

Can soil temperature direct the composition of high arctic plant communities?

Brooker, Rob* & van der Wal, René

Centre for Ecology and Hydrology, Banchory, Aberdeenshire, AB31 4BW, Scotland, UK;

*Corresponding author; Fax +441330823303; E-mail r.brooker@ceh.ac.uk

Abstract. Low temperatures exert a primary constraint on the growth of high arctic vascular plants. However, investigations into the impact of temperature on high arctic plants rarely separate out the role of air and soil temperatures, and few data exist to indicate whether soil temperatures alone can significantly influence the growth of high arctic vascular plants in a manner that might direct community composition.

We examined the response of high arctic plants of three functional types (grasses, sedges/rushes and non-graminoids) to manipulated soil temperature under common air temperature conditions. Target plants, within intact soil cores, were placed in water baths at a range of temperatures between 4.9 and 15.3 °C for one growing season. Grasses responded most rapidly to increased soil temperature, with increased total live plant mass, above-ground live mass and total below-ground live mass, with non-graminoids having the lowest, and sedges/rushes an intermediate degree of response. The ratio of above-ground live mass to total live mass increased in all growth forms. Grasses, in particular, responded to enhanced soil temperatures by increasing shoot size rather than shoot number. In all growth forms the mass of root tissue beneath the moss layer increased significantly and to a similar extent with increasing soil temperature.

These results clearly indicate that different growth forms, although collected from the same plant community, respond differently to changes in soil temperature. As a consequence, factors influencing soil temperature in high arctic ecosystems, such as global climate change or herbivory (which leads to reduced moss depth and increased soil temperatures), may also direct changes in vascular plant community composition.

Keywords: Climate change; Herbivore; Plant functional type; Soil warming; Spitsbergen.

Nomenclature: Rønning (1996).

Abbreviation: GLM = Generalized Linear Model.

Introduction

Plant productivity in the arctic is generally considered to be constrained by the prevailing low air and soil temperatures. They restrict plant growth both directly, by limiting the rate of tissue respiration and nutrient uptake (Semikhatova et al. 1992; BassiriRad 2000), and indirectly by slowing the rate of soil decomposition processes and decreasing the availability of soil nutrients (Jonasson 1983; Chapin & Shaver 1985; Nadelhoffer et al. 1991; Robinson et al. 1995).

It is likely that anthropogenic climate change, predicted to have rapid, high magnitude impacts in arctic environments, will lead to an increase in both atmospheric and soil temperatures (Houghton et al. 2001). However, experimental studies of climate change commonly include treatments that warm the whole environment, increasing both air and soil temperatures at the same time (Chapin et al. 1995; Press et al. 1998; Arft et al. 1999). Consequently, it is often difficult to determine whether the response of vascular plants to warming is due to increased soil or air temperatures alone, or to a combination of the two (Rustad et al. 2001). Some natural components of high arctic environments may influence soil temperature without having a concomitant impact on air temperature. For example, the presence of grazers such as *Branta leucopsis* (Barnacle geese) or *Rangifer tarandus platyrhynchus* (Svalbard reindeer) can reduce the depth of the thick moss layer, a major component of many high arctic plant communities, thereby increasing soil temperatures but not air temperatures (van der Wal et al. 2001).

As well as considering the response of overall productivity to changes in soil temperature, we should consider the possibility that soil temperature might direct plant community composition. It has been suggested that the influence of soil temperature on growing season length might alter plant community structure (BassiriRad 2000 and references therein). If the degree of response of arctic vascular plants to changes in soil temperature is not constant between species or growth forms, then soil temperature may also act in this alternative way to control plant community composition.

It is important, therefore, both for predicting the impacts of climate change in the Arctic and for understanding the processes currently controlling high arctic ecosystems and community composition, to understand the impact of enhanced soil temperatures on the growth of high arctic vascular plants in isolation from the effects of air temperatures.

In this study we examine the short-term responses of high arctic vascular plants to changes in soil temperature, under conditions of common air temperature, to determine whether changes in soil temperature *alone* might lead to significant changes in the growth of high arctic vascular plants. Rather than looking for the species specific responses of plants to manipulated soil temperature, we examine the occurrence of growth-form specific responses. The examination of response patterns at the level of the plant growth form is an important step in determining the likely impact of increased soil temperature, as it enables between-site extrapolation without knowledge of the response of individual species (Chapin et al. 1996; Arft et al. 1999). We tested the hypothesis that high arctic vascular plant species respond in a growth form specific manner to increased soil temperature, independent of air temperature. For this we grew 11 high arctic vascular plant species at a range of soil temperatures (4.9 - 15.3 °C), but all with similar air temperatures, and examined the response of the above- and below-ground tissues of three growth forms: grasses, sedges/rushes and non-graminoids.

