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The performance of different populations of the green spruce aphid (*Elatobium abietinum* Walker) at different temperatures

GUÐMUNDUR HALLDÓRSSON
Iceland Forest Research Station, Mógilsá, IS-270 Mosfellsbær, Iceland
MAUREEN DOCHERTY
University of Ulster, School of Environmental Studies, Colerain, BT52 1SA, Northern Ireland, UK
EDDA SIGURDÍS ODDSDÓTTIR
Iceland Forest Research Station, Mógilsá, IS-270 Mosfellsbær, Iceland
and
KEITH R. DAY
University of Ulster, School of Environmental Studies, Colerain, BT52 1SA, Northern Ireland, UK

SUMMARY

The performance of different populations of the green spruce aphid at temperatures below and above zero was studied in laboratory experiments. A significant difference in growth rate of different aphid populations at 15°C was observed, as aphids from Ireland and Iceland had significantly lower growth rates than aphids from France and Denmark. No differences in survival of major aphid populations at potentially lethal temperatures were found. The implications of these findings on the adaptation strategies of the aphids are discussed.

Key words: adaptation, aphid populations, cold hardiness, growth rate, temperature.

YFIRLIT

*Lifun og þroskunarhraði mismunandi stofna sitkalúsar (*Elatobium abietinum *Walker) við mismunandi hitastig*

Lifun og þroskunarhraði mismunandi sitkalúsarstofna var rannsakaður við mismunandi hitastig undir og yfir frostmarki. Marktækur munur reyndist vera á þroskunarhraða mismunandi stofna við 15°C, þar sem þroskunarhraði sitkalúsarstofna frá Írlandi og Íslandi reyndist vera marktækt minni en þroskunarhraði stofna frá Frakklandi og Danmörku. Engan slíkan mun var að finna á lifun mismunandi stofna við frystingu á því hitasviði sem að jafnaði er banvænt fyrir sitkalýs. Í greininni er fjallað um hvernig túlka beri þessar niðurstöður með tilliti til aðlögunarhæfni sitkalúsar.

INTRODUCTION

The green spruce aphid is a major pest on spruce in many countries, especially in regions with a maritime climate, where it develops anholocyclicly throughout the year (Straw *et al.*, 1998; Carter and Halldórsson, 1998). Distribution is by aleates, which are produced at high population levels, especially during the spring peak (Carter and Cole, 1977). *E. abiet-*

inum populations in North-west Europe have been found to be divided genetically into four major groups (Guðmundur Halldórsson *et al.*, unpublished data). Aphids from Norway comprised the first group, aphids from Denmark and Iceland comprised the second group, aphids from Brittany, Normandy and Wales the third group, and the fourth group consisted of aphids from England, Scotland and North-west Ireland.

The influence of different environmental factors on the population dynamics of *E. abietinum* has been reviewed by Day and Kidd (1998). Temperature is a major factor in the population dynamics (Carter, 1972; Powell and Parry, 1976; Crute and Day, 1990) and information on the influence of temperature on growth and survival of the aphid is therefore essential for modelling the population development of the aphid. The influence of temperature on the developmental rate of *E. abietinum* has been studied by Cunliff (1924) and Hussey (1952). They found that the generation time at 15°C was 18–24 days.

The influence of low temperatures on aphid survival has been the subject of many studies in the laboratory as well as of field studies (Beier-Petersen, 1962; Ohnesorge, 1961; Carter, 1972; Powell and Parry, 1976). Field observations in Denmark and Great Britain show that *E. abietinum* outbreaks are not to be expected if the lowest minimum temperature of the winter falls below –8°C (Beier-Petersen, 1962; Ohnesorge, 1961). This minimum seems to be considerably lower in Iceland (Carter and Halldórsson, 1998). The frost tolerance is influenced by the host plant, as ice nucleation always starts in the gut content. The frost tolerance of unfed first instar aphids is therefore significantly greater than that of aphids that have started feeding, and the frost tolerance of aphids that have been removed from the host plant is greater than that of aphids on host plants (Powell, 1974). Both Carter (1972) and Parry (1979) have showed that acclimatization occurs in *E. abietinum* in the autumn / early winter but the importance of this is debated as it has been argued that an increase in freezing point temperatures caused by imbibition of plant sap will mask these acclimatization changes in feeding aphids (Parry, 1979).

