ORIGINAL PAPER

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Factors limiting the distribution of *Acyrthosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen

Abstract The distribution of the high arctic aphid *Acyrthosiphon svalbardicum* was found to have a distinct limit in the Kongsfjorden area of Spitsbergen; the probability of site occupancy increased with distance from the fjord mouth and decreased with distance from the shore. Superimposed on this general distribution pattern, sites that cleared of snow early in the polar summer were more likely to be occupied by aphids. The phenology of the aphid was significantly affected by small changes in microclimate over distances of a few metres. The aphid only occurs in the warmer parts of the region, but laboratory cultures were successfully reared on plant material collected from colder regions that the aphid does not presently occupy. These observations suggest that the local distribution of *A. svalbardicum* is determined by summer thermal conditions. On a smaller scale, within patches where the aphids occurred, densities were higher on flowers and flowering shoots than on non-flowering shoots.

Introduction

Insects in the high Arctic are thought to be surviving at the extreme limits of their range with regard to abiotic conditions (Downes 1962), although this has been clearly demonstrated for only a few species. Further, it is probable that the realised and fundamental niches of phytophagous insects in the high Arctic coincide closely because their low abundance makes competitive exclusion unlikely, and parasitism and pedation pressures are thought to be low (Ryan 1981; but see also Kukal and Kevan 1987).

The aphid *Acyrthosiphon svalbardicum* Heikinheimo is endemic to Svalbard and feeds on *Dryas octopetala* L. (Heikinheimo 1968; Strathdee et al. 1993b). Survival in this extreme environment is only possible because of the aphids' unusual biology (Strathdee et al. 1993c). Studies were carried out around the research base of Ny Ålesund, in the Kongsfjorden district. An analysis comparing historical meteorological data with thermal budget (above 0°C) requirements of *A. svalbardicum* demonstrated that in some years this species was threatened by local extinction due to unfavourable summer conditions (Strathdee et al. 1933a). Indeed, a decrease in average summer temperature of 2 deg C would lead to local extinction within a few years as the first-born sexual morphs would fail to mature, mate and lay overwintering eggs.

Conditions are warmer during summer in the inner fjord than the outer fjord at Ny Ålesund and these thermal gradients are reflected in vegetation type, although the aphid's host plant *D. octopetala* is ubiquitous throughout the region (Brattbakk 1986). Similarly, land closer to the shore is warmer than further inland due to the changing elevation and the proximity of snow fields and glaciers. Superimposed on these gradients are local differences in microclimate reflecting aspect and winter snow accumulation. Further, the population of *A. svalbardicum* studied previously was found in one of the warmer areas, which cleared of snow early in the season. These observations suggest that it is possible that at sites in cooler parts of the region, or in which the growing season is shorter, the aphid would be unable to produce any eggs in some years, threatening local extinction. On a smaller scale, there is a preferential allocation of nutrients to flower heads in *D. octopetala* that may affect the within-patch distribution and abundance of the aphid. This paper identifies

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patterns in the distribution of *A. svalbardicum* and considers possible explanations.

Materials and methods

Aphid developmental phenology and microclimate

Several patches of *D. octopetala* were found on a south facing slope in Ny Ålesund that progressively cleared of snow from the top of the slope to the bottom 5 m over 1 to 2 weeks in May 1992. There was no vegetation on the ground between the patches. The six largest patches of *D. octopetala* were selected (labelled A–F in Fig. 1) and four 10-cm-diameter vegetation samples taken from each patch in early July 1992. The arthropod fauna was heat extracted using Burkhard funnels into an alcohol-glycerol (70:30) solution and the population density and age-structure of the aphids assessed.