Material and Methods

The response of high arctic vascular plant growth forms to soil temperature was studied in a greenhouse erected in Longyearbyen, Spitsbergen (78°N 16°E). Mean greenhouse temperature was 8.6°C (SD ± 2.2 °) during the experiment, and was kept close to natural ambient temperature (6.6 ± 2.2°C) by covering lower windows with aluminium foil, and keeping windows and doors open. At the start of the growing season, 13-16 June 2000, 11 target plant species (Table 1) were excavated in intact soil cores (5 cm diameter), to a depth of approximately 8 cm from an east facing slope located at the mouth of Bjørndalen (ca. 25 m a.s.l.) near to Longyearbyen. Cores contained both the target plant species (in the center of each core) and any neighbouring vascular plants within the 5 cm diameter of the core. The sampled plant community at Bjørndalen is a moss tundra community (Rønning 1996), containing a low number (compared to temperate systems) of sparsely distributed vascular plant species. Neighbouring species are not strongly associated or dissociated at this

site (pers. obs.). Therefore, variation in target plant responses due to varying neighbour identity was similar among all target species. All cores were taken from within a 100 m × 100 m area, and were therefore sampled from within a single moss dominated valley floor community. Species were chosen to broadly represent the source vascular plant community, with the target species accounting for approximately 80% of the total vascular plant cover within the Bjørndalen site. For simplicity we use the generic name for each target plant species throughout the text.

Cores were taken at least 1 m apart and, in some cases, contained more than one shoot of the target species. Several growth response parameters are therefore expressed on a per shoot basis. With creeping, prostrate species side branches as well as roots are inevitably cut by the coring process. However, all target species survived within the cores, indicating that in all cases we sampled minimum viable units for each species. Additionally, we might expect strongly laterally spreading species, such as the grasses, to suffer the most damage from the severing of lateral shoots. In the temperature manipulation study grasses actually show the greatest positive response to increased temperature (see Results section). If there has been any effect of the root coring process it will be to cause an underestimation of the response of strongly spreading species.

All soil cores were placed in close fitting, open top 10 cm deep plastic bags from which the vegetation could grow without restriction. The cores were placed in water baths such that only the top 2 cm of the cores was above the water, the temperature of the water bath setting soil temperature, whilst the plastic bag prevented the core from soaking. Cores were initially placed in water baths of ambient temperature for two days, after which a range of temperatures were set and maintained throughout the season by controlling the relative flow of chilled and warmed water to each of the 12 water baths. Water temperatures were recorded every other day and mean values were 4.9, 5.0, 5.4, 6.0, 6.1, 7.3, 8.9, 10.4, 11.7, 11.9, 13.9 and 15.3 °C in the 12 baths across the experimental period of nearly 8 weeks. Each water bath contained six cores of each target species except for *Deschampsia*, with only four cores per bath. Cores were kept damp by spraying with tap water every day.

On 11 August 2000, all soil cores were taken from the water baths and frozen prior to transportation to the UK. Cores were analysed during October 2000. Following thawing, the target plant tissue within the cores was sorted into live above-ground tissue (stems and leaves) and all below-ground tissue (roots and rhizomes).

All cores contained a moss layer, which had a mean thickness of 51 mm (SE ± 15 mm), composed largely of the live and dead material of *Aulacomnium turgidum*,

Hylocomium splendens, *Sanionia uncinata* and *Tomentypnum nitens*, and lay over a mineral soil layer. Vascular plants commonly place below-ground tissues (roots and rhizomes) both within this moss layer and in the mineral soil beneath (Table 1). Therefore, harvested below-ground tissues were subdivided into those from either within the moss layer or beneath the moss layer of each core. Comparison of the mass of below-ground tissues within and beneath the moss layer provides an indication of the depth at which plants are placing below-ground tissues within the soil cores. Tissue mass was recorded following drying at 70 °C for three days. The live above-ground material of all non-target vascular plants within each core was also harvested and treated similarly. The number of shoots (at the moss surface) of all species except *Equisetum* and *Salix* were recorded.

Data analysis

The differential response of plant growth forms to simulated soil warming was determined using regression of final mass and associated ratios (e.g. ratio of live above-ground to total plant mass) against mean water bath temperature and plant growth form. The three growth form categories were grasses, sedges/rushes and non-graminoid species (apart from *Salix* and *Equisetum* all perennial, non-woody forb species; Table 1), a classification based on that of Chapin et al. (1996). Data from three pairs of water baths, those at 4.9 and 5.0 °C, 6.0 and 6.1 °C and 11.7 and 11.9 °C, were combined prior to analysis. The combined mean water bath temperature for these pairs was used in the analysis.

