

Aphid–willow interactions in a high Arctic ecosystem: responses to raised temperature and goose disturbance

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Abstract

Recently, there have been several studies using open top chambers (OTCs) or cloches to examine the response of Arctic plant communities to artificially elevated temperatures. Few, however, have investigated multitrophic systems, or the effects of both temperature and vertebrate grazing treatments on invertebrates. This study investigated trophic interactions between an herbivorous insect (*Sitobion calvulum*, Aphididae), a woody perennial host plant (*Salix polaris*) and a selective vertebrate grazer (barnacle geese, *Branta leucopsis*). In a factorial experiment, the responses of the insect and its host to elevated temperatures using open top chambers (OTCs) and to three levels of goose grazing pressure were assessed over two summer growing seasons (2004 and 2005). OTCs significantly enhanced the leaf phenology of *Salix* in both years and there was a significant OTC by goose presence interaction in 2004. *Salix* leaf number was unaffected by treatments in both years, but OTCs increased leaf size and mass in 2005. *Salix* reproduction and the phenology of flowers were unaffected by both treatments. Aphid densities were increased by OTCs but unaffected by goose presence in both years. While goose presence had little effect on aphid density or host plant phenology in this system, the OTC effects provide interesting insights into the possibility of phenological synchrony disruption. The advanced phenology of *Salix* effectively lengthens the growing season for the plant, but despite a close association with leaf maturity, the population dynamics of the aphid appeared to lack a similar phenological response, except for the increased population observed.

Keywords: climate change, grazing, herbivory, phenology, *Salix polaris*, *Sitobion calvulum*, Svalbard, trophic mismatch

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Introduction

Several experimental studies have used open top chambers (OTCs) or cloches to investigate the effects of climate warming on the phenology and growth of Arctic plant communities, both with and without nutrient supplementation (Robinson *et al.*, 1998; Arft *et al.*, 1999; Jónsdóttir *et al.*, 2005b; Hollister *et al.*, 2005a,b). The effects of grazing on these communities by vertebrates such as reindeer and geese are also relatively well documented (e.g. Alsos *et al.*, 1998; Skarpe & van der Wal, 2002; Fox & Bergersen, 2005; Post & Pederson, 2008; Rinnan *et al.*, 2009; Evju *et al.*, 2010). In contrast, studies that incorporate plant-feeding and soil dwelling invertebrate responses are relatively scarce (Coulson *et al.*, 1996; Webb *et al.*, 1998; Bale, 1999; Roy *et al.*, 2004; Adler *et al.*, 2007; Bokhorst *et al.*, 2008; Hågvar & Klanderud, 2009; Nash *et al.*, 2013) and have often been

inserted retrospectively into the experimental design of plant experiments (Sjursen *et al.*, 2005; Dollery *et al.*, 2006; Post & Pederson, 2008). However, the role of invertebrates in mediating changes in vegetation communities during a warming climate is potentially important (Post & Pederson, 2008; Zvereva *et al.*, 2010).

This article reports an experimental investigation, using OTCs, of trophic interactions within a three-component system involving an herbivorous insect [the aphid *Sitobion calvulum* Ossiannilsson (Homoptera: Aphididae)], a woody perennial host plant [the polar willow *Salix polaris* WG (Salicaceae)] and a selective vertebrate grazer [the barnacle goose *Branta leucopsis* Bechstein (Anseriformes: Anatidae)]. The responses of the insect and its host plant to rising environmental temperatures, reflected in their timing of development and population densities were investigated under three levels of grazing disturbance by barnacle geese. The general aim of this study was to evaluate the mechanisms by which climate change may act differentially among interacting trophic levels (Watt &

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McFarlane, 2002; Voigt *et al.*, 2003). The study forms part of the EU funded FRAGILE project (Fragility of Arctic goose habitat: impact of land use, conservation and elevated temperature) in Adventdalen, Svalbard.

Polar willow, *S. polaris*, a prostrate shrub, is frequently the dominant plant species in high Arctic tundra plant communities throughout northern circum-polar regions (Bliss & Matveyeva, 1992; Elven & Elvebakk, 1996). Field experiments show that on Svalbard it responds positively to raised temperature as displayed in its increased reproductive output and increasing percentage cover (Robinson *et al.*, 1998; Dormann *et al.*, 2004). Physiological models, however, suggest that a disproportionate increase in respiration over photosynthesis at higher temperatures might result in reduced net primary productivity (Muraoka *et al.*, 2002). *Salix polaris* is dioecious but there is no evidence to suggest differences in the growth performance of male vs. female plants (Dormann & Skarpe, 2002).

Vertebrate grazing on *Salix* dominated plant communities may have contrasting effects. Selective removal of coexisting plant species by grazing may, through competitive release, lead potentially to enhanced growth performance by *Salix*, particularly when growing in a low productivity environment (Dormann & Brooker, 2002; Olofsson *et al.*, 2002; Dormann *et al.*, 2004). Alternatively, neighbouring species may shelter and thereby facilitate growth of *Salix* and their selective removal could lead to lowered willow performance (Dormann & Brooker, 2002; Klanderud & Totland, 2004). Evidence for such overall effects in field and phytotron experiments with *Salix* on Svalbard is mixed (Dormann & Brooker, 2002; Dormann *et al.*, 2004).

Grazing of *Salix* by reindeer in 1 year may produce knock-on effects the following year. These include reductions in leaf numbers, total leaf biomass, individual leaf biomass and number of inflorescences, coupled with no change in leaf phenolic concentration but an increase in leaf nitrogen content (Skarpe & van der Wal, 2002). Length of growing season and the timing of browsing *per se*, however, appear to have little effect on the concentrations of these chemicals (Skarpe & van der Wal, 2002). The grazing response strategy appears to be one of compensatory growth (similar to that of graminoids in the same experiment, see Cooper *et al.*, 2006) rather than enhanced chemical defence. In contrast to reindeer, barnacle geese feed to a limited extent on *Salix* buds early in the year, but generally feed selectively on grasses, as well as mosses and nonwoody herbaceous plants when preferred species are not available (Alsos *et al.*, 1998; Fox & Bergersen, 2005; Cooper *et al.*, 2006; Kuijper *et al.*, 2006; Soininen *et al.*, 2010) and thus their effect on *Salix* growth is likely to differ somewhat from

that of reindeer. Their presence in an experimental setting may have other disturbance effects, however, such as trampling and indirect biomass removal. We therefore refer to this treatment as 'goose presence' rather than 'goose grazing'.

The rare aphid *S. calvulus* (previously named *Acyrtosiphon calvulus*) is endemic to Svalbard and breeds on *S. polaris* at a number of high Arctic sites within and adjacent to Isfjord, Spitsbergen (Ossiannilsson, 1958; Heikinheimo, 1968; Hodkinson *et al.*, 2004). Close phenological synchrony between the aphid life cycle and the seasonal growth phases of its host plant allows the aphid, unusual among Arctic insects, to complete two obligatory generations per year (Gillespie *et al.*, 2007). The phloem sap-feeding aphid overwinters as eggs that hatch coincident with bud burst in *Salix* and the first generation fundatrices develop on the expanding willow leaves. These viviparous fundatrices give rise (asexually) to males and females, starting at around the onset of leaf senescence. Mated females continue to develop and lay overwintering eggs, attached to *Salix* leaves, throughout the period of leaf senescence (Hodkinson *et al.*, 2004; Gillespie *et al.*, 2007). Previous work has shown that another High Arctic aphid on Svalbard, *Acyrtosiphon svalbardicum* Heikinheimo (Homoptera: Aphididae), responds positively to experimentally elevated temperature in terms of phenology and population density (Strathdee *et al.*, 1993), but no studies have investigated the additional effects of the presence of vertebrates.

