The distribution, abundance and host plant relationships of *Salix*-feeding psyllids (Homoptera: Psylloidea) in arctic Alaska

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ABSTRACT. 1. Five species of psyllid occurred on seven species of *Salix* at Meade River, Alaska. Studies were made on the two common species *Psylla palmeni* Löw and *P.phlebophyllae* Hodkinson. The former feeds on the phanerophytes *Salix pulchra*, *S.lanata*, *S.alaxensis* and *S.glauca*, the latter on the chamaephytes *S.phlebophylla* and *S.reticulata*.

2. Both *P.palmeni* and *P.phlebophyllae* had a 1-year life cycle and nymphal development took place on the female *Salix* catkin. The life cycle was generally closely synchronized with the period of catkin development. However, only a few eggs were laid on *S.glauca*.

3. Seasonal perturbation of the host plant by flooding, ice movement and blown sand prevented psyllids breeding in certain areas colonized by the host plant.

4. In *P.palmeni* densities and 'feeding pressure', measured as biomass of psyllids per gram of catkin, on the different host plants followed the sequence *S.pulchra* > *S.lanata* > *S.alaxensis* > *S.glauca*. In *P.phlebophyllae* densities and feeding intensities were similar on *S.phlebophylla* and *S.reticulata* and grazing intensity was comparable with *P.palmeni* on *S.pulchra*.

5. A highly significant negative correlation was found between psyllid density and catkin dry weight in *S.pulchra*, *S.phlebophylla* and *S.reticulata*, suggesting that psyllid feeding is affecting catkin growth.

6. Predation of psyllid nymphs by syrphid larvae was heavy but there was no evidence of parasitism.

7. The life history strategies of the five psyllid species are discussed within the context of the constraints imposed by the arctic environment.

Introduction

This work forms part of the integrated programme 'Research on Arctic Tundra Environments' (RATE) designed to quantify the intensity and impact of herbivore grazing on tundra vegetation. The 'Rate' study area is

situated adjacent to Meade River, approximately 100 km south of Point Barrow on the arctic slope of northern Alaska (70° 25' N, 157° 5' W). In contrast to the well-studied coastal tundra I.B.P. sites at Barrow and Prudhoe Bay, Meade River has a significantly warmer climate and in consequence a much richer flora and fauna (see MacLean, 1975b; MacLean & Pitelka, 1971).

The main objectives of this study were to

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TABLE 1. Host plant relationships of *Salix*-feeding psyllids at Meade River

	<i>Psylla palmeni</i> Löw	<i>Psylla zaecevi</i> Sulc.	<i>Psylla macleani</i> Hod.	<i>Psylla phlebophyllae</i> Hod.	<i>Trioza atkasookensis</i> Hod.
<i>Salix pulchra</i> Cham.	X	X			
<i>S. lanata</i> L.	X	X			X
<i>S. glauca</i> L.	X				
<i>S. alaxensis</i> (Anderss.) Cov.	X		X		
<i>S. niphoclada</i> Rydb.*	X				X
<i>S. reticulata</i> L.				X	
<i>S. phlebophylla</i> Anderss.				X	
<i>S. hastata</i> L.*					
<i>S. arctica</i> Pall.*					

* Uncommon species — few plants available.

investigate the distribution, abundance and phenology of the jumping plant lice (Psylloidea) associated with dwarf willows (*Salix* species) and to measure their impact on their host plant. The Psylloidea is a group of small, host specific, phloem feeding insects which often occur at very high densities on dicotyledenous plants, particularly in arctic or alpine situations (Hodkinson, 1973a, unpublished; Koponen, 1973, 1978; Koponen & Ojala, 1974).

The Alaskan willows are particularly diverse; Hultén (1968) records fifty-six species for the region. Similarly the associated psyllids exhibit parallel diversification; twenty-one species are recorded by Hodkinson (1978). At Meade River five psyllid species are associated with nine *Salix* species: their host plant relationships are summarized in Table 1.

Both *Psylla palmeni* Löw and *Psylla phlebophyllae* Hodkinson were common and widespread, *Psylla zaecevi* Sulc and *Trioza atkasookensis* Hodkinson were widespread but uncommon, whereas *Psylla macleani* Hodkinson was found at only one restricted locality. Hence attention was focused mainly on the two common species.

Psylla palmeni and *P. zaecevi* are widely distributed throughout the far northern region of the Palaearctic and the latter species also occurs as a relic population in the mountains of northern India (Klimaszewski, 1973; Mathur, 1975). *Psylla phlebophyllae* and *T. atkasookensis* are also recorded from the arctic regions of eastern Siberia (Hodkinson, unpublished) whereas *P. macleani* occurs only in Alaska (Hodkinson, 1978).

