Population Dynamics Features
of Willow-feeding Aphids

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Willow-feeding aphid colonies were sampled on scattered trees *(Salix alba)* from April until November, in 1999. The collected individuals belonged to 9 aphid species of 3 families *(Lachnidae, Chaitophoridae, Aphididae).* The aphid populations showed two peaks in May and in October. The indirect negative effect of the rainfall seems to be responsible for this temporal pattern. The Shannon diversity also exhibited spring and autumn peaks during the year. The willow-feeding aphid guild seasonally rearranged, different species were dominant in each period. Four types of population dynamics of the 9 species were established based on the abundance changes. The time of appearance of different morphs in two dominant species was compared, they belonged to *Pterocomma genus.* In spring, there were uncoordinated schedule in the development of populations of *P. pilosum konoi* and *P. rufipes,* the different morphs of *P. pilosum konoi* increased earlier. In autumn both species reached their peaks simultaneously, but there were fewer individuals of *P. pilosum konoi* for a longer time. This species was more vulnerable to aphid parasitoids in each season.

Keywords: Aphids, coexistence, diversity, guild structure, seasonality, weather variables.

Aphids are among the favourite objects of insect population dynamics studies. Their population density can fluctuate considerably over different spatial and temporal scales (Hales et al., 1997). A number of studies deals with the abundance changes between years (Honek, 1991; Woiwod and Hanski, 1992; Brown and Schmitt, 1994; Sequeira and Dixon, 1997; Thacker et al., 1997; Jarosik and Dixon, 1999). There is a well-demonstrated auto-correlation in abundance between consecutive years (Sequeira and Dixon, 1997). The within-year population dynamics of aphids were less studied (Dixon, 1987).

In temperate regions there is synchronization between vegetation development and aphid life cycles. Bud burst and leaf fall of plants mark the beginning and the end of the aphid season (Dixon, 1987). The general seasonal dynamics of most aphids can be described with two abundance peaks in spring and autumn, and commonly there is a drastic summer decrease. In spring, parthenogenetic reproduction and overlapping of generations are common to most aphid species, resulting high densities (Sequeira and Dixon, 1997). However, in early spring parasitoids can reduce the rate of increase of populations in the consecutive periods (Tomanovic et al., 1996). The possible reasons of summer decrease are as follows: migration of alatae, high temperature, natural enemies (predators, parasitoids and entomopathogens), poor-quality food (leaf age) and density-dependent competition (Szalay-Marzsó, 1969; Dixon, 1977, 1987; Honek, 1987; Thompson, 1988; Sequeira and Dixon, 1997). The importance of these factors is very variable depending on the life

history of various aphid species. Certain aphids are able to reproduce on woody hosts in summer (Dixon, 1977). Sexual morphs occur in autumn before leaf fall as a result of low temperature and short day length (Szalay-Marzsó, 1969; Dixon, 1977, 1987; Ward et al. 1984).

Density dependence is common in aphids, because they can reach very high abundances (Woiwod and Hanski, 1992; Dixon, 1998). Regulation can be observed only by extreme densities, but the population may be well limited by density-independent factors (e.g. weather) (Strong, 1986). The population density is influenced by the different growth and reproductive rates of the different aphid stages and morphs (Hales et al., 1997).

Aphid life cycles are complex. These insects are highly polymorphic and have many generations. The morphs differ not only in external morphology but in biology, even within a morph there is variation. This phenotypic variation is responsible for the success of aphids (Dixon, 1977). Each morph is adapted preferentially to either dispersal, reproduction or survival (Dixon, 1987).

This paper presents the seasonal dynamics of aphid populations living on *Salix alba.* The main aimes of this study were as follows: (1) comparison of the life cycles of species, (2) study of the effect of weather conditions on the abundance changes of aphids, (3) establishment of the temporal changes of species diversity, (4) investigation of the re-arrangement of the phloem-sucking guild during the year, (5) separation of the population dynamics strategies of coexistent species, (6) to reveal interspecific competition differences between life cycles of closely related, similarly behaving species, (7) establishement of the preference of parasitoids.

Materials and Methods

In 1999, we collected aphid colonies from dispersed willow trees *(Salix alba)* in the Great Hungarian Plain, in the vicinity of Kiskőrös. 33 trees were examined from 7th April until 10th November fortnightly as a rule, but in July and August there were only three sampling because of the aestivation period of aphids. Aphids were collected from 10 randomly selected shoots from the canopy of each tree and aphids found were preserved in 70% ethil-alcohol. Aphid species were identified by phase contrast microscope. We counted the different morphs, fundatrices, apterous and alate viviparous females, males, sexual females, larvae with external wing pads and larvae. We did not draw distinction between instars. The number of infected aphids (with aphid parasitoid) was also recorded.

