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Distribution of the Aphid *Hyalopterus pruni* GEOFFR. within and between Habitats of Common Reed *Phragmites australis* (CAV.) TRIN. ex STEUDEL as a Result of Migration and Population Growth

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With 5 Figures and one Table

Key words: Aphid migration, host plant selection, population development

Abstract

The aphid *Hyalopterus pruni* migrates to its secondary host Common Reed in late spring and early summer. Reed fields are known to be more heavily infested at the edges compared to the centre, as the migrants are attracted to the colour of the reed. There is also evidence that reeds growing at wet sites are more heavily infested than at dry sites. This paper shows that both processes interact in determining the distribution of aphids in different habitats.

The observations were carried out in the vast reed field of the Zuidelijk Flevoland polder (The Netherlands) during a number of years after its reclamation in 1968. In the period of migration flying aphids were caught with sticky traps situated in and around the reed field. The distribution of aphids on the reed was determined at different times during the season along transects through the centre of the polder. The existence early in the season (June) of a higher infestation at the edges than in the centre of the field was confirmed. The density of winged aphids in this early period was higher in wet than in dry habitats, which may have been a result of a preference of the settling migrants for reed standing in water. Later in the season (August) the dry habitat still had a relatively low infestation in the centre, but at the wet sites the infestation was high everywhere. This could be attributed to the much quicker population growth that was found in the wet habitat and subsequent short range movement of newly born winged aphids.

Introduction

The Mealy Plum aphid, *Hyalopterus pruni*, hibernates on *Prunus* species, especially plum trees. In spring there are a few generations of wingless aphids on the leaves of the plum trees. In the period from the end of May to early July winged aphids (also called *alatae*) appear, which migrate to *Phragmites australis*. DILL (1937) gives an account of the life history of the species. The timing of migration depends on the condition of the food plant and the density of the aphids on the leaves. The timing may therefore differ between years. The active flight of migrating aphids is slow, but they can be transported passively by wind over long distances. When landing on a plant the aphid probes the surface of the leaf or the upper layer of cells with its stylet and may either accept it and settle or reject it and resume flight, until it finds an acceptable host plant (DIXON 1973).

The early generations born on the reed are also wingless, but in later generations winged aphids are born. These may migrate to other reed shoots. Winged males and *gynoparae* born on reed at the end of summer return to the *Prunus*. The timing depends on the condition of the reed (PINTERA 1973).

Studies on the distribution of *Hyalopterus pruni* on reed usually deal with the distribution within a reed field or the infestation of reed fields growing in different habitats.

Several authors (DILL 1937; SKUHRAVY 1981; VOGEL 1984; TSCHARNTKE 1989a; OSTENDORP 1993) mention or have documented a decline in infestation from the edges of reed fields to the centre. Many aphids probably alight as soon as they encounter reed, as a reaction to its colour (MOERICKE 1969).

Another phenomenon is that reed growing on dry soil was found to be less infested than reed growing in water (PINTERA 1973; BIBBY et al. 1976; SKUHRAVY 1981). This may be caused early in the season by selection behaviour of migrants shortly after landing, or later in the season as a result of differences in population growth.

However, the distribution of aphids in reed vegetation may be the result of several processes working at different periods of the life cycle. Behaviour during migration and at the moment of landing is probably significant, but the popu-

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lation growth on reed and behaviour of alate aphids born on reed may also have an effect. Based on the distribution of infested plants in the Zuidelijk Flevoland polder (The Netherlands) at the end of the summer of 1968 it has previously been suggested (MOOK 1971a; see also Fig. 2) that both an edge effect at landing and a difference in population growth play a role. This paper aims to give an account of what takes place during the whole summer season.

Study area and Methods

In the last new polder (Zuidelijk Flevoland) which was reclaimed in 1968 from the large central lake of The Netherlands (the IJsselmeer, formerly Zuiderzee; see Fig. 1), Common Reed was sown from an aeroplane. Starting with a few plants per square metre, germinated in May 1968, the originally very open reed vegetation developed by 1971–1972 into a large and dense reedfield. This reedfield was gradually cultivated from the edges of the polder. In the early years after drainage the situation in the polder was favourable for the study of the migration of *Hyalopterus*, because no *Prunus* species were present. Therefore migration to the reed of necessity originated each year from the adjacent old land. The observations were carried out in 1968, 1969 and 1971 through 1973.