Site Description

The Meade River area is topographically diverse with polygonized tundra, lake basin, dry ridge, bluff, sand dune and river edge habitats occurring in close proximity. The distribution of *Salix* reflects this habitat diversity and study sites were chosen accordingly. *Salix pulchra* is found mainly in the wetter more stable areas, in drained lake basins and around low centred polygons. *Salix phlebophylla* and *S. reticulata* occur together on the drier, more exposed ridges but the latter species also extends into the wetter lake basins. *Salix lanata*, *S. alaxensis* and *S. glauca* occur most commonly in disturbed situations, mainly along river margins. Both *S. phlebophylla* and *S. reticulata* are chamaephytes, reaching a maximum height of about 4 cm, whereas the remaining species are phanerophytes reaching a maximum height of about 1 m, except *S. alaxensis* which reaches about 2 m in sheltered micro-habitats on the Dune site.

Mine Site. Previous disturbance associated with mining activities had produced a diverse mixture of *Salix* spp. which made this site an ideal experimental area for the main comparative studies. The dominant vegetation was *S. pulchra*, *S. lanata*, *S. alaxensis*, *S. glauca* and *S. reticulata* with less *S. niphoclada*. The 50 x 50 m sampling area was marked out as a 1 m² grid.

Dry Ridge. This was the main dry site containing *Salix phlebophylla* and *S. reticulata* growing in a mixed chamaephyte shrub community. The 10 x 10 m sampling area along the ridge crest was marked out as a 1 m² grid.

Lake Basin. This was the main wet site, subject to waterlogging when spring snow melted. *Salix pulchra* was dominant but *S. reticulata* was also abundant. The 10 × 100 m sampling area was marked out as a 1 m² grid.

Ice Scrape. This disturbed site along the edge of Meade River, was subject to ice scrape as the river ice melted. The willows were partially flattened and there was little or no ground vegetation. *Salix alaxensis* grew in a narrow strip along the edge of the river with a wider belt of *S. lanata* behind it. The *S. lanata* extended into an undisturbed area with a well-developed ground flora. A sampling grid was not marked out.

Sand Dunes. On this area *Salix alaxensis* grew in bare sand on a well-developed dune system adjacent to Meade River.

Atkasook Village. A single colony of *Psylla macleani* was discovered on this site at the end of the 1976 season on *S. alaxensis* growing in a mixed *Salix* community adjacent to Meade River. No further studies were made on this site.

Sampling Methods

A preliminary survey of the distribution of psyllid eggs on the willows at the various sites was carried out from 20 June to 3 July 1976. A minimum of nine catkin-bearing stems was removed from the plant and the number of eggs on the catkins (♂ or ♀), on the woody stem and on the green buds or leaves (depending on phenological state) was recorded. At the same time, a semi-quantitative assessment of adult psyllid abundance on each *Salix* was made by taking ten sweep net samples (twenty sweeps per sample). Adult sampling was continued throughout the season to obtain material for investigation of ovary maturity. All data on female maturity are based on a minimum of fifty dissected females per host plant for each sample date.

Subsequently, each *Salix* species on the Mine, Dry Ridge and Lake Basin sites was sampled for psyllids at regular intervals during the summer of 1976. For each *Salix* species a minimum of twenty-four random samples was taken. Each sample was stratified to include three components: a female catkin,

the current year's growth on the catkin bearing stem, and the current year's growth on a non-catkin bearing stem. The number of psyllid eggs and nymphs on each was then counted separately. Catkins of *S. pulchra*, *S. lanata*, *S. alaxensis* and *S. glauca* at the Mine Site were also sampled for *P. palmeni* nymphs on two occasions during July 1977.

Preliminary sweep netting and egg sampling on 14 July 1976 suggested that psyllids were absent from the Ice Scrape site. To investigate the distribution of psyllids there a transect was made on 2 August 1976 from the riparian *S. alaxensis* through to the unaffected *S. lanata*. At 10 m intervals along three separate transect lines a sweep net sample for adults (twenty sweeps) was taken together with a four catkin sample which was examined for nymphs. It also became apparent that *P. phlebotomiae* nymphs were absent from *S. reticulata* growing on the wet Lake Basin although they were abundant on the same *Salix* species 60 m away on the Dry Ridge. Thus, to examine the distribution of *P. phlebotomiae* along a wet-dry gradient, eight catkins were taken at 10 m intervals (5 m up the slope) along a transect rising from the Lake Basin to the Dry Ridge on 3 August 1976.

Similarly, preliminary egg sampling of *S. alaxensis* at the Sand Dune site on 27 June 1976 suggested that psyllids were likewise absent from this site. Thus twenty-five random composite samples, as previously described, were taken on 31 July 1976.

During the period when eggs were present all *Salix* samples were hand sorted. In later samples nymphs were extracted from catkins in modified Berlese-Tullgren funnels. Straight heat extraction, as used successfully for other psyllid species (Hodkinson, 1973a; Harris, 1971), was found to be inappropriate as direct heat caused older catkins to burst, trapping the nymphs. This problem was overcome by suspending the catkin over water in a polystyrene cup using a pin driven into the cup base: the water then served as the collection fluid. Extraction efficiency, estimated by counting the remaining dead psyllids on twenty catkins after extraction, was at least 96%.

The phenological state of each *Salix* at each of the four main study sites was observed at regular intervals throughout the 1976 and

1977 seasons and recorded as dates of first occurrence of each stage of development.