The synchrony of the aphid and willow life stages highlights the close association between plant and insect in this study system. Furthermore, the complexity of potential effects of both goose presence and raised temperature on the physiology of *Salix* summarized above indicates that this relationship could be at risk of disruption in a changing environment (Bale *et al.*, 2002; Watt & McFarlane, 2002). The two null hypotheses tested were as follows: (i) raised temperature has no impact on the growth, population abundance and synchrony of the willow and its associated aphid and (ii) this impact is unaffected by the presence of barnacle geese and their limited grazing on willow.

Materials and methods

Experimental design

The FRAGILE experiment was established on 1 June 2003, just after snow melt on mesic and wet tundra (78°10'N, 16°07'E) in Adventdalen, Spitsbergen, Svalbard. The initial experimental design, detailed by Cooper *et al.* (2004, 2006), comprised five separate blocks, within each of which there were six treatment

combinations, with each treatment replicated five times on separate plots (of 2×2 m). Treatment factors were temperature (comparing ambient [A] with warming using open top chambers [T]; Arft *et al.*, 1999) and goose presence (comparing untreated [0h] plots with those subjected to presence of barnacle geese in the plots for 1 h [1h = normal presence level] or 5 h [5h = high presence level]). The plot treatment combinations thus used were named 0hA, 1hA, 5hA, 0hT, 1hT and 5hT. The surface temperature was measured by Tinytag data loggers (Gemini, Chichester, UK) in the no-goose plots in each block to determine the mean temperature effect of the OTCs. The goose presence treatment was applied twice in 2003 and also in 2004 (24–29 June and 25–31 July), but only once in 2005 (28 June to 3 July). Geese behaved normally and the resulting grazing pressure was similar to that found in normal grazing situations and in overgrazed areas on Svalbard (Kuijper *et al.*, 2006).

The work presented in this article was carried out only at the mesic site and only during the summers 2004 and 2005. Within each treatment plot a central subplot of 75×75 cm (0.56 m²) was identified. On each field site visit, a 100 square grid quadrat of the same dimensions was placed over the subplot. Five nonadjacent predetermined grid squares of the grid quadrat, each measuring 7.5 cm \times 7.5 cm, were used for subsequent recording of willow and aphids. The same squares were used every time.

Salix phenology, biomass and reproduction

The phenology of *Salix* was observed at regular intervals (weekly or less) throughout the growing seasons 2004 and 2005 for all grid squares. On each occasion, all leaves in each grid square (5 squares \times 25 plots = 150 squares in total) were counted and placed into one of five phenological categories: (i) 'bursting' – bud burst but leaves not exposed; (ii) 'furled' – leaf not yet unfurled; (iii) 'unfurled' – leaf fully expanded/mature (leaf pair opened to 90–180 degrees); (iv) 'senescing' – leaf showing onset of senescence (yellow spotting) and (v) 'senesced' – leaf fully senescent (yellow). The leaf counts were then summed for the 5 grid squares in each subplot. Phenological advancement for each subplot on each date was expressed using a phenological index adapted from Fischer (2000) in which the frequency distributions of each of the five defined phenological categories were converted into cumulative probability functions (between 0 and 1). These functions return the probability of finding a leaf in a particular stage or earlier. The probability functions for each category were then summed to give the overall phenological index on a rising scale from 0 to 5.

On 27 June 2005, an indication of *Salix* reproductive success was obtained by counting the number of male and female flowers per subplot and the number of ovaries per flower. On 8 July 2005, the number of seed capsules set was counted and the length of up to 5 catkins per subplot was measured. On 13 July 2005, just before the onset of senescence, vegetative growth was recorded by measuring the length and width of 20 randomly selected mature leaves within the subplots, from areas not subjected to the repeated counting of phenological stages. Leaves were selected using random numbers: the first

number dictated a square on the grid quadrat (1–95), and the second dictated the leaf to be selected from that square (1–20), counting from left to right and beginning at the top left corner. The measured leaves were then picked and oven-dried at 100 °F for 24 h and weighed to establish their dry mass. This drying process provides a more reliable estimate of biomass than fresh weight as it excludes the water content in the leaf material which may fluctuate between leaves and cannot be controlled for.

Aphid populations

Total aphid numbers were counted by direct field observation on the grid squares outlined above throughout the 2004 and 2005 growing seasons at the same time as *Salix* leaf counts. Previous studies showed that this reliably estimated population density (Gillespie *et al.*, 2007).

Data analysis

The data from the 5 grid squares in each subplot were summed for each time point and all data were then analysed using R 2.13 (R Development Core Team, 2011) with the *car* package (Fox & Weisberg, 2011). Data for phenology, total leaf number per subplot, aphid number per subplot [transformed using $\log(n + 1)$ to normalize the data] and flower/ovary number per subplot were analysed separately using a fully factorial nested repeated measures ANOVA, with plots nested within treatment blocks. Date, surface temperature and goose presence were treated as within subject effects and the experimental plots as a between subject effect. Data were tested for sphericity using Mauchly's test. Where they failed to conform for a particular factor or factor interaction then the Greenhouse-Geisser epsilon value was used to correct the numerator and denominator degrees of freedom for the succeeding *F*-test. Flower data, leaf size and leaf weight data were analysed using a fully factorial nested ANOVA, with plots nested within treatment blocks.

While it is recognized that more complex Linear Mixed Effects Models may also provide a suitable way of analysing these data, possibly using degree days instead of time as a covariate, attempts to parameterize such models were compromised by the violation of one or more model assumptions during model validation. In addition, degree day calculations are only available for plots with 0h goose presence treatment. The more conservative approach above using all of the data was therefore adopted. Similar problems were encountered when attempting to examine the treatment effects on the *Salix*–aphid interaction. However, it was possible to specify a Linear Mixed Effects Model using the *nlme* package in R (Pinheiro *et al.*, 2013) with aphids [$\log(n + 1)$] as the response variable and temperature treatment, number of mature (unfurled) leaves and degree days as explanatory variables (0h goose presence plots only). Mature leaves was the only *Salix* variable not correlated with degree days, and provides a useful proxy for development stage as mature leaves occurred during every week of data collection. In this model, block was treated as a random factor, and an auto-regressive [AR(1)] correlation

structure was fitted to take account of the auto-correlation associated with repeated measures data. Finally, due to patterns in the plots of model residuals vs. fitted values (residual variance increased with larger fitted values violating the homogeneity of variance assumption), a heterogeneity structure was added to the model which allowed for a different variance for each week of data collection.