Data were analysed using the GLM (Generalized linear model) procedure, SAS version 8.0 (Anon. 1999). Mass data and derived variables for each species were

normalized to remove species effects by subtracting the mean per species (of all samples) from each data point and dividing the resulting value by the species specific standard deviation. Mean values for each species at each temperature step were calculated to avoid pseudo-replication. These mean values were regressed in an additive fashion, weighted by the number of replicates for each species at each temperature step (to account for variation in the power of the estimates of the mean species values) against increasing soil temperature alone, temperature and growth form (with species nested within growth form) and finally the interactive effect. In those cases with significant temperature - growth form interactions direct *post-hoc* comparisons between growth forms were performed using the contrast option within GLM. Although replication at the growth form level is low (a consequence of natural species paucity in the source community) the analysis, weighted as it is by the frequency of observations, is conservative and as such increases confidence in the results.

Both *Salix* and *Equisetum* might be expected to respond differently to the 'forbs' that compose the rest of the non-graminoid group (Chapin et al. 1996). To examine whether this was the case, and whether there were also species specific responses to temperature in either the grasses or the sedges/rushes groups, preliminary analyses were conducted on data from all three growth-form groups separately. GLM analysis, conducted in an identical manner to the full analysis described above but introducing only species and temperature into the regression model, indicated no significant interactive effects of temperature and species on the response of any growth parameter to increased soil temperature, other than in the sedges/rushes group for the mass of below-ground tissue beneath the moss layer

Table 1. Target species and the allotted growth forms as used in the soil temperature manipulation experiment and data analysis. Also shown are the mean values for the above-ground and below-ground tissue mass (both within and beneath the moss layer) for each species, expressed as a percentage of total mass. Means are calculated from all samples in all water baths at the end of the experiment with standard errors given in parentheses.

Species	Growth form	% Above-ground	% Below-ground in moss layer	% Below-ground beneath moss layer
<i>Alopecurus borealis</i>	Grass	7.9 (0.40)	67.67 (1.80)	24.39 (1.73)
<i>Deschampsia alpina</i>	Grass	8.25 (0.63)	69.44 (2.33)	22.31 (2.09)
<i>Carex rupestris</i>	Sedge/rush	6.79 (0.47)	89.29 (0.82)	3.92 (0.64)
<i>Luzula arctica</i>	Sedge/rush	18.24 (1.93)	75.69 (2.28)	6.07 (1.18)
<i>Cerastium regelii</i>	Non-graminoid	38.97 (2.45)	60.97 (2.45)	0.06 (0.05)
<i>Equisetum arvense</i>	Non-graminoid	11.05 (0.88)	72.79 (2.42)	16.16 (2.50)
<i>Polygonum viviparum</i>	Non-graminoid	7.58 (0.63)	91.87 (0.68)	0.55 (0.21)
<i>Ranunculus sulphureus</i>	Non-graminoid	11.84 (0.76)	69.84 (1.58)	18.32 (1.25)
<i>Salix polaris</i>	Non-graminoid*	15.89 (0.85)	80.31 (1.53)	3.79 (1.22)
<i>Saxifraga hircifolia</i>	Non-graminoid	13.82 (1.45)	84.50 (1.76)	1.67 (0.70)
<i>Stellaria crassipes</i>	Non-graminoid	37.13 (2.32)	61.49 (2.28)	1.38 (0.28)

*All non-graminoids are low-stature perennial forbs, apart from *S. polaris* and *E. arvense* (see text for details of its treatment in the data analysis).