Results

Phenology of *Salix* species

Seasonal development of the willows was rapid within the 2½ month growing season (Fig. 1). On the basis of phenology the species were divided into two groups; group 1 with catkins appearing before leaves (*S. pulchra*, *S. lanata* and *S. alaxensis*) and group 2 with catkins appearing after the leaf buds have broken (*S. glauca*, *S. phlebophylla* and *S. reticulata*). Group 1 species were the first to com-

mence growth. On the Mine Site catkins of group 1 species appeared at least 14 days before group 2 species whereas at the Lake Basin the difference was reduced to 10 days. On the Dry Ridge Site group 1 species were rare but catkin appearance in group 2 species was at least 9 days later than group 1 species at the Mine Site. Catkin appearance in group 1 species on the Ice Scrape Site was delayed by 4–5 days compared to the Mine Site, although development to maturity was more rapid.

The period between catkin appearance and catkin burst represents the period favourable for psyllid growth (see later). In group 1 species at the Mine Site this was 40–43 days and in group 2 species on the Dry Ridge

FIG. 1. Phenology of willows on the four study sites for 1976 and 1977. Open bars = catkins present, leaves absent; stippled bars = leaves present, catkins absent; cross-hatched bars = leaves and immature catkins present together; black bars = catkins burst. The numbers represent days between catkin appearance and catkin burst.

36–41 days. *Salix glauca* (group 2) is atypical in that catkin burst is delayed and good estimates of time of ripening are difficult to obtain.

At Meade River the temperature threshold for *Salix* growth was about 6°C. In 1977 the growing season began 10 days earlier than in 1976 and this is reflected in the advanced phenology of the willows in that year (Fig. 1). However, the actual development time of catkins to maturity remained almost constant between years.

The life cycle of Psylla palmeni and P. phlebophyllae

The life history of *P. palmeni* on *S. pulchra*, *S. lanata*, *S. alaxensis* and *S. glauca* at the Mine Site and on *S. pulchra* at the Lake Basin during 1976 is shown in Fig. 2. At snow melt in mid-June, prior to the commencement of *Salix* growth, sexually mature *P. palmeni* adults were present on the plant. Oviposition on catkins occurred as soon as they appeared (see later); the eggs hatched and the nymphs passed through five instars before the first new generation adults appeared in late July. These adults remained sexually immature at least until late August. It was not possible to investigate the mode of overwintering as the site was inaccessible during the winter. However, adults probably overwinter in the litter layer or in rolled dead leaves attached to the plant. The closely related *Psylla moscovita* Andr., which has a similar life history on *Salix repens*, hibernates in this manner (Hodkinson, unpublished).

The time between first appearance of eggs and first appearance of new generation adults varied between 40 and 41 days. This period, making due allowance for observational error, is very close to the estimated life of the female catkin (40–43 days in phenological group 1 willows). Therefore, if the psyllid is to complete its life cycle within a female catkin (see later) there must be almost perfect phenological synchronization between the two. This is achieved by *P. palmeni* being ready to oviposit the moment the catkin appears. This strategy results in the vast majority of eggs being laid on the phenological group 1 willows *pulchra*, *lanata* and *alaxensis*. On the Mine Site *Salix glauca* and

FIG. 2. Changes in nymphal instar composition and adult female maturity for *P. palmeni* and *P. phlebophyllae* on different *Salix* species during 1976.

S. reticulata were 16 and 14 days later respectively in producing catkins by which time the majority of *P. palmeni* females were spent. There is some evidence, however, that a small number of eggs were laid on *S. glauca* and that these developed into adults late in the season. *Salix glauca* may thus act as a 'safety net' species on which *P. palmeni* can reproduce, albeit at a low level, in years when synchronization with group 1 species breaks down.

Psylla phlebophyllae on *S. reticulata* and *S. phlebophylla* at the Dry Ridge had a very similar life cycle to *P. palmeni*, except that eggs were not laid until the catkins emerged, 12 days later than *S. pulchra* on the Mine Site and the first adults emerged 6 days later than *P. palmeni* (Fig. 2). Again there was close

synchrony between the life cycle and the life of a female catkin: the time taken to pass from first egg to first adult was 36 days compared with a catkin life of 39 and 41 days for *S.phlobophylla* and *S.reticulata* respectively.

Life cycle of Psylla zaecevi, P.macleani and Trioza atkasookensis

The scattered data collected on these species suggest that all overwinter as adults and pass through a single generation each year. *Trioza atkasookensis* nymphs were always found in pit galls on leaves and never in catkins, whereas *P.zaecevi* nymphs were always found in catkins, often in association with *P.palmeni*. While no data are available for nymphal development of *P.macleani* at Meade River, late instars nymphs were collected from female *S.alaxensis* catkins at Fairbanks (Hodkinson, 1978).