The aim of this study was to establish the difference between aphid populations in: (a) the growth rate at above-zero temperatures and (b) survival at sub-zero temperatures. Aphids from four different regions were involved in both studies. These populations were from: (a) the British Isles, (b) France, (c) Denmark and (d) Iceland. Studies on the growth rate of aphids at temperatures above zero were conducted at the University of Ulster, whereas studies on the survival of aphids at sub-zero temperatures were conducted at the Iceland Forest Research Station.

MATERIALS AND METHODS

Growth rate at temperatures above zero

One-year-old Sitka spruce (line 1902 from improved, but generally available forestry stock) were grown in a potting mixture of three parts peat, three parts composted bark, and two parts perlite and ground magnesium limestone at 1 kg m^{-3}. The slow-release fertilizer, Osmocote Plus 12:14 Spring formulation, was added at a rate of 3 kg m^{-3} and plants were watered daily. Trees were maintained in a controlled environment cabinet at 15°C, 70% RH, 16L:8D, and light levels of 1544.4±48.9 lux from overhead grid-lighting.

Aphids were obtained by collection from Sitka spruce in each of the four countries, Iceland (Reykjavík), Northern Ireland (Grange Park Forest, Co Londonderry), Denmark (Hørsholm) and France (Forest of Monnaye, Normandy). Although the aphid populations were not derived from a single lineage, the national isolates were expected to be regionally representative and are henceforth referred to as aphid provenances. The provenances were kept for several weeks in the same laboratory to eliminate cultural differences between them. Each first instar nymph, selected from a provenance, was weighed on a microbalance to the nearest 0.001 mg, and placed individually onto a needle of a spruce shoot within a fine-mesh nylon sleeve on a single branch. The sleeved experimental shoot unit was approx. 4 cm in length and bore approx. 50 needle leaves. Experimental aphids from each of four provenances were randomised to each of four branches on 15 trees, in order to control for the effect of individual trees on aphid performance. Each aphid was re-weighed after 7 days and again when 50% of the aphids in a treatment had passed their final moult (after approx. 16 days).

Mean relative growth rate (Adams and van Emden, 1972) was calculated as:

$$\text{MRGR } (\mu g\ \mu g^{-1}\ day^{-1}) = [\ln(\text{final weight}) - \ln(\text{initial weight})] / \text{number of days between weighings}$$

Adult aphids were removed upon production of a first nymph, and the following additional information obtained. The total developmental time, from first instar to first reproduction, was recorded (prenatal development), the adult was weighed and embryos present in the abdomen were counted. Only those trees with all four aphids alive at the end of the experiment were used in the analysis. A two-way analysis of variance, taking account of country of origin, host tree and country × tree interaction, was performed on the data.

Survival at temperatures below zero

The frost tolerance of green spruce aphid populations established on host plants of different origin was studied under controlled conditions. Four different populations of aphids were collected from Sitka spruce in: (a) Southeast Iceland (Hornafjörður), (b) UK (Alice Holt), (c) Denmark (Hørsholm) and (d) France (Forest of Monnaye, Normandy). These populations were expected to be regional. All aphid populations were sampled in the summer/autumn of 1998. The aphids were sent to the Iceland Forest Research Station where they were kept under natural conditions outside the research station to eliminate cultural differences. For comparison, aphids were collected in Reykjavík, Southwest Iceland in January 1999. These aphids were transferred directly from the field onto test plants.