Results

Temperature elevation

Mean daily air temperatures at 0.5 m aboveground (1 June to 31 August) were retrieved online (www.unis.no) for the old Northern lights station ('Nordlysstasjon', 78° 12' 6" N, 15° 50' E) in Adventdalen, the nearest weather station to the study site (approximately 7.5 km away) and annual differences were analysed using a two-sample *t*-test. During the period of study, there was a significant difference in mean daily air temperature between the 2 years (2004 = 5.2 °C ± 0.3; 2005 = 6.0 °C ± 0.2; *t* = -2.27, *P* = 0.03). Surface temperatures from the 0hA and 0hT plots were analysed using a one-way ANOVA with Block as an error term. Temperatures in 0hT plots were significantly higher than those in 0hA plots in both years by about 1 °C, and temperatures differed significantly between years (Table 1).

Salix phenology and growth

The phenology of *Salix* was significantly advanced by raised temperature compared to ambient in both 2004 and 2005 (Table 2). The phenology index advancement (Fig. 1) shows advanced bud burst in OTCs. Figs. 2 and 3 illustrate the advancement in terms of the early leaf stages. However, the onset of senescence which occurred in week 7 in 2004 (15th July 2004) and week 6 in 2005 (11th July 2005) did not differ between temperature treatments and this is reflected in the latter stages of phenology index curves (Fig. 1). Full senescence was not reached by the end of the study period in both years, but

the number of fully senescent leaves did not differ between treatments at any stage in the season. The effect of the goose presence was not significant, although in 2004 the temperature/presence interaction was significant, that is, in OTCs, *Salix* phenology was more advanced at both levels of goose presence (1hT and 5hT) but at ambient temperatures goose presence retarded phenology. In 2005, there was a significant date/presence interaction, suggesting that goose presence retarded phenology during later weeks, that is, new leaves emerged later in the season following goose presence/grazing to compensate for lost biomass. Effects of temperature and goose presence on leaf number were nonsignificant in both years (Table 2). Date and the date/temperature interaction were significant in both years.

In 2005, there was a significant positive effect of OTC on leaf length ($F_{1,20} = 8.30$, $P < 0.01$), leaf width ($F_{1,20} = 9.11$, $P < 0.01$) and dry leaf weight ($F_{1,20} = 6.88$, $P = 0.016$), but no significant effects of goose presence or temperature/goose presence on leaf length or mass. There were no treatment effects on any of the reproductive counts or on the phenology of reproductive parts.

Aphid abundance

Aphid densities were consistently higher in 2004 than in 2005 across all treatments and log (*n* + 1) aphid numbers showed a significant response to OTCs in both years, and date/temperature only in 2004 (Table 3). Enhanced temperature produced a significant increase in aphid densities in both 2004 (Ambient: 1.8 ± 0.1, Raised: 2.6 ± 0.1; $F_{1,388} = 24.0$, $P < 0.001$) and 2005 (Ambient: 1.6 ± 0.1, Raised: 2.0 ± 0.1; $F_{1,328} = 9.3$, $P = 0.002$). Fig. 1 indicates that this increase occurred in the earliest part of the summer in 2004 and throughout the summer in 2005. Goose presence reduced aphid number but this trend was nonsignificant.

Salix and aphid interaction

In 2004, there was a significant positive effect of temperature treatment ($F_{1,121} = 17.6$, $P = 0.0001$) and

Table 1 Mean differences in surface temperature for the 2 years of study between 0hA plots and 0hT plots, with standard errors and results of ANOVA tests between plot types (column *F* and *P* values) and between years (row *F* and *P* values). Summer temperatures were calculated from 1 June to 31 August and means were calculated from hourly data. 'n' refers to the number of paired plots for which temperature data were available

Year	0hA mean summer temperature °C	SE	0hT mean summer temperature °C	SE	<i>F</i> value	<i>P</i> value
2004 (<i>n</i> = 4)	8.8	0.1	9.6	0.1	48.8	<0.001
2005 (<i>n</i> = 3)	9.2	0.1	10.5	0.1	174.8	<0.001
<i>F</i> value	171.1		132.0			
<i>P</i> value	<0.001		<0.001			

Table 2 Summary of the main ANOVA effects of date (weekly counts from 3 June to 26 August in 2004, and 6 June to 15 August in 2005), OTC and goose presence on the total leaf number per subplot and growth phenology of *Salix polaris* (Fischer index) in 2004 and 2005. Degrees of freedom (df) are corrected using Greenhouse-Geisser epsilon where necessary ($n = 5$)

Factor/Interaction	Leaf number			Leaf phenology		
	df	F	P	df	F	P
2004						
Date	4.0, 80.9	123.26	<0.001	4.6, 92.7	1946	<0.001
Temperature	1, 20	0.51	ns	1, 20	49.8	<0.001
Goose presence	2, 20	1.60	ns	2, 20	0.27	ns
Date × goose presence	8.1, 80.9	1.56	ns	9.3, 92.7	1.57	ns
Date × temperature	4.0, 80.9	3.44	0.012	4.6, 92.7	9.34	<0.001
Temperature × goose presence	2, 20	0.77	ns	2, 20	8.05	0.003
Temperature × goose presence × date	8.1, 80.9	0.37	ns	9.3, 92.7	1.67	ns
2005						
Date	4.47, 89.4	213.12	<0.001	3.7, 73.0	1358	<0.001
Temperature	1, 20	3.19	ns	1, 20	9.66	0.006
Goose presence	2, 20	0.59	ns	2, 20	1.14	ns
Date × goose presence	8.9, 89.4	1.44	ns	7.3, 73.0	2.68	0.015
Date × temperature	4.47, 89.4	3.45	<0.001	3.7, 73.0	2.94	0.030
Temperature × goose presence	2, 20	0.84	ns	2, 20	0.82	ns
Temperature × goose presence × date	8.9, 89.4	0.90	ns	7.3, 73.0	1.28	ns

mature leaves ($F_{1,121} = 61.4$, $P < 0.0001$) on the abundance of aphids. There was also a significant negative effect of degree days on aphid abundance ($F_{1,121} = 169.4$, $P < 0.0001$). The interaction between mature leaves and degree days was also significant with a small negative effect ($F_{1,121} = 11.9$, $P < 0.001$), suggesting that more aphids occur when there are a greater number of mature leaves earlier in the season.

In 2005, only the number of mature leaves was significant in explaining the abundance of aphids ($F_{1,102} = 129.7$, $P < 0.0001$). There was a slight positive effect of both temperature treatment and degree days, but these effects were not significant (temperature: $F_{1,102} = 3.3$, $P = 0.072$; degree days: $F_{1,102} = 3.9$, $P = 0.051$).

Discussion

Salix phenology

Elevated temperature via OTC treatment significantly advanced the phenology of *Salix* in both years. However, Figs 2 and 3 show that the advancement occurred in the first part of the season between the bud burst and mature leaf phases. This concurs with previous findings from OTC experiments in tundra areas in a meta-analysis of ITEX studies; dormancy tends to break early occurred in the first 2 years of artificial warming in deciduous shrubs and woody species, and in the first 3 years in High Arctic species (Arft *et al.*, 1999). The timing of onset and full senescence was unaffected by the OTC treatments (graphs not shown). Senescence

also tends to be unaffected in the above species groups as this is likely to respond to photoperiod cues (Arft *et al.*, 1999; Cooper *et al.*, 2011).