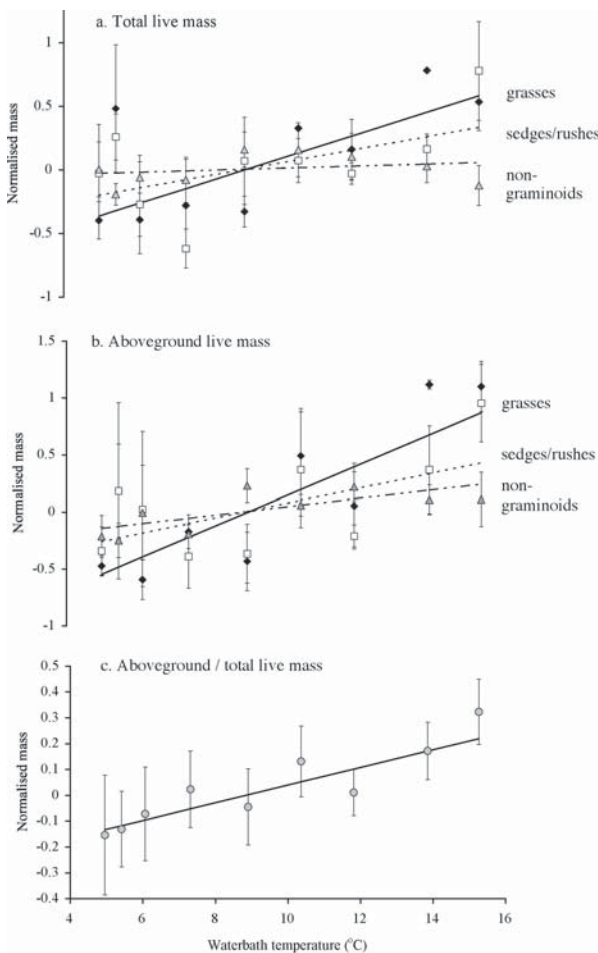


Fig. 1. The response of mean, normalized (a) total live mass, (b) above-ground live mass and (c) above-ground / total live mass to increasing soil temperature ($^{\circ}\text{C}$) in either three growth forms of high arctic plants (grasses (\blacklozenge), sedges/rushes (\square) and non-graminoids (\triangle) or for all three growth forms combined (\circ). Growth form means are calculated from individual species means for each temperature. Error bars show the standard error for the growth form means. In those cases where means have been calculated for pairs of waterbaths (see text), the pooled standard errors for the means have been used. At each temperature $n=2$ for grasses and sedges/rushes and $n=7$ for non-graminoids, apart from at temperatures of 5.0°C , 6.1°C and 11.8°C , where $n=4$ and 14 , respectively.

(species $F_{1,14}=9.68$, $P<0.01$). Therefore, for all growth parameters, the species within the grasses and non-graminoid group responded identically to increased temperature. In addition the nesting of species within growth form within the GLM analysis accounts for variation between species thereby increasing the robustness of the analysis. However, both *Salix* and *Equisetum* were excluded from the analysis of variables that involved shoot number, as this was recorded for neither species.

Results

There was a significant positive response of total plant mass to increasing soil temperature ($F_{1,97}=7.33$, $P<0.01$). The rate at which total plant mass increased differed significantly between the three growth forms ($F_{2,85}=4.04$, $P<0.05$; Fig. 1a), being greater in grasses than in non-graminoids ($F_{1,85}=7.13$, $P<0.001$). The rate of increase in sedges/rushes was intermediate between the other two growth forms and did not differ significantly from either grasses ($F_{1,85}=1.12$, $P=0.292$) or non-graminoids ($F_{1,85}=2.27$, $P=0.136$).

Above-ground live mass of the target species was positively correlated with increased soil temperature ($F_{1,97}=24.09$, $P<0.0001$), with the rate of response again differing significantly between the three growth forms ($F_{2,85}=4.31$, $P<0.05$; Fig. 1b). As with total live mass the rate of response of grasses was significantly greater than that of non-graminoids ($F_{1,85}=8.50$, $P<0.01$) and the response of sedges/rushes did not differ significantly from either grasses ($F_{1,85}=2.89$, $P=0.093$) or non-graminoids ($F_{1,85}=0.86$, $P=0.355$). With increasing temperature, above-ground live mass accounted for a significantly greater proportion of total target plant mass ($F_{1,97}=9.27$, $P<0.01$; Fig. 1c); this response was similar in the three growth forms ($F_{2,85}=1.33$, $P=0.270$). The above-ground live mass of all non-target species from the cores also increased significantly with increasing soil temperature ($F_{1,97}=47.48$, $P<0.001$) irrespective of the growth form of the target plant within the core ($F_{2,85}=1.01$, $P=0.369$).

Increases in the above-ground mass of target species were largely driven by changes in the size of, rather than the number of, individual shoots especially for the grasses. The mass of above-ground live tissue per shoot had a highly significant positive response to increasing soil temperature ($F_{1,79}=15.97$, $P<0.001$). This response differed significantly between the three growth forms ($F_{2,69}=3.54$, $P=0.05$) being greater in grasses than in either non-graminoids ($F_{1,69}=6.25$, $P<0.05$) or sedges ($F_{1,69}=5.32$, $P<0.05$). The response of sedges and non-graminoids did not differ ($F_{1,69}=0.04$, $P=0.835$). However, there was a sizeable trend toward a significant increase in the number of shoots of the target plants per core with increasing soil temperature ($F_{1,79}=3.41$, $P=0.069$), a pattern that did not differ significantly between growth forms ($F_{2,69}=1.41$, $P=0.250$; Fig. 2).