We used climate data to analyse the potential environmental correlates of the population dynamics. The rainfall and the temperature data derived from a meteorological station, 20 km from the investigated area. The amount of rainfall (in mm) and the average of the daily maximum temperatures two weeks before the sampling date were taken into account.

To determine the changes of diversity the Shannon formula was used. We have computed Spearman rank correlation coefficients between the changes of the abundance of aphids and the climate data.

Results

During 1999 63,051 individuals of 9 aphid species belonging to 3 families *(Lachnidae, Chaitophoridae* and *Aphididae)* were collected. The most frequent aphid species were *Chaitophorus vitellinae* (Schrank), *Pterocomma rufipes* (Hartig), *Pterocomma pilosum konoi* Hori and *Tuberolachnus salignus* (Gmelin). Seven out of the 9 species are monoecious, the two *Cavariella* species [(*C. aegopodii* (Scopoli) and *C. theobaldi* (Gillette and Bragg)] are heteroecious *(Table 1).*

Table 1

Individual number and host alternation of the 9 species living on *Salix alba*

Species	Abbreviation	Individual number	Host alternation
Chaitophorus vitellinae	Ch vit	22921	monoecious
Pterocomma rufipes	Pt ruf	16262	monoecious
Pterocomma pilosum konoi	Pt pil	14069	monoecious
Tuberolachnus salignus	T sal	4932	monoecious
Chaitophorus salijaponicus niger	Ch nig	2072	monoecious
Cavariella theobaldi	C theo	1208	heteroecious
Plocamaphis flocculosa brachysiphon	P floc	669	monoecious
Cavariella aegopodii	C aego	37	heteroecious
Pterocomma salicis	Pt sal	24	monoecious

The aphid populations on willow trees showed two peaks in May and October based on both the number of shoots with aphid colonies and individual number of aphids *(Fig. 1).* The figure shows that in the autumn the individual number of aphids had began to increase earlier than the number of infected shoots. At that time the size of population started to increase intensively and the dispersion was followed later by the growth of colony size.