Site location and occupancy

To map the distribution of *A. svalbardicum* around Ny Ålesund, samples of *D. octopetala* were taken from 42 sites in the area during July 1992. One 10-cm-diameter vegetation sample was collected from each of 12 randomly selected patches within a 20 m × 20 m area at each site and the arthropod fauna extracted as before. All the main areas of *D. octopetala* within the region were included in the survey and results were analysed using binary logit (Systat, Logit), comparing presence and absence with distance to the shore and distance to the fjord mouth (measured from the point Kvadehuken).
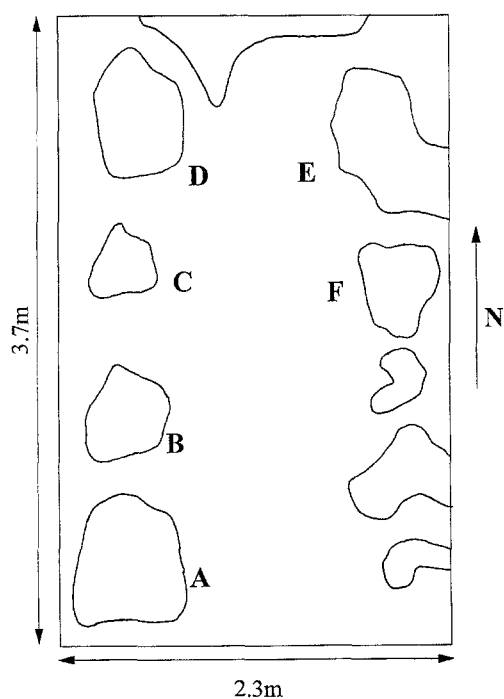

Fig. 1 Map of clumps of *Dryas octopetala* on a south facing slope in Ny Ålesund

Date of snow clearance

To test the hypothesis that the date of snow clearance affects site occupancy, 13 sites within a region where the aphid occurred were selected. The date of first patch clear of snow at each site was recorded during the period mid-May to mid-June, and aphid occupancy at these sites was assessed in mid-July (the time of peak aphid density) by taking twelve 10-cm-diameter samples at random from each site and extracting the arthropod fauna as before.

Within patch distribution

On 29 June 1992, soon after aphid egg hatch at the study site, samples of *D. octopetala* were taken from a coastal ridge within Ny Ålesund where the aphid occurred. The plant material was stored in a refrigerator (5 ± 2°C) to limit movement of the aphids before analysis. Individual shoots of the *D. octopetala* were hand-sorted under a binocular microscope, and densities of aphids on flowering and non-flowering shoots recorded.

Aphid rearing on plant material from unoccupied sites

In experiments on *A. svalbardicum*'s life-cycle, aphids were reared on *D. octopetala* collected from sites that were known to be unoccupied in order to maintain the hygiene of the lineages being studied. Plant shoots were kept in water using the methods described by Austin et al. (1993) as *D. octopetala* proved difficult to propagate.

Results

Developmental phenology and microclimate

The distribution and density of *A. svalbardicum* in the six patches of *D. octopetala* on a south facing slope (Fig. 1) are given in Table 1. First and second instar nymphs were found only in cores containing adult aphids with one exception (one of the cores from D). At the time of sampling, most of the fundatrices at the top of the slope had matured to adulthood and some had started to reproduce as evidenced by the large number of nymphs in patches B–F. The number of adults tended to be higher in patches furthest up the slope, and the ratio of first and second instar nymphs to adults was also highest at the top of the slope. Collectively, these points demonstrate that aphid phenology was advanced at the top compared with the bottom of the slope.

Site location and occupancy

The distribution of *A. svalbardicum* around Ny Ålesund is mapped in Fig. 2 and these data are summarised in Fig. 3. Binary logit analysis of the presence or absence data for the aphids at 42 sites (Table 2) indicated a clear distribution limit in which aphids occurred on the inner (and not outer) fjord ($P = 0.015$) and close to the shore ($P < 0.005$).

Table 1 Local distribution and density of *Acyrthosiphon svalbardicum* on clumps of *Dryas octopetala* on a south facing slope (mean ± SE). The ratio (1 + 2)/(A) (number of first and second instars per adult) indicates the length of time since the fundatrices matured to adulthood-the higher the number the longer the time

Patch	Aphid instar					Total 3 to adult	(1 + 2)/A
	1	2	3	4	Adult		
A	0	0	4.0 ± 1.3	4.3 ± 1.4	0.5 ± 0.3	8.8	0
B	7.0 ± 3.2	0	0.3 ± 0.3	0.5 ± 0.3	5.5 ± 0.6	6.3	1.1
C	7.3 ± 1.7	0.5 ± 0.5	0.3 ± 0.3	0.3 ± 0.3	3.3 ± 0.8	3.9	2.4
D	13.3 ± 4.4	0.8 ± 0.3	0	0	3.3 ± 1.1	3.3	4.3
E	35.8 ± 4.6	3.3 ± 1.6	0.5 ± 0.5	0.8 ± 0.5	5.5 ± 1.3	6.8	7.1
F	9.3 ± 5.1	0.8 ± 0.5	0.5 ± 0.5	0.5 ± 0.3	3.8 ± 1.6	4.8	2.7