The plant material was 5 year old Sitka spruce plants of the provenances Homer, Alaska and Cordova, Alaska. The test plants of the Homer provenance consisted of a single family – Homer-6-10, whereas the Cordova test plants consisted of two families – Cordova-20-2 and Cordova-20-3. One cage/aphid population was put on each plant. Aphids were transferred to the cages in the period between 13th January and 13th February 1999, ca 15 aphids/cage. Aphid populations were randomly assigned to the cages on each plant. The Cordova-20-2 plants were infested with aphids of all populations, whereas Cordova-20-3 and Homer-10-6 were only infested with aphids from Southeast Iceland and Denmark (Table 1). This was due to shortage of aphids from other populations. After transferring the aphids, the test plants were placed in a greenhouse under natural light conditions at 5°C until the first week of March. All cages were then inspected and dead individuals removed just before the freezing experiment started.

The experiment was carried out at the Möðruvellir research station in a domestic freezer modified with a hot gas bypass to minimize temperature variations (Timbers and Canon, 1977; Guðleifsson and Björnsson, 1989). Temperature in the freezer was automatically recorded at 5 min intervals. The freezer was adjusted to 1°C and the test plants placed in it. The temperature was then adjusted to a programmed temperature decrease (1°C/h). Plants with aphids were removed from the treatment in batches, each batch consisting of one randomly selected plant/family, i.e. one plant of Cordova-20-2, one of Cordova-20-3 and one of Homer-6-10. There was therefore only one measurement/treatment at each sampling. The first batch was removed when the temperature had reached ca –8°C and thereafter plants were removed at ca 1°C intervals until the temperature had reached ca –16°C. The actual temperature at each sampling was automatically recorded. After removing the plants

Table 1. Assignment of aphid provenances onto the plant material.
1. tafla. Röðun mismunandi sitkalúsarstofna á tilraunaplöntur af mismunandi uppruna.

Aphid provenance	Cordova-20-2	Plant material Cordova-20-3	Homer-6-10
Denmark	x	x	x
France	x		
UK	x		
Iceland – East	x	x	x
Iceland – West	x		

from the freezing experiment they were warmed up stepwise, by placing them in increasing temperature levels. This process consisted of 3 levels, –4°C, 0°C, 4°C. The plants stayed for 2 hours at each level, with the exception of the last level where they stayed until the aphids could be examined. The aphids were removed from the needles and examined under the stereoscope and identified as belonging to three different age groups: 1st instar, 2–4th instar and adults. For analysis the last two groups, 2–4th instar and adults were merged into one group termed "older aphids". The number of dead and living aphids within each age group was counted.

Data analysis. The number of survivors in a cage follows a binomial probability distribution. The data were analysed, using the logit transformation, as a generalized linear model in Genstat. The linear effects of the factor combinations of temperature and populations (or trees) are additive effects on the transformed scale. The significance of an effect is tested by deleting it from the full model, using the socalled deviance as a test statistic, i.e. the logarithmic transformation of the likelihood ratio test, dev.= –2 log(L/Lo). Under the null hypothesis of zero effect the deviance follows a chi-squared distribution. In this experiment, however, the hypothesis of equal probability of survival in cages with equal treatment was rejected. This is a common problem in biological data of this kind. There is an extra-binomial residual variation among cages that should be included as a component of error for testing model effects. The approach used here was to arrange the deviances in a table analogous to an analysis of variance table where the deviances replace the sums of squares, and tests, analogous to F-tests, were based on deviance ratios between the mean deviance of effect, i.e., the deviance divided by its degrees of freedom, and the residual deviance. As the number of aphids per cage can, in general, be considered adequate and the probability of survival is rarely close to zero or one, this ratio can with fairly good confidence be tested as if it were an F-test.

RESULTS

Growth at temperatures above zero

Both country of origin (aphid provenance) and host tree, had a statistically significant effect on aphid performance (Table 2).

