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Plant growth response to direct and indirect temperature effects varies by vegetation type and elevation in a subarctic tundra

Jonathan R. De Long, Paul Kardol, Maja K. Sundqvist, G. F. (Ciska) Veen and David A. Wardle

J. R. De Long (orcid.org/0000-0002-7951-4818)(jonathan.de.long@slu.se), P. Kardol, M. K. Sundqvist, G. F. Veen and D. A. Wardle, Dept of Forest Ecology and Management, Swedish Univ. of Agricultural Sciences, SE-901 83, Umeå, Sweden. MKS also at: Dept of Ecology and Environmental Science, Umeå Univ., SE-901 87, Umeå Sweden. GFV also at: Dept of Terrestrial Ecology, Netherlands Inst. of Ecology, PO Box 50, NL-6700 AB, Wageningen, the Netherlands.

There has been growing recent use of elevational gradients as tools for assessing effects of temperature changes on vegetation properties, because these gradients enable temperature effects to be considered over larger spatial and temporal scales than is possible through conventional experiments. While many studies have explored the direct effects of temperature, the indirect effects of temperature through its long-term influence on soil abiotic or biotic properties remain essentially unexplored. We performed two climate chamber experiments using soils from a subarctic elevational gradient in Abisko, Sweden to investigate the direct effects of temperature, and indirect effects of temperature via soil legacies, on growth of two grass species. The soils were collected from each of two vegetation types (heath, dominated by dwarf shrubs, and meadow, dominated by graminoids and herbs) at each of three elevations. We found that plants responded to both the direct effect of temperature and its indirect effect via soil legacies, and that direct and indirect effects were largely decoupled. Vegetation type was a major determinant of plant responses to both the direct and indirect effects of temperature; responses to soils from increasing elevation were stronger and showed a more linear decline for meadow than for heath soils. The influence of soil biota on plant growth was independent of elevation, with a positive influence across all elevations regardless of soil origin for meadow soils but not for heath soils. Taken together, this means that responses of plant growth to soil legacy effects of temperature across the elevational gradient were driven primarily by soil abiotic, and not biotic, factors. These findings emphasize that vegetation type is a strong determinant of how temperature variation across elevational gradients impacts on plant growth, and highlight the need for considering both direct and indirect effects of temperature on plant responses to future climate change.

Plant performance and community composition respond greatly to increasing elevation, largely as a result of decreasing temperature (Körner 2007). Changes in temperature that occur across an elevational range of a few hundred meters are typically on par with predicted rises in global surface temperatures of around 3°C over the next century (IPCC 2013), making elevational gradients valuable tools for studying the effects of global climate change (Fukami and Wardle 2005). Performing experiments along elevational gradients while controlling for other potentially confounding variables can have an advantage over manipulative experiments for assessing ecosystem responses to temperature change because they are better able to assess community and ecosystem processes over longer timeframes and larger spatial scales than is otherwise possible (Wolkovich et al. 2012, Sundqvist et al. 2013). For this reason, the use of elevational gradients has become increasingly recognized as an effective space for time substitution tool for determining how factors such as nutrient availability, plant and soil community composition, and species interactions of above- and belowground ecosystem components change with climatic factors (Richardson et al. 2005, Sanders et al. 2007, Bahram et al. 2012). However, despite recent advances in this field (Callaway et al. 2002, Defossez et al. 2011, Wagg et al. 2011), there is still a lack of knowledge on how abiotic and biotic factors directly and indirectly drive plant growth across elevational gradients.

It is well recognized that plant performance is driven by both soil abiotic and biotic factors, but these conditions are not static and plants exist in a complex, ever-evolving interactive relationship with the soil (Aerts and Chapin 2000, Bardgett and Wardle 2010). Soil abiotic conditions altered by plants include mineral nutrient availability (Bezemer et al. 2006), hydrological properties (Bardgett and Wardle 2010) and soil structure (Angers and Caron 1998). Meanwhile, soil biotic properties driven by plants include densities and communities of soil pathogens (van der Putten et al. 1993), mycorrhizal fungi (Klironomos 2002), and the decomposer biota that mineralizes nutrients required for plant growth (Ayres et al. 2009). The legacy of effects that plant species exert on both abiotic and biotic belowground properties and their interactions have consequences for subsequent plant growth and community development (Kardol et al. 2007, Manning et al. 2008, van de Voorde

et al. 2011). Further, interactions between plants and soils also depend both upon environmental context (Gustafson and Casper 2004) and temporal scale (Kardol et al. 2013). While plant–soil interactions are increasingly being recognized as important for understanding how ecosystems function (van der Putten et al. 2013), very little is known about how plant–soil interactions vary with elevation, and more specifically, whether shifts in these interactions are primarily driven by abiotic and/or biotic soil properties. Although two recent studies have explored how variation in soil pathogens or mycorrhizal fungi across elevational gradients affect seedlings of forest tree species (Defossez et al. 2011, Wagg et al. 2011), no study to date has explored how plant–soil linkages respond to elevation for tundra ecosystems, including in the subarctic which is the region expected to be most impacted by future global climate change (IPCC 2013).

In the present study we sought to advance our understanding of how soil abiotic and biotic properties interact with climate to influence plant performance along a well-established elevational gradient ranging from 450 to 900 m in subalpine birch forest and subarctic tundra in northern Sweden (Sundqvist et al. 2011a, b, Milbau et al. 2013). Along this gradient, a mosaic of two markedly differentiated ground-layer vegetation types occurs at all elevations, both within the birch forest and above the treeline, namely heath, which is dominated by ericaceous dwarf-shrubs, and meadow, which is dominated by graminoid and herbaceous species. The heath vegetation is characterized by lower pH, lower mineral nitrogen (N) and higher phosphorus (P) availability than is the meadow vegetation (Björk et al. 2007, Sundqvist et al. 2011a, b). Previous work along the elevational gradient utilized in this study has found contrasting responses to increasing elevation (i.e. decreasing temperature) between the two vegetation types. Specifically, with increasing elevation there are linear decreases in plant-available N and P, increasing fungal to bacterial ratios and low species turnover for the heath vegetation, while the meadow vegetation shows declining P availability, idiosyncratic N availability, a hump-shaped fungal to bacterial ratio, and high species turnover (Sundqvist et al. 2011a, b). Average temperatures during the growing season across this gradient change approximately 3°C from 450 m to 900 m (Sundqvist et al. 2011a), with observed mean annual 2012 growing season temperatures decreasing from 13.5°C to 9.7°C from the 450 m and 900 m elevations (Supplementary material Appendix 1), making this gradient ideal for comparing climate and soil drivers of plant performance across a temperature range that is on par with expected future increases over the coming century (IPCC 2013).

