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Mutual influences between aphids on a joint host plant

With 3 text figures

1. Problem

Many aphid species are found in dense colonies at the preferred sites on their host plants. Such aggregations are the result of locating a special point or position on the host plant and of negative or positive geotaxis, and often involve aggregation behaviour as well. *Acyrtosiphon pisum* (HARRIS) aggregations can even be induced by an artificial diet and in darkness (STRONG 1867). The massing of thousands of individuals in a single patch leads to the question of whether intraspecific competition arises. Interspecific competition is another problem (JERMY 1985). According to EASTOP (1986), about 4000 species of aphids are known and the vast majority (99%) have an obviously restricted range of host plants, which in most cases is expressed as host specificity at about the subgeneric level. Many plants are hosts of more than one aphid species and may be settled in addition by polyphagous and oligophagous species, thus giving rise to potential interspecific competition. According to our experience, a kind of allelopathy is discernible in some cases. However, other observations give the impression that sometimes a sort of mutual stimulation occurs.

2. Intraspecific competition

JERMY (1985) came to the conclusion that intraspecific competition for food may occur in phytophagous insects if coexisting individuals with identical resource requirements are localized on a limited food source. He points to the role of such intraspecific feeding competition in phytophagous insects as a possible density-dependent population regulation factor. In aphids, this density-controlled effect induces dispersal because in many, but not all, species crowding results in the proliferation of alatae.

Direct intraspecific competition involving aggression and fighting is known in some Pemphigidae. For three consecutive years, about 15 years ago, I found thousands of greyish black 1st instar fundatrices as described by LAMPEL (1960) for *Pemphigus spyrothecae* (PASS.) in April beneath a row of poplar trees (*Populus nigra pyramidalis*) that were simultaneously heavily infested by the galls of *P. spyrothecae*. At first I thought these larvae might have been blown down by the wind. However, the paper of AOKI and MAKINO (1982)

offered another explanation. These two authors observed 1st instar fundatrices of *Epipemphigus niisimae* which had settled on the midrib of a leaf on *Populus maximowiczii* before gall formation. When a second larva intruded, the original occupant and the invader fought in the developing cecidium often until one was overcome and died; such a fight between two 1st instar fundatrices is shown by a photo in the paper. The same paper quotes similar observations by other authors concerning *Pemphigus betae* and other Pemphigidae. In Switzerland and Austria, the 1st larvae of the 2nd generation following the fundatrix of *Pemphigus spyrothecae* are sometimes even real soldiers with thickened legs that successfully attack predators entering the galls (AOKI & KUROSU 1986).

The first-instar fundatrices of *Pemphigus betae* DOANE render an instance for intraspecific competition evoked by marked territorial behaviour. This aphid performs host alternation with *Populus angustifolia* in North America. 83% of the newly hatched 1st-instar stem mothers immigrate over a 3-day period to immature leaves on the *P. angustifolia* trees immediately after bud burst. However, only 1.6% of the tree's leaves were large enough to warrant 100% optimal settlement (WHITHAM 1978). The establishment site is restricted to the upper side of the leaf base on the midrib. When two or more larvae occupy the same leaf, they arrange themselves linearly along the midrib. In most cases, the largest stem mother wins the superior basal position by defending a linear territory of about 3 mm at the base of the leaf blade. The outcome of these interactions between competing first-instar stem mothers is determined by kicking and shoving contests, and they move "like boxers in a ring" (WHITHAM 1979).

A peculiar type of intraspecific aggression is exhibited by *Astegopteryx bambucifoliae* (Thelaxidae, Hormaphidinae, Cerataphidini) on its secondary host e.g. bamboos, and related aphids (AOKI & KUROSU 1985). A walking aptera becomes an attacker and jostles a stationary individual whose stylets are inserted into the plant tissue. The attacker butts the stationary aphid with the apices of its head horns and clasps it with its forelegs. The attacked insect performs a "headstand" by raising its abdomen. The attacker then usually stops butting and sooner or later goes away, but in about 26% of the cases the attacker succeeded in driving its competitor away.

3. Interspecific competition

TAMAKI & ALLEN (1969) observed that *Aphis gossypii* depressed the growth rate of *Macrosiphoniella sanborni* in mixed colonies on *Chrysanthemum morifolium*. However, the retardation did not lead to the disappearance of *M. sanborni*, but to a relatively stable equilibrium phase. On the other hand, *Myzus persicae* can be completely suppressed by *M. sanborni* and/or *A. gossypii*. These phenomena are attributed by the two authors to interspecific competition. Nevertheless a kind of allelopathy as described below cannot be excluded, and this is not included in competition in the strict sense.

JERMY (1985) studied interspecific competition in general in phytophagous insects and concluded that the incidence of regular interspecific competition is very limited even between species with identical resource requirements. We can confirm this in the case of the aphids. For instance the umbels of *Pastinaca sativa* are often heavily colonized by *Cavariella theobaldi* (GILETTE & BRAGG) and *Aphis fabae* SCOP. s. lat. together. In July, 1987, I found plants of *Arctium lappa* settled jointly by *Aphis fabae mordwilkoii* BÖRNER & JANISCH and *Brachycaudus cardui* (L.). The dense mixed colonies persisted until the remigrantes appeared in the proceeding season.