Fig. 2 Map of distribution of *A. svalbardicum* in the Kongsfjorden area of Spitsbergen (*o* aphids present, *x* aphids absent)
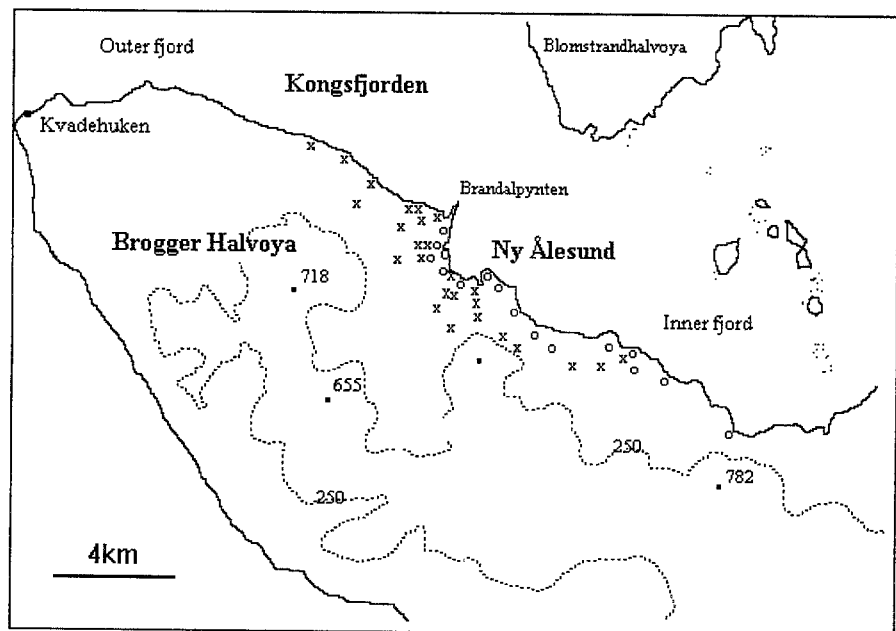
Snow clearance and occupancy

Of the 13 sites investigated, only the 7 that cleared of snow before the end of May were occupied. In the analysis of aphid occurrence at 13 sites with different times of snow clearance, there was a higher occupancy at sites that cleared of snow before the end of May than at sites where snow remained later in the year (Fisher's exact test $N = 13$, $P < 0.05$).

Within patch distribution

A significantly larger number of nymphal fundatrices fed on shoots with flower buds than on vegetative shoots (27 aphids per 100 flowering shoots compared with 5 aphids per 100 vegetative shoots, $\chi^2 = 21$, $P < 0.005$).

Aphid rearing on plant material from unoccupied sites

Aphids developed and reproduced on plant material collected from unoccupied sites, even though the plant material was not potted plants, showing that the distribution is not limited by host plant quality.

Discussion

Within patch distribution

The higher concentration of nymphal fundatrices on flower buds compared to vegetative shoots suggests that flowers are preferred feeding sites, selected either by oviparae at the time of egg laying in the previous summer or by nymphs soon after egg hatch. Whatever
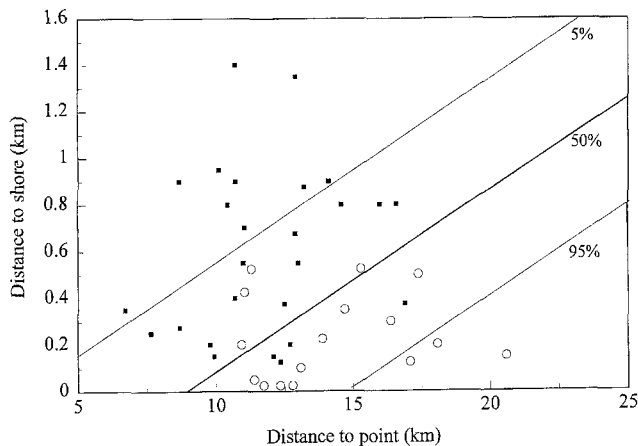
Fig. 3 Plot of distribution of sites tested for aphid occurrence (O aphids present, ■ aphids absent). *Diagonal lines* are plots of equal confidence of finding an aphid at a site as predicted by binary logit analysis model given in Table 2