We set up two experiments that each used soils from, and plant species occurring along, this elevational gradient in growth chambers programmed to mimic temperatures across the gradient to test the following three hypotheses: 1) seedlings grown both at temperatures characteristic of lower elevations and in soils from lower elevations will grow larger than seedlings grown at temperatures and in soils from higher elevations. This is because, in addition to the direct positive effect of temperatures on plant growth (Anderson and McNaughton 1973), soils from lower elevations that have developed under warmer temperatures will be more conducive to plant growth through having higher fertility and soil biological activity compared to higher elevations (Sveinbjörnsson et al. 1995); 2) seedling responses to variation in temperature and soil will differ between vegetation types, with seedlings grown in heath soils displaying a stronger, unidirectionally declining growth response to both decreasing temperature and soils from increasing elevations than will seedlings grown in meadow soils. This is based upon previous findings of abiotic and biotic factors known to affect plant growth declining more linearly with increasing elevation in heath than meadow soils (Sundqvist et al. 2011a); 3) soils from lower elevations (and thus developed under warmer temperatures) will have more positive effects on plant growth both due to the abiotic effect of higher nutrient availability (Hart and Perry 1999), and through supporting a soil biotic community that is more conducive to mineralizing nutrients for seedling growth (Liu and Wang 2010). To further elucidate this linkage, we assessed mycorrhizal colonization of the seedlings, which we expect to be greater in plants grown in soils from lower elevations and at higher temperatures (Rillig et al. 2002, Kytoviita and Ruotsalainen 2007). By testing these hypotheses in a controlled climate chamber scenario, we intend to further our mechanistic understanding of how plants in tundra ecosystems respond to shifts in temperature on the order of those predicted to occur with global climate change within the next century.

Methods

Study site

This study was conducted along an elevational gradient on the northeast-facing slope of Mount Suorooaivi (1193 m), located approximately 20 km south of Abisko, Sweden (68°21′N, 18°49′E). The climate is subarctic with a yearly growing season of approximately three months. Temperature measurements from the elevational gradient show air temperature declines by around 3°C from 450 to 900 m (Sundqvist et al. 2011a) (Supplementary material Appendix 1). Mean annual precipitation (Abisko Scientific Research Station) has been 310 mm between 1913–2000, with highest precipitation occurring in July (51 mm) and lowest in April (12 mm) (Kohler et al. 2006). The tree line is situated at 500–600 m and is composed of *Betula pubescens* ssp. *czerepanovii*. Parent soil material consists of salic igneous rocks and quartic and phyllitic hard schists. The landscape is made up of a mosaic of co-dominant heath (composed mainly of woody dwarf ericaceous shrubs and *Betula nana*) and meadow (composed mainly of herbaceous and graminoid species) vegetation types.

Soil collection for experiment 1 and 2

Between June 21 and 29 in 2012, five plots of 1×1 m were established at each of three elevations, i.e. 450, 700 and 900 m, for each of the heath and meadow vegetation types. The mean distance between plots within vegetation types and within elevations was ca 48 m with the maximum distance between the two plots furthest apart being ca 140 m. Considering the high level of heterogeneity over

short distances observed in this study system (Björk et al. 2007), it is expected this distance is sufficient to ensure independence between plots (Sundqvist et al. 2012). Due to the high volume of soil required, soil was collected adjacent to each plot in the root zone (= upper 10 cm) from 27–31 August 2012 for use in experiment 1 and 2. A total of 60 l per vegetation type per elevation was collected and stored frozen (–18°C) for six weeks; these freezing conditions are well within the range of what these soils experience during the winter.

Soil abiotic and biotic properties

We characterized soil properties in five replicate plots in each of three elevations in each of the two vegetation types to aid interpretation of plant growth response to soils. For each of the five plots at each elevation for each vegetation type, 3–6 cores were taken on 2 July 2012 with a 45 mm diameter PVC corer from within each of the plots to a depth of 10 cm to yield a minimum 0.2 l soil. For each core the depth of the humus layer was measured; cores were then bulked within plots and kept at 4°C overnight before being passed through a 4 mm mesh sieve to remove plant matter and stones. Soil pH was determined on a subsample of fresh soil (2.5 g dry weight) after shaking for 12 h in 40 ml deionized water. Gravimetric moisture content was determined after drying (105°C, 24 h) and soil organic matter (SOM) content was determined after combustion in a muffle furnace (550°C, 4 h). A subsample of soil was dried (60°C, 72 h), ground with a ball mill and analyzed for total carbon (C) and nitrogen (N) by dry combustion using an elemental analyzer and phosphorus (P) with nitric–perchloric acid digestion analyzed by inductively coupled plasma (ICP) (Spark 1996).

For each subsample of soil, soil microbial communities were characterized by phospholipid fatty acid (PLFA) analysis. We extracted PLFAs from each subsample after freeze-drying and grinding, according to Frostegård et al. (1991). Abundance of PLFAs is expressed in nmol g^{-1} organic matter (OM). We used i14:0, 14:0, i15:0, a15:0, 15:0, i16:0, 16:1ω9, 16:1ω7c, 16:1ω7t, i17:0, a17:0, 17:1ω8, cy17:0, 17:0, 18:1ω7, cy19:0 as indicators for bacteria and 18:2ω6 as an indicator for fungi (Frostegård and Bååth 1996).

Experiment 1: growth in unsterilized soils

To test the effects of temperature, soil legacy effects and vegetation type on seedling growth, a full factorial growth chamber pot experiment was set up with four factors: 1) three temperatures simulating the temperature characteristics of the three elevations; 2) soils from three elevations; 3) soils from two vegetation types within each elevation, i.e. heath and meadow; and 4) two graminoid species, with five replicates of each treatment combination. This yielded a total of 180 pots, each serving as a separate experimental unit.

For this experiment, collected stored field soils were thawed, processed by removing large stones and roots and then thoroughly homogenized within each vegetation type per elevation (Pizano et al. 2011). Subsamples of soil were put into plastic pots (each 8 × 8 × 10 cm deep, with a total volume of 490 ml), each containing a drainage layer at the bottom of 150 ml sterilized sand and the remaining volume filled with the collected field soil; there were 30 pots for each elevation × vegetation type combination. Two species, *Deschampsia flexuosa* (more prevalent in heath vegetation) and *Festuca ovina* (more prevalent in meadow vegetation), which occur across the entire elevational gradient, were selected as phytometers. In addition to producing high quality litter, grasses respond quickly to changes in temperature and nutrients (Dormann and Woodin 2002). Thus, changes in grass species growth and/or abundance due to climate change may have important impacts on tundra ecosystem processes and functioning. A seed source was selected from outside of the soil collection sites to control for potential confounding effects of coadaptation with climatic or soil conditions. Seeds were obtained from natural sources through a seed company (*Deschampsia flexuosa* and *Festuca ovina*) and surface sterilized in a 1% sodium hypochloride solution for 1 min, rinsed, and sown in autoclaved sand. After germination the seedlings were placed in 4°C to arrest growth until transplantation into the experimental pots. For each of the two species, five seedlings were transplanted into half of the pots for each elevation × vegetation type combination. We used five seedlings per pot to ensure that even with some seedling mortality there would be sufficient surviving seedlings in each pot for measurement, which would enable us to avoid loss of statistical power.