When apterae of *Acyrtosiphon pisum* are allowed to select between *Vicia faba* leaflets settled with *Megoura viciae* and aphid-free ones, no significant differences were observed (HOLTFRETER 1980).

4. Mutual stimulation

Drepanosiphum platanoides reared in clip-cages on the upper surface of *Acer pseudo-platanus* leaves whose undersides were settled by aestivating larvae of *Periphyllus acericola* were heavier after 14 days than on leaves uninfested by *P. acericola* (SHEARER 1976).

Feeding aphids induce biochemical transformations in the plant tissue. When *Aphis fabae* SCOP. is feeding in large colonies on leaves of *Vicia faba*, amino acids accumulate at the feeding site. This increase in amino acids is due mainly to locally induced proteolysis of leaf protein and partly to translocation from other organs of the plant (POEHLING 1985).

In experiments with *Sitobion avenae* (F.), which in nature preferably colonizes the ears of cereals and other Gramineae, 36% of the plant N accumulated in the ears of infested winter wheat, whereas the ears of aphid-free plants contained only 23% of the total N of the plants (JAHN et al. 1985). This higher N content implies improved nutrition, and *S. avenae* living on ears or panicles are therefore much bigger and also more strongly pigmented than individuals forced to develop on leaves (Fig. 1).

Amino acids and soluble nitrogen are present in high concentrations in galls (DIXON 1983). Their high nutritive value permits colonization also by aphids which are otherwise found rarely, if at all, on the gall producer's host. Thus, I have found well established colonies with large individuals of *Sitobion avenae* (F.) on *Holcus lanatus* at the cecidium of *Holcaphis holci* H. R. L. Likewise, I have seen dense colonization of *Brachycaudus cardui* (L.) on the galls of *Schizoneura lanuginosa* HARTIG, on *Ulmus campestris*. *Aphis fabae* on apple seedlings galled by *Dysaphis devecta* retained a constant body size for 4 successive

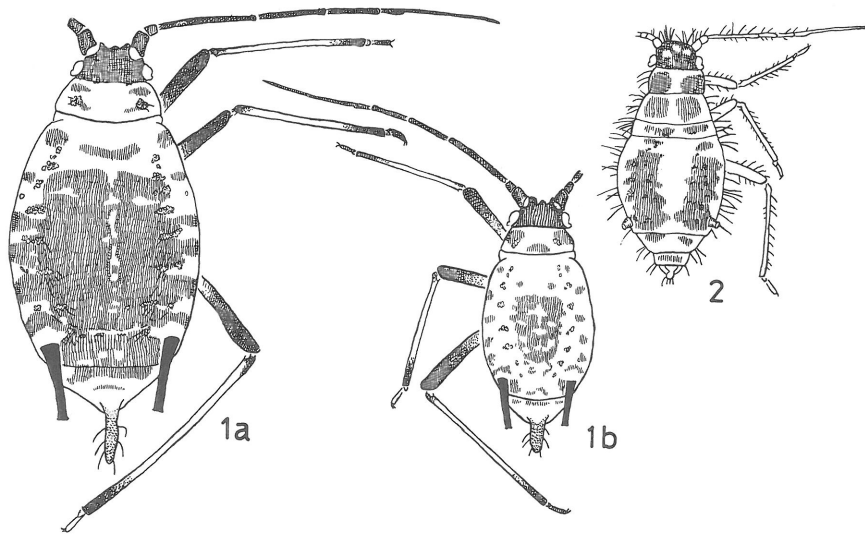


Fig. 1: *Sitobion avenae*: a. from oat panicles. — b. from culture on *Poa annua* without inflorescences. — Fig. 2: *Chaitophorus leucomelas*: Magnification 25× in 1, 30× in 2

generations, whereas in the absence of *D. devector* the size was distinctly smaller even in the first generation. In the IIIrd generation *A. fabae* required twice as long to attain adult stage without *D. devector*. Development of the leaf galls promotes shed of amino acids (FORREST 1971).

Chaitophorus leucomelas KOCH is monophagous on *Populus nigra*, especially the *pyramidalis* form, where it is often found on the surface of *Pemphigus* galls. At Rostock in a group of *Populus pyramidalis* which did not bear *Pemphigus* galls, *Chaitophorus leucomelas* was found exclusively in more or less dense colonies under the leaf vaginations produced by the fungus *Taphrina populina*.

5. Allelopathy

It has been observed in the laboratory and in the field insectary that in unintentionally mixed colonies one taxon can completely suppress the other. BLACKMAN (1979) reviewed the notices of some authors who alleged to have observed transformations of one race or species into another. He emphasizes the difficulties of avoiding contamination of aphid cultures by alien aphids from outside sources even in the laboratory because first-instar aphids are very easily overlooked. To the best of his belief, a single first-instar intruder may take over a culture. We can corroborate BLACKMAN'S observation.