During the first two years, most of the soil on which the reed plants grew was wet, but there were a few dry sites bordering deposits of sand or mixed soil. In later years most reed habitats became dry and wet sites became restricted to ditches and a few areas with shallow water.

Infestation of the reed was recorded along transects across the polder, which were different between years because of the changing situation (due to the process of reclamation). The transect (A–B) used in 1968 and 1969 is shown in Fig. 1. Due to the inaccessibility of the terrain, and as during the visits other species were also censused, it was not possible to cover the whole transect within a few days, but the census period was as short as possible and there was no influence of the census date on the results. During the census of 1968 (17 September to 9 October) separate plants originating from a single seed could still easily be distinguished, and the percentage of infested plants was determined by examining at least 100 plants per site where the infestation was high and 200 plants were it was low. During the early migration period of 1969 (13–23 June), the number of winged aphids (i.e. migrants) were counted on at least 250 shoots per site; more shoots (up to 1000) were examined where the aphid density was low.

Another transect was used in 1971 (sites 1–6, see Fig. 1; the area to the east of site 6 was already cultivated). These sites were easily accessable by road, hence all the data could be gathered within a day. At each of the 6 stations 50 or 100 shoots were examined in a wet habitat (a ditch) and 100 or 200 shoots on adjacent dry banks. In this paper the data for the six stations are added, so that means are given for 300 or 600 shoots in the wet and 600 or 1200 shoots in the dry habitat. The percentage of infected shoots was determined twice a week from the end of May to mid June, weekly from mid June to early August and once every 10 days in August and early September. Unwinged and winged aphids were counted until late June and early August, respectively, when they became too numerous.

In 1971–1973 sticky traps were used to catch migrating aphids. These consisted of a piece of stove pipe (painted white) with a diam-