For the 15 pots for each elevation × vegetation type × species combination, five replicate pots were placed in each of three growth chambers, whose conditions were set to mimic temperature conditions as observed at 450, 700 and 900 m along the elevational gradient during the 2012 growing season (Supplementary material Appendix 1). Average minimum and maximum temperatures recorded were 5.0°C and 13.5°C; 4.1°C and 12.3°C; and 3.8°C and 9.7°C, at the 450 m, 700 m and 900 m sites, respectively. Weekly average maximum and minimum temperature were derived from equations of the trend lines of regressions as shown in Supplementary material Appendix 1. Diurnal temperature cycles in the growth chambers were set by hourly increments between minimum and maximum values. Minimum temperature values lower than 5°C were set to 5°C due to climate chamber system constraints. Relative humidity was set to 90% in all chambers and photosynthetically active radiation (PAR) and hours of daylight were set in each growth chamber to represent conditions measured from mid June to mid September 2012 in the vicinity of the elevational gradient used in our study (using data derived from Abisko Scientific Research Station, Abisko, Sweden for PAR; and the Swedish Meteorological and Hydrological Institute for day length) (Supplementary material Appendix 2). Each of the five replicates of each treatment combination was randomly assigned to a position in a block within each chamber. Pots were rotated systematically between chambers (i.e. entire temperature treatments moved between chambers) on a weekly basis to control for any artifacts resulting from differences between growth chambers that were independent of treatment. Pots were watered as necessary throughout the experiment (usually every other day) to eliminate moisture as a limiting factor, and were weeded as necessary.

After 12 weeks the three largest individual seedlings in each pot were harvested. Three rather than five seedlings were selected to avoid biases given that there was some mortality.

However, mortality was less than 1.5% of the 2400 total seedlings planted and randomly distributed across all treatments, making it unlikely to have contributed to biases introduced by potential intraspecific competition among seedlings. Roots were carefully washed and separated from the shoots. Samples were oven dried at 60°C for a minimum of 48 h, weighed and the average biomass of the three seedlings from each pot was treated as one data point in subsequent analyses. Upon harvest and before drying, a subsample of root tissue was taken from plants in all pots containing soils from the 450 and 900 m elevations that were grown in chambers that mimicked the 450 and 900 m temperature conditions, to check for arbuscular mycorrhizal fungi (AMF) colonization. When a subsample of root was taken for this purpose, the wet weight of both the subsample and of the remaining roots in the pot were measured, as well as the oven dry weight of the remaining roots, to enable determination of oven dry weight of the subsample. Subsamples used for mycorrhizal assessment were stored in 50% ethanol at 4°C until cleared, stained and mounted on slides (Omar et al. 1979, Koske and Gemma 1989). Colonization was assessed in 100 random fields of intersection (with the vertical crosshair eyepiece) per slide at 40 × magnification (McGonigle et al. 1990).

Experiment 2: growth in sterilized and inoculated soils

To separate the contribution of abiotic and biotic components of soil effects from contrasting elevations and vegetation types, a full factorial experiment was set up with four factors: 1) three growth chamber temperatures simulating the temperature characteristics of the three elevations; 2) soil from the two vegetation types, heath and meadow; 3) four soil inocula treatments, including sterilized soil without inocula and with inocula from each of three elevations; and 4) two graminoid species, with five replicates (or ten for sterilized uninoculated soil treatments) of each treatment combination. This yielded a total of 300 pots with each pot serving as a separate experimental unit.

For this experiment, collected stored field soils were thawed, processed by removing large stones and roots and then thoroughly homogenized within each vegetation type per elevation, as per experiment 1. We took an equal subsample of soil from all plots within each vegetation type from all elevations and combined them into two bulk soils, one representing heath and the other representing meadow. The bulk soils were then sent for γ-irradiation at 25 kGy. Gamma irradiation is a method of soil sterilization that has been shown to effectively sterilize soils while exerting minimal impacts on other soil properties (Berns et al. 2008). By comparing sterilized soils to reinoculated soils, the effects of abiotic versus biotic soil factors on plant growth can be effectively separated (Kardol et al. 2007).

For each of the vegetation types we prepared four inoculation treatments (i.e. inoculation with unsterilized soil from each of the three elevations or with sterilized soil). A volume of 10% unsterilized soil from each elevation or sterilized soil was mixed with the bulked sterilized soil. We bulked the unsterilized soil inocula within each elevation's vegetation type because we were interested in the composite effect of an elevation's soil biota, rather than within-site heterogeneity (Gundale et al. 2014). Plant performance in the pots inoculated with unsterilized soils relative to the corresponding sterilized soils allows for a quantification of the effect of soil biota (Kardol et al. 2007, Gundale et al. 2014). Prepared soils were then placed into plastic pots as per experiment one, yielding a total of 30 pots per vegetation type × soil inoculum treatment, except for the bulked sterilized soils for which there were 60 pots per vegetation type. Half of the pots of each soil treatment were planted with one of the two grass species, as per experiment 1. Five replicates of all vegetation × inoculum × species combinations (or ten for the sterilized soil treatments) were randomly assigned positions within five blocks (two replicates of sterilized soil treatments assigned each block) and placed in each of the three climate chambers set to mimic conditions observed along the gradient at 450, 700 and 900 m sites, as per experiment 1. Maintenance, rotations, chamber settings, duration of experiment, harvesting and AMF measurements were the same as described in experiment 1.

Statistical analyses

To test for the effects of vegetation type and elevation on soil abiotic and biotic variables, we used two-way ANOVA. For experiment 1, we used four-way ANOVA to test for the effects of temperature, soil origin, vegetation type and species, and all possible interactions (all as fixed factors and with block as a random factor) on root biomass, shoot biomass, total biomass, root to shoot ratio and mycorrhizal colonization. For experiment 2, data were also analyzed by four-way ANOVA as described above, but with soil inoculum treatment and not soil origin as a factor. For all ANOVAs, whenever significant main or interactive effects were found, differences among means were further explored using Tukey's h.s.d. at $p = 0.05$. For all analyses data were transformed whenever necessary to meet the assumptions for parametric testing. All statistical analyses were performed in SPSS (PASW statistics 21.0).

Results

Soil abiotic and biotic properties

Of the soil abiotic properties, SOM, pH, C:N, C:P and N:P were significantly affected by vegetation type, with heath soils having larger values than meadow soils for all variables except pH (Supplementary material Appendix 3). Additionally, SOM, pH and C:N were significantly affected by elevation. At 700 m elevation SOM peaked and pH generally increased with increasing elevation for both heath and meadow soils. The C:N generally decreased with increasing elevation for heath soils, while C:N showed no significant differences between elevations in meadow soils. No significant interactive effects of elevation × vegetation type were detected.

Bacterial and fungal PLFA and the ratio of fungal to bacterial PLFAs were all significantly affected by vegetation type, with meadow soils generally having higher bacterial PLFA values and heath soils having higher fungal PLFA values and fungal to bacterial ratios (Supplementary material Appendix 3). Soil origin (i.e. elevation) also significantly influenced microbial properties; both bacterial and fungal PLFAs were lowest in soils from the highest elevation in

meadow soil, while fungal PLFAs were highest at the 700 m plots for the heath soils, although only significantly different from the 900 m soils. Fungal to bacterial ratios showed a hump-shaped relationship in the heath and meadow soils, peaking at the 700 m plots (Supplementary material Appendix 3), although this relationship was only significant in the meadow soils. No significant interactions between elevation and vegetation type were detected.