The distribution of psyllids on the different willows at each site

Table 2 summarizes the presence or absence of *P.palmeni* and *P.phlebophyllae* on all sample sites. Absence is generally defined as there being no egg, nymph or adult found in any sample on a particular site throughout the study period. However, a few eggs and nymphs of *P.palmeni* were present on *S.reticulata* at the Mine Site early in the season but were absent from a later sample. The data to

TABLE 2. Presence (+) and absence (–) of *P.palmeni* and *P.phlebophyllae* on different willows at different sites as revealed by the intensive sampling programme

	<i>P.palmeni</i>	<i>P.phlebophyllae</i>
Mine site		
<i>S.pulchra</i>	+	–
<i>S.lanata</i>	+	–
<i>S.glaucia</i>	+	–
<i>S.reticulata</i>	–?	–
<i>S.alaxensis</i>	+	–
Lake Basin		
<i>S.reticulata</i>	–	–
<i>S.pulchra</i>	+	–
Dry Ridge		
<i>S.reticulata</i>	–	+
<i>S.phlebophylla</i>	–	+
Ice Scrape		
<i>S.lanata</i>	–	–
<i>S.alaxensis</i>	–	–
Dunes		
<i>S.alaxensis</i>	–	–

support these overall conclusions are presented in the following sections.

Preliminary observations on the distribution of psyllid eggs on the host plant

Table 3 illustrates the distribution of *P.palmeni* and *P.phlebophyllae* eggs on the various willows at all sample sites. These data demonstrate that psyllid eggs are highly aggregated on male and female catkins and that

TABLE 3. Distribution of *P.palmeni* and *P.phlebophyllae* eggs on various willows at the different sites. A = abundant (a minimum average of more than fifty eggs per sample unit); I = infrequent (less than twenty eggs found in all sample units); 0 = total absence of eggs from the sample; (–) = the plant had not reached or had grown beyond a particular phenological stage.

Site	<i>Salix</i>	Psyllid	Date	n	♂ Catkin	♀ Catkin	Stem	Green bud	Leaves
Mine	<i>S.pulchra</i>	<i>P.palmeni</i>	20.vi.76	28	A	A	0	0	–
	<i>S.lanata</i>	<i>P.palmeni</i>	20.vi.76	30	A	A	0	0	–
	<i>S.glaucia</i>	<i>P.palmeni</i>	8.vii.76	18	0	0	0	0	–
Dry Ridge	<i>S.reticulata</i>	<i>P.phlebophyllae</i>	29.vi.76	36	A	A	0	–	I
	<i>S.phlebophylla</i>	<i>P.phlebophyllae</i>	29.vi.76	19	A	A	0	–	I
Sand Dune	<i>S.alaxensis</i>	<i>P.palmeni</i>	27.vi.76	9	0	0	0	–	0
Lake Basin	<i>S.pulchra</i>	<i>P.palmeni</i>	1.vii.76	10	–	A	0	–	0
Ice Scrape	<i>S.lanata</i>	<i>P.palmeni</i>	3.vii.76	10	0	0	0	–	0

very few are laid on the rest of the plant. This is not surprising on willows in which the catkin appears before the leaves and in which initially only the catkin is available to the gravid female for oviposition, but it also applies to those willows whose catkins appear after the leaves. Female psyllids must therefore actively seek catkins for oviposition. However, eggs were laid abundantly on both male and female catkins even though the former withered and dropped from the plant before the eggs hatched. This represents a major source of mortality in the populations of both *P. palmeni* and *P. phlebophyllae*. It was only on the female catkins that the psyllids were able to continue their development.

Distribution of psyllid nymphs within the host plant

Table 4 summarizes the density of *P. palmeni* and *P. phlebophyllae* nymphs on catkin, catkin bearing shoot and non-catkin bearing shoot for each *Salix* at each site during 1976. Except for the odd end of the season sample, when numbers were small, the densities remained consistently very much greater on catkins than on the rest of the plant (see Table 4). Moreover, most of the nymphs found on the catkin shoot were associated with leaf axils right at the base of the catkin stalk. To test whether instar composition varied between the different plant parts an index of advancement (*I*) on a scale 1–5 was calculated for every sample where

$$I = \frac{\sum_{i=1}^5 \frac{n_i \times i}{T}}$$

where n = number of animals in instar i ;
 T = total number of nymphs present;
 i = instar code (instar 1 = 1 . . . instar 5 = 5).

This index was used to compare instar composition on the catkin against those on the catkin shoot and non catkin shoot using a paired comparison 't' test. No significant differences between plant parts were demonstrated (Table 4).

To test the null hypothesis that there is no linear relationship between numbers of nymphs on catkins and numbers on catkin

shoots a correlation analysis was carried out for all willows at each site on each date. A significant correlation was found in only three instances, for *P. palmeni* on *S. pulchra* at the Lake Basin on 27 July 1976 ($r = 0.43$, $P < 0.05$), and for *P. phlebophyllae* on *S. reticulata* at the Dry Ridge on 27 July 1976 and 5 August 1976 ($r = 0.44$, $P < 0.05$; $r = 0.46$, $P < 0.05$) respectively.

Thus results indicate that nymphs remain highly aggregated on catkins throughout their life cycle. Those on the rest of the plant are probably vagrants from the catkin as their instar composition is not significantly different from that on the catkin. There is no evidence to suggest that a late psyllid cohort may develop on the leaves.

