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Shrub expansion may reduce summer permafrost thaw in Siberian tundra

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Abstract

Climate change is expected to cause extensive vegetation changes in the Arctic: deciduous shrubs are already expanding, in response to climate warming. The results from transect studies suggest that increasing shrub cover will impact significantly on the surface energy balance. However, little is known about the direct effects of shrub cover on permafrost thaw during summer. We experimentally quantified the influence of *Betula nana* cover on permafrost thaw in a moist tundra site in northeast Siberia with continuous permafrost. We measured the thaw depth of the soil, also called the active layer thickness (ALT), ground heat flux and net radiation in 10 m diameter plots with natural *B. nana* cover (control plots) and in plots in which *B. nana* was removed (removal plots). Removal of *B. nana* increased ALT by 9% on average late in the growing season, compared with control plots. Differences in ALT correlated well with differences in ground heat flux between the control plots and *B. nana* removal plots. In the undisturbed control plots, we found an inverse correlation between *B. nana* cover and late growing season ALT. These results suggest that the expected expansion of deciduous shrubs in the Arctic region, triggered by climate warming, may reduce summer permafrost thaw. Increased shrub growth may thus partially offset further permafrost degradation by future temperature increases. Permafrost models need to include a dynamic vegetation component to accurately predict future permafrost thaw.

Keywords: active layer thickness, *Betula nana*, climate warming, ground heat flux, permafrost degradation, tundra vegetation

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Introduction

Climate change has caused rapid environmental changes at northern high latitudes (Serreze *et al.*, 2000; Hinzman *et al.*, 2005; McGuire *et al.*, 2006). Atmospheric warming is expected to continue in the future, especially in the Arctic region (ACIA, 2004). Climate models predict a mean annual temperature rise of 5 °C in the Arctic by the end of this century (IPCC, 2007). A rise in temperature may have important consequences for the stability of permafrost soils, which are thought to store twice as much carbon as is currently present in the atmosphere (Schuur *et al.*, 2008). Siberian permafrost soils in particular contain a significant reservoir of easily decomposable organic carbon (Zimov *et al.*,

2006). Given that the decomposition of organic matter is largely controlled by permafrost conditions (Goulden *et al.*, 1998), there are fears that if the permafrost thaws, much of the carbon stored will be released to the atmosphere (Mack *et al.*, 2004; Dutta *et al.*, 2006). Thawing permafrost might thus trigger important feedback effects between further climate change and soil carbon release (Schuur *et al.*, 2008).

Permafrost warming has been observed in some Arctic regions in recent decades (Osterkamp & Romanovsky, 1999) and it is expected that the thickness (Anisimov *et al.*, 1997) and extent (Lawrence & Slater, 2005) of permafrost will decrease drastically because of climate warming. However, vegetation cover and soil properties play an important role in protecting permafrost from degradation because of atmospheric warming (Walker *et al.*, 2003; Yi *et al.*, 2007). A north–south transect study in Alaskan tundra showed little

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correspondence between summer air temperature and the thaw depth of the soil, also called the active layer thickness (ALT), perhaps due to the insulating effects of vegetation and soil on permafrost (Walker *et al.*, 2003). It is unclear how permafrost will respond to a warmer climate: a recent discovery of ancient permafrost that survived several warm geological periods suggests that vegetation cover may help protect permafrost from climate warming (Froese *et al.*, 2008).

Climate change will probably cause large-scale vegetation changes in the Arctic: especially a further expansion of deciduous shrubs is expected with continued warming (Walker *et al.*, 2006). Palaeo records show that in the past, shrubs occurred at higher latitudes than today (Bigelow *et al.*, 2003). Evidence has been presented of recent increased shrub growth in Alaskan tundra, which seems to be in response to higher temperature (Sturm *et al.*, 2001b; Tape *et al.*, 2006). On a broader scale, satellite reflectance data show increased photosynthetic activity in northern high latitudes (Myneni *et al.*, 1997), especially in tundra areas (Goetz *et al.*, 2005). This Arctic greening is thought to be related to temperature changes (Stow *et al.*, 2004; Jia *et al.*, 2006) and is partly attributed to shrub expansion in the Arctic (Tape *et al.*, 2006).

Experimental studies have observed increased shrub growth with higher air temperature (Hobbie & Chapin, 1998). One deciduous shrub species that is expected to proliferate in the future in response to increasing temperature and nutrient availability is *Betula nana* (Bret-Harte *et al.*, 2008). Long-term studies in which fertilization and warming treatments were applied to tussock tundra showed a shift in vegetation composition towards dominance by *B. nana* (Chapin *et al.*, 1995; Henry & Molau, 1997).