Experiment 1: growth in unsterilized soils

Total plant biomass was significantly affected by temperature, soil origin, species and vegetation type (Table 1). *Festuca ovina* produced larger total biomass than did *Dechampsia flexuosa* and meadow soils produced higher total biomass than did heath soils (Fig. 1). There was a significant temperature × vegetation type interactive effect, because for both species total biomass declined with decreasing temperature for the meadow soils (Fig. 1b, d), but was unresponsive to temperature for the heath soils (Fig. 1a, c). There was also a significant soil origin × vegetation type effect because for the meadow, the highest biomass occurred for soils originating from 450 m, while for the heath, biomass did not show consistent responses to soil origin (Fig. 1). There was also a three-way interaction between temperature, soil origin and vegetation type, and a four-way interaction between these three factors and species. This is because plants grown in meadow soils from 450 m and at 450 m temperatures (i.e. soils from the warmest elevation, grown in the warmest temperatures) produced the largest biomass with *D. flexuosa* following a more unidirectionally declining trend with increasing elevation of soil origin and temperature than did *F. ovina*, while for the heath soil plants generally showed non-significant growth responses to temperature and soil origin for both species (Fig. 1). Root growth responded in essentially the same manner as total biomass (Table 1, Supplementary material Appendix 4). The one exception was an additional marginally significant three-way interactive effect of temperature, soil origin and species. Shoot growth also generally responded in the same manner as total biomass; the only exception was a lack of significance of species (Table 1, Supplementary material Appendix 5).

The root to shoot biomass ratio was significantly affected by temperature, soil origin, vegetation type and species (Table 1). Overall, *F. ovina* produced larger root to shoot ratios than did *D. flexuosa* and heath soils produced much higher root to shoot ratios than did meadow soils (Fig. 2). There was a significant interactive effect of soil origin × species because *D. flexuosa* generally had higher root to shoot ratios in soils from 900 m than in soils from 450 m and 700 m, while those for *F. ovina* did not show any consistent response to soil origin (Fig. 2). There was also a significant interactive effect of temperature × soil origin because the 900 m temperature (i.e. coldest) consistently produced plants with lower root to shoot ratios in 700 m soils, while the other temperatures had varying responses to soil origin. Further, there was a significant interactive effect of species × vegetation type because root to shoot ratios were more consistently higher for *F. ovina* than for *D. flexuosa* in heath soils than in meadows soils (Fig. 2). Finally, there was a significant interactive effect of vegetation type × temperature because for both species the root to shoot ratio was highest overall for the 900 m temperature (i.e. coldest) for heath soils but not for meadow soils (Fig. 2).

Mycorrhizal colonization was significantly affected by soil origin and vegetation type but not by temperature or species (Table 1), with plants grown in 900 m soils generally showing higher colonization than those grown in 450 m soils and plants grown in meadow soils displaying an overall higher colonization than those grown in heath soils (Supplementary material Appendix 6). There was a significant interactive effect of soil origin and vegetation type because 450 m soils

Table 1. Results of ANOVA (F-value with p-value in brackets) testing effects of temperature (450, 700, 900 m), soil origin (450, 700, 900 m), species (*Deschampsia flexuosa*, *Festuca ovina*) and vegetation type (heath, meadow soils) on plant biomass in Experiment 1; DF error = 140 except for AMF colonization where DF error = 60. For arbuscular mycorrhizal fungi (AMF) colonization, ANOVA was performed only on 450 m and 900 m temperature and soil origin treatments so DF = 1 for all treatment factors. Significant p-values ($p \leq 0.05$) in bold.

	DF	Total biomass[a] F-value (p)	Root biomass[a] F-value (p)	Shoot biomass[a] F-value (p)	Root to shoot ratio[a] F-value (p)	AMF colonization[b] F-value (p)
Temperature (T)	2	17.8 (**<0.001**)	9.2 (**<0.001**)	22.9 (**<0.001**)	6.6 (**0.002**)	0.7 (0.409)
Soil origin (O)	2	69.0 (**<0.001**)	64.0 (**<0.001**)	57.0 (**<0.001**)	9.6 (**<0.001**)	5.8 (**0.020**)
Species (S)	1	4.1 (**0.045**)	18.7 (**<0.001**)	0.1 (0.791)	50.1 (**<0.001**)	1.8 (0.181)
Vegetation type (V)	1	1196.3 (**<0.001**)	720.4 (**<0.001**)	1351.3 (**<0.001**)	194.3 (**<0.001**)	35.3 (**<0.001**)
Block	4	2.5 (**0.043**)	2.2 (0.070)	2.8 (**0.029**)	2.6 (**0.038**)	0.5 (0.739)
O × S	2	1.4 (0.258)	2.5 (0.085)	1.4 (0.249)	3.7 (**0.026**)	0.6 (0.426)
T × O	4	0.4 (0.824)	1.3 (0.271)	0.3 (0.890)	3.9 (**0.005**)	0.8 (0.383)
O × V	2	107.3 (**<0.001**)	83.9 (**<0.001**)	101.0 (**<0.001**)	1.1 (0.345)	12.5 (**0.001**)
T × S	2	0.4 (0.644)	0.7 (0.502)	0.4 (0.691)	1.1 (0.346)	1.2 (0.288)
S × V	1	0.9 (0.354)	0.3 (0.616)	3.7 (0.057)	4.5 (**0.036**)	1.8 (0.182)
T × V	2	17.5 (**<0.001**)	21.0 (**<0.001**)	10.8 (**<0.001**)	5.1 (**0.008**)	5.8 (**0.019**)
T × O × S	4	2.3 (0.065)	2.6 (**0.039**)	2.2 (0.077)	2.0 (0.092)	1.8 (0.185)
O × S × V	2	0.3 (0.710)	1.2 (0.307)	0.9 (0.915)	1.8 (0.176)	0.1 (0.721)
T × O × V	4	5.5 (**<0.001**)	6.9 (**<0.001**)	4.6 (**0.002**)	1.1 (0.362)	4.1 (**0.048**)
T × S × V	2	1.5 (0.219)	1.5 (0.235)	2.0 (0.146)	1.9 (0.150)	1.1 (0.290)
T × O × S × V	4	4.2 (**0.003**)	3.9 (**0.005**)	4.2 (**0.003**)	1.3 (0.284)	0.8 (0.372)

[a]Data ln(x) transformed before analysis.
[b]Data ln(x + 1) transformed before analysis.