To reveal the background of the aphids' population dynamics we compared the abundances of aphids with the changes of rainfall *(Fig. 2).* The abundance minimum was in rainy summer, but this period of the year may be adversed because of the high temperature, too. There was no significant correlation computed by Spearman rank correlation coefficient between the amount of rainfall and the individual number of aphids, but the negative relation is evident between them, mainly in the summer and autumn periods. Therefore, we established two categories based on the amount of the rainfall. We compared the number of aphids of those two weeks periods when rainfall was above 40 mm with those of below 40 mm. There was significant difference in the individual number between the rainy and the less rainy periods used Mann-Whitney test ($z = -3.06$, $p < 0.01$). The changes of aphid abundance also did not show any significant correlation with the maximum mean temperatures (average of the daily maximum temperatures). However, there was significant difference between number of aphids of the optimal (18–25 °C) and sub-
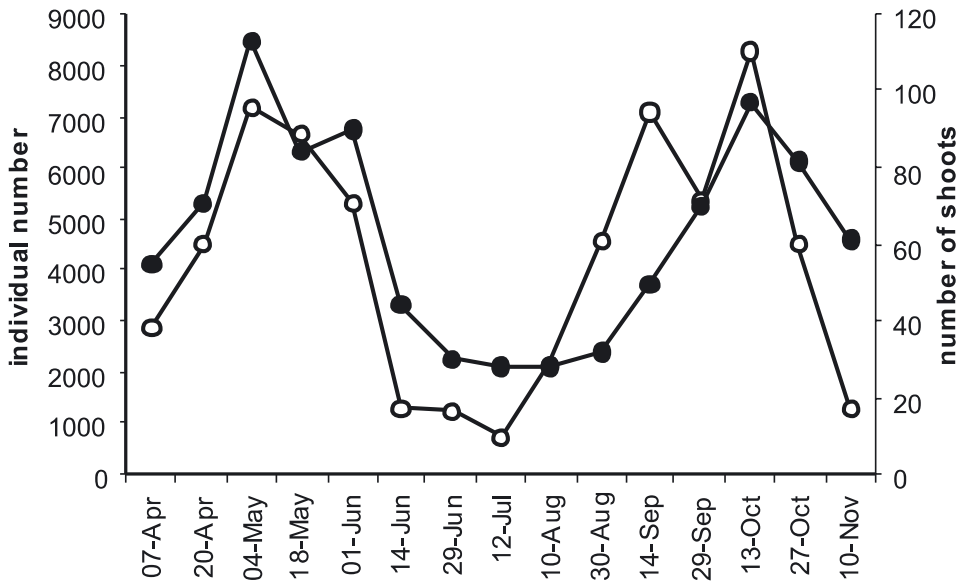
Fig. 1. Seasonal dynamics of aphids based on the individual number (open circles)
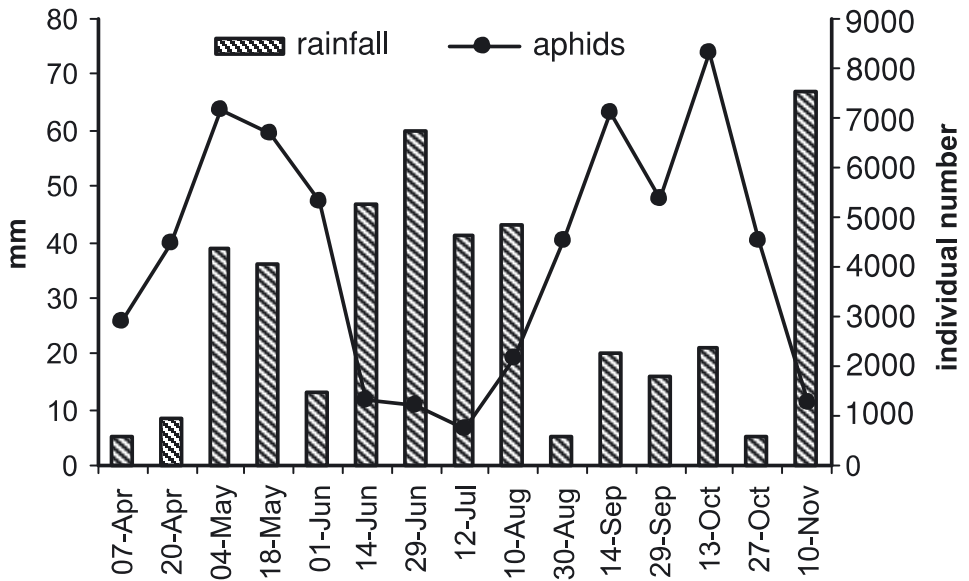and occupied shoots (solid circles)

Fig. 2. The changes of rainfall throughout the year compared
with seasonal dynamics of aphids

optimal periods (z = –2.1988, p < 0.05). Analysing the relation between climate data and population dynamics of the frequent species being present throughout the year (*Chaitophorus vitellinae, Ch. salijaponicus niger, Pterocomma rufipes* and *P. pilosum konoi*), only the abundance of *P. rufipes* (z = –2.26, p < 0.05) and *P. pilosum konoi* (z = –2.51, p < 0.05) showed a significant negative relation with the amount of rainfall. The temperature has a detectable effect only on *Ch. vitellinae* (z = –2.54, p < 0.05).

Similarly, the Shannon diversities exhibited two peaks, one in spring and one in autumn *(Fig. 3).* In summer both the number of the individuals and the number of species decreased. In October eight species were present.
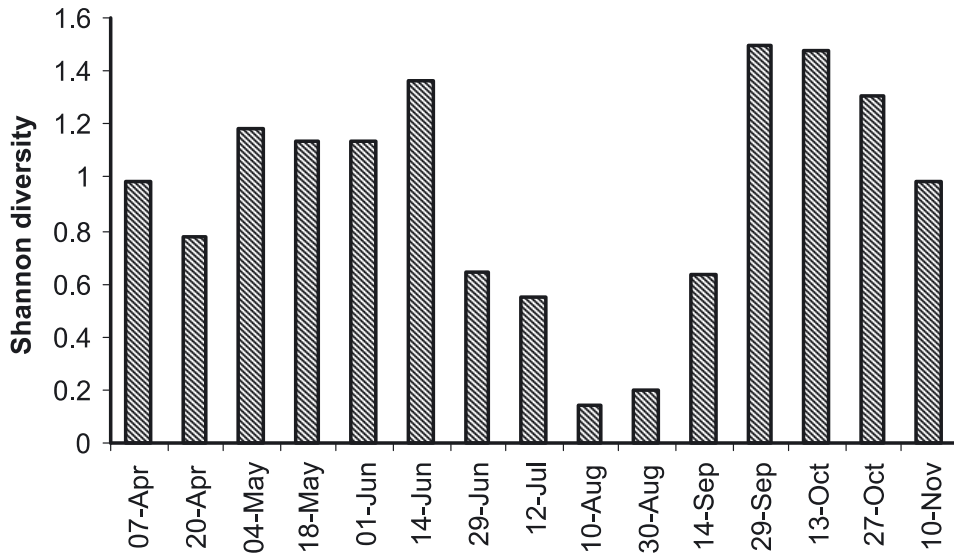