Aphids from Iceland and Northern Ireland grew more slowly than those from France and Denmark (Figure 1). Adult weight and the number of embryos produced by each, were unaffected by country of origin or tree (Table 2). Using initial weight as a covariate, aphids from the different countries showed significantly different pre-reproductive periods (Figure 2), although the average time until reproduction among the replicate trees was very variable but was not statistically significant. Using adult weight as a covariate in the analysis, the total number of embryos (red-eyed and non-eyed) did not differ significantly between

Table 2. Summary of ANOVA for the performance of aphid provenances replicated among individual trees. (NS represents P>0.05).
2. tafla. Fjölbreytugreining á þroskunarhraða mismunandi sitkalúsarstofna á einstökum trjám. (NS táknar að P>0,05).

Performance measure	Independent factor	df	F	P
MRGR	Aphid provenance	3.12	4.56	0.024
	Tree	4.12	4.31	0.022
Adult weight	Aphid provenance	3.12	0.69	NS
	Tree	4.12	1.63	NS
Pre-natal period	Aphid provenance	3.11	5.78	0.013
	Tree	4.11	2.84	0.077
Number of embryos	Aphid provenance	3.12	1.17	NS
	Tree	4.12	1.90	NS

countries of origin or between trees. There was no relationship between adult weight and embryo count, using either total, red-eyed or non-eyed embryos.

Survival at temperatures below zero

The total number of aphids/treatment/sampling ranged from 1 to 93 for 1st instar nymphs and from 5 to 95 for the older stages, most cages did however contain more than 20 aphids (Tables 3–6). This was to be expected as the aphids had ca 1 month to settle on the plants and these differences reflect differences in aphid establishment success and aphid survival. In general the survival of aphids followed a logistic curve. Survival of older aphids decreased relatively slowly as temperature fell from –7.9°C to –12.3°C. As the temperature was further decreased to –14.2°C there was an abrupt fall in the survival of older

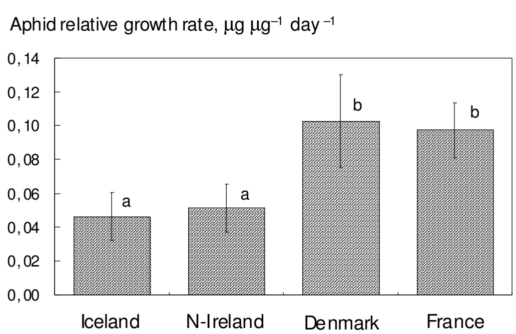

Figure 1. The relative growth rates (MRGR) of aphids from four countries (provenances), maintained in controlled environments. Vertical bars indicate SE. Different letters indicate significant differences between provenances (P<0.05).
1. mynd. Hlutfallslegur þroskunarhraði sitkalúsarstofna frá fjórum löndum (sitkalúsarkvæmi) við stýrðar umhverfisaðstæður. Lóðrétt strik sýna staðalfrávik. Mismunandi bókstafir sýna marktækan mun milli stofna (P<0,05).

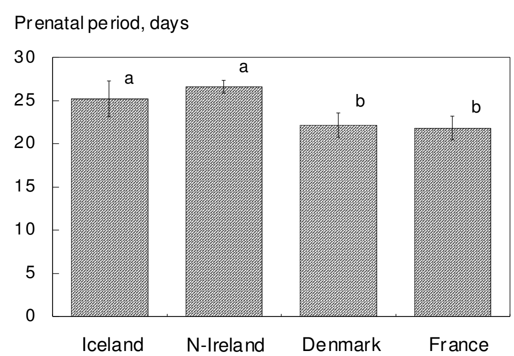

Figure 2. The prenatal period (development time until adulthood) of aphids from four countries (provenances), maintained in controlled environments. Vertical bars indicate SE. Different letters indicate significant differences between provenances (P<0.05).
2. mynd. Þroskunartími fram að kynþroskastigi fyrir sitkalúsarstofna frá fjórum löndum (sitkalúsarkvæmi) við stýrðar umhverfisaðstæður. Lóðrétt strik sýna staðalfrávik. Mismunandi bókstafir sýna marktækan mun milli stofna (P<0,05).