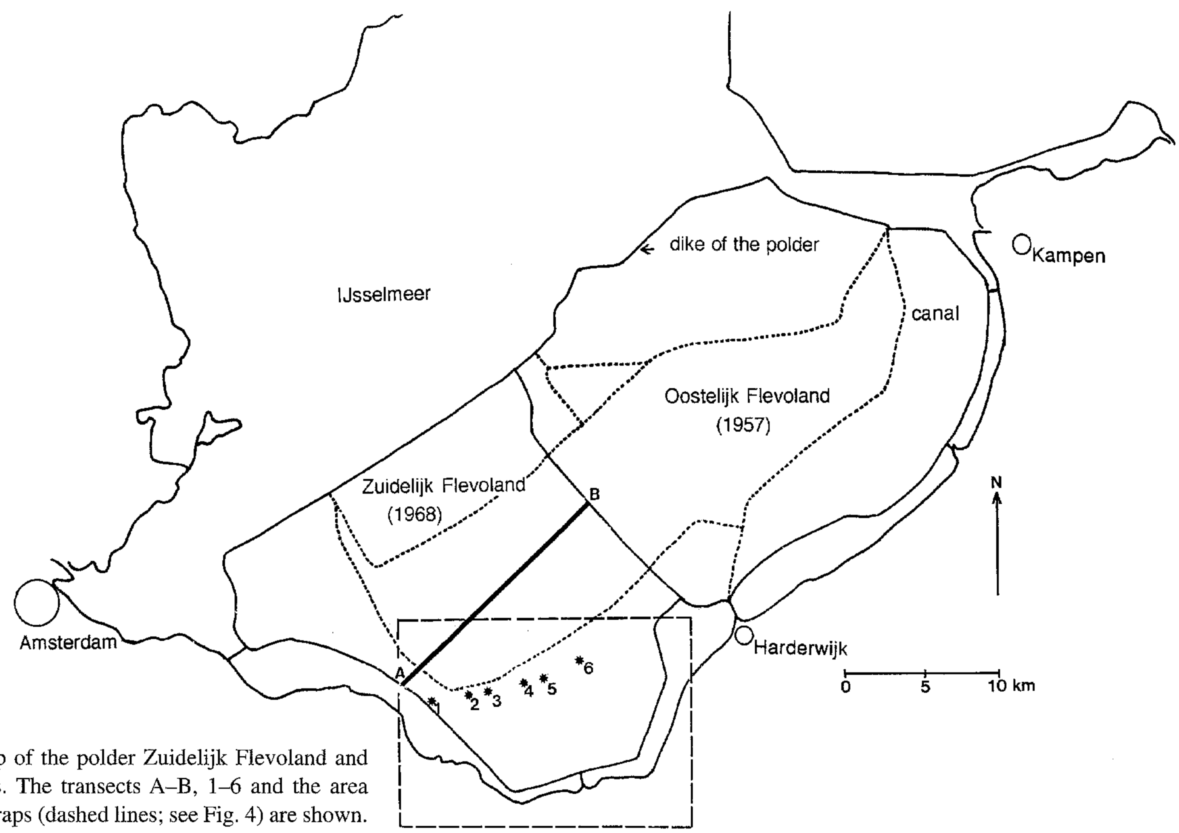


Fig. 1. Map of the polder Zuidelijk Flevoland and surroundings. The transects A–B, 1–6 and the area with sticky traps (dashed lines; see Fig. 4) are shown.

eter of 14 cm and 30 cm long covered by a sheet of translucent plastic which was coated with a sticky material (tanglefoot). The base of the traps was approximately 2 m above the ground. Two traps were used at each site. The sticky sheets were renewed every four days during the migration period in June and early July. The same transect (1–6) was used in 1971 and 1972. The western edge of the reedfield was at site 1 in 1971 and at site 2 in 1972; in both years the eastern edge was at site 6. However, it should be mentioned that the sampling sites were not immediately at the edge of the reed field, but at least 50 m away from it. In 1973 the traps were placed in a grid covering the southern part of the polder. The edges of the reed field in that year are given in Fig. 4 (A, B). Data on wind direction were collected from nearby stations operated by the polder authorities or the Royal Dutch Meteorological Service.

Results and Discussion

The results of the first census in late September and early October 1968 along the Transect A–B through the centre of the polder are shown in Fig. 2. A clear decrease is apparent in the percentage of infested plants in dry habitats, with high percentages near the bordering dyke (A) and gradually lower percentages towards the centre of the polder. However, no decrease was found in wet habitats, but between 80 and 100% of the plants were infested. It may be that the census period was rather late in the season, when in other years plants would already have been abandoned by the aphids. However, 1968 was exceptional because the plants were still very young, having germinated in May and they all had fresh green shoots. Pintera (1973) mentions that while normally the aphids disappear at the end of August, aphids on green sprouts can survive until late autumn, long after the usual period of remigration. Our results were not influenced by the moment of census, the water level however was important. The sites at a distance between 10 and 11 km were all sampled on the 27th of September. At a site on sandy soil well above the waterlevel no aphids were found; on clay soil with deep cracks from previous drying, but with some water in the cracks, 5.5 per cent of the shoots had aphids, while on clay with 8 cm of water above the soil 87 per cent of the plants were infested.

The following year a comparable census was carried out, but earlier in the season. During the period of migration in June 1969 the distribution of winged aphids (all of which were probably migrants coming from the primary host) was sampled along the transect A–B (Fig. 3). Lower densities were also found from the western edge of the field (A) inwards, but this time in both dry and wet habitats. However, at the more distant sites there was a tendency towards higher percentages in wet habitats.

These two results suggest that at least three processes may be at work that influence the distribution of aphids on reed during the summer season.

(1) The decrease from the edge of the polder to the centre is probably caused during the migration period. This could be due to either a passive behaviour of the aphids as an effect of the distance travelled, or to active landing behaviour as a reaction to stimuli from the reed.
(2) The slightly higher densities in June 1969 (Fig. 3) of winged aphids on wet compared to dry standing reed further from the western edge of the polder suggest that the aphids prefer to settle on wet standing reed, but this does not, however, explain the great differences in infestation of wet and dry reed later in the season (cf. Fig. 2). This could possibly be caused by
(3) differences in population growth on wet and dry standing reed and by behaviour of (winged) aphids of later generations.