There was also a nearly significant trend toward an overall positive effect of increasing soil temperature on total root mass ($F_{1,97}=3.84$, $P=0.053$). As for above-ground mass, the rate of response to increasing soil temperature differed significantly between the three growth forms ($F_{2,85}=3.80$, $P<0.05$; Fig. 3a), being greater in grasses than in non-graminoids ($F_{1,85}=6.67$, $P<0.05$), with sedges/rushes differing from neither

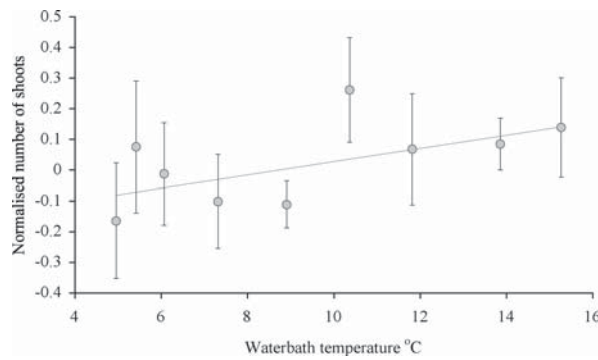


Fig. 2. The response of mean, normalized number of shoots to increasing soil temperature (°C) for 11 species of high arctic plant. Growth form means are calculated from individual species means for each temperature. Error bars show the standard error for the means. In those cases where means have been calculated for pairs of waterbaths (see text), the pooled means and standard errors for the means have been used. $n = 11$ except for temperatures of 5.0°C, 6.1°C and 11.8°C, where $n = 22$.

grasses ($F_{1,85} = 1.02$, $P = 0.315$) or non-graminoids ($F_{1,85} = 2.18$, $P = 0.144$).

Tissue mass *within* the moss layer was unaffected by increasing soil temperature ($F_{1,97} = 0.000$, $P = 0.945$) for all three growth forms ($F_{2,85} = 2.18$, $P = 0.120$; Fig. 3b). However, tissue mass *beneath* the moss layer increased significantly with increasing soil temperature ($F_{1,97} = 70.44$, $P < 0.001$), although again this response did not differ between the three growth forms ($F_{2,85} = 2.34$, $P = 0.103$; Fig. 3c). Therefore, as soil temperatures increase a greater proportion of the total root mass is found below the moss layer in the mineral soil, irrespective of growth form.

Discussion

Increasing soil temperature has a clear growth-form specific effect on high arctic vascular plants as represented by the suite of 11 species used in this study. Total plant mass increased with increasing temperature more rapidly in grasses than in non-graminoids, with sedges and rushes responding at an intermediate level between these two groups. This growth form-specific response is composed primarily of changes in live above-ground tissue mass, which increased as a result of increasing mass per shoot, especially in the grasses, although there was also a sizeable but non-significant trend of increasing shoot number. As demonstrated by the increase in the proportion of plant mass that was contributed by shoot tissue, the response of root mass to increased soil temperature was less pronounced than that of shoots.

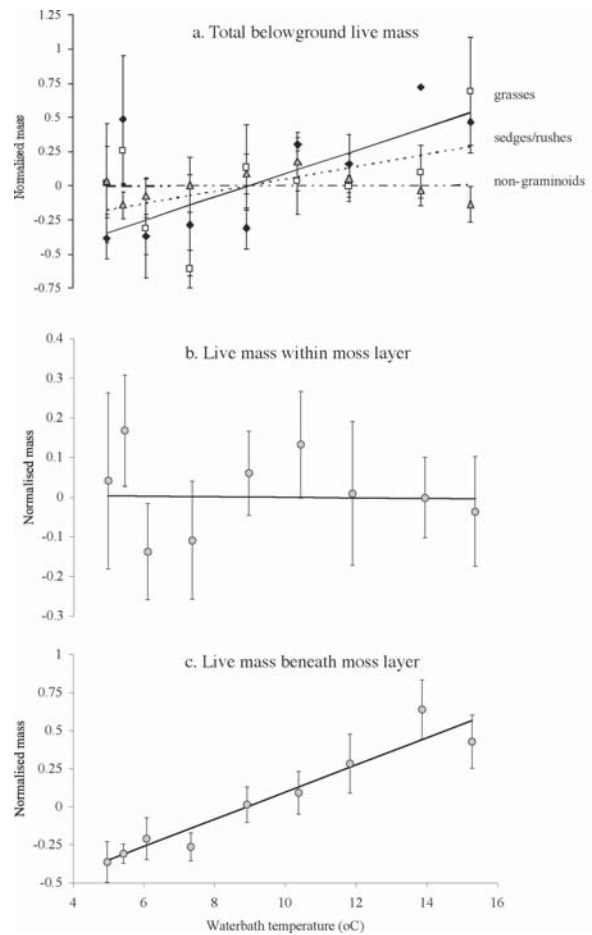


Fig. 3. The response of mean, normalised (a) total below-ground live mass, (b) below-ground live mass within the moss layer and (c) below-ground live mass beneath the moss layer to increasing soil temperature (°C) in either three growth forms of high arctic plants (grasses (◆), sedges/rushes (□) and non-graminoids (△) or for all three growth forms combined (○). Growth form means are calculated from individual species means for each temperature. Error bars show the standard error for the growth form means. In those cases where means have been calculated for pairs of waterbaths (see text), the pooled standard errors for the means have been used. At each temperature $n = 2$ for grasses and sedges/rushes and $n = 7$ for non-graminoids, apart from at temperatures of 5.0°C, 6.1°C and 11.8°C, where $n = 4$ and 14 respectively.