Fig. 3. Dynamics of aphids' Shannon diversity

The order of species rank based on the number of occupied willow trees was different throughout the year, than in the particular seasons *(Fig. 4).* For example, *Chaitophorus vitellinae* was found on most of the trees throughout the year, but it had the first rank only in the summer. The *Pterocomma* species were forced back in the summer, but their distributions were different in the cooler seasons: in the spring *P. rufipes* occupied more trees but in the autumn *P. pilosum konoi.* The behaviour of anholocyclic *Tuberolachnus salignus* was interesting. This is one of the most distributed species throughout the year. However, this species appeared in the middle of September and spread within a few weeks. We can say that the structure of the aphid community rearranged throughout the year, considering mainly the frequent species. This phenomenon is probably due to the different features of population dynamics of the aphid species.
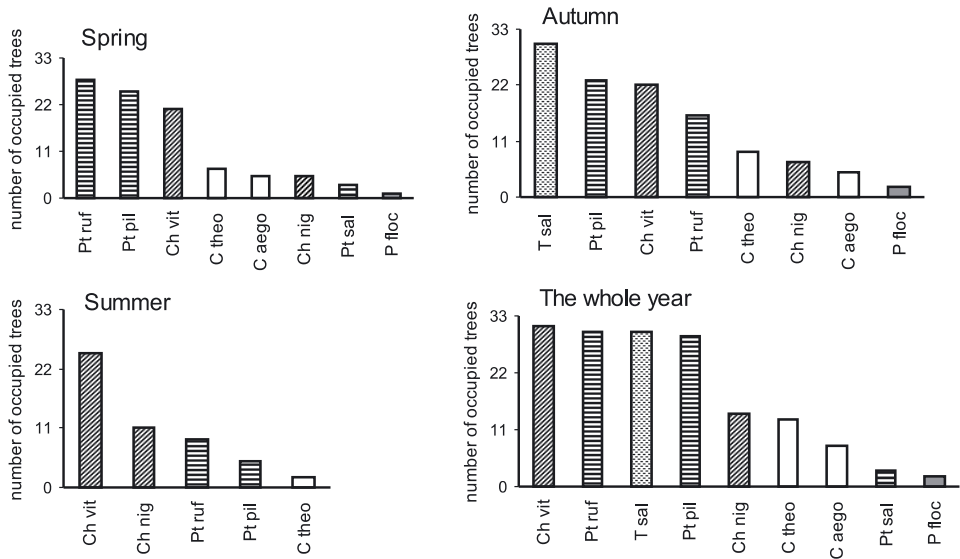
Fig. 4. The order of rank of aphid species based on the occupation of willow trees,
seasonally (spring: 04.07–06.01. summer: 06.14–08.30. autumn: 09.14–11.10.)
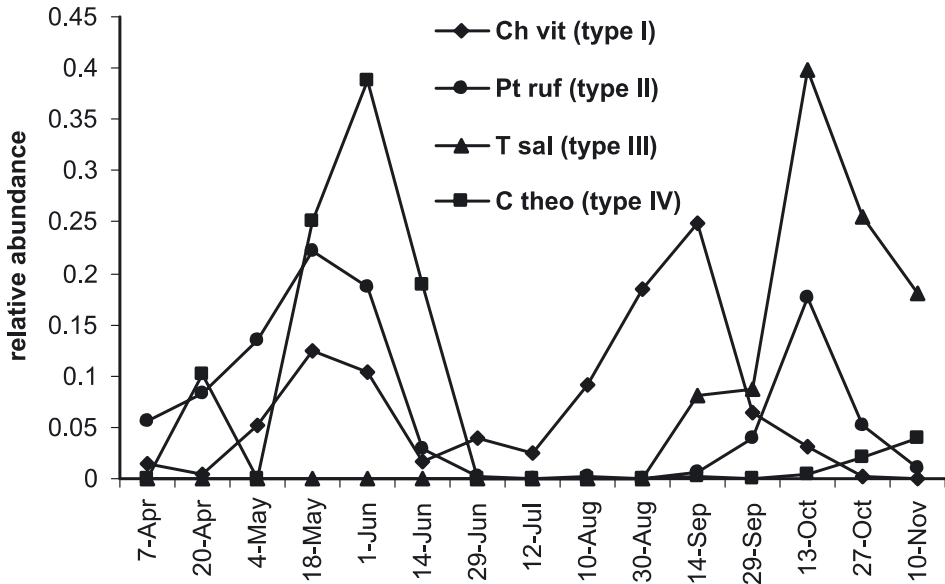and the whole year