The pattern of *Salix* phenology advancement effectively lengthens the growing season for this species. This may benefit the plant in creating more time for seed maturation, dispersal and enhanced reproductive success (Jones *et al.*, 1997; Cooper *et al.*, 2011; Mallik *et al.*, 2011), or in providing “enemy-free space” as long as aphid phenology, or that of other consumers, does not change in parallel (Both *et al.*, 2009; Singer & Parmesan, 2010).

Advanced phenology, however, may also be detrimental for the plant, particularly if it leads to greater synchronization with herbivores, bringing peak availability of palatable plant parts in line with maximum consumer abundance (Miller-Rushing *et al.*, 2010; van der Putten *et al.*, 2010; Jepson *et al.*, 2011). In addition, arctic plants that respond to warming with earlier development tend to have lower N and P pools after 3 years of treatment (Michelsen *et al.*, 1996; Welker *et al.*, 1997), although there have also been reports of the converse (e.g. *Carex bigelowii*, Jónsdóttir *et al.*, 2005a). This latter point may explain why phenology was less advanced in 2005, the third consecutive year of warming, than in 2004 (0.14 phenology index units difference vs. 0.08 units). This difference may also be owing to differing weather patterns between the 2 years. Fig. 4 shows cumulative positive degree days for both years plotted against time (May and June) calculated from the Adventdalen weather station.

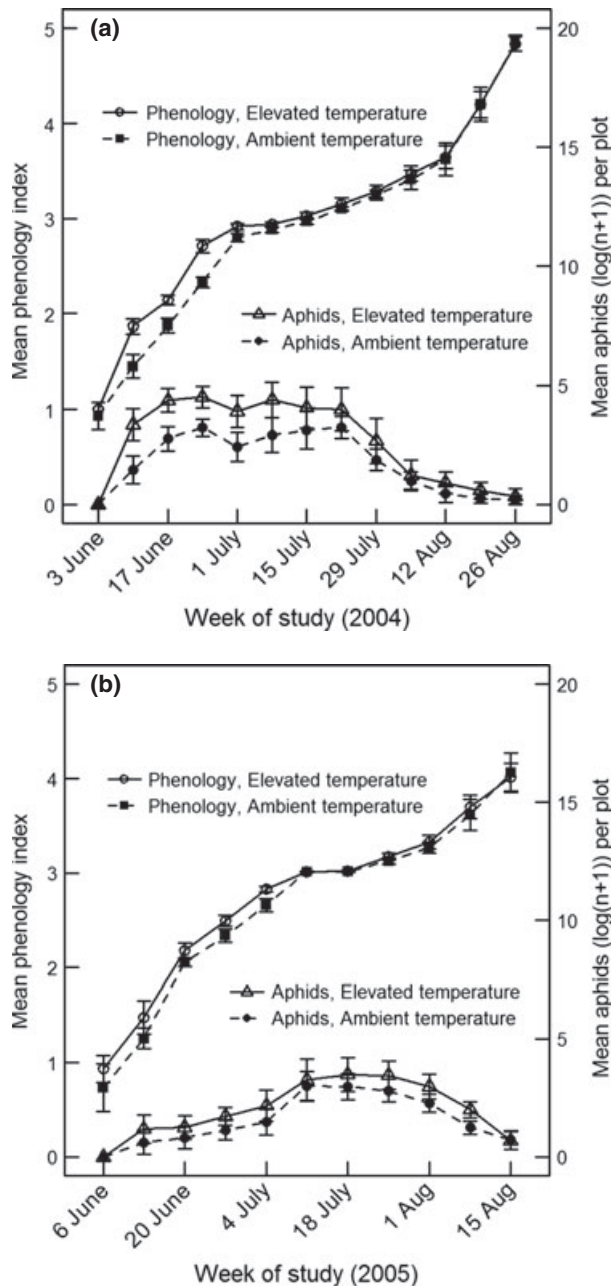


Fig. 1 The phenological index of *Salix polaris* (left-hand axis) and abundance of *Sitobion calvulum* (right hand axis) plotted over time for (a) 2004 and (b) 2005. Data shown are marginal means for each week of study with 95% confidence intervals.

While 2005 was initially warmer from around 15 May, temperatures did not increase appreciably until around 4 June compared to 22 May in 2004. This cold start to the 2005 growing season is likely to have impacted bud burst, leaf maturation and aphid emergence. Plot surface temperature data are incomplete for parts of May in both years, but the same general patterns are shown in both temperature treatments.

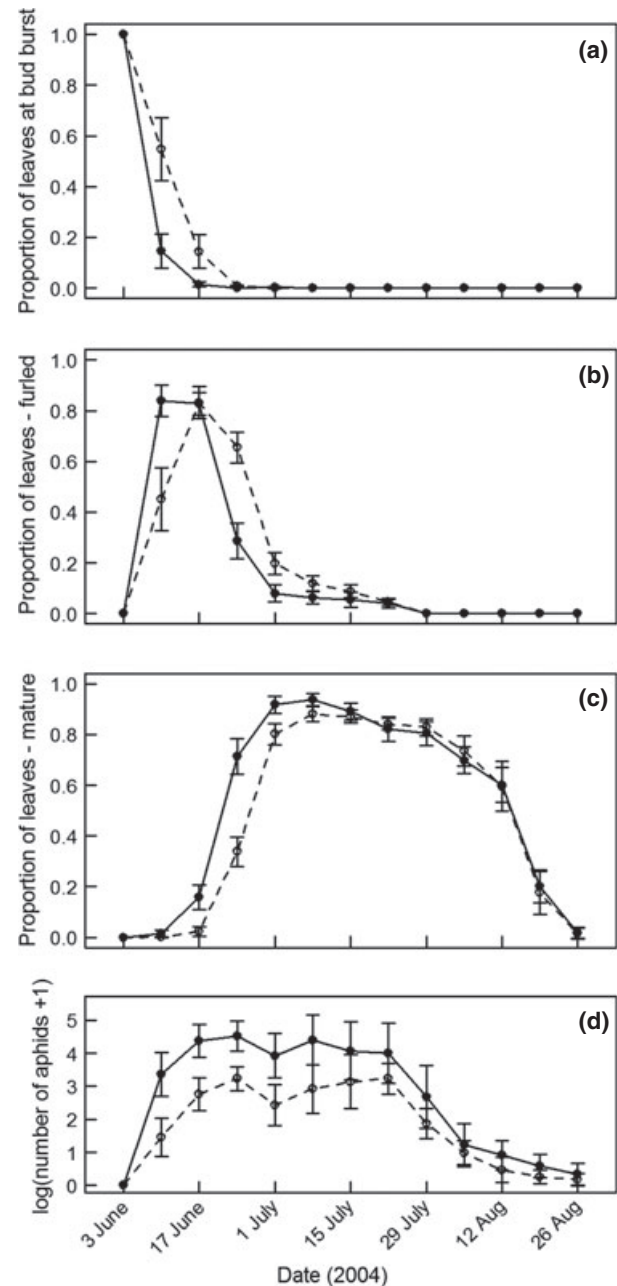


Fig. 2 The proportion of *Salix polaris* leaves in the phenological stages of (a) bud burst; (b) furled leaves and (c) mature leaves, and (d) abundance of *Sitobion calvulum* plotted over time for OTC (solid lines and circles) and ambient plots (dashed lines and open circles) during 2004. Data shown are marginal means for each week of study with 95% confidence intervals.