Significant increases in the mass of roots further down the cores, i.e. beneath the moss layer, were consistent between all growth forms. Importantly, we found this response even though the air temperature conditions were the same for all plant species. Therefore, differences in soil temperature alone were sufficient to drive these growth form specific responses.

We cannot tell whether the general increase in plant mass results from either direct temperature driven effects on root growth, effects on root uptake processes

or because of increased microbial activity, increased decomposition rates and increased plant nutrient availability. The comparative unresponsiveness of root mass and the significant increase in the ratio of live above-ground mass to total plant mass indicate that factors other than the direct impacts of temperature on root growth, for example soil nutrient availability, must in part be driving the overall increase in plant size. Manipulations of temperature and nutrient availability in arctic environments have suggested that nutrient limitation is the primary growth restricting factor, and has a stronger relative impact than soil temperature *per se* (e.g. Chapin et al. 1995; Shaver & Jonasson 1999). However, Havström et al. (1993) showed that the relative importance of the direct and indirect effects of temperature may be dependent upon the environment in which they are examined. In their study of *Cassiope tetragona* growth under conditions of enhanced temperature, they found that at high latitudes temperature had a comparatively stronger direct effect, whilst at low latitudes nutrient-driven effects were more important. Therefore, further research is clearly needed to determine the exact mechanisms driving the response to increased soil temperature observed in this study.

Irrespective of the mechanism, increased live shoot mass mainly occurred via increased mass per shoot rather than an increase in the number of shoots. This means that, as an immediate response to warming, plants increased the size rather than the number of shoots. Field experiments have demonstrated that some arctic plants, e.g. *Carex bigelowii*, can respond positively to fertilizer addition in terms of shoot number as well as shoot size (Carlsson & Callaghan 1990; Brooker et al. 2001). However, the potential short-term responsiveness of shoot number in many arctic species may be constrained because the number of leaves and shoots produced in a given year is pre-determined at the end of the previous year's growing season (Callaghan & Emanuelsson 1985; Callaghan et al. 1997). Given this limitation, and the short duration of the experiment, the trend toward increased shoot number for all growth forms (Fig. 2) may indicate the start of a potentially sizeable response. However, this trend was similar for all growth forms. Therefore, although increased shoot number would lead to an overall increase in vascular plant cover, the relative abundance of species in communities such as that at Bjørndalen may still be more responsive to changes in shoot size.

The dangers of extrapolation to the field from controlled environment (in this case greenhouse) biomass responses have been highlighted in previous studies (Aerts & Chapin 2000). However, the responses that we detected are very much in line with responses detected in whole community temperature manipulations in the

field. For example, Zhang & Welker (1996) found that an artificial atmospheric warming of 5 °C, with an associated soil warming of 3 °C, led to a 25% increase in the biomass of grasses in just a five week period in Tibetan alpine tundra community. Although Hartley et al. (1995) found that, following an initial increase in decomposition rates and plant growth, soil warming had no detectable impact on these factors by the fifth year of manipulation, other studies have shown sustained long-term, as well as short-term, responses by graminoids, particularly to artificial warming or fertilization (Dormann & Woodin 2002 and references therein). For example, after five seasons of fertilization at a sub-arctic dwarf shrub heath site there was an 18-fold increase in the abundance of *Calamagrostis lapponica* (Parsons et al. 1995; Press et al. 1998). Similarly, two years after fertilizer addition to a tussock tundra community at Kuparuk Ridge, Alaska, there was an increase in the biomass of *Calamagrostis* species from 0.01 to 6.7 g.m⁻² (Chapin & Shaver 1986). In some long-term fertilizer and temperature manipulation experiments in low arctic communities on the Alaskan North Slope, initial expansion of grasses was reversed by the development of the *Betula nana* dwarf shrub canopy (Chapin et al. 1995). In the high arctic communities of Spitsbergen the environment is more severe and woody growth forms are capable of developing only in particularly sheltered and nutrient enriched habitats (Rønning 1996) or with an extremely prostrate morphology, e.g. *Salix polaris*. As a result, plant communities are not dominated by taller dwarf shrubs and the expansion of grasses may go unchecked by competition for either light or soil nutrients. In these high arctic environments, where biological interactions between vascular plants have a far smaller modulating effect on growth responses to abiotic factors, there may be a more direct and reliable link between the results of controlled growth chamber or greenhouse experiments and community processes in the field.