Because of point 1 (behaviour during migration) more detailed observations on the distribution of migrating aphids were made with the use of sticky traps. The small scale ob-

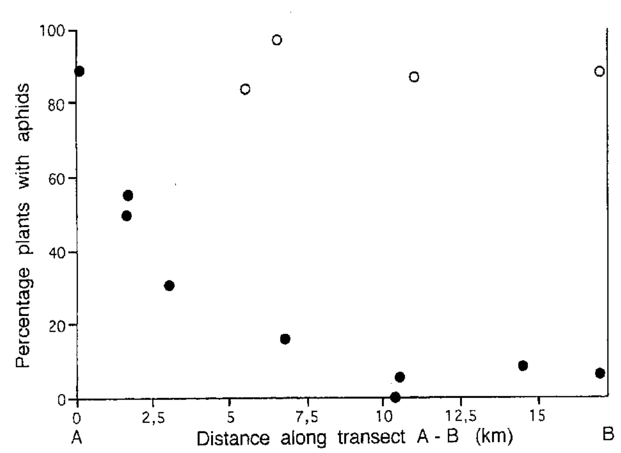


Fig. 2. Percentage of reed plants infested by aphids (late September–early October 1968) along the transect A–B through the Zuidelijk Flevoland polder (see Fig. 1). ○ wet habitat, ● dry habitat.

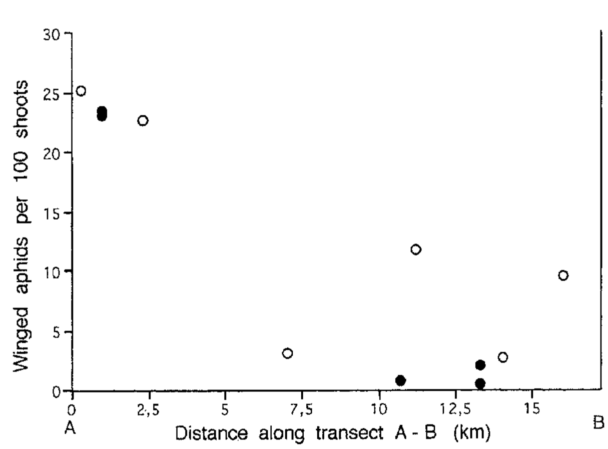


Fig. 3. Number of aphids per 100 reed shoots (mid June 1969) along the transect A–B through the Zuidelijk Flevoland polder (see Fig. 1). ○ wet habitat, ● dry habitat.

servations of 1971 and 1972 are interesting, because it became evident that our idea of prevailing south-westerly winds during the migration period may be false (Table 1). In 1971, except for the first few days, the wind was from the east during nearly the whole period between 28 May and 11 June. In the period 23 June to 3 July 1972 it was nearly always west to south west.

In order to have a better insight into the behaviour of migrating aphids with respect to reed, the distribution also needs to be known of migrants outside the reed field. To this