The distribution of psyllids between sites

Fig. 3 shows the distribution of *P. palmeni* along the Ice Scrape transect. No nymphs or adults were found on either *S. alaxensis* or *S. lanata* within the area affected by ice scrape but both became common once the unaffected *S. lanata* was reached. This strongly suggests that *P. palmeni* is prevented from breeding on the Ice Scrape. This may be because *Psylla palmeni* overwinters as an adult and becomes active in spring as snow melt occurs. Overwintering adults will require protected hibernation sites in the ground vegetation/litter layer and these sites are absent from the Ice Scrape. Furthermore, ice movement over the host plant and surface flooding, at a time when adults are becoming active, will further minimize their chances of survival. A similar lack of suitable hibernation sites may explain the apparent absence of *P. palmeni* from *S. alaxensis* at the Sand Dune site during 1976 where any leaf litter falling to the ground in autumn is soon blown away.

The success of *P. palmeni* on *S. alaxensis* at the Mine Site is probably because the *Salix* community is subject to little or no natural disturbance. The plants are old and large, probably the residual colonizers following the cessation of mining activity. In the more natural unstable habitats of *S. alaxensis*, *P. palmeni* has few chances of reproducing.

Fig. 4 illustrates the distribution of *P. phlebophyllae* on *S. reticulata* along the Lake Basin–Dry Ridge transect. Nymphs

TABLE 4. Abundance of *P. palmeni* and *P. phlebophyllae* on various Salices at the different sites during 1976 (error terms are SE)

Site	Salix	Psyllid	Date	n	Wt catkin (mg)	Psyllids catkin ⁻¹	Wt catkin shoot (mg)	Psyllids catkin shoot ⁻¹	Wt non catkin shoot (mg)	Psyllids non catkin shoot ⁻¹	Catkin v Rest 'r'	Index of advancement paired 'r'
Mine	<i>pulchra</i>	<i>palmeni</i>	17. vii. 76	21	101±14	160.8±17.2	104±9	6.1±1.9	165±12	1.90±0.41	•	n.s.
	<i>pulchra</i>	<i>palmeni</i>	30. vii. 76	24	124±13	17.3±2.6	148±14	2.7±0.5	194±20	2.45±0.55	•	n.s.
	<i>lanata</i>	<i>palmeni</i>	22. vii. 76	27	397±24	47.3±3.2	173±18	1.14±0.30	302±40	0.85±0.34	•	n.s.
	<i>lanata</i>	<i>palmeni</i>	31. vii. 76	24	308±30	3.7±0.3	227±33	1.79±0.30	308±23	0.83±0.23	•	n.s.
	<i>alaxensis</i>	<i>palmeni</i>	25. vii. 76	24	368±20	3.5±0.7	536±38	1.17±0.34	679±52	0.37±0.22	•	n.s.
	<i>glaucia</i>	<i>palmeni</i>	23. vii. 76	27	85±7	0.30±0.17	150±9	0.22±0.09	183±15	0.18±0.12	n.s.	n.s.
	<i>glaucia</i>	<i>palmeni</i>	10. viii. 76	24	153±16	1.79±0.96	282±42	0.02±0.09	247±30	0.08±0.08	n.s.	n.s.
	<i>reticulata</i>	<i>palmeni</i>	23. vii. 76	25	21.5±2.8	1.44±1.19	73±6	0	69±7	0	•	—
	<i>reticulata</i>	<i>palmeni</i>	1. viii. 76	25	—	0	—	0	—	0	—	—
	<i>pulchra</i>	<i>palmeni</i>	27. vii. 76	24	150±7	15.1±3.2	95±10	0.92±0.33	121±12	0.29±0.18	•	n.s.
Lake Basin	<i>reticulata</i>	<i>palmeni</i>	31. vii. 76	25	24.2±2.8	0	67±7	0	57±7	0	—	—
	<i>alaxensis</i>	<i>palmeni</i> ?	31. vii. 76	25	—	0	—	0	—	0	—	—
Dry Ridge	<i>phlebophylla</i>	<i>phlebophyllae</i>	22. vii. 76	24	21.6±9.1	17.8±2.8	17.8±2.8	2.8±0.4	28.3±4.5	0.21±0.10	•	n.s.
	<i>phlebophylla</i>	<i>phlebophyllae</i>	28. vii. 76	25	25.8±6.3	7.8±1.4	15.9±2.0	0.72±0.23	17.2±3.0	0.16±0.09	•	n.s.
	<i>phlebophylla</i>	<i>phlebophyllae</i>	4. viii. 76	25	32.5±4.0	4.6±0.7	24.6±3.5	0.68±0.21	30.2±3.4	0.64±0.10	•	n.s.
	<i>phlebophylla</i>	<i>phlebophyllae</i>	16. viii. 76	24	27.0±2.0	0.4±0.2	17.4±1.8	0.25±0.11	27.2±2.9	0.25±0.20	n.s.	n.s.
	<i>reticulata</i>	<i>phlebophyllae</i>	27. vii. 76	25	27.7±3.5	7.2±1.3	78±6	0.24±0.10	75.0±10	0.08±0.08	•	n.s.
	<i>reticulata</i>	<i>phlebophyllae</i>	5. viii. 76	25	22.0±3.5	0.5±0.1	57±8	0.08±0.06	60.5±7	0.08±0.06	•	n.s.
	<i>reticulata</i>	<i>phlebophyllae</i>									•	n.s.