Table 3. Total number of older aphids on Cordova-20-2 plants.
3. tafla. Heildarfjöldi eldri lúsa á Cordova-20-2 plöntum.

Temperature, °C	UK	Denmark	France	Iceland-East	Iceland-West
–7.9	37	42	14	48	11
–8.9	51	53	42	12	48
–10.0	54	95	34	71	24
–11.2	32	88	29	88	48
–12.3	34	28	23	29	5
–13.6	9	63	32	13	12
–14.2	67	34	21	47	35
–15.5	62	49	26	27	38
–16.2	89	72	37	81	62

Table 4. Total number of 1st instar nymphs on Cordova-20-2 plants.
4. tafla. Heildarfjöldi fyrsta stigs gyðla á Cordova-20-2 plöntum.

Temperature, °C	UK	Denmark	France	Iceland-East	Iceland-West
–7.9	16	12	11	20	12
–8.9	24	44	16	7	8
–10.0	16	93	18	33	18
–11.2	21	88	21	33	19
–12.3	6	13	15	14	3
–13.6	3	14	5	1	4
–14.2	16	15	10	17	24
–15.5	11	7	12	15	14
–16.2	32	24	17	26	34

aphids and only a few of the older aphids survived –14.2°C or lower temperatures (Figure 3). A significant difference was found in the survival of older aphids from different populations (P<0.001). This difference was due to the lower survival of aphids from the Iceland-West population. There was a tendency for better survival of the Iceland-East and the French population at –13.6°C, but no significant difference was found in the survival of aphids from different populations if the Iceland-West population was excluded (P=0.25). The LD-50 value for older aphids was –10.6°C for the Iceland-West population, but –12.6°C for the other populations.

Survival of 1st instar nymphs followed a similar curve as that of older aphids, except that survival of 1st instar nymphs was higher than that of older aphids at all temperatures below –10°C. Survival at –10°C was however surprisingly low and this tendency could also be seen for the older aphids. At –14.2°C survival of 1st instar nymphs had fallen below 30% (Figure 4). Survival of 1st instar nymphs was similar for all populations and all plant material and no significant differences were found in the survival of 1st instar nymphs from different populations (P=0.07). There was however a tendency for lower survival of 1st instar nymphs from the Iceland-West population.

Survival of aphids from the Danish and Iceland-East populations on plant material of different origin followed similar curves (Figures 5 and 6). At –11.2°C, –12.3°C and –13.6°C there was a tendency for lower survival of

Table 5. Total number of Danish and Iceland-East aphids on Cordova-20-3 plants.
5. tafla. Heildarfjöldi lúsa af dönskum og austur íslenskum stofni á Cordova-20-3 plöntum.

	Denmark		Iceland-East	
Temperature, °C	1st instar	Older aphids	1st instar	Older aphids
–7.9	8	14	24	14
–8.9	14	28	9	13
–10.0	9	37	4	14
–11.2	8	24	22	40
–12.3	18	13	15	10
–13.6	5	26	1	19
–14.2	6	18	20	28
–15.5	30	20	9	23
–16.2	8	6	4	21

Table 6. Total number of Danish and Iceland-East aphids on Homer-6-10 plants.
6. tafla. Heildarfjöldi lúsa af dönskum og austur íslenskum stofni á Homer-6-10 plöntum.

	Denmark		Iceland-East	
Temperature, °C	1st instar	Older aphids	1st instar	Older aphids
–7.9	51	33	29	64
–8.9	27	39	27	21
–10.0	45	45	39	32
–11.2	12	26	47	43
–12.3	21	24	27	43
–13.6	6	19	12	27
–14.2	5	20	30	41
–15.5	18	33	17	17
–16.2	24	13	44	26

older aphids on Homer-6-10 plants (Figure 5). These differences were not significant and no significant difference was found in the survival of aphids on different plant material (P=0.12).