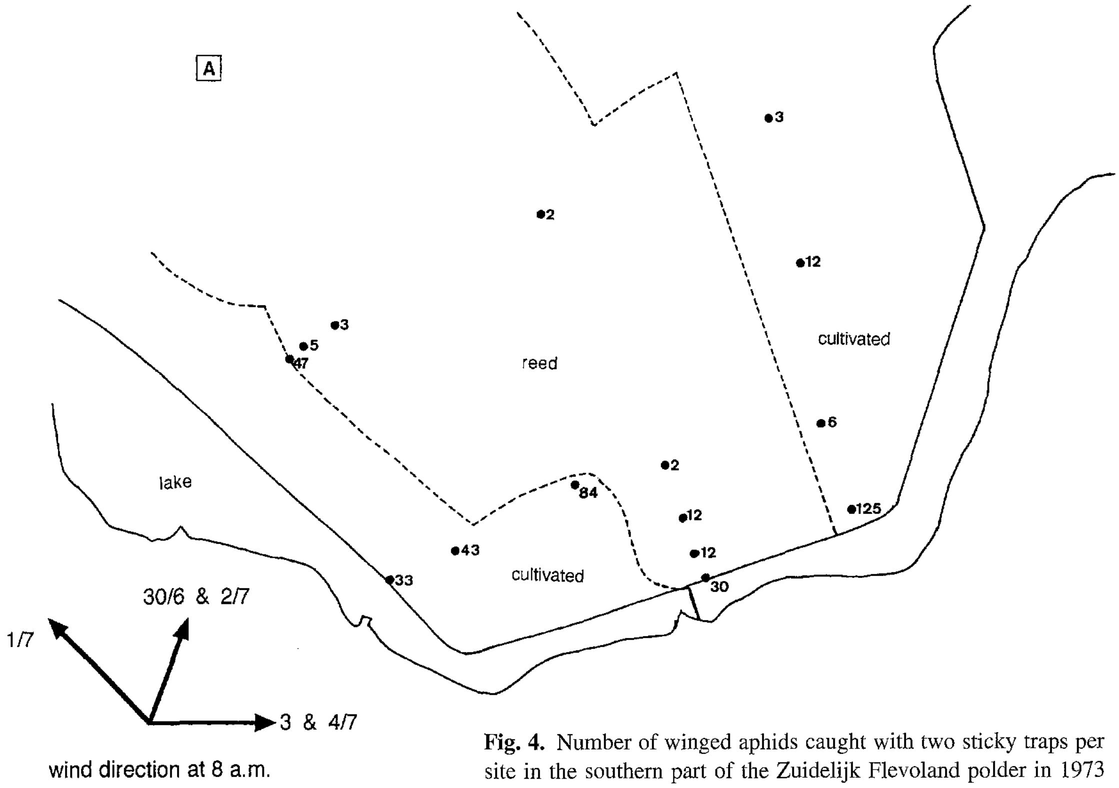
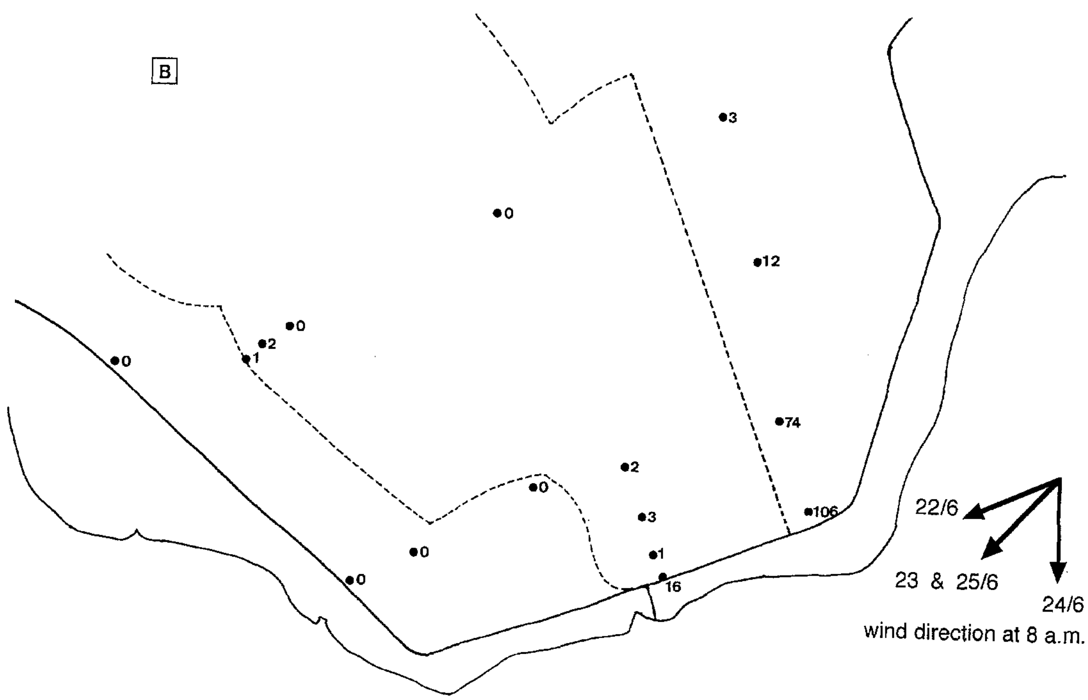


Fig. 4. Number of winged aphids caught with two sticky traps per site in the southern part of the Zuidelijk Flevoland polder in 1973 (see Fig. 1). **A**: Period 30 June to 3 July; **B**: period 22 to 25 June. The main wind directions on the different days are indicated.



end sticky traps were placed in a grid in and around the reed field in June–July 1973.

In Fig. 4 the results of two periods are shown during which the wind came from a specific direction. It is evident that the direction of the wind had a major influence on the distribution of aphids over the traps. Fig. 4 A (in a situation with winds predominantly from the south-west) clearly demonstrates that the number of aphids declined sharply as the distance from the edge of the reed field increased and not from the edge of the polder. These results suggest that stimuli from the reed were much more important in inducing the aphids to land than the distance travelled. Fig. 4 B shows clearly that the traps on the lee-side of the reed field caught few or no aphids.