* Significant at $P < 0.05$ level.

FIG. 3. Distribution of nymphs and adults of *P. palmeni* along the Ice Scrape transect on 2 August 1976.

were absent from the Lake Basin but appeared as soon as the transition on to the Dry Ridge was reached. Flooding of the Lake Basin during spring snow melt ensures that the dwarf *S. reticulata* is completely inundated at the time when *P. phlebohyllae* adults would be becoming active and they appear unable to survive and reproduce in these conditions. In contrast *P. palmeni* on the Lake Basin appears able to move to its taller host plant *S. pulchra* and thereby largely avoid the effects of flooding.

Thus, on a broad scale, a combination of naturally occurring physical events appears to be acting to prevent both *P. palmeni* and *P. phlebohyllae* from breeding in areas which at first sight, on the basis of host plant availability, might be considered suitable.

The failure of psyllids to recolonize these sites once the disturbances have passed suggests that the rate of dispersal out of the more

FIG. 4. Distribution of nymphs of *P. phlebohyllae* on *S. reticulata* along the Lake Basin-Dry Ridge transect on 3 August 1976.

FIG. 5. Index of advancement of *P. palmeni* on various willows at the Mine Site during 1976 and 1977. $\circ$, *S. pulchra*; $\bullet$, *S. lanata*; $\square$, *S. glauca*; $\blacksquare$, *S. alaxensis*.

favourable areas is too low to overcome the host plant synchronization demands placed on the psyllid.

Seasonal differences in development rates of *P. palmeni* at the Mine Site

The contrast between a late (1976) and an early (1977) growing season permits a comparison between the progression of psyllid development and host plant phenology. In the early season *S. alaxensis* was the first to commence growth (Fig. 1) and psyllid development on this species, as indicated by the index of advancement, was advanced over *S. pulchra*, *S. lanata* and *S. glauca* (Fig. 5). However, in the late season *S. alaxensis* commenced growth after *S. lanata* and *S. pulchra* (Fig. 1) and in consequence the development of *P. palmeni* nymphs on these species remained advanced relative to *S. alaxensis* (Fig. 5). In both years psyllid development was latest on *S. glauca* but the difference was most accentuated in the late season.

Relative abundance and feeding intensity of psyllids on the different willows

Catkin and shoot size varies considerably between different willows. For instance, the biomass ratios of catkins of *S. lanata*, *alaxensis*, *pulchra*, *glauca*, *reticulata* and *phlebohylla* were 15:15:5:5:1:1 respectively. Thus psyllid numbers per sample unit do not give a meaningful comparison of numbers per standard unit of habitat. Furthermore, it proved logistically impossible to sample all

TABLE 5. Abundance of *P. palmeni* on *Salix* catkins at the Mine Site 1977 (error terms are SE)

<i>Salix</i>	Date	n	Weight of catkin (mg)	Psyllids catkin ⁻¹
<i>pulchra</i>	3.vii.77	58	140 ± 10	34.8 ± 4.1
	17.vii.77	60	228 ± 18	7.2 ± 1.5
<i>lanata</i>	4.vii.77	56	327 ± 24	7.8 ± 1.1
	18.vii.77	59	356 ± 23	7.9 ± 3.3
<i>alaxensis</i>	1.vii.77	50	455 ± 30	3.3 ± 0.8
	15.vii.77	60	428 ± 24	0.69 ± 0.17
<i>glauca</i>	6.vii.77	57	36.8 ± 7.1	0.25 ± 0.06
	19.vii.77	50	122 ± 13	0.58 ± 0.14

willows on the same date to provide a direct comparison of psyllid abundance, and sample dates are staggered for the different species. However, a few general conclusions can be drawn from a straight comparison of numbers (Table 4). On the Mine Site during 1976 numbers of *P. palmeni* nymphs per catkin were greater on *S. pulchra* than on *S. lanata* or *S. alaxensis*, but these three species as a group supported much larger populations than *S. glauca* or *S. reticulata*. The data for the latter were distorted by a large batch of eggs from a single catkin in the 23 July sample. The 1977 catkin data (Table 5) show an identical sequence of abundance on the different willows.

Numbers of *P. palmeni* on *S. pulchra* were of a comparable order of magnitude on the Mine Site and the Lake Basin despite a slightly larger catkin size at the latter. On the Dry Ridge numbers of *P. phleboaphyllae* per catkin were approximately equal on both *S. phleboaphylla* and *S. reticulata*.