The lack of goose presence effect on phenology can be explained in part by the timing of the goose treatment, which began after the completion of the bud burst and furled leaf stages, that is, the leaf stages that contributed most to the advanced index. In addition, *Salix* has a high tolerance to mechanical damage

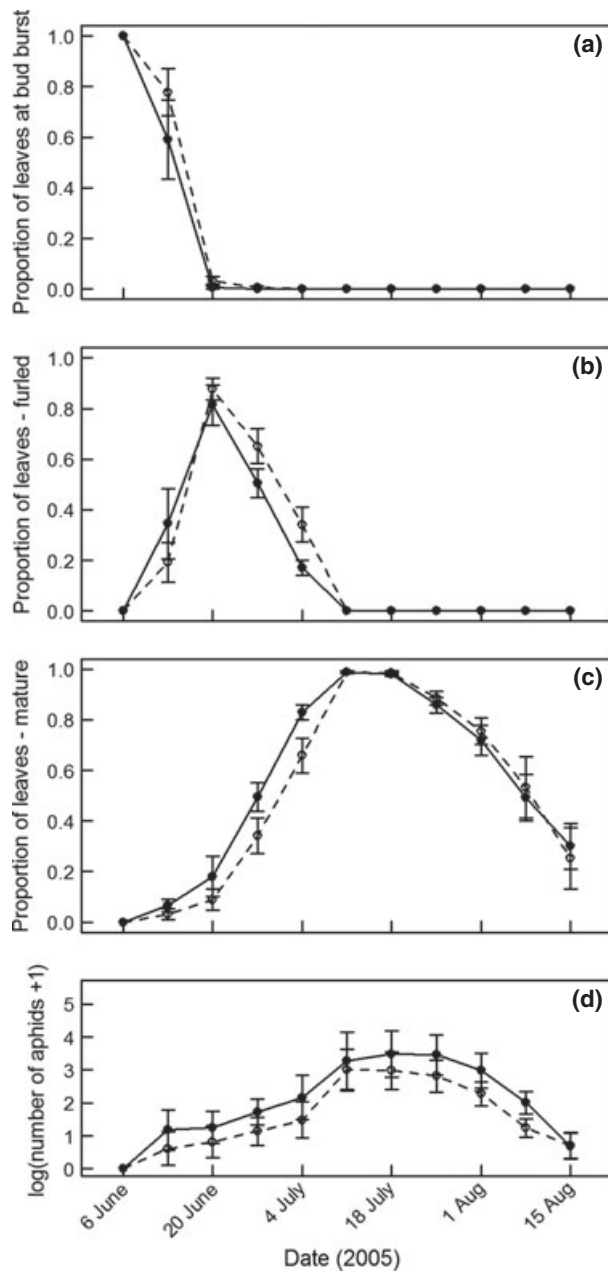


Fig. 3 The proportion of *Salix polaris* leaves in the phenological stages of (a) bud burst; (b) furred leaves and (c) mature leaves, and (d) abundance of *Sitobion calvulum* plotted over time for OTC (solid lines and circles) and ambient plots (dashed lines and open circles) during 2005. Data shown are marginal means for each week of study with 95% confidence intervals.

(Dormann, 2003), with the ability to activate dormant buds to compensate for tissue loss, relocating resources to growth at the expense of reproduction following simulated browsing (Skarpe & van der Wal, 2002). The lower leaf number in 2005 may support this explanation: compensation for two sessions of grazing pressure in 2004 through activation of dormant buds may have

Table 3 Summary of the main ANOVA effects of date, temperature and goose presence on the population abundance ($\log n + 1$) (aphids per subplot) of *Sitobion calvulum* in 2004 and 2005. Degrees of freedom (df) are corrected using Greenhouse-Geisser epsilon where necessary

Factor	df	F	P
2004			
Date	5.2, 104.2	161.85	<0.001
Temperature	1, 20	43.04	<0.001
Goose presence	2, 20	1.88	ns
Date \times goose presence	10.4, 104.2	1.18	ns
Date \times temperature	5.2, 104.2	7.11	<0.001
Temperature \times goose presence	2, 20	0.72	ns
Temperature \times goose presence \times date	10.4, 104.2	0.95	ns
2005			
Date	5.8, 116.1	112.0	<0.001
Temperature	1, 20	9.56	0.006
Goose presence	2, 20	1.93	ns
Date \times goose presence	11.6, 116.1	1.22	ns
Date \times temperature	5.8, 116.1	1.71	ns
Temperature \times goose presence	2, 20	0.15	ns
Temperature \times goose presence \times date	11.6, 116.1	1.07	ns

resulted in fewer available buds for the following year. However, leaf number was also reduced in the goose-free plots lending further support to the weather pattern explanation above (Fig. 4).

There were interaction effects of goose presence with elevated temperature in 2004 and with date in 2005, which may be artefacts of the goose presence experiment design and the index formula. For example, in 2004, phenology was more advanced in the OTC plots subject to goose presence than in ambient plots. At the point of the first goose presence session in this year, the proportion of leaves in the furred stage was lower in OTC plots owing to phenological advancement, and the subsequent removal of the remaining leaves by goose disturbance would have increased the phenology index. In 2005, the presence/date interaction suggested retarded phenology in weeks long after the only goose presence session, so a longer term effect of mechanical trampling disturbance as well as nutrient enrichment via faeces deposition on phenology should not be ruled out.

Salix biomass and reproduction

Despite the lack of treatment effect on total leaf number in 2005, leaves from OTC plots weighed more and were larger than those from ambient plots, as shown for

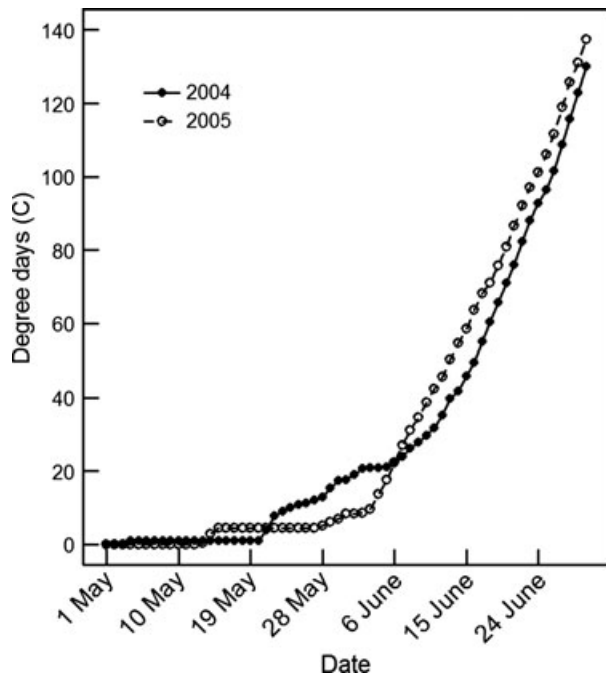


Fig. 4 Cumulative positive degree days in the Adventdalen valley during May and June of 2004 (solid circles) and 2005 (open circles). Data are taken from the northern lights station ('Nordlissstasjon') in Adventdalen, approximately 7.5 km from the study site.

other *Salix* species (Post & Pederson, 2008; Hudson *et al.*, 2011) and other Arctic shrubs (Walker *et al.*, 2006; Lin *et al.*, 2010). This may reflect an increased availability or uptake of nutrients (Rinnan *et al.*, 2009), which is expected under warming conditions (Lloyd & Taylor, 1994; White *et al.*, 1999). Unlike in some of these studies though, goose presence and disturbance did not counteract the warming response, possibly owing to geese selectively feeding (and in this case selecting plants other than *Salix*), rather than the generalist grazing of reindeer. The greater biomass of leaves from warmed plots may also have resulted from increased photosynthetic rates and water use efficiency (Day *et al.*, 2008; Hudson *et al.*, 2011). The lack of response of *Salix* reproduction to treatments found here is also similar to findings for other deciduous shrubs, probably because the pre-formation of flower buds prevents the detection of a short term response (Arft *et al.*, 1999).

