

Short communication

## Odour communication of *Rhopalosiphum padi* on grasses

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### Introduction

There is ample field evidence on the mobility of apterous aphids, suggested as part of a spacing mechanism leading to better exploitation of the food resource (Hodgson, 1991). Thus, a considerable proportion of apterae of *Sitobion avenae* (Fabr.), *Metopolophium dirhodum* (Wlk.) and *Rhopalosiphum padi* (L.) were found walking on the ground in cereal fields (Sopp *et al.*, 1987; Wikteliuss, 1989).

Although apterous aphids walking on the soil surface may also be the result of weather conditions, such as rain or wind (Araya & Fereres, 1991) or escape reactions after disturbance by predators (Nault & Phelan, 1984; Arakaki, 1989), adult apterous aphids of *R. padi* (Wikteliuss, 1989), *S. avenae* (Sopp *et al.*, 1987), and *Aphis fabae* (Scop.) (Way & Banks, 1967) have been observed leaving the plants spontaneously. This emigration of apterae seemed to be induced by crowding. A spacing pheromone would contribute to resource management and can be active even at moderate population densities.

In the present paper we report on the odour communication of alatae and apterae of *R. padi* on one of its summer hosts.

### Materials and methods

**Aphids.** Multiclinal stock cultures of *R. padi* were kept on oats in a greenhouse at temperatures between

18 and 22 °C and a light regime of L18:D6. Aphids to start the cultures were collected in June 1992 in a barley field south of Uppsala, Sweden.

**Olfactometer technique.** In previous studies of aphid pheromones, an olfactometric technique based on the mobility of aphids has been successfully employed (Pettersson, 1970). In brief, aphids are enclosed in an arena permeated by air coming from each of its four stretched out corners and drawn out through a hole above the center of the arena. The arena is divided into five zones, a central quadratic zone and four arm zones. Each arm zone is permeated only with air from a stimulus tube attached to that specific corner. The position of the test aphid individual in the arena is observed at intervals long enough to permit one individual to move from one place to another in the arena. Standard time intervals between observations were three minutes. The experiment was started 10 min after the aphid was introduced into the arena. After ten observations, the experiment was concluded and the cumulative number of visits in each arm zone computed and used as one replicate. If an individual was completely inactive between two consecutive observations, it was discarded. Test individuals and stimulus were changed between replicates. The construction of the olfactometer has been described in detail earlier (Pettersson, 1970). In the present studies, only one test individual at a time was placed in order to avoid social effects. Comparisons of cumulated visiting frequencies between the four arm zones were made using non-

parametric statistics using Wilcoxon one-tailed rank-sum test for two groups.

**Leaf settling test.** The experimental arrangement consisted of a 12 mm thick Styrofoam (Frigolite) plate with holes placed over a tray with water. Oat leaves cut from seedlings in decimal growth stage 20 (Zadoks *et al.*, 1974) and reaching the water in the tray, were placed through the holes in the plate, and held in place by a piece of foam. The surface around the leaves was covered with a filter paper, over which polyethylene rings (2 mm high  $\times$  15 mm diameter) painted with glue were placed in order to prevent the migration of aphids between different leaves at the base. Aphid groups of different sizes were placed at the base of each leaf and every 10 minutes a record was made of the number of aphids walking on the leaf. Each experiment consisted of six observations separated by 10-minute intervals. Two experiments were carried out where aphids had available for movement oat leaves of two different areas of c. 2.3 and 4.5 cm<sup>2</sup>.

## Results and discussion

The olfactometer results showed that odour from alatae of *R. padi* caused an arresting effect on conspecific alatae, and that odour from apterae had a repellent effect on conspecific apterae (Table 1). The latter effect cannot be interpreted in terms of alarm pheromones, since the repellent response was not observed when the same number of aphids was used without an oat leaf (Table 1).

The effects described above were apparent only when the aphids were on their host plant. It is unlikely that the effects are due to changes in the plant's chemistry since the time elapsed between aphids being placed on the test plant and the start of the experiment was typically as short as 15 min. Additionally, the following experiment was performed: the oat leaf on which 10 apterous individuals had shown repellency towards one test aptera ( $P = 0.008$ ) was tested against a fresh oat leaf using another test aptera. Differences obtained from 9 replicates were not statistically significant ( $P = 0.91$ , results not shown).