the selection mechanism this relationship is advantageous to the aphid, as developing flower heads act as nutrient sinks and therefore often offer favourable feeding sites to sap-feeding insects. Flower heads may also offer warmer microsites that would allow accelerated development (Kevan 1975). Increased nutrition has been shown to be positively correlated with aphid size in many cases (Watt 1979), which itself is correlated with reproductive rate (Wratten 1977; Watt 1979); however, in *Metopolophium dirhodum* the opposite was found (Watt 1979). Further, the mean rate of development, relative growth rate and intrinsic rate of increase of *Sitobion avenae* are higher in individuals reared on ears of corn compared to flag leaves (Acreman and Dixon 1989). As we carried out the sampling at the beginning of the season, as soon as nymphs were present, it seems likely that the oviparae select these sites at the end of the previous season, and must therefore be able to identify shoots that will produce a flower in the following year. The increase in flowering shoots of the host plant reported by Wookey et al. (1993) in response to a simulated warming of 2 deg C would provide a greater abundance of preferred feeding sites for increased numbers of aphids resulting from climate warming (Strathdee et al. 1993a).

General distribution

The survey of aphid occurrence along the southern shore of Kongsfjorden indicates a clearly demarcated limit to the distribution, even though *D. octopetala* is ubiquitous in this region. Superimposed on the general distribution pattern of *A. svalbardicum*, it is evident that site occupancy is more likely in areas that clear of snow early in the summer. There are a number of possible explanations for this clearly defined distributional limit, which will be considered in turn.

1. Host plant quality: It is possible that the aphid is unable to live on *Dryas octopetala* in cold sites and from under deep snow because the plant material is unsuitable as a host, due to poor nutrient status. This, however, is unlikely as the aphid was successfully reared during laboratory experiments on plant material collected from unoccupied sites.

2. Restricted colonisation: *A. svalbardicum* is unusual amongst aphids in that it does not produce winged forms in response to crowding, which limits its ability to disperse to new areas (Strathdee et al. 1993c). Although this factor may play some part in limiting the rate of spread of the population, it explains neither the absence of aphids from sites that clear of snow late in the summer nor the shape of the present distribution. If this was the underlying mechanism behind the present distribution, the aphid would have spread approximately equal distances inland as along the coast.

3. Winter thermal conditions: Some Arctic species (e.g. *Epirrita autumnata* in the sub-Arctic; Tenow and Nilssen 1990) are limited in their distribution by winter conditions, due to insufficient cold hardiness. This is not the case in *A. svalbardicum* as site occupancy is higher in areas that accumulate little snow and which are thus exposed to the lowest winter temperatures, than at those sites protected from low air temperatures by insulating snow.

4. Summer cold injury: Cold periods with sub-zero temperatures occur during summer in the high Arctic, which may cause injury or death in the active stages of aphids that have a low level of cold hardiness (Knight et al. 1986; Hutchinson and Bale 1994). However, summer active stages of Arctic aphids are more cold hardy than their temperature counterparts and are able to

Table 2 Binary logit analysis of *A. svalbardicum* patch occupancy. Distances in km. RHO^2 is equivalent to R^2 in linear regression analysis but values as low as 0.2 are considered a good fit (Hensher and Johnson 1984) (N_1 number of occupied patches, N_2 number of unoccupied patches)

	Parameter estimate	SE	T-ratio	P	RHO^2	N_1	N_2
Constant	− 4.346	2.402	− 1.810	0.070	0.426	16	26
Distance to shore	− 6.212	2.092	− 2.969	0.003			
Distance to Kvadehuken point	0.481	0.198	2.428	0.015			
Model $\chi^2 = 23.791$, $df = 2$, $P < 0.001$							

survive the lowest summer temperatures occurring in their environment without suffering mortality or sublethal effects (Bale et al. 1994).

5. Summer thermal conditions: The aphid was found only in the warmest areas i.e. close to the shore and towards the inner fjord (Fig. 2). Previous results have shown that even in warmer sites the aphid is threatened with local extinction due to insufficient thermal budget to complete the life-cycle in the coldest years (Strathdee et al. 1993a). It is likely that in the unoccupied areas in the harshest years the aphid would be unable to complete the two generations necessary for the production of overwintering eggs to continue the population to the next year.