Aphid populations

Aphid abundance was not significantly affected by goose presence, but in both years aphid populations were significantly greater in OTCs compared with ambient plots: even expressed on a logarithmic scale, this approximates densities of 150% (2004) and 133%

(2005) of control. Strathdee *et al.* (1993) found (using cloches smaller than our OTCs) similar effects of warming on the other endemic aphid on Svalbard, *Acyrtosiphon svalbardicum*, with an 11-fold increase in egg production under temperature elevation. However, the two species are not directly comparable as *A. svalbardicum* may exhibit an extra generation to that of *S. calvulum* (Strathdee *et al.*, 1993; Gillespie *et al.*, 2007) in favourable conditions.

The more rapid early-season increase in aphid populations within OTCs compared to ambient plots is interesting as the aphid only has a life cycle consisting of two generations, the second of which starts at the beginning of July (Gillespie *et al.*, 2007). Populations at the beginning of the season are therefore likely to be entirely made up of fundatrices emerging from eggs laid the previous season or migrating to the warmer plots. Greater numbers in OTC plots at the start of the season are therefore likely to occur due to an increase in egg laying during the previous season (warming treatments started in 2003), an increase in survival of eggs and/or fundatrices in OTC plots, or recruitment of fundatrices attracted to the more favourable conditions of the OTC plots (Moise & Henry, 2010).

Furthermore, despite the greater overall abundance of aphids in OTC plots over the summer and greater population growth during the early part of the season (Fig 1), data suggest that OTCs did not greatly affect population dynamics in the latter half of the season. Previous work (Gillespie *et al.*, 2007) showed that when *S. calvulum* fundatrices reach reproductive maturity in early July, they may produce a mean number of offspring of up to 29.4 ± 2.8 per individual over 5 weeks in natural enemy exclusion tubes. Despite this reproductive potential, the aphid populations in both years did not grow rapidly at this later stage of the season, suggesting high mortality or low reproduction in both treatments. At this point in the season, the period of leaf maturity in *Salix*, soluble nitrogen availability to the aphid may be considerably reduced and this is also likely to be a limiting factor to populations.

While the positive temperature effect of OTCs on aphid population abundance is strong, particularly in 2004, it is difficult to separate the direct effects of temperature from indirect effects mediated through host plant factors such as phenology and leaf biomass (Bale *et al.*, 2002). For example, while the extended growing season and advanced immature stages of the host plant could contribute to enhanced aphid populations in OTC plots through knock-on effects on host plant characteristics (Kudo *et al.*, 1999), the same effects could also constrain populations later in the season by disrupting the synchrony between the insect and its host (Hodkinson *et al.*, 1979; Hodkinson, 1997, 2005;

Mjaaseth *et al.*, 2005). A subtle shift in leaf chemistry that explains improved aphid performance early in the season also cannot be discounted. Aphid nutrition is complex, often involving host plant amelioration and relying on symbionts to synthesize essential amino acids (e.g. Sandstrom & Moran, 1999). In this study, information on the leaf chemistry changes is not available.

A carry-over effect on aphid densities between successive years might also have been expected. However, in the related species *A. svalbardicum*, an initial major population increase with warming during year one was followed, as in this experiment, by a declining warming effect in later years as populations of predators and parasitoids gradually increased (Bale, 1999; Dollery *et al.*, 2006). In particular, generalist soil surface dwelling predators, such as mesostigmatic mites and spiders, which normally feed on soil Collembola, are easily able to switch their feeding to aphids feeding on a plant species that grows closely adjacent to the soil surface.

An alternative explanation for the observed aphid populations is that insects may have been attracted to the more favourable conditions of the OTCs, and repelled from the plots with heavy disturbance by geese. These possibilities suggest that the responses of aphid numbers to treatments may exaggerate expected future densities under a changing climate (Moise & Henry, 2010).

Synchrony of Salix and aphid phenology

The results of the mixed effects models demonstrate that the aphid is tightly associated with its host plant, with the number of mature leaves significantly affecting the abundance of aphids in both years. The significant mature leaves by degree days interaction in 2004 suggests that this is particularly evident early in the season when leaves are maturing and when degree days are lower (although not too low, as in 2005). However, the lack of a significant interaction between the temperature treatment and the number of mature leaves suggests that the association is unlikely to be disrupted by elevated temperatures, at least in the short term. Furthermore, the lack of a significant effect of temperature in the 2005 mixed effects model may be an artefact of the cold start to the season, but may also indicate that both plant and aphid are capable of adapting their phenology to elevated temperatures, although longer term data are required to confirm this.

Maintenance of phenological synchrony is supported by other evidence presented in this and other studies. The aphid studied here requires temperatures of at least 4 °C for egg hatch to occur in large numbers (Gillespie *et al.*, 2007), and this temperature was

reached earlier in OTC plots than in ambient controls (data not shown). Furthermore, the growth and reproduction stages of the aphid which coincide with *Salix* leaf expansion are periods when nitrogen in soluble form is mobilized within the plant and is optimally available to the aphid (Gillespie *et al.*, 2007). It is likely therefore that egg hatch at least is advanced under temperature elevation for this aphid, and that aphid population expansion will be able to continue to match leaf expansion. This period of egg hatch/bud burst could be vital to maintaining or improving synchrony between the species as shown for some sub-Arctic moth species and their mountain birch host (Jepson *et al.*, 2011). Previous work on the High Arctic aphid *A. svalbardicum* also demonstrated that aphid phenology was advanced under elevated temperatures, due to a greater number of degree days in which to develop and reproduce (Strathdee *et al.*, 1993). However, the evidence here is not clear-cut. The patterns in population data appear to show that aphid phenology is unaltered in OTC plots: patterns in aphid population dynamics in both years appear to be similar between treatments, with simultaneous early season peak abundances (Figs 2 & 3). This could infer a disruption in the phenological synchrony of the two species under elevated temperature conditions. The problem with the use of these data for phenology studies, however, is that it does not include data on any individuals that emerged too early or too late and therefore did not survive (Both *et al.*, 2009). Thus, detailed conclusions about the disruption of synchrony cannot be made without (i) knowledge of the required precision of the phenological synchrony between the two species (Miller-Rushing *et al.*, 2010); (ii) finer resolution data on aphid and plant phenology at the beginning of the season (Both *et al.*, 2009); (iii) knowledge of the baseline synchrony (i.e. whether the ambient control situation is a state of synchrony or asynchrony) (Miller-Rushing *et al.*, 2010; Singer & Parmesan, 2010), and (iv) the extent to which predator and parasitoid phenology has changed (Both *et al.*, 2009).