No response was observed of alatae towards apterae, or of apterae towards alatae, either alone or on oat leaves (Table 1).

When an increasing number of apterae on excised oat leaves served as the stimulus against oat leaves control, repellency towards a test aptera increased linearly

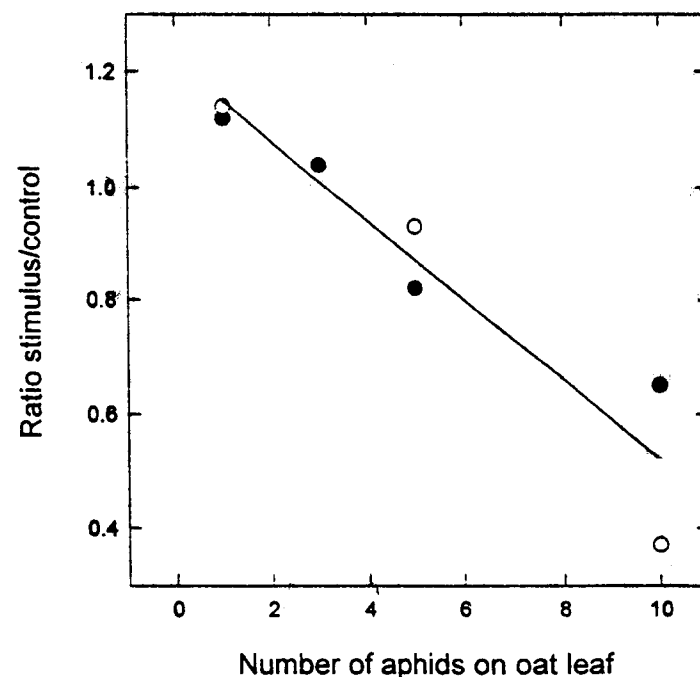


Fig. 1. Effect of different-sized groups of apterous *R. padi* located on an excised oat leaf (●) or on an undamaged oat seedling (○), on the behaviour of an individual test *R. padi* aptera in an olfactometer  $r^2 = 0.90$ . For each point on the graph  $n = 12$ .

(Fig. 1). The same effect was observed when undamaged oat seedlings were used as substrate, the points for both experiments falling on the same regression line (Fig. 1). Two possible explanations for these effects are: i) apterae always produce an odour repelling other apterae. In this alternative, the total stimulus produced would be proportional to the number of aphids emitting it, and only when present above a certain threshold (in the present case, the production by 5 aphid individuals), it would be perceived by the test aptera; ii) apterae produce a repellent stimulus only when their population density raises above a certain threshold (reached in this case at 5 aphids on an oat leaf of c. 2.3 cm<sup>2</sup>).

In order to test these alternatives, the same number of apterae serving as stimulus were used at two different densities, by varying the area of the leaf a given number of aphids was offered to move on. Repellency was measured as the mean number of unsettled aphids. Figure 2 shows the combined results from the two experiments, using aphid density as the independent variable. The curve drawn shows the existence of a threshold aphid density (c. 4 aphids/cm<sup>2</sup>) above which restlessness within the aphid cohort becomes density-dependent.

These results partly challenge earlier reports on the advantages of conspecific colonies of feeding aphids (Way, 1973; Way & Cammell, 1970; Chongrattaname-teekul *et al.*, 1991; Klingauf & Sengonca, 1970; Turchin & Kareiva, 1989). Our results may be related

Table 1. Olfactometer experiments with individual test alatae or individual test apterae of *Rhopalosiphum padi* placed in the arena

| Stimulus applied                   | Test alatae                     |    |       | Test apterae                    |    |      |
|------------------------------------|---------------------------------|----|-------|---------------------------------|----|------|
|                                    | Average visits in arm zones (#) | n  | P     | Average visits in arm zones (#) | n  | P    |
| 5. <i>R.p.</i> alatae on oat leaf  | 3.4                             | 12 | 0.009 | 2.3                             | 10 | 0.85 |
| oat leaf                           | 1.8                             |    |       | 2.4                             |    |      |
| 5. <i>R.p.</i> alatae              | 2.7                             | 12 | 0.12  | 2.5                             | 10 | 0.71 |
| blank                              | 2.1                             |    |       | 1.5                             |    |      |
| 5. <i>R.p.</i> apterae on oat leaf | 2.7                             | 10 | 0.26  | 1.5                             | 10 | 0.05 |
| oat leaf                           | 2.2                             |    |       | 2.7                             |    |      |
| 5. <i>R.p.</i> apterae             | 2.4                             | 10 | 0.54  | 3.0                             | 10 | 0.07 |
| blank                              | 2.2                             |    |       | 2.1                             |    |      |