Increased shrub cover in the Arctic is expected to have major implications for the energy exchange between land surface and atmosphere (Chapin *et al.*, 2005): for example, because the denser and relatively dark shrub canopy has a lower albedo and absorbs more solar radiation than the short tundra vegetation (Eugster *et al.*, 2000). The resulting increased atmospheric heating will positively feed back to further regional warming (Chapin *et al.*, 2005) and cause further vegetation changes (Thompson *et al.*, 2004). However, higher air temperature does not necessarily lead to higher soil temperature: it has been demonstrated that increases in air temperature sometimes lead to vegetation changes that offset the effect of air warming on soil temperature (Walker *et al.*, 2003; Yi *et al.*, 2007). Although the effects of shrubs on soil processes in the winter have been studied (Sturm *et al.*, 2001a, 2005; Wahren *et al.*, 2005; Pomeroy *et al.*, 2006), less is known about the effects of increased shrub growth on permafrost thaw during summer.

Our aim was to determine the direct effects of *B. nana* on permafrost thaw during summer. Therefore, we conducted a field experiment in which *B. nana* shrubs were removed in 2007 from the tundra vegetation. We expected that plots with much shrub cover would absorb more solar radiation than plots with less shrub cover (Beringer *et al.*, 2005), but wondered whether this would be offset by a reduction in the partitioning of energy into ground heat flux, because of increased canopy shading. In this paper, we describe the net outcome of these processes on the seasonal thawing of permafrost and ground heat fluxes in plots from which *B. nana* had been removed compared with control plots with high natural *B. nana* cover.

Materials and methods

Site description

The experiment took place in the Kytalyk nature reserve (70°49'N, 147°28'E) in the Indigirka lowlands in north-east Siberia, Russia. The *B. nana* removal experiment, where we measured permafrost thaw and soil heat fluxes, was set up in moist tussock-shrub tundra approximately 30 km northwest of the town Chokurdakh, 150 km south of the Arctic Ocean. The research site is located within the continuous permafrost zone in the Yakutia region, where permafrost thickness ranges between 100 and 500 m (Balobaev & Lyubomirov, 1999).

Regional climate data (Chokurdakh airport weather station, 1999–2006) show mean annual air temperatures of -10.5°C and average July temperatures of 10.4°C . The mean annual precipitation is 212 mm (Van der Molen *et al.*, 2007), mostly falling during the summer months. July is the wettest month: average precipitation is 37 mm (Van Huissteden *et al.*, 2005).

The Circumpolar Arctic Vegetation Map (Walker *et al.*, 2005) classifies the vegetation of the research area as tussock-sedge tundra, dominated by *Eriophorum vaginatum* and dwarf shrubs, with high moss cover (G4). We conducted our study in two distinct sites, which differ in their relative abundance of graminoid and deciduous shrub vegetation (Table 1). One site is located in the former bed of a drained thermokarst lake, where elevated areas dominated by *B. nana* alternate with wet areas dominated by *Eriophorum angustifolium*, *Carex aquatilis* and *Sphagnum* species. The other site is located on top of a ridge, probably representing a Pleistocene river terrace surface (Van der Molen *et al.*, 2007). This site is adjacent to but 20–30 m higher than the former lakebed site and has more homogeneous moist tussock tundra vegetation in which *E. vaginatum* is the dominant graminoid, with abundant shrubs of *B. nana*, *Salix pulchra* and *Ledum palustre*. In both sites,

Table 1 Plant species cover, determined using point intercept measurements, in summer 2007, before *B. nana* removal, and in summer 2008, after *B. nana* removal