The thermal environment of polar regions is heterogeneous during both winter and summer, and the selection of microhabitats can have profound effects on the thermal regimes experienced by organisms (Downes 1962; Coulson et al. 1993). Site selection is a trade-off between the risk of cold injury due to exposure to low temperatures in winter and the thermal budget available during the summer. Sites that accumulate deep snow and are thus insulated from the lowest winter air temperatures clear of snow later in the summer, whereas those that remain virtually uncovered experience the lowest winter air temperatures directly, but clear earlier, maximising summer heat budgets (Coulson and Strathdee, unpublished data). The overall thermal budget of a habitat during summer is the product of the length of the growing season and the ambient temperature (a function of many variables such as latitude, incident radiation, air temperature, vegetation type, aspect and elevation). Larvae of Arctic Lepidoptera frequently hibernate in exposed areas where little snow accumulates (Johansen 1911) and the eggs of mosquitoes are laid where the snow melts most rapidly (Corbet 1967). By contrast, many species rely on the insulating effect of snow cover for survival (e.g. Monro 1935). It is probable that A. svalbardicum is absent from sites that accumulate deep snow during winter because this reduces the available thermal budget during summer. Indeed, the differences in phenology over a few metres on a south facing slope illustrate the importance of micro-climate on the seasonal success of A. svalbardicum. Retardation of development caused by a late clearance of snow may prevent the aphid from producing eggs by the end of the season, causing local, temporal extinction. The importance of this interaction is supported by survey of dates of snow melt in which the aphid was more likely to occur at sites that were clear of snow before the end of May.

In combination, these results suggest that the present geographical limit is determined by summer thermal conditions alone. There are few critical studies that demonstrate that the distribution of a phytophagous insect is determined by thermal conditions (Strong

et al. 1984). Temperature plays an important role in the distribution of the white admiral butterfly (Ladoga camilla L.) in southeast England (Pollard 1979). It is not, however, climate per se that limits the distribution but its effect on predation by birds. With low summer temperatures development is slow, giving birds more time to prey on caterpillars and pupae, hence imposing high mortality. A second example, the thimbleberry aphid (Masonaphis maxima Mason) was given by Gilbert (1980). Like A. svalbardicum, this species has a minimum life-cycle (three generations) through which it has to pass to produce overwintering eggs. Further, colonisation across gaps of 1 km or more requires an extra two generations as the migrants are unable to produce sexual morphs, so the aphid may be unable to survive in new areas during the year of colonisation, even though the normal three generation life-cycle would be possible in all years. Similarly MacLean and Hodkinson (1980) showed that the distribution of psyllids in Alaska is limited by the length and temperature of the growing season; the thermal requirement to complete the univoltine life-cycle defines the northerly extent of a number of species.

In studies of distribution, a commonly used methodology is transplant experiments (e.g. Gilbert 1980). However, such experiments would not be of much value in this case as they are unlikely to be carried out in the extremely cold years that would limit the distribution. Thus, after moving the aphid to a presently unoccupied site, it is likely it would survive for a number of seasons until a severe summer occurred producing conditions too cold for any eggs to be laid. It would therefore be difficult to interpret the results of transplant experiments unless the populations were followed at experimental sites for many years.

Conclusions

To survive the harsh polar winter, aphids must overwinter as eggs because the active stages are not sufficiently cold hardy. The life-cycle of A. svalbardicum is well adapted to this constraint and the short polar summer, with the fundatrix giving rise directly to both sexual morphs, an observation so far unique in the Aphidinae (Strathdee et al. 1993c). It seems likely that current thermal conditions around Ny Ålesund are at the limit of those in which an aphid with a fundatrix generation can survive; the life-cycle can only be further truncated by the production of sexual morphs directly from overwintering eggs. In combination, the survey work presented here shows that factors including summer thermal regime and nutrient availability influence the distribution of A. svalbardicum, on both a wide ranging and more local scale on Spitsbergen. The results demonstrate that the distribution of A. svalbardicum is presently limited by summer thermal

conditions, and that the aphid survives only at sites with little or no snow cover that have maximal summer thermal budgets, but are exposed to the lowest winter temperatures. Like other species at the limit of their geographic range (e.g. Thomas 1993), *A. svalbardicum* is restricted to specific microhabitats. It is likely that in the high Arctic, where thermal conditions are particularly severe, the limit to the distribution of many invertebrates is defined by thermal conditions alone.

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