Not only do the responses found within field based temperature manipulation studies concur with the findings of our experiment, the incubation temperatures used within this study fall within the range of soil temperatures that occur naturally within moss dominated high arctic ecosystems. Data from a survey of 14 moss dominated communities across Spitsbergen (van der Wal & Brooker unpubl.), conducted during July and August 2000, showed a range of sub-moss layer soil temperatures of between 0.9 °C and 15.2 °C (mean temperature 6.6 °C, SD = 2.7 °C; *n* = 569). In addition, they found that at great moss depths, and hence colder soils, grasses made up a lower proportion of the total vascular plant flora. Therefore, the responses that we observed in the greenhouse are not the result of expos-

ing these plants to unrealistic soil temperatures, and can be considered as indicating the 'natural' responses of these species to changes in soil temperature.

These results suggest that with environmental warming, as expected from climate change, increased soil temperature *alone* would be sufficient to drive changes in high arctic vascular plant community composition. However, our results are not only of interest for predicting the future impacts of climate change in high arctic ecosystems, but may also contribute to our understanding of current plant community control mechanisms in high arctic environments. As mentioned, thick moss mats can insulate and reduce the temperature of arctic soils, especially in areas with continuous or widespread permafrost (Dyrness 1982), which in turn can retard the growth of vascular plants (van der Wal et al. 2001). Herbivores, such as reindeer and geese, decrease the depth of the moss layer both by grazing and trampling, leading to an increase in soil temperatures (van der Wal et al. 2001; van der Wal & Brooker unpubl.). Given the growth form specific response of high arctic vascular plants to changes in soil temperatures detected in this study, the impacts of herbivores on the moss layer, and subsequently soil temperature, may play a role in regulating vascular plant community composition. However, the exact mechanism by which the presence of herbivores could be regulating community composition needs further study. As mentioned, enhanced soil temperatures will have a direct impact on the rate of plant tissue processes, whilst also increasing the rate of decomposition and the availability of soil nutrients. Soil nutrient availability may also be enhanced by herbivores through mechanisms unrelated to soil temperature, for example by deposition of faeces. All of these factors may promote vascular plant growth, possibly in growth form specific ways. In order to understand the regulation of high arctic vascular plant community composition by large herbivores, we therefore need to understand the relative importance of these related processes in controlling plant growth.

Conclusions

High arctic vascular plants respond to enhanced soil temperatures in a growth form specific manner even when air temperatures remain unaltered. Therefore, factors that determine soil temperatures in high arctic communities might not only determine the overall productivity of these systems, but may also play a role in regulating the composition of their vascular plant communities. Future research should examine: 1. The exact nature of the mechanism by which soil temperatures influence plant growth (i.e. the involvement of changes

in soil nutrient availability and impacts on physiological processes) and 2. The relative importance of soil temperatures compared to other drivers of community composition (such as air temperatures and biotic interactions) in high arctic environments.

Acknowledgements. We are grateful to the staff of UNIS in Longyearbyen, particularly Jörn Dybdahl, Øyvind Hamre, Fred Hansen and Rolf Langvatn, for their extraordinary support in providing a newly erected greenhouse (twice) at 78° North. Kasper Hanke and friends took great care of the plants in the greenhouse. We thank in particular Jane Palmer and Anita van der Wal for their services to root washing. Steve Albon, Phil Hulme and two anonymous referees provided useful comments on earlier versions of the paper, and David Elston and Steve Palmer provided invaluable statistical advice. This study was funded by NERC (GR9/4773).