Location	2007				2008			
	Former lakebed		Ridge		Former lakebed		Ridge	
Treatment	Control	Removal	Control	Removal	Control	Removal	Control	Removal
<i>Growth form/species</i>								
Deciduous shrub	61.8 ± 3.5	66.4 ± 5.6	41.5 ± 8.1	47.7 ± 8.1	67.4 ± 2.4*	16.5 ± 3.1	32.6 ± 4.9*	9.5 ± 1.1
<i>Arctostaphylos alpina</i>	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.4 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.9 ± 0.9
<i>Betula nana</i>	59.4 ± 3.6	60.1 ± 5.1	31.8 ± 7.5	39.9 ± 8.6	65.1 ± 2.2*	12.8 ± 3.7	26.6 ± 4.6*	5.8 ± 0.9
<i>Salix</i> spp.	2.3 ± 1.5	6.0 ± 2.0	5.8 ± 2.5	5.5 ± 1.4	2.3 ± 0.9	2.9 ± 1.3	2.6 ± 0.8	1.8 ± 0.6
<i>Vaccinium uliginosum</i>	0.0 ± 0.0	0.3 ± 0.3	3.6 ± 0.6	1.9 ± 1.2	0.0 ± 0.0	0.7 ± 0.6	3.2 ± 0.9	1.0 ± 0.5
Evergreen shrub	7.4 ± 2.7	10.2 ± 6.9	81.8 ± 7.6	72.7 ± 5.0	8.0 ± 2.6	12.6 ± 9.6	68.0 ± 2.3	71.8 ± 6.3
<i>Dryas octopetala</i>	0.0 ± 0.0	0.0 ± 0.0	1.2 ± 0.9	2.0 ± 1.4	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 0.4	2.0 ± 1.1
<i>Ledum palustre</i>	0.6 ± 0.3	0.3 ± 0.2	38.5 ± 7.5	34.5 ± 4.8	0.6 ± 0.3	0.3 ± 0.3	33.6 ± 5.1	34.5 ± 7.8
<i>Vaccinium vitis-idea</i>	6.9 ± 2.6	9.9 ± 6.8	42.0 ± 9.0	36.2 ± 6.3	7.4 ± 2.6	12.3 ± 9.3	33.7 ± 5.7	35.3 ± 4.6
Graminoid	10.7 ± 3.3	12.0 ± 4.2	22.9 ± 5.4	27.9 ± 6.4	9.6 ± 1.2	12.4 ± 1.4	11.1 ± 2.7	13.6 ± 2.4
Forbs	0.1 ± 0.1	0.0 ± 0.0	0.6 ± 0.3	0.6 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 0.5	0.3 ± 0.2
Moss	57.1 ± 7.2	57.2 ± 6.2	56.5 ± 8.4	52.8 ± 5.8	80.7 ± 3.1	82.6 ± 2.3	61.8 ± 4.5	66.4 ± 3.7
Lichen	21.5 ± 7.3	15.8 ± 2.9	23.9 ± 4.3	23.4 ± 3.0	29.3 ± 5.9	23.1 ± 3.8	28.3 ± 5.4	25.5 ± 3.9
Total litter	46.4 ± 4.6	52.0 ± 5.1	40.1 ± 5.2	36.2 ± 4.8	62.9 ± 2.1	55.5 ± 5.2	33.7 ± 8.8	41.3 ± 5.2

Data are means ± SE ($n = 5$ plots) per location (former lakebed and ridge) and treatment (control, no *B. nana* removed; removal, *B. nana* removed).

Salix species: *Salix fuscescens*, *Salix glauca* and *Salix pulchra*. Graminoid species: *Arctagrostis latifolia*, *Calamagrostis holmii*, *Eriophorum vaginatum*, *Carex aquatilis* ssp. *stans* and *Poa pratensis*. Forbs: *Pedicularis lapponica*, *Petasites frigidus*, *Pyrola rotundifolia*, *Rubus chamaemorus*, *Saxifraga punctata* and *Valeriana capitata*. Moss species include: *Aulacomnium turgidum*, *Dicranum polysetum*, *Hylocomium splendens*, *Polytrichum* sp. *Ptilidium ciliare*, *Rhizidium rugosum* and *Tomenthypnum nitens*. Lichen species include: *Cetraria* sp., *Cladonia* sp., *Cladonia* sp., *Sterocaulon* sp. and *Thamnolia vermicularis*.

All data are in percentage of the total number of grid points within the circular 10 m diameter plots.

Significant differences in plant species cover between plots with different treatments within each location for both years are shown * $P < 0.05$.

Table 2 Vegetation characteristics and snow depth in the control and removal plots, measured in 2008

Location	Former lakebed ($n = 5$ plots)		Ridge ($n = 5$ plots)	
	Control	Removal	Control	Removal
<i>Betula nana</i> height (cm)	20.6 ± 1.1*	10.3 ± 0.4	15.4 ± 1.4*	7.4 ± 0.4
Moss layer thickness (cm)	5.3 ± 0.3	4.3 ± 0.5	4.6 ± 0.1	4.2 ± 0.5
Snow depth, May 3 (cm)	26.1 ± 1.6	33.0 ± 3.6	33.4 ± 3.8	27.0 ± 0.8

Data are mean values ± SE.

Significant differences between plots with different treatments within each location are shown * $P < 0.05$.

the subsoil is a silty clay overlain by 10–15 cm of highly organic soil carpeted with a layer of moss approximately 4–5 cm thick (Table 2).