Fig. 5. Relative abundance changes of four willow-feeding aphids representing four types
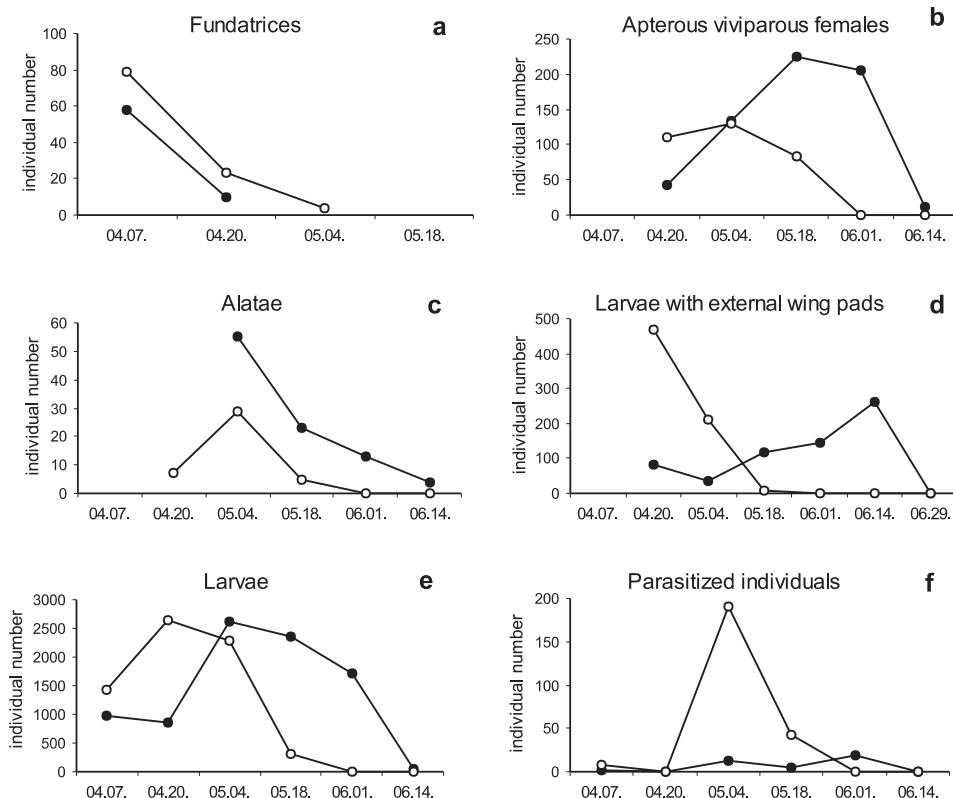of population dynamics (for details see text)

Fig. 6. The abundance changes of different morphs (a–e) and parasitized individuals (f)
of *Pterocomma pilosum konoi* (open circles) and *P. rufipes* (solid circles), in spring

The aphid species living on willow trees can be classified in different types of popu-
lation dynamics *(Fig. 5)*. The *Ch. vitellinae* represented a special type: in the spring it had
a lower peak, then the number of the individuals decreased moderately (in summer this
species is dominant), in the autumn it reached a large population density. The second type
of population dynamics showed two peaks too, but the spring peak was higher and the
summer decrease was stronger (*Ch. salijaponicus niger, P. rufipes* and *P. pilosum konoi*). In
the third type those species can be classified which were present only in the autumn in the
canopy of willows (*Tuberolachnus salignus* and *Plocamaphis flocculosa brachysiphon*).
The previous species were monoecious. The two host-alternating species (*Cavariella
theobaldi* and *C. aegopodii*) disappeared from willow trees in July after the spring increase
(they migrate to the secondary hosts), and they appeared again in October in a smaller
number of individual.

There may be difference among similarly behaving species in the appearance time
of their various morphs (fundatrices, apterous and alatae viviparous females, sexual
morphs). We analysed the occurrence of the temporal shifts. The two *Pterocomma* species

proved to be convenient, because their population sizes were comparable, and their colour, size, feeding site and population dynamics were similar.