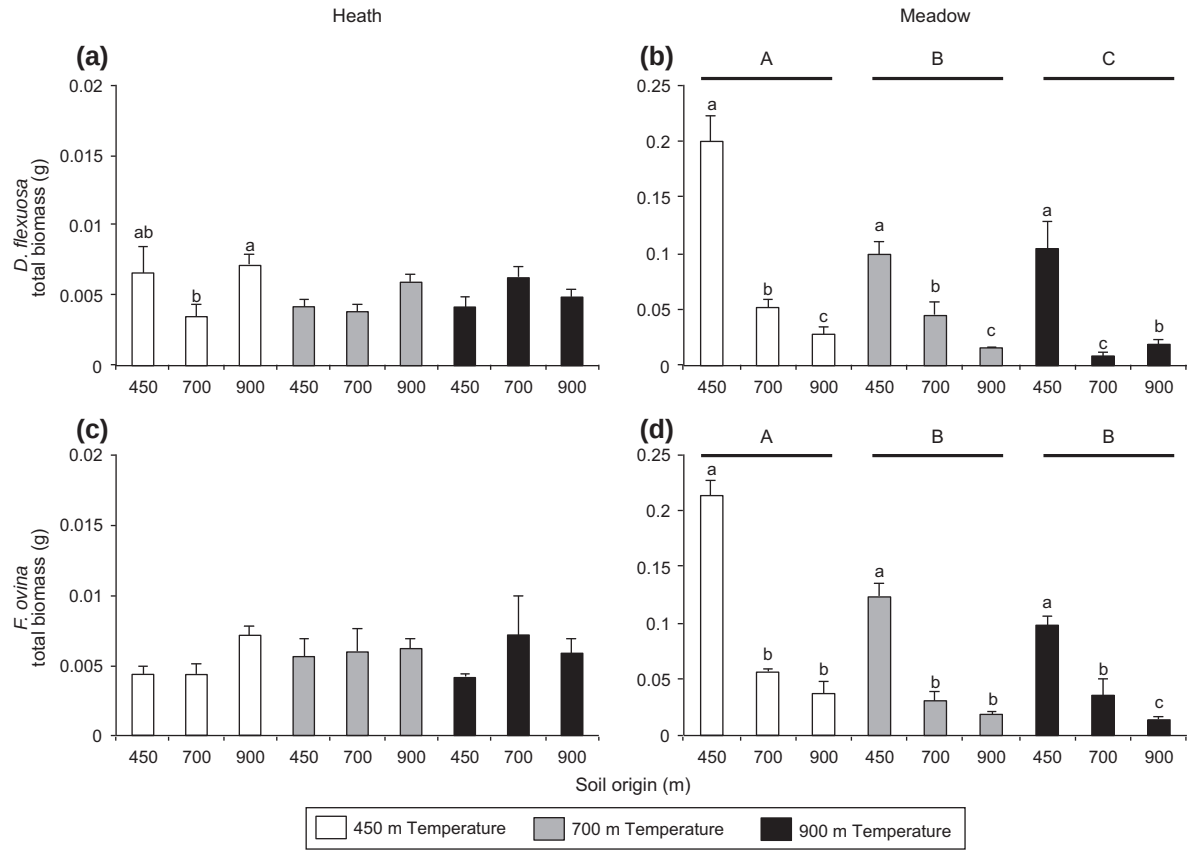

Figure 1. Total biomass of *D. flexuosa* and *F. ovina* grown at 450, 700 and 900 m temperatures in unsterilized soils from heath and meadow vegetation types originating from 450, 700 and 900 m elevations (numbers on horizontal axis indicate soil origin). Within each panel groups of three bars topped with the same capital letter do not differ at $p \leq 0.05$, and for each group of three bars, bars topped with the same lower case letter do not differ at $p \leq 0.05$ (Tukey's h.s.d. with Bonferroni correction). Data shown are mean ± SE. Note different scales on the vertical axes for soils from heath and meadow vegetation.

generally produced plants with higher colonization than 900 m soils for heath vegetation, while meadow soils showed the opposite pattern (Supplementary material Appendix 6). There was also a significant interaction between temperature and vegetation type because plants grown in heath soils showed overall higher mycorrhizal colonization at 450 m temperatures (i.e. warmest), while plants grown in meadow soils showed the opposite pattern (Supplementary material Appendix 6). In addition, there was a marginally significant temperature × soil origin × vegetation type effect because at 450 m temperatures (but not at 900 m temperatures) higher mycorrhizal colonization was observed in plants grown in 450 m soils in the heath, but this pattern was reversed (i.e. higher colonization in 900 m soils) in meadow soils (Supplementary material Appendix 6).

Experiment 2: growth in sterilized and inoculated soils

Total biomass was significantly affected by temperature, inoculum origin, and vegetation type, but not species (Table 2). Overall, 450 m temperatures (i.e. warmest) produced larger plants and meadow soils produced higher total biomass than did heath soils (Fig. 3). Although inoculated soils generally produced larger plants than did sterile soils, differences between inoculum origins were not significant. There was, however, a significant interactive effect of inoculum origin × plant species, because living soil inocula increased overall *D. flexuosa* biomass more than *F. ovina* biomass (Fig. 3). The interactive effect of temperature × inoculum origin effect was marginally significant, but largely idiosyncratic. Further, there was a significant interactive effect of inoculum origin × vegetation because plants grown in meadow soils responded more consistently favorably to living soil inocula than did plants grown in heath soils (Fig. 3). A significant interactive effect of temperature × species also occurred because although both species produced their greatest biomass at the 450 m temperature, this effect was more pronounced for *D. flexuosa* (Fig. 3). The interactive effect of species × vegetation type was also significant because *F. ovina* showed a greater disparity in total biomass between heath and meadow soils than did *D. flexuosa* (Fig. 3). Root biomass responded in the same manner as did total biomass, except that species also emerged as a significant main effect because root biomass was generally greater for *F. ovina* than for *D. flexuosa*, and that none of the interaction terms were significant except for inoculum origin × species (Supplementary material Appendix 7). Shoot biomass responded the same as total biomass (Table 2, Supplementary material Appendix 8).

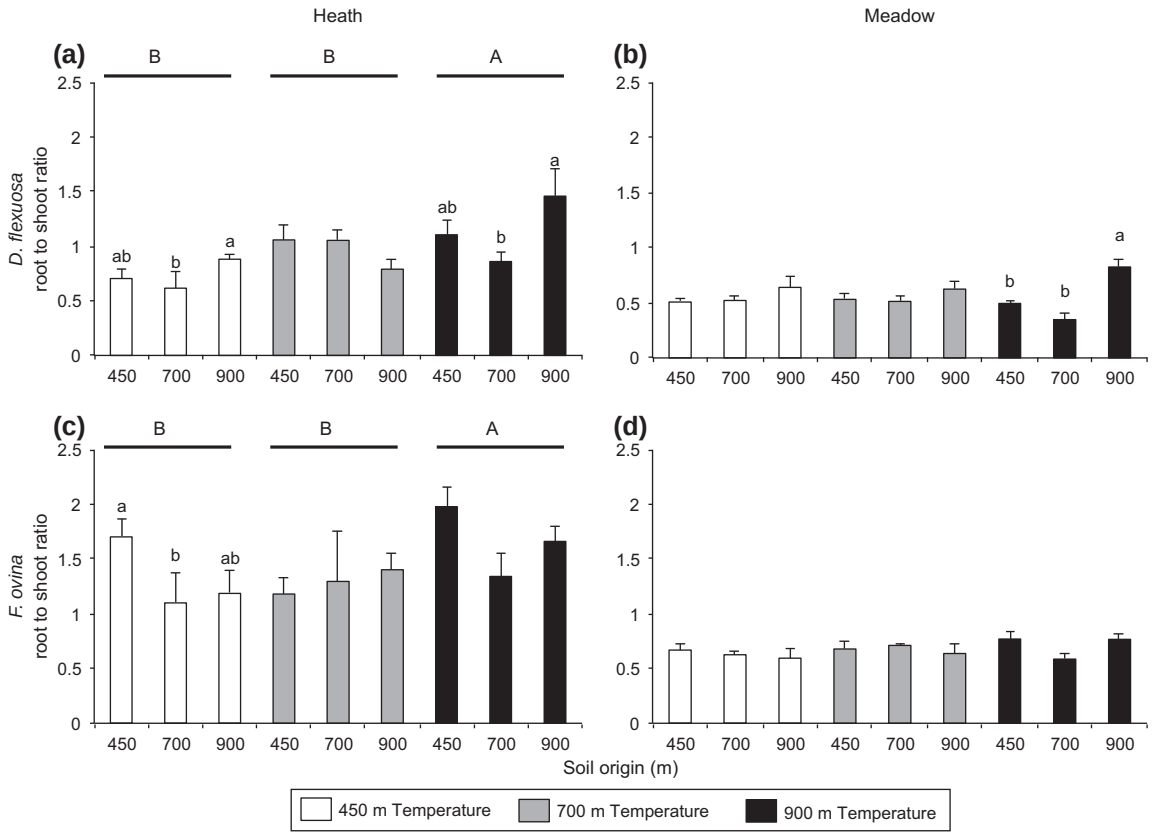

Figure 2. Root to shoot ratio of *D. flexuosa* and *F. ovina* grown at 450, 700 and 900 m temperatures in unsterilized soils from heath and meadow vegetation types originating from 450, 700 and 900 m elevations (numbers on horizontal axis indicate soil origin). Within each panel groups of three bars topped with the same capital letter do not differ at $p \leq 0.05$, and for each group of three bars, bars topped with the same lower case letter do not differ at $p \leq 0.05$ (Tukey's h.s.d. with Bonferroni correction). Data shown are mean ± SE.

