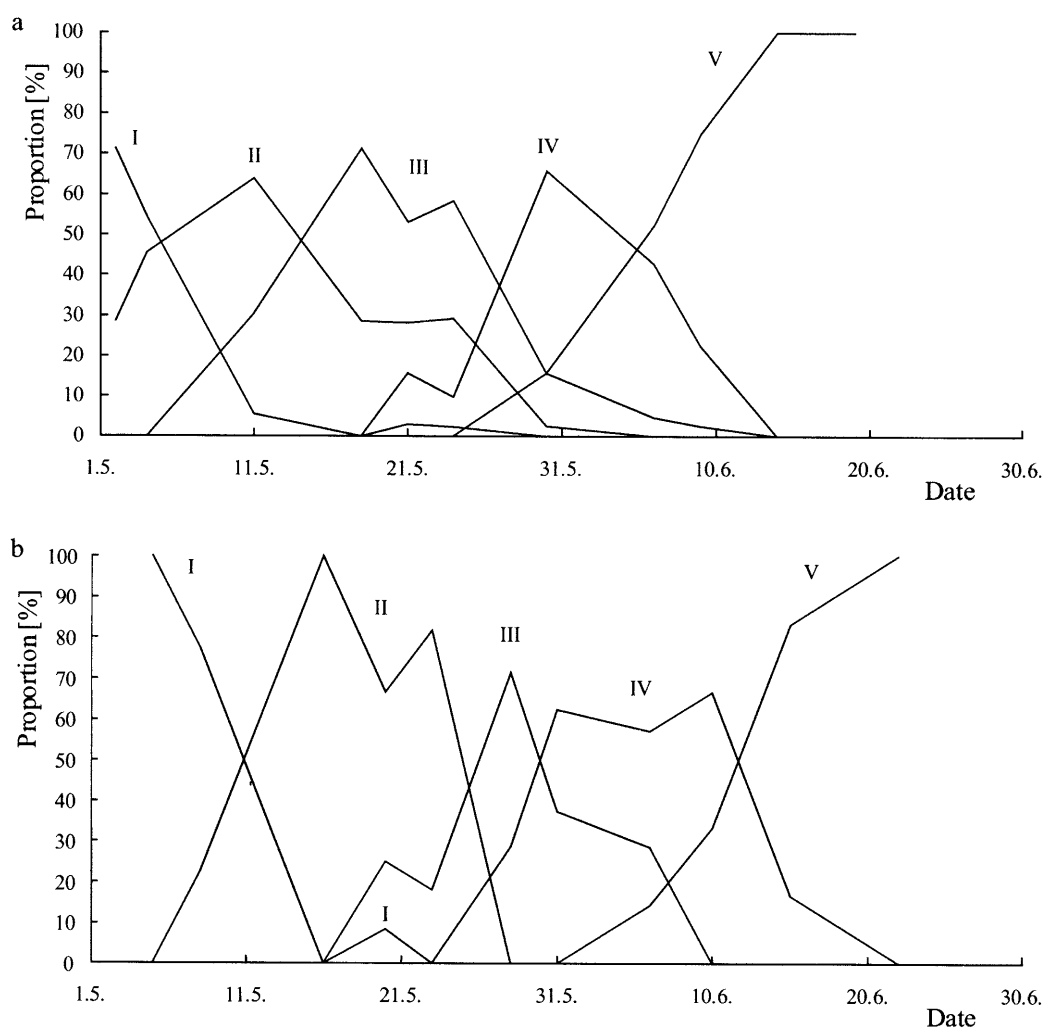


Fig. 2. Phenology of the instars (I-V) of *Neophilaenus albipennis* in (a) Br2 and (b) Br498.

able growth of the host plant, nymphs remained within a fairly restricted zone at the base of the vegetation layer.

After an examination of 386 spittle masses, more than one spittle mass per plant stem was found on only one occasion (two nymphs at instar IV). All other nymphs lived aggregated or singly in one spittle mass per stem. The nymphs were regularly found in tall and dense vegetation. The analysis of the vegetation structure showed that vegetation was taller at locations where nymphs were found, in contrast to random samples in the patches (Table 2).

