Species at the edge of their range: The significance of the thermal environment for the distribution of congeneric Craspedolepta species (Sternorrhyncha: Psylloidea) living on Chamerion angustifolium (Onagraceae)

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Abstract. There is much current discussion about the factors that control the distribution and abundance of animal species, particularly at the edges of their range. The significance of temperature for survival and development is compared in two closely related psyllid species (Craspedolepta nebulosa and C. subpunctata) living on the same host plant (Chamerion angustifolium) (Onagraceae) but displaying different distributions along latitudinal and altitudinal gradients. The following measurements were made at critical periods during the life cycle (a) winter supercooling points (SCPs), (b) tolerance of short (1 min) and long term (1–25) days exposure to sub-zero temperatures above the SCP, (c) tolerance of short term exposure to high spring/summer temperatures and (d) comparative field development rates among species and sites during the early critical part of the growing season. Successful completion of the life cycle is related to heat availability during the growing season. This appears to limit the distribution of the Craspedolepta species, rather than their survival response to thermal extremes. No significant differences were found between the two species in the supercooling point or in their long and short term survival responses at low or high temperatures.

INTRODUCTION

There is much current discussion about the factors that control the distribution and abundance of animal species, particularly at the edges of their range. Attention has recently focused on the importance of the spatial configuration and abundance of the host plant (Gaston, 1996) and on the insect’s trophic flexibility (Quinn et al., 1997). The significance of temperature as a limiting factor and its possible role in shifting the competitive balance between species has been somewhat neglected, despite its importance in an era of changing global temperatures (Whittaker & Tribe, 1996; Hodkinson & Bird, 1998; Hodkinson et al., 1998). Davis et al. (1998) have recently argued that physiological models of single species response to changing climate fail to reflect how climate can act differentially on interacting species, particularly as it affects their distributional range. This paper compares the significance of temperature for the survival and development of two closely related and potentially competing psyllid species living on the same host plant. It shows how temperature may act to determine the distribution of these species along latitudinal and altitudinal gradients.

The jumping plant-lice or psyllids Craspedolepta nebulosa (Zetterstedt) and Craspedolepta subpunctata (Förster) are host specific on rosebay willow-herb or fireweed [Chamerion angustifolium (L.) J. Holub] (Onagraceae). Both species have broad north circumpolar distributions (Joumet & Vickery, 1979; Hodkinson, 1980; MacLean & Hodkinson, 1980; Ossiannilsson, 1992) and their ranges overlap, with the two often found abundantly on the same plant. Furthermore, C. nebulosa and C. subpunctata have almost identical annual life cycles (Fig. 1), suggesting a potentially strong competitive interaction (Lal, 1934; Heslop-Harrison, 1937; Lauterer & Baudys, 1968; Bird & Hodkinson, unpubl.). Eggs are laid on above ground shoots in late spring, before the rosebay commences flowering (Sampo, 1975). The hatching larvae migrate to feed on the roots, where they develop to the fourth instar before the onset of winter. As the rosebay commences growing in the following year the overwintered larvae move onto the growing shoots. The moult to the final (fifth) instar is rapid and adults emerge soon afterwards. The distribution of the two species along latitudinal and altitudinal transects (Table 1) shows that C. nebulosa extends to higher latitudes and altitudes than C. subpunctata but that neither species occupies the full geographical range of its host plant (Hodkinson & Bird, 1998). MacGarvin (1982) attempted to establish a relationship between host plant patch size and abundance for C. subpunctata without apparently realising that larvae spend most of the year on the roots rather than the leaves. Craspedolepta nebulosa is, by contrast with C. subpunctata, typically smaller and darker (Table 2). Mature adults of the former are greyish with extensive black or dark
TABLE 1. Presence (+) and absence (-) of C. nebulosa and C. subpunctata in large samples (minimum of 100 C. angustifolium plants on at least 2 separate occasions) at sites along a latitudinal transect and up an interlinking altitudinal gradient on the Hardangervidda, Norway (Hodkinson & Bird, 1998). Suitable host plants occur abundantly at all sites.