Further information with respect to the questions 2 and 3 mentioned above – respectively, preference for wet standing reed to settle on and influence of population growth – is given in the data on infestation and population density in 1971 (Fig. 5 A, B). As the overall trend of the data of the six dry and six wet sites sampled are highly comparable, separate data are not given. Three conclusions can be reached from these figures.

In the first place the percentage of infested shoots and the mean number of winged aphids per shoot at the start of the season was much greater in the wet than in the dry habitat, although these habitats were close to each other (approximately 10 metres). This result confirms the hypothesis that aphids when settling have a preference for shoots standing in water.

Secondly, it can be seen that in the wet habitat a fair level of infestation was reached after a short period, which more or less persisted until the beginning of July. Data on the density of unwinged aphids were not collected for the entire period, but in June the leaves were not very crowded. By the end of June the mean density of aphids in the wet habitat was about 30 per infested shoot. Nevertheless many winged aphids appeared in the wet site which apparently redistributed themselves over nearby shoots, thus causing a sharp rise of the percentage infested shoots and the number of winged aphids per 100 reed shoots. The shoots in the dry habitat show a similar picture, but at a much lower level. By the end of June the infestation was still extremely low. We assume that the quick

Table 1. Catches of winged *Hyalopterus pruni* with two sticky traps per site along a transect in a reed field in the Zuidelijk Flevoland polder in the migration periods of 1971 and 1972 (sites see Fig. 1). In both years the eastern edge of the reed field was at site 6. The western edge was at sites 1 and 2 respectively in 1971 and 1972.

Period	Site					
	1	**2**	**3**	**4**	**5**	**6**
28 May–11 June 1971	13	7	29	6	10	56
23 June–3 July 1972	5	62	2	4	3	3
7 July–12 July 1972	0	13	1	0	1	0