A source of bright green *Lipaphis erysimi pseudobrassicae* (DAVIS) taken from cabbage in 1980 in the Sudan was reared on *Capsella bursa-pastoris*. On 11th July, 1984, the culture proved to be contaminated by a few dark olive green *Lipaphis erysimi* (KALT.) s. str. Apparently the intruding aphids were not removed completely, and in September the culture comprised exclusively the dark olive green *erysimi* s. str. A culture of an anholocyclic *Myzus persicae* (= *M. antirrhinii* MACCHIATI sensu BLACKMAN 1987) held in a greenhouse on *Rumex obtusifolius* was handed over to another team. About three months later the culture contained only *Myzus ascalonicus* DONC., *M. persicae* having completely disappeared. The same thing happened with a holocyclic strain of *M. persicae* which had been reared artificially during winter in a parthenogenetic generation sequence. Supervision was lax, however, and after about three months this culture also consisted exclusively of *M. ascalonicus*.

This kind of disappearance of one species (or subspecies) cannot be considered a result of competition because there is no evidence of either physical aggression or food deprivation. Very probably a substance in the saliva of one species has a detrimental effect on the food uptake of the other species. It is well known that Aphididae are generally phloem suckers. Aphids secrete two types of saliva through their stylets. While feeding, they emit a coagulating material which forms the sheath of the stylet canal and, in addition, a non-coagulating watery saliva (MILES 1959). As demonstrated with *Dysaphis devector* and *Myzus persicae*, salivary components injected by aphids are transported both upwards and down wards inside the plant (FORREST & NOORDINK 1971).

The salivas of 8 aphid species differed in their content of diverse amino acids and phenolic compounds, and the saliva of *Myzus ascalonicus* was characterized by a particular high level of phenolic substances (SCHÄLLER 1968). Free phenolic compounds in winter wheats bring about a high antibiosis against aphids (NIRAZ et al. 1987) and may also be responsible for the suppression of *M. persicae* on *Rumex* after settlement of *M. ascalonicus*. A behavioural component may also be involved, however, for *M. persicae* generally lives

scattered on the plants and does not form dense colonies like *M. ascalonicus*. Therefore, the behaviour of *M. persicae* may cause it to retreat from the crowded *M. ascalonicus* aggregations.

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Summary

In view of the massing of one or more aphid species together on a single plant, the occurrence of reciprocal effects may be anticipated. The proliferation of alatae in crowded colonies appears to be a consequence and a means of avoiding intraspecific competition. Intraspecific competition involving physical aggression is known only for some Pemphigidae and Hormaphidinae. It is not uncommon for two aphid species to colonize the same plant together without exhibiting signs of interspecific competition. The higher nitrogen content of the plant tissue either induced directly by sucking or caused by galling may stimulate the settlement or growth even of another aphid species. A kind of allelopathy has been observed in special cases in which an immigrant aphid species or race dislodges another. Obviously, this mechanism is based on biochemical properties of the intruder's saliva.

Zusammenfassung

In Hinblick auf das Massenaufreten einer oder mehrerer Blattlausarten zusammen an ein und derselben Pflanze können gegenseitige Wechselwirkungen erwartet werden. Verstärktes Auftreten von Geflügelten bei Überbesiedelung erscheint als die Folge oder als Mittel zur Vermeidung von intraspezifischer Konkurrenz. Intraspezifische Konkurrenz in Verbindung mit direktem Angriff ist nur bei manchen Pemphigidae und Hormaphidinae bekannt. Nicht selten besiedeln zwei Blattlausarten eine Pflanze gemeinsam ohne daß Anzeichen für interspezifische Konkurrenz erkennbar sind. Erhöhter Stickstoffgehalt in der Pflanze entweder als Direktwirkung des Saugens oder auf dem Wege über Gallbildung fördert Ansiedelung und Wachstum sogar einer anderen Blattlausart. Eine Art von Allelopathie wurde in besonderen Fällen beobachtet, wobei eine zugewanderte Blattlausart oder -rasse eine andere verdrängt. Dieses Verschwinden beruht auf biochemische Eigenschaften im Speichel des Eindringlings.

Резюме

Название работы: Взаимодействие тлей на одном растении-хозяине

При массовом появлении одного или нескольких видов тлей на одном и том же растении-хозяине можно ожидать взаимодействия. Усиленное появление крылатых при перенаселенности растения, может быть, является следствием или средством избежания внутривидовой конкуренции. Внутривидовая конкуренция в связи с прямым наступлением известна только при некоторых Pemphigidae и Hormaphidinae. Нередко 2 вида тлей заселяют одно растение, не показывая признаков межвидовой конкуренции. Повышение содержания азота в растении, обусловленное или сосанием тлей или образованием галлов, способствует даже заселению растений другим видом тлей и его размножению. В особых случаях обнаружили признаки вроде аллелопатии, причем переселившийся вид или переселившаяся раса вытесняют других тлей. Это вытеснение, по-видимому, обосновано биохимическими свойствами слюны «переселенца».

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