TABLE 1. Position above ground of the nymphs of *Neophilaenus albipennis* at the host plant stem and stem length (mean and standard deviation).

Instar	Height above ground (cm)	Stem length (cm)
I	1.5 ± 0.7 (n = 18)	15.9 ± 5.8
II	1.9 ± 0.9 (n = 97)	18.7 ± 6.5
III	2.4 ± 1.1 (n = 67)	20.3 ± 6.7
IV	3.3 ± 1.5 (n = 28)	26.0 ± 9.0
V	4.8 ± 3.2 (n = 47)	29.4 ± 5.9

Aggregation

The nymphs of *N. albipennis* were aggregated in the spittle masses; up to 4 nymphs per spittle mass were discovered (Fig. 3). The highest aggregation occurred in instar I where 63.4% lived in aggregations in Br498, 44.4% in Br2. In Br498 19.5% of instar I lived twosome in the spittle, 39.0% threesome and 4.9% foursome. In Br2 instar I did not aggregate beyond twosomes. Patch differences were less pronounced for later instars. The degree of aggregation generally decreased with successive instars. The degree of aggregation declined from instar I to instar III and varied from 9.0 and 14.8% for instar IV and V. Instar IV and V were never found aggregated beyond threesomes.

In addition to *N. albipennis*, nymphs of the spittlebug *Philaenus spumarius* (Linnaeus, 1758) were recorded. In 4 out of 368 spittle masses examined (1.1%), the nymphs of both species were found in the same spittle mass. Beyond instar III, however, no nymphs of *P. spumarius* were found together with *N. albipennis*.

Mortality

The mortality of the nymphs decreased from instar I to instar IV (Table 3). The highest mortality rate was found