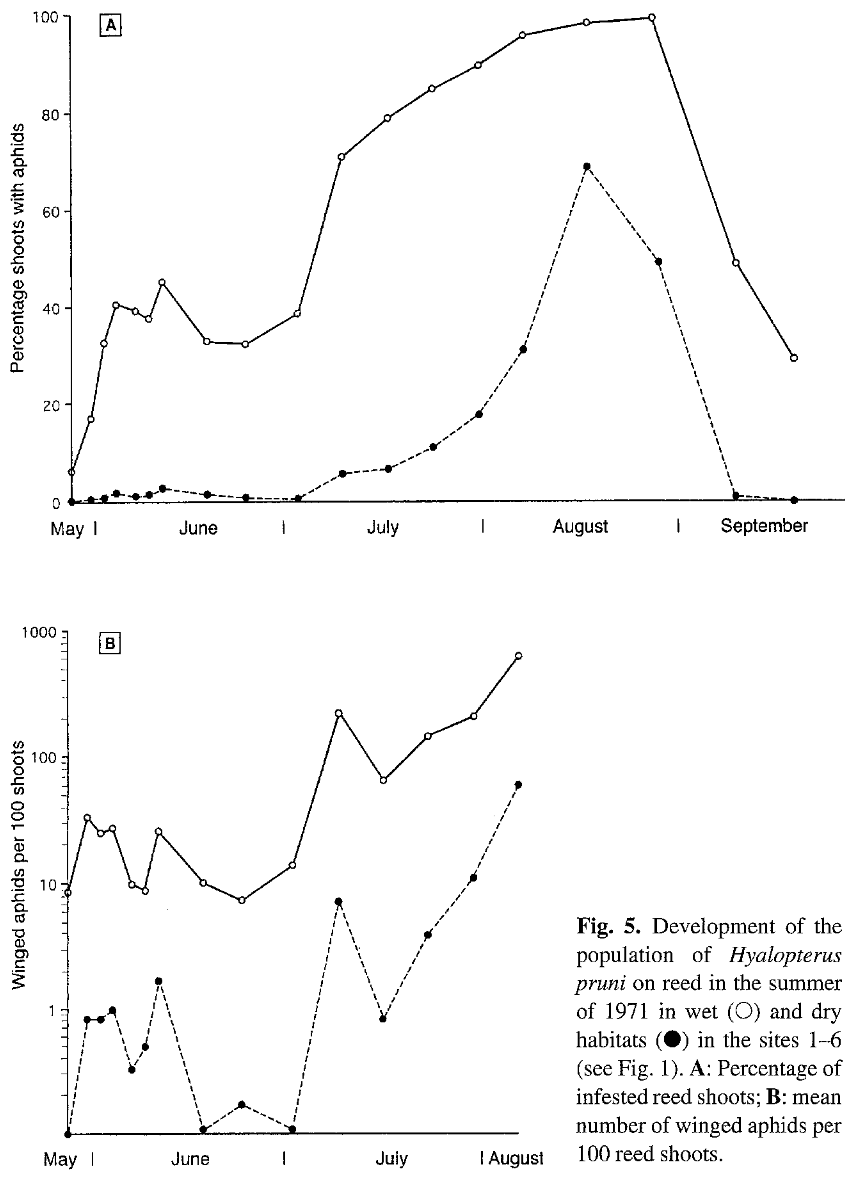


Fig. 5. Development of the population of *Hyalopterus pruni* on reed in the summer of 1971 in wet (○) and dry habitats (●) in the sites 1–6 (see Fig. 1). **A**: Percentage of infested reed shoots; **B**: mean number of winged aphids per 100 reed shoots.

rise from mid July onwards is caused by winged aphids born in the wet sites invading the reed on the dry banks. A really high infestation (of 70% of the shoots) did not occur before mid August. Finally it can be seen that at the end of the season the percentage infested shoots dropped, after mid August in the dry and after late August in the wet habitat.

These findings show that also with regard to population development reed shoots standing in the water are much more favourable for the aphids than reed standing dry.

We have no data on predation by insects or birds. Reed aphids have been found to be an important part of the diet of some species of birds at least in the migration period (BIBBY et al. 1976). It should be kept in mind that the stagnation of population growth in June could have been caused by predation in the breeding season of the birds. For instance, the Reed Warbler (*Acrocephalus scirpaceus*) and, to a lesser extent, the Sedge Warbler (*A. schoenobaenus*) breed until late July and may feed high proportions of aphids to their young (BIBBY & THOMAS 1985; GLUTZ VON BLOTZHEIM 1991). Although we have no indications that these species had a high population density in the vicinity of our six sampling sites, it cannot be ruled out that the sudden population growth in July could coincide with the end of the breeding season and a relaxation of predation pressure.

General Discussion

The results support the conclusions of previous workers (DILL 1938; TSCHARNTKE 1989 a) concerning the decrease in aphid density with distance from the edges of reed fields. However, there are differences which can be attributed to the specific circumstances in the reed vegetation of the polder. TSCHARNTKE (1989 a), who gives the most detailed results, found that in July the infestation approximately 15 metres inwards from the edge of a reed field was 80% lower than at the edge. We did not find such a sharp decrease, because the distances between our sample sites were much greater and thus not suitable to observe a steep gradient. In 1973 one of our trapping sites was at the (western) edge of the field (see Fig. 4 A) and the nearest sampling point, where the count was about 90% lower (5 against 47) was nearly 400 m inwards. Similar results were found at the southern border (Fig. 4 A and B). Our data of 1969 (Fig. 3), which were also obtained during the migration period, suggest that the decrease was not as sudden as found by TSCHARNTKE. However, in that year and even more so in 1968, the reed vegetation was still in an early stage of development and thus very open. By 1971 the vegetation was still not completely closed in parts of the polder, this applied particularly to the vegetation we studied that year in and near the ditch. Nevertheless it can be concluded from the catches with sticky traps in 1973 that the decrease from the edge inwards is the result of a reaction of the migrating aphids to stimuli from the reed. In view of the findings of MOERICKE (1969) that migrants of *H. pruni* preferably alight on specific colours and also have a preference for the grey-green leaves of reed to the yellow-green leaves of e.g. sugar beet, it can be safely assumed that the colour of reed is an important stimulus in inducing the aphids to alight. The sticky trap results suggest that many reed aphids migrate at low heights, which may help to explain the strong effect of the edge of a closed vegetation.