DISCUSSION

The present study indicates that at 15°C growth rates of Icelandic and Irish aphids are lower than those from France and Denmark and that the prenatal period of the Icelandic and Northern Ireland aphids is correspondingly longer. This is unlikely to have affected reproductive rate between aphids from different countries because fecundity among recent adults was similar among all aphid provenances. Initial reproductive rate during early adult life is of greater importance in determining the value of r_m, the intrinsic rate of natural increase, than that achieved over the entire lifetime (Barlow, 1962), so fecundity here was probably a good measure of reproductive potential.

Faster rates of growth were not achieved at the expense of adult weight, as is possible in different seasons of tree growth. Day *et al.* (unpublished data) show that, although aphids in mid-summer grow relatively rapidly compared with aphids in spring, their final weight (and consequently fertility) is much lower and contributes little to population growth at this time of the year. The main consequence of faster growth rates among the aphid provenances from France and Denmark is a reduction in generation time and the amplification this brings to higher population rates of increase (Dixon, 1987). It would be anticipated, therefore, that anholocyclic spruce aphids from more continental regions of Europe, represented here by France and Denmark, could achieve higher population maxima in a specified time before budburst. After this a decline in spruce needle sap nutrients invokes a syndrome of demographic change resulting in a dramatic decline in aphid population density by mid-summer (Parry, 1974; Fisher and Dixon, 1986).

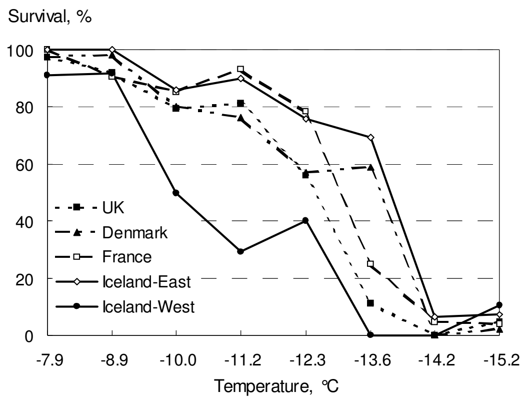

Figure 3. Survival of older aphids at different temperatures on Cordova-20-2 plants.
3. mynd. Lifun eldri lúsa við mismunandi hitastig á Cordova-20-2 plöntum.

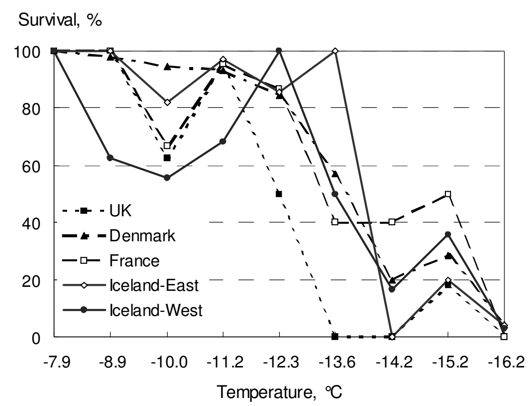

Figure 4. Survival of 1st instar nymphs at different temperatures on Cordova-20-2 plants.
4. mynd. Lifun fyrsta stigs gyðla við mismunandi hitastig á Cordova-20-2 plöntum.

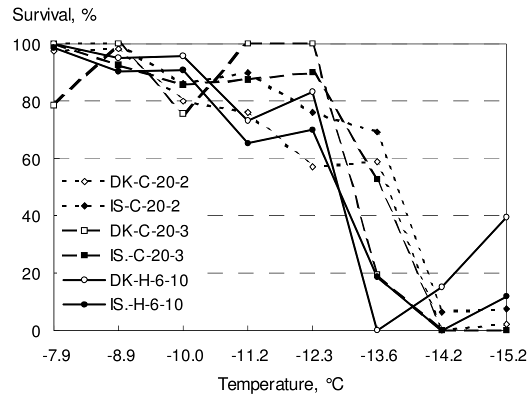

Figure 5. Survival of older aphids of the Danish (DK) and Iceland-East (IS) populations at different temperatures on Cordova-20-2, Cordova-20-3 and Homer-6-10 plants.
5. mynd. Lifun eldri lúsa af dönskum og austur íslenskum stofni við mismunandi hitastig á Cordova-20-2, Cordova-20-3 og Homer-6-10 plöntum.