References

- Anon. 1999. *SAS/STAT User's Guide, Version 7.0*. SAS Institute Inc., Gary, NC, US.
- Aerts, R. & Chapin, F.S.I. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.* 30: 2-69.
- Arft, A.M. et al. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecol. Monogr.* 69: 419-511.
- BassiriRad, H. 2000. Kinetics of nutrient uptake by roots: responses to global change. *New Phytol.* 147: 155-169.
- Brooker, R.W., Carlsson, B.Å. & Callaghan, T.V. 2001. *Carex bigelowii* Torrey ex Schweinitz (*C. rigida* Good., non Schrank; *C. hyperborea* Drejer). Biological Flora of the British Isles. *J. Ecol.* 89: 1072-1095.
- Callaghan, T.V. & Emanuelsson, U. 1985. Population structure and processes of tundra plants and vegetation. In: White, J. (ed.) *The population structure of vegetation*. Junk, Dordrecht, NL.
- Callaghan, T.V., Jonasson, S. & Brooker, R.W. 1997. Arctic clonal plants and climate change. In: de Kroon, H. & van Groenendael, J. (eds.) *The ecology and evolution of clonal plants*. Backhuys, Leiden, NL.
- Carlsson, B.Å. & Callaghan, T.V. 1990. Programmed tiller differentiation, intracolonial density regulation and nutrient dynamics in *Carex bigelowii*. *Oikos* 58: 219-230.
- Chapin, F.S. III & Shaver, G.R. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 66: 564-576.
- Chapin, F.S. III & Shaver, G.R. 1986. Effect of fertilizer on production and biomass of tussock tundra, Alaska, USA. *Arct. Alp. Res.* 18: 261-268.
- Chapin, F.S. III, Shaver, G., Giblin, A., Nadelhoffer, K. & Laundre, J.A. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694-711.
- Chapin, F.S. III, Bret-Harte, M.S., Hobbie, S.E. & Zhong, H. 1996. Plant functional types as predictors of transient

- responses of arctic vegetation to global change. *J. Veg. Sci.* 7: 347-358.
- Dormann, C.F. & Woodin, S.J. 2002. Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Funct. Ecol.* 16: 4-17.
- Dyrness, C.T. 1982. *Control of depth to permafrost and soil temperature by the forest floor in black spruce/feathermoss communities*. United States Department of Agriculture Forest Service, Pacific and Northwest Forest and Range Experiment Station Research Note PNW-396. Department of Agriculture Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, US.
- Hartley, A.E., Neill, C., Melillo, J., Crabtree, R. & Bowles, F.P. 1995. Plant performance and soil nitrogen mineralization in response to simulated climate change in subarctic dwarf shrub heath. *Oikos* 86: 331-343.
- Havström, M., Callaghan, T.V. & Jonasson, S. 1993. Differential growth responses of *Cassiope tetragona*, an arctic dwarf shrub, to environmental perturbations among three contrasting high- and subarctic sites. *Oikos* 66: 389-402.
- Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J. & Xiaosu, D. 2001. *Climate change 2001: The scientific basis*. Cambridge University Press, Cambridge, UK.
- Jonasson, S. 1983. Nutrient content and dynamics in north Swedish shrub tundra areas. *Holarct. Ecol.* 6: 295-304.
- Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R. & Laundre, J.L. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. *Ecology* 72: 242-253.
- Parsons, A.N., Press, M.C., Wookey, P.A., Welker, J.M., Robinson, C.H., Callaghan, T.V. & Lee, J.A. 1995. Growth responses of *Calamagrostis lapponica* to simulated environmental change in the sub-arctic. *Oikos* 72: 61-66.
- Press, M.C., Callaghan, T.V. & Lee, J.A. 1998. How will European arctic ecosystems respond to projected global environmental change? *Ambio* 27: 306-311.
- Robinson, C.H., Wookey, P.A., Parsons, A.N., Potter, J.A., Callaghan, T.V., Lee, J.A., Press, M.C. & Welker, J.M. 1995. Responses of plant litter decomposition and nitrogen mineralization to simulated environmental change in a high arctic polar semi-desert and a subarctic dwarf shrub heath. *Oikos* 74: 503-512.
- Rønning, O.I. 1996. *The flora of Svalbard*. Norsk Polar Institut, Oslo, NO.
- Rustad, L.E. et al. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental warming. *Oecologia* 126: 543-562.
- Semikhatova, O.A., Gerasimenko, T.V. & Ivanova, T.I. 1992. Photosynthesis, respiration and growth of plants in the Soviet Arctic. In: Chapin, F. S. III, Jeffries, R.L., Reynolds, J.F., Shaver, G.R. & Svoboda, J. (eds.) *Arctic ecosystems in a changing climate: An ecophysiological perspective*. Academic Press, London, UK.
- Shaver, G.R. & Jonasson, S. 1999. Response of Arctic ecosystems to climate change: results of long-term field experiments in Sweden and Alaska. *Polar Res.* 18: 245-252.
- van der Wal, R., van Lieshout, S.M.J. & Loonen, M.J.J.E. 2001. Herbivore impact on moss depth, soil temperature and arctic plant growth. *Polar Biol.* 24: 29-32.
- Zhang, Y. & Welker, J.M. 1996. Tibetan alpine tundra responses to simulated changes in climate: aboveground biomass and community responses. *Arct. Alp. Res.* 28: 203-209.

Received 7 May 2002;

Revision received 27 January 2003;

Accepted 27 January 2003.

Co-ordinating Editor: C. Leuschner.