<table>
<thead>
<tr>
<th>Location</th>
<th>C. nebulosa</th>
<th>C. subpunctata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ainsdale, UK</td>
<td>53°30'N</td>
<td>+</td>
</tr>
<tr>
<td>Geilo, Norway</td>
<td>60°40'N</td>
<td>+</td>
</tr>
<tr>
<td>Tromsø, Norway</td>
<td>69°30'N</td>
<td>+</td>
</tr>
</tbody>
</table>

Altitudinal transect

<table>
<thead>
<tr>
<th>Site</th>
<th>Altitude (m)</th>
<th>C. nebulosa</th>
<th>C. subpunctata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geilo</td>
<td>749</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Haugastøl</td>
<td>988</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Gråkallen</td>
<td>1,100</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Finse</td>
<td>1,222</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Our study examined the factors that might determine the distribution limits of the species. The following measurements were made at critical periods during the life cycle: (a) winter supercooling points (SCPs), (b) tolerance of short (1 min) and long term (1-25 days) exposure to low temperatures above the SCP, (c) tolerance of short term exposure to high spring/summer temperatures and (d) comparative field development rates between species and sites during the early critical part of the growing season.

**METHODS**

**Field sampling of populations**

Populations of C. nebulosa and C. subpunctata were sampled at weekly intervals during 1993 at Ainsdale, Merseyside, UK and at 3 sites, Geilo, Haugastøl and Finse along the altitudinal gradient in the Hardangervidda region of southern Norway (Table 1). Each sample comprised 50 plants of C. angustifolium from which the psyllids were removed, identified and counted. Development rates of psyllids among species and sites was compared using a modification of the Index of Development (I) on a scale of 1-6 as defined by Hill & Hodkinson (1995)

\[ I = \frac{1}{n_i} \left( \frac{1}{T} \sum_{i=1}^{n_i} t_i \right) \]

where \( T \) = total number of eggs and larvae present, \( i \) = instar code (instar 1 = 1, instar 2 = 2, adult = 6), and \( n_i \) = number of individuals in instar \( i \).

A similar set of samples were taken from a dense population of C. angustifolium growing on a steep south-facing slope near Haugastøl, Norway. This slope was chosen because of its favourable aspect and the fact that it is covered by snow throughout the winter and that snowmelt proceeds gradually from the top to the bottom of the slope. Plants growing at the top of the slope were free of snow earlier and were phenologically well-advanced over those growing at the bottom of the slope. Thirty plants were taken at weekly intervals from the top, middle and bottom of the 10 m slope and the psyllids extracted and counted as before.

Winter soil (surface, 3 and 6 cm depths) and air shade temperatures (30 cm above ground) were recorded continually throughout one winter at Ainsdale, UK (1993/4) and Finse, Haugastøl and Geilo, Norway (1994/5) using microthermistor probes (FM-S) linked to Grant Squirrel MQW32 or SQ32 data loggers. Standard long-term meteorological data for the Norway transect sites were obtained from det Norske Meteorologiske Institutt.

**Sources of experimental material**

Supercooling point (SCP) determinations were carried out on C. nebulosa and C. subpunctata from Ainsdale, Merseyside, UK and on C. nebulosa from Tromsø, Norway. Short-term low and high temperature survival experiments were conducted on larvae of both psyllid species from Ainsdale and on adult and larvae of C. nebulosa from Tromsø, collected at time of spring emergence. Larvae are difficult to find in the soil and the normal method of heat extraction during winter alters their physiology. They can only be collected reliably as they become active towards the end of winter. Long-term survival experiments were conducted on larvae in intact soil cores taken at Ainsdale in February.

**Supercooling points**

Supercooling points were determined, where appropriate, for the overwintering and spring-active stages of both C. nebulosa and C. subpunctata (fourth and fifth instar larvae and adults) using the method described by Coulson et al. (1995b). C. nebulosa is colour dimorphic in the fifth instar, existing as both yellow and brown forms, with the paler form becoming, counter intuitively, more abundant at higher latitudes and altitudes (Bird & Hodkinson, unpubl.). This difference is apparently unrelated to time in the stage and serves no immediately discernible purpose. When sufficiently abundant, as at Tromsø, SCPs for each phenotype were initially determined separately but as the data were not significantly different they were later pooled.

**Survival at low temperature – short term exposure**

Survival was measured by cooling animals in small tubes at 1°C min-1 from a starting temperature of 5°C to preselected sub-zero temperatures as described by Coulson et al. (1995b). Animals were held at that temperature for 1 min and then raised back to the starting temperature at the same rate. Each tube contained five animals and the treatment was replicated 6 times at each temperature. After treatment psyllids were returned to their host plant in moistened petri dishes and survival was recorded after 48 h, when normal behaviour could be observed.