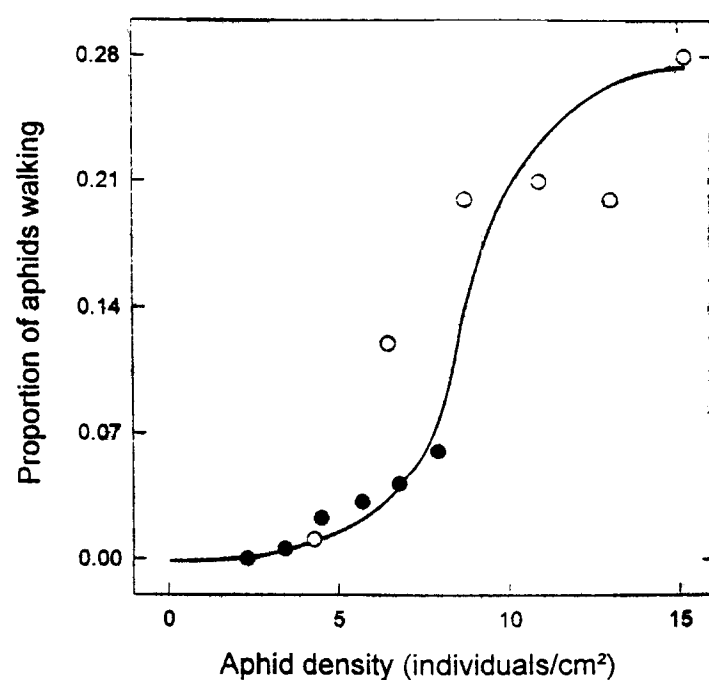


Fig. 2. Effect of density of apterae of *R. padi* on the settling behaviour of apterae of *R. padi*. Points in the graph are averages of replicates of six observations made at 10-minute intervals during one hour. The leaf surface area available to aphids was 2.3 cm<sup>2</sup> (o;  $n = 3$  for each point) or 4.5 cm<sup>2</sup> (•;  $n = 4$  for each point).

to a resource management strategy to reduce intraspecific competition. This mechanism would only be active at high aphid densities on the plant, when the advantages of aggregation in a short time perspective are over-compensated by poorer development possibilities offered by an over-exploited substrate. Aggre-

gation stimuli are more likely to affect the behaviour at low population densities when the resource is not limiting, when the aphid has recently landed on the plant and may need to modify the substrate in order to reach sustained feeding (Miles, 1987), or when the recently landed aphid seeks protection from predators (Arakaki, 1989).

The development of alate individuals and hence the dispersion of the aphid colony may be caused by the build up of high population densities (Lees, 1967; Dixon & Glen, 1971; Watt & Dixon, 1981; Ankersmit & Dijkman, 1983), as well as by changes in food quality (Harrewijn, 1978; Howard & Dixon, 1992). However, the time frame for this process is orders of magnitude slower than that which may be obtained as a response to a volatile stimulus. The capacity of apterae to react to overcrowding before poor food conditions start to prevail, is definitely of positive adaptive significance.

A fast means of intraspecific communication conveying the message of poor food quality or over-exploited resource would also be to the advantage of aphid individuals approaching a given feeding site, since evaluation of a plant as a potential host through probing and feeding is time consuming, requiring of the order of several minutes to hours (Givovich & Niemeyer, 1991; 1994). Interestingly, apterous *R. padi* spent considerably less time probing on wheat

seedlings when they were placed in high numbers on the seedlings than when placed singly on them (Chongrattanameteekul *et al.*, 1991).

The present investigations show that there is a density dependent spacing behaviour in apterae of *R. padi*. At high population densities odour stimuli produce an avoiding behaviour and increased mobility. We suggest this constitutes a mechanism serving a food resource management strategy.

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