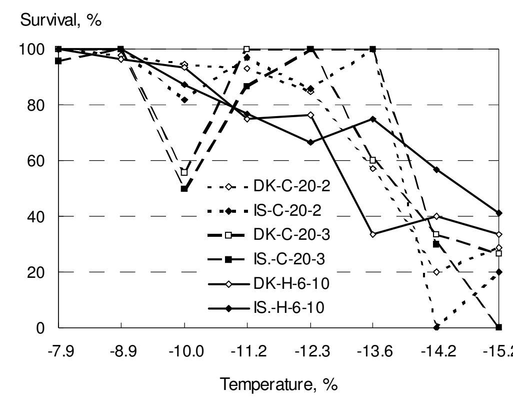

Figure 6. Survival of 1st instar nymphs of the Danish (DK) and Iceland-East (IS) populations at different temperatures on Cordova-20-2, Cordova-20-3 and Homer-6-10 plants.
6. mynd. Lifun fyrsta stigs gyðla af dönskum og austur íslenskum stofni við mismunandi hitastig á Cordova-20-2, Cordova-20-3 og Homer-6-10 plöntum.

Differences similar to those found in growth rates at 15°C were not found in the survival of different aphid populations at potentially lethal subzero temperatures, with the exception of the Iceland-West population. The low survival of this population was however most likely caused by different pre-treatment of this population as it was sampled directly from trees within the city of Reykjavík just prior to transferring into the cages. This was probably caused by the influence of the host plants on the frost tolerance of the aphids as suggested by Parry (1979). This influence of the host plant seems therefore to have masked any differences in the frost tolerance of the aphid itself or such differences did not exist. The fact that no differences in the performance of 1st instar nymph could be found indicates that there were no differences in frost tolerance of the aphid itself. These findings must however be considered in the view of the fact that the 1st instar nymphs consisted of unfed and fed individuals. The differences observed in the frost tolerance of 1st instar nymphs and older aphids did however show that a considerable proportion of the 1st instar nymphs must have been unfed individuals. Some differences in frost tolerance of 1st instar nymphs and older aphids could therefore be expected had any significant differences of that kind existed.

No influence of plant material on the frost tolerance of aphids could be found. Such differences had been expected as the Homer provenance has been shown to be more resistant to frost in the middle of the winter than the Cordova provenance (Skúlason *et al.*, 2000) and the supercooling point of the needles of the Homer plant material could therefore be expected to be lower than that of the Cordova plant material. This contradicts the observations of Parry and Powell (1977) who claimed that the frost tolerance of different trees was one of the major reasons for different susceptibility of spruce to the green spruce aphid.

Lethal winter temperatures does therefore seem to cause random mortality of different genotypes rather than to select specific genotypes, whereas higher temperatures seem to select better adapted genotypes effectively. Similar selection may happen at temperatures relatively close to the freezing point. The low growth rate of the Irish and the Icelandic population compared to that of the Danish and the French populations indicate that this ability was lost due to a selection pressure that favoured some other abilities at the expense of growth rate at 15°C. It must be kept in mind in this context that both the Irish and the Icelandic populations were introduced from the European continent. The present study indicates that this putative gain was not in frost tolerance. The green spruce aphid belongs to a group of insects termed chill-susceptible (Bale, 1993) and prolonged periods at relatively low, but not lethal, temperatures are known to have a considerable negative influence on green spruce aphid populations (Powell and Parry, 1976). Studies need to be carried out to determine whether the Irish and Icelandic population have gained any advantages at these temperature regimes at the expense of growth rate at higher temperatures.

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