The root to shoot ratio was significantly affected by inoculum origin, vegetation type and species but not temperature (Table 2). Overall, inoculated soils produced higher root to shoot ratios than did sterilized soils, heath soils had higher root to shoot ratios than did meadow soils, and *F. ovina* produced larger root to shoot ratios than did

Table 2. Results of ANOVA (F-value with p-value in brackets) testing effects of temperature (450, 700, 900 m), inoculum origin (450, 700, 900 m; sterile control), species (*Deschampsia flexuosa*, *Festuca ovina*) and vegetation type (heath, meadow soils) on plant biomass in Experiment 2; DF error = 248 except for AMF colonization where DF error = 60. For arbuscular mycorrhizal fungi (AMF) colonization, ANOVA was performed only on 450 m and 900 m temperature and inoculum origin treatments so DF = 1 for all treatment factors. Significant p-values ($p \leq 0.05$) in bold.

	DF	Total biomass[a] F-value (p)	Root biomass[a] F-value (p)	Shoot biomass[a] F-value (p)	Root to shoot ratio[a] F-value (p)	AMF colonization[b] F-value (p)
Temperature (T)	2	33.9 (**<0.001**)	17.5 (**<0.001**)	33.4 (**<0.001**)	0.4 (0.648)	5.1 (**0.028**)
Inoculum origin (O)	3	24.4 (**<0.001**)	53.6 (**<0.001**)	13.6 (**<0.001**)	40.7 (**<0.001**)	0.6 (0.454)
Species (S)	1	2.2 (0.141)	25.4 (**<0.001**)	0.0 (0.874)	48.5 (**<0.001**)	2.1 (0.157)
Vegetation type (V)	1	144.7 (**<0.001**)	73.9 (**<0.001**)	168.1 (**<0.001**)	6.3 (**0.013**)	19.5 (**<0.001**)
Block	4	4.3 (**0.002**)	3.1 (**0.015**)	4.2 (**0.003**)	0.9 (0.444)	0.8 (0.532)
O × S	3	21.1 (**<0.001**)	25.0 (**<0.001**)	19.6 (**<0.001**)	4.0 (**0.009**)	2.1 (0.154)
T × O	6	2.3 (**0.033**)	1.4 (0.224)	2.2 (**0.040**)	0.4 (0.868)	0.0 (0.912)
O × V	3	16.6 (**<0.001**)	1.8 (0.146)	23.2 (**<0.001**)	18.2 (**<0.001**)	0.2 (0.623)
T × S	2	3.7 (**0.026**)	2.1 (0.124)	3.300 (**0.038**)	0.4 (0.671)	5.3 (**0.025**)
S × V	1	6.5 (**0.011**)	0.9 (0.347)	7.7 (**0.006**)	3.1 (0.082)	2.9 (0.095)
T × V	2	1.8 (0.171)	1.3 (0.266)	2.1 (0.130)	0.6 (0.575)	4.0 (0.051)
T × O × S	6	0.8 (0.569)	0.4 (0.851)	0.9 (0.507)	0.8 (0.561)	1.2 (0.275)
O × S × V	3	1.2 (0.320)	0.8 (0.514)	1.2 (0.309)	2.8 (**0.041**)	1.4 (0.241)
T × O × V	6	1.0 (0.416)	0.9 (0.532)	0.9 (0.500)	0.5 (0.845)	0.1 (0.712)
T × S × V	2	0.8 (0.450)	1.5 (0.225)	0.6 (0.566)	0.9 (0.394)	6.6 (**0.013**)
T × O × S × V	6	0.7 (0.667)	0.5 (0.796)	0.7 (0.659)	0.2 (0.961)	0.7 (0.404)

[a]Data ln(x) transformed before analysis.
[b]Data ln(x + 1) transformed before analysis.