The *Salix* responses with respect to phenology, leaf number and biomass may be useful in future studies of community responses to predicted climate change. Hudson *et al.* (2011) studied the effects of enhanced temperature on a number of Arctic plant species including *Salix arctica* over 16 years, and found that contrary to previous suggestions (Arft *et al.*, 1999), short-term responses to warming were sustained over the longer term. Similarly, Elmendorf *et al.* (2012a,b) found that patterns in biome-wide vegetation change since 1980 were generally congruent with observations made by plot-level tundra warming studies. While data are lacking to draw conclusions on the precise mechanisms behind aphid population growth within OTCs,

or on the phenological synchrony between aphid and host, the system studied provides insights which are worthy of further study.

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References

- Adler LS, de Valpine P, Harte J, Call J (2007) Effects of long-term experimental warming on aphid density in the field. *Journal of the Kansas Entomological Society*, **80**, 156–168.
- Alsos IG, Elvebakk A, Gabrielsen GW (1998) Vegetation exploitation by barnacle geese *Branta leucopsis* during incubation on Svalbard. *Polar Research*, **17**, 1–14.
- Arft AM, Walker MD, Gurevitch J *et al.* (1999) Responses of tundra plants to experimental warming: metaanalysis of the international tundra experiment. *Ecological Monographs*, **69**, 491–511.
- Bale JS (1999) Impact of climate warming on arctic aphids: a comparative analysis. *Ecological Bulletins*, **47**, 38–47.
- Bale JS, Masters GJ, Hodkinson ID *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1–16.
- Bliss LC, Matveyeva NV (1992) Circumpolar Arctic Vegetation. In: *Arctic Ecosystems in a Changing Climate. An Ecophysiological Perspective* (eds Chapin FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J) pp. 59–89. Academic Press, San Diego.
- Bokhorst S, Huiskes A, Convey P, Van Bodegom PM, Aerts R (2008) Climate change effects on soil arthropod communities from the Falkland Islands and the Maritime Antarctic. *Soil Biology and Biochemistry*, **40**, 1547–1556.
- Both C, van Asch M, Bijlsma RG, van den Burg AB, Visser MC (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology*, **78**, 73–83.
- Cooper EJ, Jónsdóttir IS, Chaput D *et al.* (2004) Climate change and goose grazing on Svalbard's tundra. The ACIA International Symposium on Climate, Reykjavik, Iceland, 9–12 November 2004. Extended Abstracts, AMAP Report 2004, 4, pp. 3.
- Cooper EJ, Jónsdóttir IS, Pahud A (2006) Grazing by captive Barnacle geese affects graminoid growth and productivity on Svalbard. *Memoirs of National Institute of Polar Research, Special Issue*, **59**, 1–15.
- Cooper EJ, Dullinger S, Semenchuk P (2011) Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. *Plant Science*, **180**, 157–167.
- Coulson SJ, Hodkinson ID, Webb NR *et al.* (1996) Effects of experimental temperature elevation on high arctic soil micro-arthropod populations. *Polar Biology*, **16**, 147–153.
- Day TA, Ruhland CT, Xiong FS (2008) Warming increases aboveground plant biomass and C stocks in vascular-plant-dominated Antarctic tundra. *Global Change Biology*, **14**, 1827–1843.
- Dollery R, Hodkinson ID, Jónsdóttir IS (2006) Impact of warming and timing of snow melt on soil microarthropod assemblages associated with *Dryas*-dominated plant communities on Svalbard. *Ecography*, **29**, 111–119.
- Dormann CF (2003) Consequences of manipulations in carbon and nitrogen supply for concentration of anti-herbivore defence compounds in *Salix polaris*. *Ecoscience*, **10**, 312–318.
- Dormann CF, Brooker RW (2002) Facilitation and competition in the high Arctic: the importance of the experimental approach. *Acta Oecologica*, **23**, 397–401.
- Dormann CF, Skarpe C (2002) Flowering, growth and defence in the two sexes: consequences of herbivore exclusion for *Salix polaris*. *Functional Ecology*, **16**, 649–656.
- Dormann CF, van der Wal R, Woodin SJ (2004) Neighbour identity modifies effects of elevated temperature on plant performance in the High Arctic. *Global Change Biology*, **10**, 1587–1598.
- Elmendorf SC, Henry GHR, Hollister RD *et al.* (2012a) Plot scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, **2**, 453–457.
- Elmendorf SC, Henry GHR, Hollister RD *et al.* (2012b) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, **15**, 164–175.
- Elven R, Elvebakk A (1996) Part 1. Vascular plants. In: *Vascular plants. A Catalogue of Svalbard Plants, Fungi, Algae and Cyanobacteria* (eds Elvebakk A, Prestrud P), pp. 9–55. Norskpolartittut Skrifter no. 198, Oslo.
- Evju M, Halvorsen R, Rydgren K, Austrheim G, Myrsetrud A (2010) Interactions between local climate and grazing determine the population dynamics of the small herb *Viola biflora*. *Oecologia*, **163**, 921–933.
- Fischer HS (2000) Multivariate analysis of phenological data. *Phytocoenologia*, **30**, 477–489.
- Fox AD, Bergersen E (2005) Lack of competition between barnacle geese *Branta leucopsis* and pink-footed geese *Anser brachyrhynchus* during the pre-breeding period in Svalbard. *Journal of Avian Biology*, **36**, 173–178.
- Fox J, Weisberg S (2011) *An R Companion to Applied Regression*, (2nd edn). Sage, Thousand Oaks, CA.
- Gillespie M, Hodkinson ID, Cooper EJ, Bird JM, Jónsdóttir IS (2007) Life history and host plant relationships of the rare endemic Arctic aphid *Acyrtosiphon calvulus*. *Entomologia Experimentalis et Applicata*, **123**, 229–237.
- Hågvar S, Klanderud K (2009) Effect of simulated environmental change on alpine soil arthropods. *Global Change Biology*, **15**, 2972–2980.
- Heikinheimo O (1968) The aphid fauna of Spitsbergen. *Annales Entomologica Fennici*, **34**, 82–93.
- Hodkinson ID (1997) Progressive restriction of host plant exploitation along a climatic gradient the willow psyllid *Cacopsylla groenlandica* in Greenland. *Ecological Entomology*, **21**, 47–54.
- Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews of the Cambridge Philosophical Society*, **80**, 489–513.
- Hodkinson ID, Jensen TS, Maclean SF (1979) The distribution, abundance and host plant relationships of *Salix*-feeding psyllids (Homoptera: Psylloidea) in Arctic Alaska. *Ecological Entomology*, **4**, 119–132.
- Hodkinson ID, Bird JM, Cooper EJ, Coulson SJ (2004) The sexual morphs of the endemic Svalbard aphid *Acyrtosiphon calvulus* (Ossiannilsson), with notes on species biology. *Norwegian Journal of Entomology*, **51**, 131–135.
- Hollister RD, Webber PJ, Tweedie CE (2005a) The response of Alaskan Arctic tundra to experimental warming: differences between short and long-term responses. *Global Change Biology*, **11**, 525–536.
- Hollister RD, Webber PJ, Bay C (2005b) Plant response to temperature in Northern Alaska: implications for predicting vegetation change. *Ecology*, **86**, 1562–1570.
- Hudson JMG, Henry GHR, Cornwell WK (2011) Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. *Global Change Biology*, **17**, 1013–1021.
- Jepson JU, Kapari L, Snorre HB, Schott T, Vinstad OPL, Nilssen AC, Ims RA (2011) Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. *Global Change Biology*, **17**, 2071–2083.
- Jones MH, Bay C, Nordenhall U (1997) Effects of experimental warming on arctic willows (*Salix* spp.): a comparison of responses from the Canadian High Arctic, Alaskan Arctic, and Swedish Subarctic. *Global Change Biology*, **3**(Suppl. 1), 55–60.
- Jónsdóttir IS, Khitun O, Stenstrom A (2005a) Biomass and nutrient responses of a clonal tundra sedge to climate warming. *Canadian Journal of Botany*, **83**, 1608–1621.
- Jónsdóttir IS, Magnússon B, Gudmundsson J, Elarsdóttir A, Hjartson H (2005b) Variable sensitivity of plant communities in Iceland to experimental warming. *Global Change Biology*, **11**, 553–563.
- Klanderud K, Totland R (2004) The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. *Journal of Ecology*, **93**, 493–501.
- Kudo G, Nordenhall U, Molau U (1999) Effects of snowmelt timing on leaf traits, leaf production, and shoot growth of alpine plants: comparisons along a snowmelt gradient in northern Sweden. *Ecoscience*, **6**, 439–450.
- Kuijper DPJ, Bakker JP, Cooper EJ, Ubels R, Jónsdóttir IS, Loonen MJE (2006) Intensive grazing by Barnacle geese depletes High Arctic seed bank. *Canadian Journal of Botany*, **84**, 995–1004.
- Lin D, Xia J, Wan S (2010) Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. *New Phytologist*, **188**, 187–198.
- Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.
- Mallik AU, Wdowiak JV, Cooper EJ (2011) Growth and reproductive responses of *Cassiope tetragona*, a circumpolar evergreen shrub, to experimentally delayed snowmelt. *Arctic, Antarctic and Alpine Research*, **43**, 404–409.