**TABLE 2. Relative body size of C. nebulosa and C. subpunctata throughout their geographical range.**

<table>
<thead>
<tr>
<th>Measurement (mm)</th>
<th>Locality</th>
<th>C. nebulosa</th>
<th>C. subpunctata</th>
<th>Authority</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length</td>
<td>Russia</td>
<td>2.6-2.8</td>
<td>3.3-3.6</td>
<td>Loginova (1964)</td>
</tr>
<tr>
<td></td>
<td>Scandinavia</td>
<td>2.5-3.4</td>
<td>2.8-4.0</td>
<td>Ossiannilsson (1992)</td>
</tr>
<tr>
<td>&quot;Czechoslovakia&quot;</td>
<td>2.6-2.8</td>
<td>3.3-3.6</td>
<td></td>
<td>Vondráček (1957)</td>
</tr>
<tr>
<td>Body length (mean)</td>
<td>N. America</td>
<td>male 2.6, female 3.1</td>
<td>male 3.5, female 3.7</td>
<td>Journet &amp; Vickery (1979)</td>
</tr>
</tbody>
</table>
ments were conducted on larval instars 4 and 5 of both species from Ainsdale and on instar 5 and adults from Tromso.

Survival at low temperatures – long-term exposure

To test the survival of overwintering psyllids in undisturbed soil samples, 9 cm diameter soil cores were taken, each incorporating the roots of a plant that was known to have supported psyllid populations in the previous summer. The cores were taken in February, at Ainsdale, UK and exposed for 2, 10 or 25 days to temperatures of -5, -10 and -15°C in unlit constant temperature cabinets. Each treatment was replicated using 6 cores and a set of equivalent control cores were maintained at 5°C for 25+ days. After each treatment, cores were returned slowly to room temperature in gradual stages over 1 week and then heat extracted for psyllids in a Burkard extractor over a 120 h period. This is the most effective method for sampling larvae, which do not appear to have a strict diapause and which can be extracted efficiently throughout the winter (Bird & Hodkinson, unpubl.). Emerging psyllid larvae were then counted. Direct counting of larvae on the roots is not feasible and it is therefore not possible to set up treatments with exactly equivalent numbers of animals. It has to be assumed that the random allocation of cores among treatments ensured that the mean number of animals in the different temperature treatments and controls at the start of the experiment was the same. This disadvantage needs to be considered when interpreting the results.

Survival at high temperature – short term exposure

Survival was measured by warming animals in small tubes at 1°C min⁻¹ from room temperature to preselected temperatures as described by Hodkinson et al. (1996). Animals were held at that temperature for 1 min and then returned at the same rate to the starting temperature. Each tube contained five animals and this treatment was replicated 5 times at each temperature. After treatment psyllids were returned to their host plant in moistened petri dishes and survival was recorded after 48 h, when normal behaviour could be observed. Experiments were conducted only on instar 5 larvae of both species as the lethal temperatures recorded were well above those they are likely to encounter under even extreme field conditions.

Statistical analysis of results

General linear model (GLM) ANOVA (Minitab) was used, where appropriate, to test for effects of species, temperature and exposure time on survival. Results were compared with parallel analyses using the Scheirer-Ray-Hare extension (for replicated experiments) of the Kruskal-Wallace test (Sokal & Rohlf, 1995). Results from this non-parametric test mirrored those from the ANOVA and are not presented.

RESULTS

The supercooling points of adults, fourth and fifth instar larvae of both C. nebulosa and C. subpunctata (Table 3) were broadly similar, independent of the site from which they were collected, with the mean value always lying within the range -20.7 to -23.5°C, and the standard deviation around the mean low, indicating a narrow spread of values. At Tromso, there was no significant difference between the yellow and brown forms of fifth instar larvae of C. nebulosa (F = 0.001, df = 23, P = 0.97) and data were combined in subsequent analyses. No significant differences were found between the samples in table 3 when compared as a single factor ANOVA (F = 1.19, df = 5, P = 0.31). Similarly when the symmetrical