To provide a direct comparison of the potential feeding intensity by psyllids the biomass of psyllids per unit biomass of plants was calculated using psyllid biomass data (Table 6). For *P. palmeni* (Fig. 6) feeding intensity was consistently greatest on *S. pulchra* both on the Mine and Lake Basin sites, being approximately 3 and 16 times greater than on *S. lanata* and *S. alaxensis* respectively on comparable dates. The figures for *S. reticulata* and *S. glauca* were consistently low. For *P. phleboaphyllae* (Fig. 6) feeding intensity was similar on both

TABLE 6. Oven dry weights of *P. palmeni* and *P. phleboaphyllae* nymphs and adults

Instar	No. weighed	Instar mean wt (µg)	
		<i>P. palmeni</i>	<i>P. phleboaphyllae</i>
Mature adult	100	238	149
5	100	88	52
4	100	28	25
3	100	14	8.0
2	100	3.9	3.1
1	100	1.5	1.4

S. phleboaphylla and *S. reticulata* and at least earlier in the season was of a comparable order of magnitude to *P. palmeni* on *S. pulchra*.

For both *P. palmeni* and *P. phleboaphyllae* psyllid biomass to catkin biomass ratios were often less than 1:100. The biomass figure at any one time represents a minimum figure for tissue production. In other psyllids the efficiency of conversion of phloem sap into body tissues is about 10% (Hodkinson, 1973a). Thus to have reached the observed biomass the psyllid population on the catkin must have consumed a weight of phloem sap at least one-tenth the weight of the catkin itself.

The effect of psyllid feeding on catkin and shoot growth

Correlation analysis was used to test the null hypothesis that psyllid density, measured as total number of psyllids per unit weight of catkin, was not related to the weight of the catkin. This analysis was carried out for each *Salix* on each site for each date during 1976 and catkins at Mine Site 1977. Several significant correlations were found: For *P. palmeni* on *S. pulchra* Mine Site 17 July 1976, 30 July 1976 and 3 July 1977 ($r = -0.71$, $P < 0.001$; $r = -0.43$, $P < 0.05$; $r = -0.40$, $P < 0.01$, respectively), for *P. phleboaphyllae* on *S. phleboaphylla*, Dry Ridge 22 July 1976 and 4 August 1976 ($r = -0.65$, $P < 0.001$; $r = -0.40$, $P < 0.05$, respectively) and for *S. reticulata* D grid 27 July 1976 ($r = -0.49$, $P < 0.05$). In every instance, including the non-significant ones, correlations were negative. The highly significant correlations occurred early in the season and tended to become non-significant towards the end of the season. These results suggest

FIG. 6. Feeding intensity of *P. palmeni* and *P. phlebotyphylae* on various willows at the different sites during 1976 and 1977.

that there is an inverse relationship between psyllid density and weight of catkin, implying that psyllids are suppressing catkin growth, i.e. the larger the psyllid population the smaller the catkin. Significant relationships were found for those species already shown to be subjected to the highest grazing intensity.

A parallel series of analyses was used to examine the relationship between psyllid density and weight of catkin bearing shoot. Significant negative correlations were found for *P. palmeni* on *S. lanata* at the Mine Site on 22 July 1976 ($r = -0.40$, $P < 0.05$) and *P. phlebotyphylae* on *S. phlebotyphylae* at the Dry Ridge on 22 July 1976 ($r = -0.57$, $P < 0.01$). These results, while not as clear cut as for the catkin, imply that the psyllids may be acting to suppress growth of the catkin bearing stem, at least in these species.

Discussion

The harsh arctic climate poses severe adaptational problems for insects (Downes, 1965). MacLean (1975a) lists low winter temperature, short growing season with associated low temperatures, low primary productivity and the weakness of photoperiod timing clues during the arctic summer as the main environmental variables to which invertebrates must adapt. He suggests that adaptation is achieved by a combination of life cycle adaptations, micro-habitat selection, metabolic and timing adaptations together with resistance to winter cold. This provides a useful framework in which to discuss adaptation in *P. palmeni* and *P. phlebotyphylae*.

The basic resource of any sap feeding phytophagous insect is its host plant. In

general growth and reproduction can only occur while the host plant itself is growing, although there is some evidence for aphids that feeding on plants can occur prior to bud burst (Hill, 1962). Thus if the plant is growing for only a short period, a high degree of phenological synchrony between insect and host plant is essential if the resource is to be fully exploited. The life cycles of both *P. palmeni* and *P. phlebotyphae* at Meade River show a high degree of synchrony with host plant phenology and this, coupled with a rapid development rate, enables them to complete a generation within the summer season. Such a life history is essentially the same as in the equivalent temperate univoltine *Salix*-feeding species *Psylla moscovita* and *P. saliceti* Förster where growth and reproduction occurs during the short period of the year when conditions are favourable (Hodkinson & White, 1979). This shows a marked contrast with the heather psyllid *Strophingia ericae* (Curtis), in which the evergreen host plant is 'available' throughout the year, and which has adapted to more rigorous climatic regimes by extending its life cycle from 1 to 2 years (Hodkinson, 1973a, b; Parkinson & Whittaker, 1975). Several adaptational features permit such a rapid life cycle. Firstly, both *P. palmeni* and *P. phlebotyphae* lie to the left of the r-k selection spectrum as defined by Southwood (1977) and possess attributes, such as high reproductive/mortality rates, necessary for the rapid exploitation of a temporary resource, albeit a somewhat restricted food resource. Secondly, the psyllids select a highly favourable micro-environment on the plant, namely the female catkin. Johnson (pers. comm.) showed that levels of soluble nitrogen, the food source of psyllids, are greater in female catkins than in any other plant component growing on the Alaskan tundra. Furthermore, the temperature regime within a developing catkin is more favourable than either air temperature or the surface temperature of adjacent leaves.