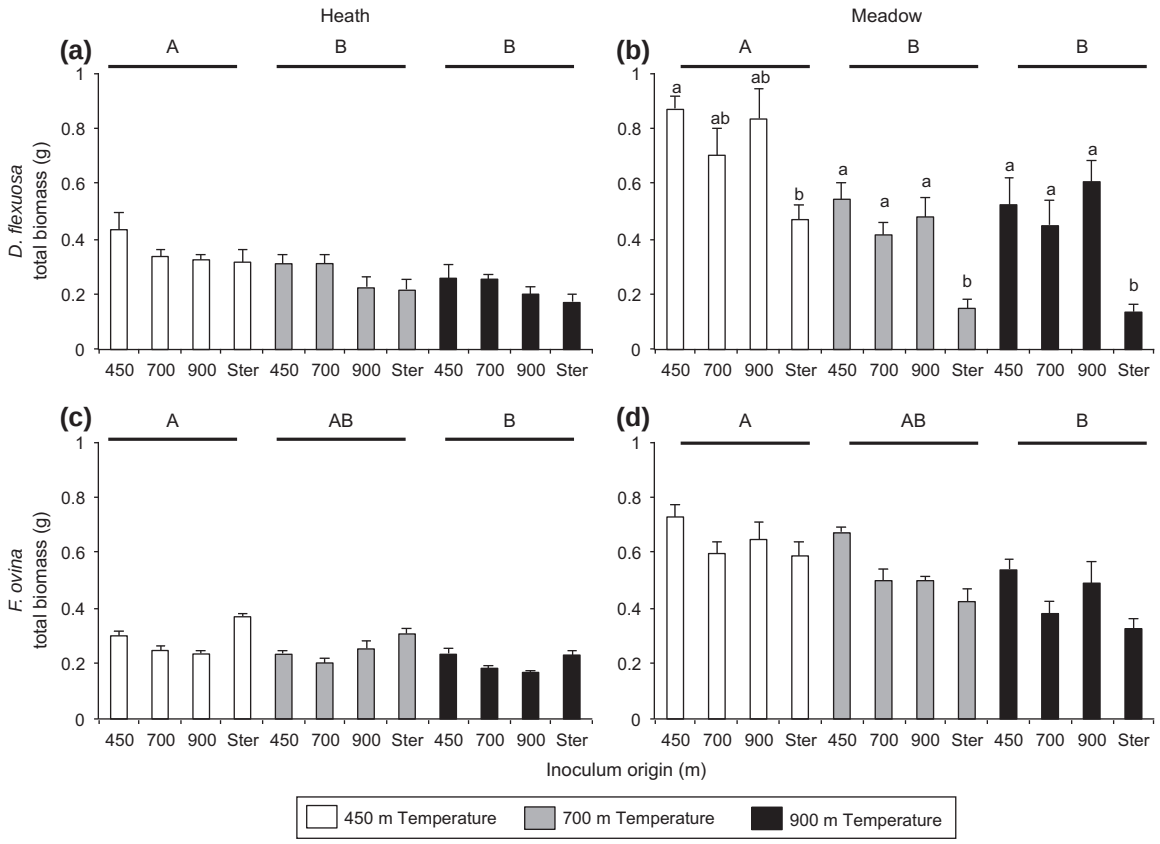

Figure 3. Total biomass of *D. flexuosa* and *F. ovina* grown at 450, 700 and 900 m temperatures in inoculated/sterile soils from heath and meadow vegetation types originating from 450, 700 and 900 m elevations (numbers on horizontal axis indicate soil origin). Within each panel groups of three bars topped with the same capital letter do not differ at $p \leq 0.05$, and for each group of three bars, bars topped with the same lower case letter do not differ at $p \leq 0.05$ (Tukey's h.s.d. with Bonferroni correction). Data shown are mean ± SE.

D. flexuosa (Fig. 4). There were also significant interactive effects of inoculum origin × species and of inoculum origin × vegetation type, as well as a three-way interactive effect of all three factors, because inoculated soils produced significantly higher root to shoot ratios than sterilized soils only in heath soils and because this trend was stronger for *D. flexuosa* than for *F. ovina* (Fig. 4).

Mycorrhizal colonization was significantly affected by temperature and vegetation type, but not species or inoculum origin (i.e. no significant difference between sterilized and inoculated soils) (Table 2). As such, in meadow soils, 900 m temperatures (i.e. coldest) led to higher colonization than did 450 m temperatures (i.e. warmest) and meadow soils resulted in higher colonization than did heath soils (Table 2, Supplementary material Appendix 6). There was a significant two-way interactive effect of temperature × species and a three way interactive effect of these two factors with vegetation type because *D. flexuosa* had the highest colonization in meadow soils in the 900 m temperature treatment (Supplementary material Appendix 6).

Discussion

In our study we explored the mechanisms underpinning how declines in temperature with increasing elevation influence plant growth. Our major findings indicate that plant growth responded to both the direct effects of temperature and its associated indirect effects via soil legacies, that these direct and indirect effects were not always closely coupled, and that plant growth responses varied among vegetation types. We also found that these soil legacy effects were driven predominantly by abiotic rather than biotic soil properties, due to the largely non-significant plant growth responses to soil communities originating from contrasting elevations. Below we explore how our findings contribute to our knowledge of plant response to elevation, and more generally, to our understanding of the impacts of future climate change in subarctic tundra ecosystems.

Consistent with our first hypothesis, higher temperatures and meadow soils from lower elevations both generated a positive effect on plant growth. This points to temperature exerting both direct and indirect effects via soil legacies in the meadow soils. Further, the positive effects of meadow soils from the lowest elevation were similar for all temperature treatments, meaning that for these soils, plant growth responses to the indirect effects of temperature via soil legacies were largely independent of the direct effect of temperature. Such legacy effects are likely to result from the greater nutrient availability that occurs at the lower, warmer elevations in this system, as has been shown in previous studies (Sundqvist et al. 2014, Vincent et al. 2014), and is likely to have resulted from higher rates of soil processes such as litter decomposition (Ayres et al. 2009) and nutrient

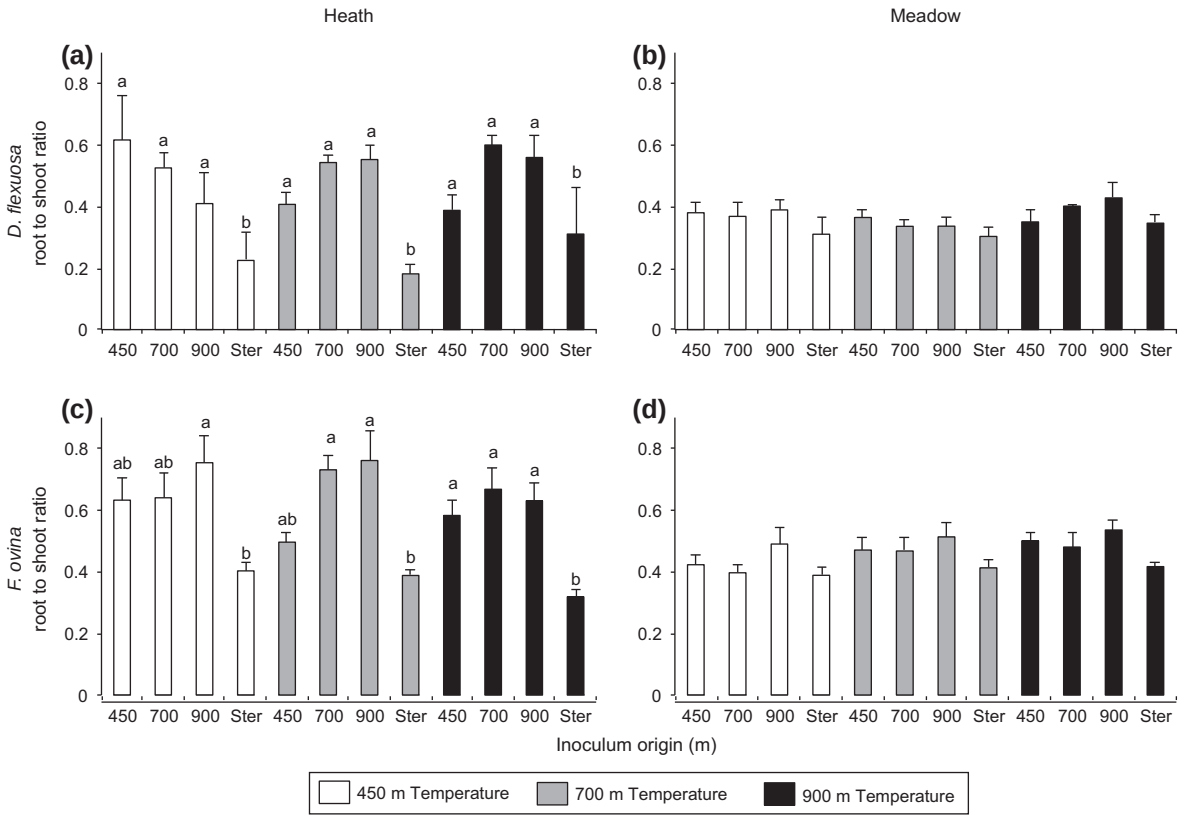

Figure 4. Root to shoot of *D. flexuosa* and *F. ovina* grown at 450, 700 and 900 m temperatures in inoculated/sterile soils from heath and meadow vegetation types originating from 450, 700 and 900 m elevations (numbers on horizontal axis indicate soil origin). Within each panel groups of three bars topped with the same capital letter do not differ at $p \leq 0.05$, and for each group of three bars, bars topped with the same lower case letter do not differ at $p \leq 0.05$ (Tukey's h.s.d. with Bonferroni correction). Data shown are mean ± SE.

mineralization (Aerts and Chapin 2000). We also found that the root to shoot ratio for plants grown in the heath soils was highest in the 900 m temperature treatment, which is consistent with low temperatures stimulating belowground biomass allocation to increase nutrient acquisition in situations where soil nutrient mineralization and supply rates are likely to be limited (Oleksyn et al. 1998, Pérez and Frangi 2000). Further, the only significant direct temperature × soil interaction effect detected in our study involved lower root to shoot ratios for *D. flexuosa* grown in soils from lower elevations at 900 m temperatures. This is most likely because soils from lower elevations often have higher nutrient availability, leading to greater investment in aboveground biomass (Pérez and Frangi 2000, Wagg et al. 2011, Vincent et al. 2014) even when temperature conditions are less conducive to plant growth. Although both direct and indirect effects of temperature were evident along this elevational gradient, these two factors did not operate in a closely coordinated way, indicating some degree of decoupling of plant growth responses to temperature and soil origin.