<table>
<thead>
<tr>
<th>Species</th>
<th>Site</th>
<th>Instar</th>
<th>SCP</th>
<th>SD</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. nebulosa</td>
<td>Tromso</td>
<td>adult</td>
<td>-20.7</td>
<td>1.5</td>
<td>18</td>
</tr>
<tr>
<td>C. nebulosa</td>
<td>Tromso</td>
<td>5th</td>
<td>-21.6</td>
<td>2.6</td>
<td>24</td>
</tr>
<tr>
<td>C. nebulosa</td>
<td>Ainsdale</td>
<td>5th</td>
<td>-22.5</td>
<td>2.4</td>
<td>34</td>
</tr>
<tr>
<td>C. nebulosa</td>
<td>Ainsdale</td>
<td>4th</td>
<td>-23.5</td>
<td>3.2</td>
<td>36</td>
</tr>
<tr>
<td>C. subpunctata</td>
<td>Ainsdale</td>
<td>5th</td>
<td>-21.8</td>
<td>2.2</td>
<td>36</td>
</tr>
<tr>
<td>C. subpunctata</td>
<td>Ainsdale</td>
<td>4th</td>
<td>-23.5</td>
<td>2.3</td>
<td>36</td>
</tr>
</tbody>
</table>

Ainsdale data set were analysed separately there were no significant effects of species, instar or species x instar on the SCP (F < 1.73, df = 1, P > 0.19).

Larvae in the low temperature short term survival experiments (Fig. 2) showed similar survival patterns in both psyllid species, with little mortality occurring below -7.5°C and significant mortality (20%) only occurring below -15°C. No larvae survived to -25°C, and just two instar 4 larvae of C. subpunctata survived -22.5°C. These experiments were analysed in two ways. Over the critical temperature range -10 to -22.5°C, short term survival data were collected for instars 4 and 5 of each species at each temperature. ANOVA of this symmetrical data set showed a strongly significant effect of temperature on survival (F = 109.7, df = 4, P < 0.001) but no significant effect of species (F = 0.64, df = 1, P = 0.44), instar (F = 0.15, df = 1, P = 0.70) or species x instar (F = 0.34, df = 1, P = 0.56). Outside the -7.5 to -22.5°C temperature range, where survival was complete and where determinations added no new information to the pattern observed, some non-critical temperatures were omitted. In a separate analysis, to make the treatments symmetrical, all data above and including -7.5°C, where survival invariably approached 100%, were grouped into a single treatment set (above -7.5°C) and the whole data set reanalysed. Again the temperature treatment effect was significant (F = 188.0, df = 5, P < 0.001) but species, instar, and species x instar effects were all non-significant (F < 0.18, df = 1, P > 0.67). By contrast, adult S. nebulosa appear less cold-tolerant than larvae with none surviving -17.5°C (Fig. 2). This is emphasised by statistical comparison of data for adults from a colder site (Tromso) with those for instar 5 larvae from a warmer site (Ainsdale) where there was a strong effect of life stage (F = 107.2, df = 1, P < 0.001), temperature (F = 53.5, df = 5, P < 0.001) and species x temperature interaction (F = 10.3, df = 1, P < 0.001).

In the long term low temperature exposure experiments (Fig. 3) the numbers of psyllids emerging from cores kept at -5°C for 25 days did not differ markedly from those emerging from untreated controls. Some C. nebulosa survived exposure down to -10°C for 25 days; none, however survived 10 days at -15°C. C. subpunctata showed a similar pattern of survival, except that two larvae survived the 10 day treatment at -15°C. The GLM ANOVA, using psyllid population data expressed as log (n+1),
Fig. 2. Percentage survival of adults and fourth and fifth instar larvae of *Craspedolepta* species when exposed for 1 min periods to sub-zero temperatures showed a significant effect of temperature on survival ($F = 9.01, df = 2, P < 0.001$) and a significant interaction between temperature and time ($F = 3.10, df = 4, P = 0.05$).

However, the effect of time alone ($F = 3.09, df = 2, P = 0.05$) and species ($F = 0.11, df = 1, P = 0.74$) were non-significant, although the former was on the verge of significance.

The response of *C. nebulosa* and *C. subpunctata* instar 5 larvae to potentially lethal high temperatures (Fig. 4), paralleled the response to low temperature. There was a highly significant effect of temperature ($F = 135.2, df = 2, F = < 0.001$) but the effects of species ($F = 0.47, df = 1, P = 0.50$) and species x temperature ($F = 2.05, df = 2, P = 0.15$) were non significant. Significant mortality was not recorded until the temperature exceeded 40°C, a temperature well in excess of the maximum recorded in the field.