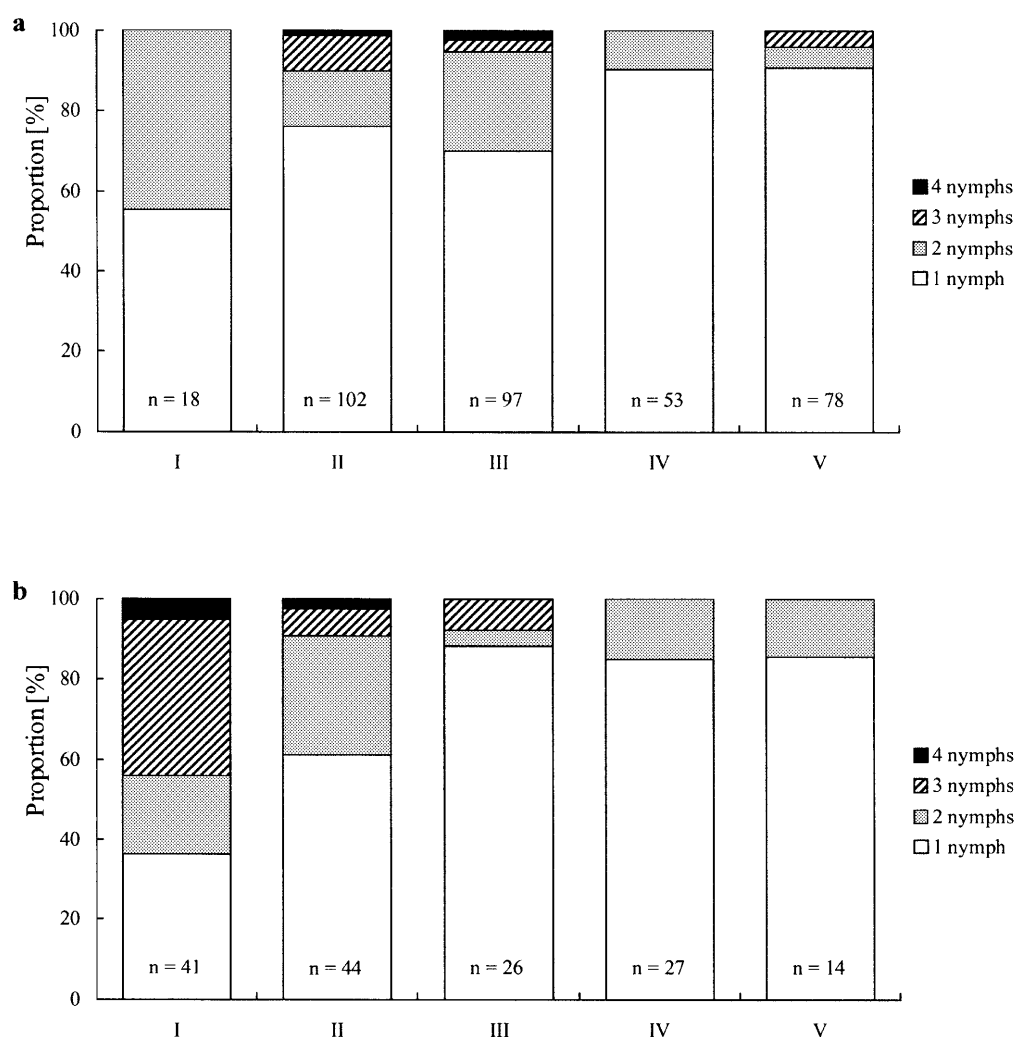


Fig. 3. Aggregation of the nymphs of *Neophilaenus albipennis* in (a) Br2 and (b) Br498.

in instar I, 0.833 in Br2 and 0.500 in Br498. The mortality of instar IV was 0.311 and 0.462 in Br2 and Br498, respectively. The overall survival rate from instar I to instar V (Fig. 4) was similar in both patches, 0.043 in Br2 and 0.085 in Br498. The mortality from instar V to the adults was only measured using the cages and was 0.167 in both patches. Thus the total survival rate from instar I to the adults was estimated at 0.036 in Br2 and 0.070 in Br498.

A significant difference in the mortality was found between aggregated and non-aggregated nymphs ($\chi^2 = 4.39$, $p = 0.036$, $n = 245$, all samples pooled). In both patches, Br2 and Br 498, the mortality was 0.090 to 0.361 lower (mean 0.205) in aggregated nymphs (Table 4). The difference between aggregated and non-aggregated nymphs was apparent in all instars I to IV and was fairly stable through the development of the nymphs. The mor-

tality was not influenced by vegetation height at the location of the nymphs. In a logistic regression analysis the vegetation height yielded no significant explanation of survival of the nymphs ($\chi^2 = 1.962$, $p = 0.161$, $n = 221$, all samples pooled).

As in free-living nymphs, nymphal mortality in the cages decreased with instar (Table 3). The mortality in instar I was 0.500 in Br2 and 0.583 in Br498 whereas in instar IV almost all nymphs survived to the succeeding instar. With the exception of instar III in Br2 and instar I in Br498, nymphal mortality in the cages was reduced. However, the total survival rate from instar I to instar IV was higher in nymphs in the cages (Fig. 4), 0.140 in Br2 and 0.176 in Br 498. Overall, however, there was no significant difference in survival between nymphs in the cages and free-living nymphs ($\chi^2 = 2.693$, $p = 0.101$, $n = 322$, all samples pooled).

TABLE 2. Comparison of the vegetation height at nymph locations and random locations using t-test.

Patch	Nymphs			Random			t-test	
	Vegetation height [cm]	S.D.	n	Vegetation height [cm]	S.D.	n	t	p
Br2	21.7	6.7	51	14.6	5.4	19	-4.068	< 0.001
Br498	17.9	6.6	18	14.8	5.2	20	-1.640	0.110