Fundatrices appeared already in early April of both species, but at *P. pilosum konoi* there were more fundratrices *(Fig. 6a)*. This is interesting because there were less apterous viviparous females of this species than of *P. rufipes*. The other morphs of *P. pilosum konoi* (apterous and alatae viviparous females, larvae with external wing pads and larvae) appeared in spring earlier and/or reached their peak sooner *(Fig. 6b–e)*. In this period, there was considerable difference in the number of parasitized individuals between the two species. Six times more parasitized specimens were found in *P. pilosum konoi* than in *P. rufipes (Fig. 6f)*. In the summer months the number of individuals of both species decreased and only apterous viviparous females and larvae could be observed in this period.
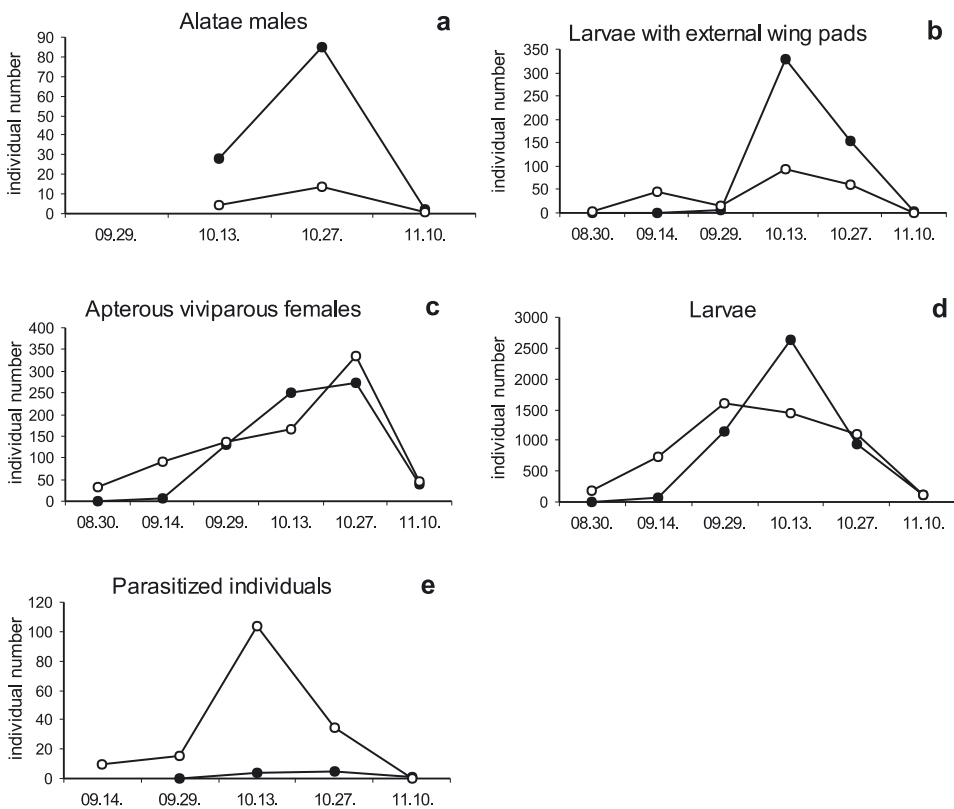

Fig. 7. The abundance changes of different morphs (a–d) and parasitized individuals (e) of *Pterocomma pilosum konoi* (open circles) and *P. rufipes* (solid circles), in autumn

In the autumn both sexual morphs and viviparous females (apterous and alatae) appeared. The sexual females were difficult to separate from the apterous viviparous females, therefore only the alatae males were analysed. (The oviparous females were

present from 27th October.) The peak of the different morphs of both species occurred at the same time *(Fig. 7a–d)* but the various morphs of *P. pilosum konoi* appeared earlier, thus, they were present longer. However, the number of these morphs was lower than of the different morphs of *P. rufipes.* The number of the parasitized aphids was also higher in the colonies of *P. pilosum konoi* (about 16 times more) in this period *(Fig. 7e).*

Discussion

In temperate regions most of the aphid species show spring and autumn peaks in their population dynamics (Szalay-Marzsó, 1969; Dixon, 1977, 1987). Similarly, we have found this kind of seasonal changes, too. Not only the host alternating species have two abundance maximum but those species also which live on woody hosts throughout the year. Demographical rates change in time, that is the cause of fluctuations (Kareiva, 1986).