The relative development rates of *C. nebulosa* and *C. subpunctata*, measured as change in the Index of Development, at Geilo (Fig. 5) diverged strongly during the critical early growth period of the host plant, with *C. nebulosa* developing the more rapidly. During this period the development index of *C. subpunctata* at Geilo was similar to that of *C. nebulosa* at Haugastol, the higher site, from where *C. subpunctata* was absent and where the growing season was significantly later. The effect of snow melt in delaying the start of the growing season is emphasised in Fig. 9, which compares soil surface temperatures at Geilo and Finse, the lower and upper sites on the transect. At the thermally more benign Ainsdale site, which is closer to the centre of the range of the two *Craspedolepta* species, there was no strong difference in the Index of Development between *C. nebulosa* and *C. subpunctata* during the critical period of early season growth (Fig. 6). This suggests that where mean temperatures are higher during the early season growth phase of the psyllid life cycles *C. subpunctata* is able to match the development rate of *C. nebulosa*.
Fig. 5. Relative development rates of *C. nebulosa* and *C. subpunctata* at two sites, Haugastel and Geilo, close to their altitudinal limit. Development is illustrated by changes in the Index of Development during the early growing season before adult emergence.

The differential effect of the timing of snow melt on the distribution of the two species is further emphasised by examining the patterns of growth and development of the psyllids along the gradient down the south-facing bank. *C. nebulosa* (Fig. 7) was found commonly as both larvae and adults on plants throughout the bank, with the timing of growth governed by differences in plant host phenol­ogy. By contrast, both larvae and adults of a sparse popu­lation of *C. subpunctata* were confined to the earliest and thermally most favourable growing site at the very top of the bank and were continually absent from plants elsewhere. This distribution and abundance pattern was repeated over three years and does not represent an initial colonisation at the top followed by later colonisation of the lower slope.

**DISCUSSION**

Collectively the physiological survival measurements and experiments demonstrated no significant differences in the abilities of *C. nebulosa* or *C. subpunctata* to sur­vive extreme low or high temperatures and it is unlikely that these factors determine the observed differences in their spatial distribution. By contrast, development rates of larvae, at sites close to the climatic limits of both spe­cies, showed strong differences between the species dur­ing the critical early season growth period from when the host plant shoot emerges above the soil surface to when flower development has clearly commenced and the plant becomes unsuitable for both larval growth and oviposi­tion. The significance of each data set contributing to these broad conclusions is discussed below.

There was no significant variation among the super­cooling points of fourth and fifth instar larvae of *C. nebu­losa* or *C. subpunctata* from Ainsdale, UK and fifth and adult instar *C. nebulosa* from Tromso, Norway. Conse­quently, there is no suggestion of adaptive differences in SCP to cope with contrasting climatic conditions across the species range. The mean SCP values for *Craspedolepta* (−20.7 to −23.5°C) lay in a similar, if slightly higher, range to those observed in other small sap­feeding Hemiptera including heather psyllids of the ge­nus *Strophingia* (−21.6 to −23.7°C) (Hodkinson et al., 1998), temperate aphids such as *Myzus persicae* (−25.0 to −26.6°C) (Bale et al., 1988), *Diuraphis noxia* (Mordvilko) (−24.9 to −26.8°C) (Butts, 1992), *Sitobion avenae* (−21.7 to −27.0°C) (Knight & Bale, 1986) and even adult glasshouse whitefly *Trialeurodes vaporari­orum* (−22.6°C, SD = 1.83, n = 25) (Hodkinson, unpubl.), although lower than in acclimated overwintering adults of the hawthorn psyllid *Cacopsylla melanoneura* (Förster) (−11.1 to −15.0°C), which possibly feeds on conifers.
nucleators in the gut, rather than any specific adaptation throughout the winter (Jackson et al., 1990). These generally low SCPs, observed in the sap-sucking sternorrhynchos Hemiptera, linked to low variability around the mean, are probably a function of common feeding behaviour and physiology, involving an absence of potential ice nucleators in the gut, rather than any specific adaptation for surviving extreme winter cold.

The short-term exposure experiments indicated that C. nebulosa and C. subpunctata in the fourth, fifth and adult instars (when measured) died at temperatures above their SCP, indicating chill susceptibility (Bale, 1993) and showing that SCP is a poor indicator of cold hardiness in these species. Chill susceptibility was most apparent in adult C. nebulosa at Tromsø where significant mortality occurred at temperatures as high as −7.5°C and none survived −17.5°C. Larvae, by contrast, were more chill tolerant, with significant mortality beginning to occur at −12.5°C, but none surviving to −25°C. Again there were no significant differences in response between the species or between the overwintering instars.