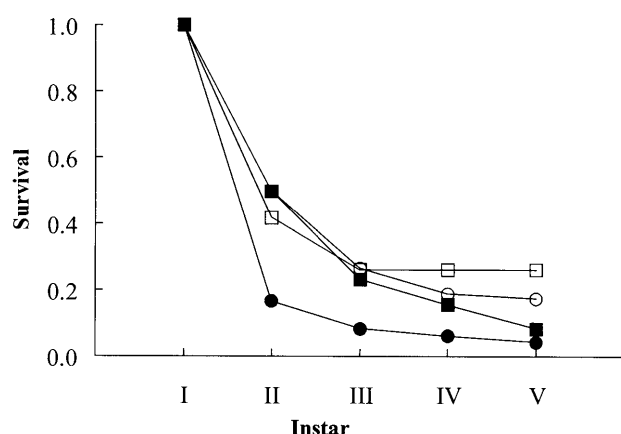


Fig. 4. Survival rate of the nymphs of *Neophilaenus albipennis* in Br2 (circles) and Br498 (squares) determined with two methods: Individual marking (solid symbols) and caging with exclusion of predators (open symbols).

DISCUSSION

Survival of the nymphs

The nymphal mortality rates decreased with instar and were similar to mortality rates estimated in other *Neophilaenus* species (Whittaker, 1965b). No substantial difference in total survival rate was found between the two patches Br2 and Br498, however, the phenology of the nymphs differed. Patch Br2 is a south facing slope with an inclination of 2 degrees, whereas the patch Br498 is north-east facing with an inclination of 25 degrees. The date of occurrence of the instars was apparently delayed in the north facing slope.

The cages used to determine nymphal mortality excluded predators. A comparison with mortality rates obtained from free-living nymphs might yield an estimate of predation rate. However, the cages could affect microclimate or host plant quality (e.g. Crafts-Brandner & Chu, 1999) and thus mortality rates of the caged nymphs. A more controlled study would be necessary to quantify possible cage-effects. Nevertheless, the results indicate that nymphal mortality of *N. albipennis* may only be little affected by predation, a conclusion concordant with existing studies on other spittlebugs. Although in some species predation by invertebrates and birds has been recorded by indirect data of prey records (Harper & Whittaker, 1976; Callan, 1980; Kristin, 1995), in all quantitative studies very low rates of predation have been found (Whittaker, 1965b, 1970, 1971; Halkka & Kohila, 1976).

Despite the observation of a clumped occurrence of nymphs in tall vegetation, the analysis of nymphal mortality in relation to vegetation height yielded no indication

TABLE 3. Stage specific mortality (q_x) of the nymphs of *Neophilaenus albipennis* determined with two methods: individual marking (IM) and caging (CA).

Instar	Br2 mortality (q_x)		Br498 mortality (q_x)	
	IM	CA	IM	CA
I	0.833 (n = 12)	0.500 (n = 2)	0.500 (n = 18)	0.538 (n = 12)
II	0.490 (n = 51)	0.467 (n = 15)	0.538 (n = 26)	0.375 (n = 8)
III	0.261 (n = 46)	0.294 (n = 17)	0.320 (n = 25)	0.000 (n = 6)
IV	0.311 (n = 45)	0.083 (n = 12)	0.462 (n = 22)	0.000 (n = 5)
V		0.167 (n = 24)		0.167 (n = 6)

of enhanced survival. Female spittlebugs of the genus *Neophilaenus* deposit their eggs in clumps on their host plants (Braasch, 1960; Whittaker, 1965b). The observed concentration of nymphs of *N. albipennis* in tall vegetation may be due to preferences of the females when laying eggs. However, differences in hibernating egg mortality between tall and low vegetation might also be responsible for the observed accumulation.

Formation of aggregations

Nymphs of *N. albipennis* on the same host plant live aggregated in their spittle masses. The degree of aggregation (maximum: 1.7 nymphs per spittle) was comparable to other spittlebugs (e.g. Whittaker (1965b) reported in *Neophilaenus lineatus* maximum 1.5 nymphs per spittle, in *Neophilaenus exclamationis* maximum 1.2 nymphs per spittle). Although spittle masses of *N. albipennis* were usually limited to the basal 5 cm of the stem and there is a high degree of overlap among instars, height on the plant increases significantly with instar. The preference of distinct parts of the host plant has also been shown by McEvoy (1986) in the two spittlebugs *Philaenus spumarius* and *Lepyronia quadrangularis*. The diameter of the *N. albipennis* spittle masses is much less than the potential distance between recorded feedings sites on the host plants. Thus, the spittle masses of several nymphs on one host plant should not necessarily be confluent. That all nymphs on that plant live aggregated in one spittle mass is evidence for strong aggregation. How does this aggregation come about? It is known that female spittlebugs of the genus *Neophilaenus* deposit their eggs in clumps in rifts like axils of their host plants (Braasch, 1960; Whittaker, 1965b). So it seems likely that the aggregation of the nymphs at the first instar may be due