The body of aphids is weakly sclerotized, therefore they are exposed to adversity of weather. Thus the environmental conditions can influence the population dynamics. Different factors have effect on the density of aphid populations in the particular phases of their life cycle. In *Myzus persicae* climatic variables influence not only the rates of development but also the flight behaviour and the activities of natural enemies (Bale et al., 1991). Thacker et al. (1997) emphasize the importance of rainfall in connection with host plant quality in summer decrease of *Aphis fabae* populations. Temperature-moisture stresses have great impacts on both carbon and nitrogen metabolism of plants (Mattson, 1980). Host quality and leaf nitrogen content of the plants affect the performance and growth rates of aphid populations (Mittler, 1958; Weber, 1985; Honek, 1991, 1994; Kindlmann and Dixon, 1994). In cereal aphids the period of summer flight activity is also influenced by the ripening of the cereals (Basky, 1998; Basky and Harrington, 2000). According to the present data, the rainfall had adverse effect on aphid populations, but this negative influence can be indirect. The climatic factors change the nutritional quality of the host plant, in this way they can affect the growth rates of aphid populations. We have shown negative, but rather significant effect of rainfall in the case of *Pterocomma* species. Temperature influence the abundance changes only of *Chaitophorus vitellinae,* the other species tolerate cooler weather.

The explanations of the summer decrease in diversity can be that the host-alternating species leave the primary host in summer and the other species decrease below detectable level. In this period aphids estivate or continue to reproduce, although at a lower rate than at the beginning of the year (Dixon, 1977). This is related to the changes of the host plant quality. The dominance of only one species, *Chaitophorus vitellinae,* can be observed, although its number decreases slightly.

The coexistent species have different demands and strategies. They divide the common habitat both in space (different feeding sites) and in time. This leads to seasonal rearrangement of willow-feeding aphid guild. Those species which appear only on few trees are rare throughout the whole year. In turn, frequent species changes their position (e.g. *Tuberolachnus salignus*).

Each aphid generation is exposed to a particular range of conditions, this has led to the generation-specific strategies (Dixon, 1987). Different species can have different temporal dynamics on the same host plant. The relative importance of biotic and abiotic factors effecting growth and reproductive rates can vary between species (Hales et al., 1997). We can classify the nine species living on *Salix alba* into four type. Naturally there is difference between heteroecious and monoecious species, but we can distinguish particular strategies within the latter group.

The population dynamics or spatial distribution of closely related, coexistent species should be different because interspecific competition can occur between them for the feeding site of higher quality. Temporal separation is one of the reducing factors of inter-specific competition. In case of gall-forming aphid guild, Inbar et al. (1995) found that fundatrices hatched in spring at various time. We studied life cycles and population dynamics of two *Pterocomma* species. The number of both species is low in summer. The species' appereance is different in spring and in autumn. In spring, temporal shift can be observed. In autumn, there is no temporal shift, but the density of *Pterocomma pilosum konoi* is lower, and it is present on the willow trees longer, than of *P. rufipes.* Our investigation site is a patchy habitat where spatial separation can occur, but we did not discuss this possibility in this paper.

The role of parasitoids in aphid population dynamics is considered variously. For example, according to Tomanovic et al. (1996) parasitoids cannot follow the population growth of aphids. However, Hales et al. (1997) claim that parasitoids have more important effect on population density than predators, therefore they should act as density dependent factors. Weisser et al. (1997) investigated the effect of weather condition on life history of the aphid parasitoid *Aphidius rosae.* They found that wind and rain influenced reproductive success and parasitization patterns of the parasitoid. The efficiency of parasitoids depends on the aphid species, too. In accordance with our study parasitoids prefer *Pterocomma pilosum konoi* in each season. This can be the possible explanation of the lower autumn density of this species.

Acknowledgements

Literature

Bale, J. S., Harrington, R. and Howling, G. G. (1991): Aphids and winter weather I. Aphids and climate change. Proceedings of the 4th ECE/XIII. SIEEC, Gödöllő 1, 139–143.

Basky, Z. (1998): Fluctuation of cereal aphid abundance in a suction trap in Hungary. In: Nieto Nafria, J. M. and Dixon, A. F. G. (eds): Aphids in Natural and Managed Ecosystems. Universidad de León, León (Spain), pp. 519–523.

Basky, Z. and Harrington, R. (2000): Cereal aphid flight activity in Hungary and England compared by suction traps. J. Pest Science 73, 70–74.