At Meade River the catkin itself has an effective 'life' equal to or only a few days longer than the time required by the psyllids to complete their development. Thus, successful completion of the life cycle demands a mechanism by which eggs are concentrated on the female catkin as soon as it appears. This

can be achieved by the sexually mature females being present on the plant at time of catkin burst and seeking out catkins for oviposition. Ovary maturation in female psyllids prior to the *Salix* flushing suggests that they are able to obtain some nutrition from stems. Female psyllids do not discriminate between male and female catkins and a significant proportion of eggs laid on the former are lost to the population when the catkin drops from the plant.

Lack of photoperiod clues at the time when psyllids emerge from hibernation suggests that synchronization with the host plant is temperature controlled. Natural selection should act to ensure that the temperature threshold for psyllid egg maturation and oviposition is close to the temperature threshold for *Salix* growth. Similarly if the psyllid population is to survive and reproduce it must complete its life cycle within the 'life' of a female catkin. The relative development rates of psyllid and catkin, taken in the context of the day degrees available for a given site, may well set the limits of psyllid distribution.

Winter snow cover on the Meade River site is thin and the willows are exposed to extreme winter temperatures. To ensure survival the psyllids must seek favourable overwintering sites, most probably in the litter layer or perhaps in rolled dead leaves remaining attached to the plant, and then return to the plant in spring. It is only the active adult stage which is capable of such movement, at least on to the taller willows.

It is generally postulated (e.g. Pianka, 1974) that arctic organisms have evolved broad, non-specialized niche-habitat requirements and that this results in the low diversity-high density situation observed among such organisms. If one considers the *Salix* community at Meade River to represent the total food resource of the psyllid community, then there is some evidence of resource partitioning, i.e. niche segregation, among the psyllid species. However, some flexibility is still retained. *Psylla phlebotyphae* occurs only on *S. phlebotypha* and *S. reticulata* whereas *Psylla palmeni* occurs only on *S. pulchra*, *S. lanata*, *S. alaxensis*, *S. glauca* and *S. niphoclada*. While there is some temporal and spatial separation of oviposition by females of each species there is sufficient overlap for oviposition on alterna-

tive willows to occur. That this does not happen suggests that both psyllids are able to discriminate between willows and are thus specific to their respective host plant series. Further resource subdivision occurs within a single host plant. On *Salix lanata*, *P. palmeni* nymphs feed on catkins whereas *Trioza atkasookensis* nymphs feed in pit galls on leaves. However, some overlap of food niches does occur, with *P. zaecevi* nymphs co-existing with *P. palmeni* nymphs on the catkins on *S. lanata* and *S. pulchra* and *P. macleani* occurring with *P. palmeni* on *S. alaxensis*, albeit at different sites.

With the exception of *P. macleani*, a scarce species, all species exhibit a degree of polyphagy. This flexibility in choice of food plant may act as a mechanism for spreading the risk and coping with year-by-year climatic variation. For instance the later developing *S. glauca* could act as a 'safety net' species on which *P. palmeni* could complete its development in years when synchrony with other hosts broke down.

The psyllid population data suggest that certain willows support higher populations than others and could therefore be considered favoured hosts. *Psylla palmeni* population densities were consistently higher on *S. pulchra* than on other *Salix* spp. In contrast, *S. lanata* and *S. alaxensis* appear to be the preferred hosts of *P. zaecevi* and *P. macleani* respectively (Hodkinson, 1978; Klimaszewski, 1973; Loginova, 1967). Thus potential niche segregating mechanisms which could act under conditions of intense competition appear to exist.

Variations in tundra topography lead to spatial separation of the different *Salix*/psyllid associations. Physical perturbation of the environment by ice movement, seasonal flooding or blown sand appears to prevent psyllids breeding in certain areas which are naturally colonized by the host plant. The heterogeneous patterns of psyllid distribution are probably further accentuated by phenological variations within a single *Salix* species, related to the aspect of the site in which it is growing.

For *S. pulchra*, *S. phlebophylla* and *S. reticulata*, those species subjected to the highest feeding pressure, psyllid populations appear to be suppressing catkin growth. The high psyllid biomass which catkins are capable of support-

ing, often of the order of 1 g of psyllid per 100 g of catkin emphasizes the fact that catkins are nutrient sinks which continually accumulate photosynthate produced elsewhere in the plant and that *P. palmeni* and *P. phlebophylla* are feeding at the site where the supply of high quality nutrients is maximal.

Predation by syrphid larvae caused considerable mortality in both *P. palmeni* and *P. phlebophylla* populations whereas no evidence of parasitism was found. This may again be a result of synchronization demands; predators such as syrphids are opportunistic generalists, feeding on any available psyllid instar as well as alternative food resources and having little need to synchronize their life cycle with that of their prey. In contrast, psyllid parasites are usually both psyllid and instar specific (Hodkinson, 1974) and host-parasite synchronization is highly vulnerable when subjected to a fluctuating environment.

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