The long-term exposure experiments suggest that for overwintering Craspedolepta species the above physiological measurements, made in the laboratory on animals removed from their natural environment, provide a poor indication of potential survival in the field, where the mode and period of exposure, as well as the exposure temperature, becomes important. Individuals of both Craspedolepta species survived −15°C for 2 days, but longer term exposures induced increasingly heavy mortality and none survived for 25 days at this lowest temperature. Temperature and the temperature x time interaction were the important determinants of mortality. There was again, however, no suggestion of differential mortality effects between the species.

How do the experimental temperature environments used relate to those experienced in the field? Fig. 8 summarises mean winter air temperatures along the Norway transect, showing that at all sites air temperature falls below that necessary to induce high mortality in both species. In the absence of a protective snow blanket it is likely, during sustained cold spells, that soil temperatures, even at 3 cm depth, will approach those of the air. This has been demonstrated for sites on Spitsbergen (−27.8°C) and on mountains near Abisko, Arctic Sweden (−15.1°C) (Coulson et al., 1995a). However, at all of the sites studied, winter minimum air temperatures sufficient to kill all Craspedolepta larvae (c. −15°C) are invariably accompanied by a thick snow blanket which provides a high degree of thermal insulation to the soil. For example, at the "coldest" site in Norway where both species occur together (Geilo, Fig. 9) the lowest winter soil temperature recorded during 1994/5 was −20°C, despite a corresponding air temperature of −20°C. Even at the higher elevation of Finse soil surface temperature did not fall below −5°C. It is unlikely, therefore, that the psyllids, even at the most continental or highest locality, experience sufficiently low soil temperatures to impact significantly on population densities. High winter mortality, linked to low temperatures, is unlikely to occur where snow cover is reliable. Only where snow cover is lacking and where soil temperatures fall below −12.5°C is there likely to be significant mortality. Migration by larvae onto the underground roots of Chamerion angustifolium thus appears to be a highly effective strategy for avoiding mortality during periods of extreme winter cold. There is also some suggestion that the spatial distribution of the host plant itself reflects a requirement for less thermally demanding microhabitats (Myerscough, 1980).

C. nebulosa and C. subpunctata also appear similarly well-adapted to survive extreme high spot temperatures in excess of those experienced naturally, at least for short exposure periods where desiccation effects are minimised. Mortality was insignificant below temperatures of 40°C and this may have some significance for survival in psyllids that live on a host plant, C. angustifolium, which in northern forests is well-known as a fire-successional species.

Survival data for extreme temperatures thus fail to explain the different spatial distribution patterns of C. subpunctata and C. nebulosa. The explanation appears to lie in the ability of the smaller and darker species C. nebulosa to develop more rapidly compared with its host plant than C. subpunctata during the critical early season phase of the life cycle. This differential effect becomes most obvious as the available thermal budget becomes shorter towards the altitudinal or latitudinal limits of the species range. At Ainsdale, within their mid-range, the two species developed almost simultaneously whereas along the Norway transect, the development rates of the species diverged strongly at the highest sites. Thus only C. nebulosa completed the critical part of its life cycle in time at the highest inhabited site (Haugastol) and the development rate of C. subpunctata at the lower site (Geilo) is similar to that of C. nebulosa at Haugastol. At the higher site the phenological interval from shoot emergence to flowering, during which the psyllid must grow, emerge as an adult, oviposit, hatch and grow through to the later larval stages capable of migrating onto the roots, is sufficient for C. nebulosa but not C. subpunctata. At low mean temperatures the latter species appears to require a longer minimum growing season, with a greater available heat budget, than C. nebulosa. These findings are rein-

Fig. 9. Winter soil surface temperatures at Geilo and Finse in 1994/95, showing the thermal buffering effect of the snow blanket.
forced by the distribution of the two species down a short embankment representing a strong gradient in the length of the growing season. *C. nebulosa* was able to utilise plants over the whole bank whereas *C. subpunctata* only occupied the very top, the precise location with the longest growing season and consequently the highest available heat budget. Thus, in this example there was little evidence that interaction between the two species affected their individual response to temperature, thereby restricting the distribution and abundance of heather psyllids (Strophingia spp.) to the UK. Funct. Ecol. (in press).


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