- Michelsen A, Jonasson S, Sleep D, Havstrom M, Callaghan TV (1996) Shoot biomass, $\delta^{13}\text{C}$, nitrogen and chlorophyll responses of two arctic dwarf shrubs to *in situ* shading, nutrient application and warming simulating climatic change. *Oecologia*, **105**, 1–12.
- Miller-Rushing AJ, Høye TT, Inouye DW, Post E (2010) The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society – Series B*, **365**, 3177–3186.
- Mjaaseth RR, Hagen SB, Yoccoz NG, Ims RA (2005) Phenology and abundance in relation to climatic variation in a sub-arctic insect herbivore–mountain birch ecosystem. *Oecologia*, **145**, 53–65.
- Moise ERD, Henry HAL (2010) Like moths to a street lamp: exaggerated animal densities in plot level global change field experiments. *Oikos*, **119**, 791–795.
- Muraoka H, Uchida M, Mishio M, Nakatsubo T, Kanda H, Koizumi H (2002) Leaf photosynthetic characteristics and net primary production of the polar willow (*Salix polaris*) in a high Arctic polar semi-desert, Ny-Ålesund, Svalbard. *Canadian Journal of Botany*, **80**, 1193–1202.
- Nash MA, Griffin PC, Hoffmann AA (2013) Inconsistent responses of alpine arthropod communities to experimental warming and thermal gradients. *Climate Research*, **55**, 227–237.
- Olofsson J, Moen J, Oksanen L (2002) Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity. *Oikos*, **96**, 265–272.
- Ossiannilsson F (1958) *Acyrtosiphon calvulus* n.sp. A new aphid (Hem. Hom.) from Spitzbergen. *Entomologisk Tidskrifter*, **79**, 66–68.
- Pinheiro J, Bates D, DebRoy S, Sarkar D R Development Core Team (2013). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-109.
- Post E, Pederson C (2008) Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences*, **105**, 12353–12358.
- van der Putten WH, Macel M, Visser ME (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B – Biological Sciences*, **365**, 2025–2034.
- R Development Core Team (2011) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Rinnan R, Stark S, Tolvanen A (2009) Responses of vegetation and soil microbial communities to warming and simulated herbivory in a subarctic heath. *Journal of Ecology*, **97**, 788–800.
- Robinson CH, Wookey PA, Lee JA, Callaghan TV, Press MC (1998) Plant community responses to simulated environmental change at a high arctic polar semi-desert. *Ecology*, **79**, 856–866.
- Roy BA, Gusewell S, Harte J (2004) Response of plant pathogens and herbivores to a warming experiment. *Ecology*, **85**, 2570–2581.
- Sandstrom J, Moran N (1999) How nutritionally imbalanced is phloem sap for aphids? *Entomologia Experimentalis et Applicata*, **91**, 203–210.
- Singer MC, Parmesan C (2010) Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society – Series B*, **365**, 3161–3176.
- Sjursen H, Michelsen A, Jonasson S (2005) Effects of long-term soil warming and fertilisation on microarthropod abundances in three sub-arctic ecosystems. *Applied Soil Ecology*, **30**, 148–164.
- Skarpe C, van der Wal R (2002) Effects of simulated browsing and length of growing season on leaf characteristics and flowering of the deciduous Arctic shrub *Salix polaris*. *Arctic, Antarctic & Alpine Research*, **34**, 282–286.
- Soininen EM, Hübner CE, Jónsdóttir IS (2010) Food selection by barnacle geese (*Branta leucopsis*) in an Arctic pre-breeding area. *Polar Research*, **29**, 404–412.
- Strathdee AT, Bale JS, Block WC, Coulson SJ, Hodkinson ID, Webb NR (1993) Effects of temperature elevation on a field population of *Acyrtosiphon svalbardicum* (Hemiptera, Aphididae) on Spitsbergen. *Oecologia*, **96**, 457–465.
- Voigt W, Perner J, Davis AJ *et al.* (2003) Trophic levels are differentially sensitive to climate. *Ecology*, **84**, 2444–2453.
- Walker MD, Wahren CH, Hollister RD *et al.* (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, **103**, 1342–1346.
- Watt AD, McFarlane AM (2002) Will climate change have a different impact on different trophic levels? Phenological development of winter moth *Operophtera brumata* and its host plants *Ecological Entomology*, **27**, 254–256.
- Webb NR, Coulson SJ, Hodkinson ID, Block W, Bale JS, Strathdee AT (1998) The effects of experimental temperature elevation on populations of cryptostigmatic mites in high Arctic soils. *Pedobiologia*, **42**, 298–308.
- Welker JM, Molau U, Parsons AN, Robinson CH, Wookey PA (1997) Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons. *Global Change Biology* (Supplement 1) **3**, 61–73.
- White A, Cannel MGR, Friend AD (1999) Climate change impacts on ecosystems and the terrestrial carbon sink: a new assessment. *Global Environmental Change*, **9**, 21–30.
- Zvereva EL, Lanta V, Kozlov MV (2010) Effects of sap-feeding insect herbivores on growth and reproduction of woody plants: a meta-analysis of experimental studies. *Oecologia*, **163**, 949–960.