Brown, M. W. and Schmitt, J. J. (1994): Population dynamics of woolly apple aphid (Homoptera: Aphididae) in West Virginia apple orchards. Environ. Entomol. 23, 1182–1188.

Dixon, A. F. G. (1977): Aphid ecology: Life cycles, polymorphism and population regulation. Ann. Rev. Ecol. Syst. 8, 329–353.

Dixon, A. F. G. (1987): Seasonal development in aphids. In: Minks, A. K. and Harrewijn, P. (eds): Aphids. Their Biology, Natural Enemies and Control. Vol. A, Elsevier Science Publishers, Amsterdam, pp. 315–320.

Dixon, A. F. G. (1998): Aphid Ecology. Chapman and Hall, London, Second edition, 300 p.

Hales, D. F., Tomiuk, J., Wöhrmann, K. and Sunnucks, P. (1997): Evolutionary and genetic aspects of aphid biology: A review. Eur. J. Entomol. 94, 1–55.

Honek, A. (1987): Effect of plant quality and microclimate on population growth and maximum abundances of cereal aphids, *Metopolophium dirhodum* (Walker) and *Sitobion avenae* (F.) (Hom., Aphididae). J. Appl. Entomol. 104, 304–313.

Honek, A. (1991): Factors determining the peak abundance of *Metopolophium dirhodum* (Homoptera: Aphididae) on cereals. Bull. Entomol. Res. 81, 57–64.

Honek, A. (1994): The effect of plant quality on the abundance of *Metopolophium dirhodum* (Homoptera: Aphididae) on maize. Eur. J. Entomol. 91, 227–236.

Inbar, M., Eshel, A. and Wool, D. (1995): Interspecific competition among phloem-feeding insects mediated by induced host-plant sinks. Ecology 76, 1506–1515.

Jarosik, V. and Dixon, A. F. G. (1999): Population dynamics of a tree-dwelling aphid: regulation and density-independent processes. J. Anim. Ecol. 68, 726–732.

Kareiva, P. (1986): Patchiness, dispersal and species interactions: consequences for communities of herbivorous insects. In: Diamond, J. and Case, T. J. (eds): Community Ecology. Harper and Row Publishers, New York, pp. 192–206.

Kindlmann, P. and Dixon, A. F. G. (1994): Evolution of host range in aphids. Eur. J. Entomol. 91, 91–96.

Mattson, W. J. (1980): Hebivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11, 119–161.

Mittler, T. E. (1958): Studies on the nutrition of *Tuberolachnus salignus* (Gmelin) (Homoptera, Aphididae) III. The nitrogen economy. J. Exp. Biol. 35, 626–638.

Sequeira, R. and Dixon, A. F. G. (1997): Population dynamics of tree-dwelling aphids: the importance of seasonality and time scale. Ecology 78, 2603–2610.

Strong, D. R. (1986): Density vagueness: Abiding the variance in the demography of real populations. In: Diamond, J. and Case, T. J. (eds): Community Ecology. Harper and Row Publishers, New York, pp. 257–268.

Szalay-Marzsó, L. (1969): Levéltetvek a kertészetben. (Aphids in Horticulture.) Mezőgazdasági Kiadó, Budapest, 1–187 pp.

Thacker, J. I., Thieme, T. and Dixon, A. F. G. (1997): Forecasting of periodic fluctuations in annual abundance of the bean aphid: the role of density dependence and weather. J. Appl. Entomol. 121, 137–145.

Thompson, J. N. (1988): Variation in interspecific interactions. Ann. Rev. Ecol. Syst. 19, 65–87.

Tomanovic, Z., Brajkovic, M., Krunic, M. and Stanisavljevic, L. (1996): Seasonal dynamics, parasitization and colour polymorphism of the pea aphid, *Acyrtosiphon pisum* (Harris) (Aphididae, Homoptera) on alfalfa in the south part of the Pannonian Area. Tiscia 30, 45–48.

Ward, S. A., Leather, S. R., Dixon, A. F. G. and Glen, D. (1984): Temperature prediction and the timing of sex in aphids. Oecologia 62, 230–233.

Weisser, W. W., Volkl, W. and Hassell, M. P. (1997): The importance of adverse weather conditions for behaviour and population ecology of an aphid parasitoid. J. Anim. Ecol. 66, 386–400.

Weber, G. (1985): Genetic variability in host plant adaptation of the green peach aphid, *Myzus persicae*. Ent. Exp. et Appl. 38, 49–56.

Woiwod, I. P. and Hanski, I. (1992): Patterns of density dependence in moth and aphids. J. Anim. Ecol. 61, 619–629.