TABLE 4. Stage specific mortality (q_x) of non-aggregated and aggregated nymphs of *Neophilaenus albipennis*.

Instar	Br2 mortality (q_x)		Br498 mortality (q_x)	
	Non-aggregated	Aggregated	Non-aggregated	Aggregated
I	0.889 (n = 9)	0.667 (n = 3)	0.667 (n = 6)	0.417 (n = 12)
II	0.528 (n = 36)	0.400 (n = 15)	0.571 (n = 14)	0.333 (n = 12)
III	0.290 (n = 31)	0.200 (n = 15)	0.350 (n = 20)	0.200 (n = 5)
IV	0.342 (n = 38)	0.143 (n = 7)	0.611 (n = 18)	0.250 (n = 4)

to clumped egg-laying rather than to active crowding over larger distances.

Causes of reduced mortality of aggregated nymphs

The nymphs of *N. albipennis* live aggregated in spittle masses and the degree of aggregation declines with increasing development as documented in most studies on spittlebugs (Oomen, 1975; Bales & Furniss, 1984; Akiyama & Matsumoto, 1986; but see Whittaker, 1965b). The aggregation of the nymphs resulted in a reduced mortality during nymphal development. Although it has been argued that aggregation may be an advantage (e.g. Matsumoto, 1990), this study is the first direct evidence for the benefit of aggregation to individual spittlebug nymphs.

In phytophagous insects it is believed that one major benefit of aggregation is a reduced predation risk (e.g. Cappuccino, 1987; Turchin & Kareiva, 1989; Lawrence, 1990). However, as the predation pressure on spittlebug nymphs generally is rather low (see above), it is unlikely that protection from predation is a major cause of the reduced mortality rates of aggregated nymphs. Thus, other reasons should explain the reduced mortality of aggregated spittlebug nymphs. One, as known from other insects (e.g. Tsubaki & Shiotsu, 1982), aggregations may have advantages for the exploitation of food resources. In spittlebugs, there may be a nutrient sink in the vicinity of other nymphs. Two, after destruction of the spittle (such as from heavy rainfall) aggregated nymphs may be able to build up the protecting spittle more quickly than single nymphs. Three, each nymph in an aggregation could reduce its contribution to the production of spittle and could thereby save energy and resources (Bales & Furniss, 1984).

The aggregation of *Aphrophora* spittlebug nymphs has been shown to increase with density (Matsumoto, 1990; Biedermann, unpubl.). However, there may be a trade-off between the benefit of aggregation and increased intra-specific competition between nymphs. At low densities, the aggregation may be beneficial. The mortality is reduced in aggregated nymphs, as shown in this study. At higher densities the aggregation (with up to 100 nymphs in some species) may be limited by feeding site availability so that intra-specific competition may increase and override the beneficial effect of aggregation. In fact, Matsumoto (1990) found the lowest mortality of the nymphs of *Aphrophora flavipes* at medium densities and thus medium aggregation. In *N. albipennis* the aggregation of up to 4 nymphs resulted in higher survival rate whereas it remains untested what happens at higher densities and aggregations.

A second possibility of a disadvantage of aggregation concerns the physiology of the host plant. The aggregation of spittlebug nymphs may be an advantage under normal conditions, where xylem is not limited. However, during longer periods of draught, the content or flow of xylem sap may be deteriorated. As a consequence, competition between nymphs in one spittle may occur and may result in the survival of the fittest nymph in the spittle.

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