Another difference compared to TSCHARNTKE'S results is that we found no decrease at all in wet habitats in 1968. TSCHARNTKE'S edge infestation was determined in a field of water reed in July and he gives no data on the distribution later in the season. Other workers have found an increase in numbers from July onwards. VOGEL (1984) shows a 20-fold increase in the catches in yellow water traps in the centre of a 20 ha reed marsh from July to August and again a more than 10-fold increase from August to September. BIBBY et al. (1976) give a detailed comparison of aphid density on reed in August, which shows that the density is high on reed in water, intermediate on reed on mud, and low to very low on reed on damp and dry ground respectively. Counts in water reed showed great variation over small distances, which were attributed to the stage of development of the reed, but nothing was said about a possible systematic variation within the field. A rapid build-up of aphid numbers was observed over a period of three weeks from late July to mid August and a decline after the first week of September. PINTERA (1973) mentions high proportions of winged aphids in early August, which he did not attribute to crowding but to a change in the nutritive conditions of the attacked shoots, induced by the aphids themselves.

These results are in agreement with our data on population development during the season. We can now reconstruct the process that leads to the distribution of infestation found late in 1968 (Fig. 2). It is probable that in the wet habitats many winged aphids are born after mid July and that these have spread to other nearby shoots, so that nearly all plants got infested irrespective of the initial density after the early migration. If one assumes that these *alatae* spread only locally with flying distances in the order of metres or, at most, tens of metres they could not have reached the dry sample sites that were at distances of at least a few hundred metres. Apparently the population growth in the dry places was much slower and therefore they could retain approximately the original distribution that was established during the early migration from *Prunus* to reed. The relatively high infestation found in August 1971 on the dry banks of the ditch can probably be explained by the proximity of the reed in the water of the ditch which was very favourable for the development of winged aphids. But even here the density of winged aphids in the ditch was much higher than on the banks.

This leads to the conclusion that the distribution of aphids on reed need not be similar in different habitats and different periods of the year. In water reed the edge infestation as described by TSCHARNTKE (1989 a) and as for instance illustrated by OSTENDORP (1993, p. 189) will probably be apparent only in early summer until July and disappear in August. In dry standing reed the initial infestation may be high at the edges, but the distribution in late season may depend on the nearness of reed favourable for the development of winged aphids in July and August.

A question that remains is what causes the difference in population growth in wet and dry habitats. Our data, and also the findings of BIBBY et al. (1976), give no clues. So far no explanation has been offered other than that reed standing in water can have young and fresh sprouts during summer which are more heavily infested than older sprouts (MOOK 1971 a; PINTERA 1973). TSCHARNTKE (1989 a) did not find a higher infestation of shoots with a greater diameter, which according to his earlier studies on other reed insects correlates with a higher nitrogen-, silicium- and water-content (TSCHARNTKE 1988, 1989 b). RAGHI-ATRI (1976) compared two stands of water reed of which the aphid density, ash content of the shoots, nitrogen content of the soil and surrounding water were determined. All four were higher in one of the two vegetations and it was concluded that aphids benefit by eutrophication of the water. However, an alternative explanation is also possible. Because the most heavily infested reed field was much smaller, with a width of approximately 50 metres and had a more open structure than the less infested field (width 200 metres) the difference in aphid density, which was determined in July, could be due to the edge effect (see TSCHARNTKE 1989 a, who found a negative correlation between aphid density in July and the size of reed beds). In the same paper a positive correlation is mentioned with doses of nitrogen in a pot experiment with reed, but no details are given. In both cases a more grey-green colour was connected with a richer environment and RAGHI-ATRI suggests that this makes it more attractive to aphids.

To explain the faster population growth in the wet habitats we have to look for differences in the food of the aphids. In the polder the soil was a rich clay with a high initial nitrogen content in all soil layers and in later years at least in the layer deeper than 0.6 m (VAN DER LINDEN 1990). The fringes of the sand deposits along the transect A–B probably had a poorer upper soil layer. The nitrogen content of the soil of the wet ditch and its dry banks, where the population growth was recorded in 1971, was probably also different. As a consequence there will have been differences in the chemical composition of the shoots. However, it is not the overall chemical composition that will be important for the aphids, but the composition of the phloem sap. In other aphid species a clear influence of nitrogen content of the phloem sap on reproduction has been found (DIXON 1973). Also the availability of the phloem sap, depending on the turgor pressure, and thus on the water regime of the plants, may be important (DIXON l.c.). Further research is required to determine which processes are important in the case of *Hyalopterus pruni*.

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