Contrary to our second hypothesis, plants grown in heath soils were less responsive to temperature and soil origin than those grown in meadow soils. Specifically, although plants grew larger in meadow soils as expected due to their higher nutrient availability relative to heath soils (Sundqvist et al. 2011a), plants in meadow soils showed a pattern of unidirectional decline in biomass when grown in soils from higher elevations, while plants in the heath soil showed no significant response. These patterns run counter to previous work along this gradient showing unidirectional declines in various soil properties with increasing elevation in heath soils but idiosyncratic responses in meadow soils (Sundqvist et al. 2011a, b). This finding indicates that plant responses to elevation cannot always be predicted by the soil conditions present. The non-responsiveness of the plants grown in heath soils from contrasting elevations signals a possible 'buffering effect' of these soils against variations in temperature, making the plants growing in them more resistant in their response to temperature change (Hudson and Henry 2010). Conversely, the declining growth response of plants in meadow soils both to temperatures and soils characteristic of higher elevations demonstrates a possible inherent adaptability of meadow vegetation to higher temperatures, and a capacity to respond more quickly to future warming (Arft et al. 1999). These results are in accordance with previous experimental warming studies showing the effects of temperature on arctic vegetation to vary across contrasting vegetation types (Hollister et al. 2005, Jonsdottir et al. 2005). As subarctic temperatures increase over the coming century (IPCC 2013), conditions may become more favorable for graminoid species, which may in turn shift plant functional group dominance. The divergent plant responses to both temperature and soil origin observed in the heath versus the meadow vegetation have potentially important

implications for understanding how the structure and function of subarctic tundra may change for contrasting vegetation types as climate change progresses.

Although heath soil inoculum had no effect on plant growth, meadow soil inoculum from all elevations stimulated growth in *D. flexuosa*, indicating that for this species, meadow soil communities from all elevations were equally beneficial. This finding is inconsistent with our third hypothesis where we predicted that soil communities from lower elevations would be more beneficial to plant growth. Our results show that the observed positive effects of meadow soils from lower elevations on plant growth cannot be due to soil biotic factors, and must be instead due to soil abiotic factors, which have previously been shown to vary along this elevational gradient (Sundqvist et al. 2011a, Vincent et al. 2014). Even though temperature may have impacted on soil biological activity, and thus influenced the current soil abiotic nutrient status across the gradient, in the short term the biotic community played little role in dictating plant growth response to the gradient soils. However, abiotic and biotic soil factors interact to drive plant growth response, thereby making strict categorical interpretation of their influences on plant performance somewhat subjective (Bardgett and Wardle 2010). It is also important to note that for the meadow soil, inoculation had a positive effect on plant biomass with decreasing temperature for *D. flexuosa*, indicating the effect of soil biota on plant growth becomes more positive with decreasing temperature independent of soil legacy effects (Wagg et al. 2011). Meanwhile, plants grown in inoculated heath soils produced higher root to shoot ratios than did their counterparts in sterilized heath soils. Greater investment in belowground biomass may signify plant responses to competition with soil microbes; as microbes outcompete plants for nutrient resources, a greater investment in root biomass is required to maintain nutrition (Jonasson et al. 1996). However, it must be noted that as is the case with most controlled experiments examining interactions between individual plant species and soil, it is possible the effects observed in this experiment may be altered in more natural settings by interactions among coexisting plant species and between abiotic and biotic factors. Generally, the meadow soil community was beneficial to plant growth independent of soil origin, while the heath soil community had no detectable effect, emphasizing the context dependency of plant growth response to biotic soil conditions.

For the mycorrhizal assessments, the highest colonization was most often observed in plants grown in meadow soils collected from 900 m elevation and grown at 900 m temperatures. This indicates a more important role of mycorrhizae with increasing elevation resulting from the associated declines in nutrient availability and temperature (Pérez and Frangi 2000). However, mycorrhizal colonization in our experiment was relatively low (≈20% of samples assessed), relative to what is typical for subarctic systems (Ruotsalainen et al. 2002), which suggests that their ecological relevance for plant nutrition and performance in the context of our experiments was also low. Additionally, the grass species considered in this experiment are known to associate with AMF (Lawley et al. 1982) and the highest colonization was found in those plants growing in meadow soils, which are known to harbor more AMF-associating species and likely to contain more AMF propagules (Gardes and Dahlberg 1996). As a result, these grass species may have been unable to form mycorrhizal associations in the heath soils, which may have contributed to the lack of differences between plants grown in inoculated vs. sterilized heath soils. If ericaceous species that typically associate with ericoid mycorrhizae, such as those commonly found on heath soils (Gardes and Dahlberg 1996), had been used in these experiments, we likely would have observed different patterns of mycorrhizal colonization and perhaps resultant changes in plant performance. It is also likely that these differences in mycorrhizal communities will restrain AMF associated plants such as grasses from invading heath systems, even as climate change advances, further supporting the idea of a "buffering effect" in heath soils (Hudson and Henry 2010).

Much is known regarding the response of plants to the direct effects of temperature, but the indirect and often long-term effects of temperature on plant growth through altering soil abiotic and biotic conditions has often been overlooked. The use of an elevational gradient in the present study allowed for comparisons between soils that have been climatically conditioned under different temperature regimes in the long term, something that is difficult or often impossible to explore in short-term, manipulative warming experiments (Wolkovich et al. 2012, Sundqvist et al. 2013). One of our primary findings is that plants are responsive to both the direct effects and indirect soil legacy effects of temperature, and that these effects do not always operate in concert. Therefore, consideration of only the direct effect of temperature on plants, such as is the case with most predictive climate change models (Cramer et al. 2001), may provide incomplete predictions about how vegetation responds to climate. Further, there is growing recognition that vegetation types differing in plant functional characteristics can show greatly contrasting responses to the same climatic factors (Díaz and Cabido 1997); our results for two distinct vegetation types reveal that this applies not only to the direct, but also the indirect, effects of a key climatic variable. Finally, our results strongly suggest that in the long term, temperature will have a greater indirect effect on plant responses through impacting on soil abiotic properties than on soil biotic properties, indicative of a decoupled response of plants and soil biota to environmental gradients and climatic factors. These findings highlight the importance of considering the direct, indirect, and interactive effects of climate, vegetation and soils to better understand and predict how subarctic ecosystems may respond to climate change (Kardol et al. 2012).

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Supplementary material (available online as Appendix oik.01764 at <www.oikosjournal.org/readers/appendix>). Appendix 1–8.