Experimental design

Observational studies that compare permafrost thawing depth and energy exchange between different ecosys-

tems along a latitudinal gradient are hampered by the fact that along the transect not only the vegetation varies, but also other important variables for permafrost thaw, such as local climate and soil conditions. We used an experimental approach that allowed the direct influence of vegetation cover changes on permafrost thaw to be observed without confounding changes to other variables important to permafrost thaw.

We selected circular plots of 10 m diameter, located in the two different sites. In total, there were 20 plots: 10 plots per site. The two sites were chosen because of their difference in relative cover of plant functional types; together the two sites cover most of the terrain types in the area. The plot size was chosen to minimize the influence of surrounding vegetation on soil heat fluxes within the plots and to enable measurements to be made of net radiation within the plots. Plots were selected pairwise on the basis of similarity in vegetation cover before removal treatment at minimum distance of 30–50 m. The average distance between plots within plot pairs was approximately 40 m and the average distance between pairs was approximately 150 m. In each site, the plots covered a total surface area of approximately 10 ha. The plots from each plot pair were randomly assigned to one of the following two treatment groups: control plots with no removal and removal plots in which *B. nana* was removed. The reason only the deciduous shrub *B. nana* was removed is because this is the most abundant shrub in the area and is expected to benefit most in tussock tundra areas under a climate warming scenario (Bret-Harte *et al.*, 2001; Van Wijk *et al.*, 2004).

The *B. nana* shrubs were removed from the removal plots between 11 July, 2007 and 3 August, 2007 by cutting back their stems until they were flush with the moss layer. The average dry biomass of *B. nana* removed was $388 \pm 72 \text{ g m}^{-2}$ on the former lakebed site and $178 \pm 65 \text{ g m}^{-2}$ on the ridge site.

Measurements

The plant species projected cover in each plot was recorded twice: in early summer 2007 before removal of *B. nana* shrubs and then again a year later. This was done by taking point intercept measurements on a grid of 13×13 points spaced 75 cm apart. The 137 grid points within the circular 10 m diameter plots were used to determine vegetation cover. To determine species presence at each point in the grid, a thin rod held vertically above the point was lowered to the ground and each plant species it touched on its descent to the ground was recorded. Multiple 'hits' of the same species at the same point counted as a single hit. To determine plant projected cover, the number of hits per species per plot was divided by the total amount of grid points within the plot.

The ALT was measured at regular intervals during the 2007 and 2008 growing season at nine points in each plot using a blunt metal probe. A modified VALERI spatial sampling scheme (<http://w3.avignon.inra.fr/valeri/>) was used to approximate the location of the points within each plot. The ALT measurements were

made in all plots during the same day. ALT was considered to be the distance between the top of the moss layer and the permafrost table.

The height of the remaining *B. nana* shrubs and the thickness of the moss layer were determined in all plots in 2008 at the same nine points where also the ALT was measured. The shrub height was considered to be the distance between the top of the shrub canopy and the moss layer and measured using a tape measure. The moss layer thickness was determined by cutting a small piece of moss ($5 \times 5 \text{ cm}$) from the moss surface. To check whether the removal treatment caused differences in snow accumulation in plots during winter, snow depth was measured at five randomly chosen points in each plot on May 3, 2008.

Net radiation (Q_n), ground heat flux (Q_g) and soil temperature (T_s) were measured simultaneously in one plot pair. We chose to relocate our two energy balance systems every 3 days to a different plot pair, in order to measure differences between control and removal plots at multiple locations. This means that we could not consistently follow seasonal developments in energy balance components. The measurements were made alternately in lakebed and ridge pairs. We could measure only seven of the 10 plot pairs (three pairs in the ridge site, four pairs in the lakebed site) because of time constraints.

For the ground heat flux measurements, per plot three soil heat flux plates (HFP01; Hukseflux, Delft, the Netherlands) and one self-calibrating heat flux Delft, plate (HFP01SC; Hukseflux) were buried in the soil at a depth of 8 cm: using a sharp knife, a soil column with a surface area of approximately $20 \times 20 \text{ cm}$ was carefully cut out. An incision was made horizontally into one side of the soil pit and the heat flux plate was inserted, ensuring that it was in good contact with the soil. Above two of the four soil heat flux plates in each plot, thermistors (T107; Campbell Scientific, Shephed, UK) were installed at depths of 2 and 5 cm below the moss surface to measure the soil temperature and calculate the heat flux storage in the soil above the heat flux plates. The heat flux storage Q_s was calculated using the profile integration method (Van Boxtel, 1986), by calculating the heat flux from changes in temperature over time interval Δt measured by the thermistors buried at 2 and 5 cm:

$$Q_s = \frac{C_s}{\Delta t} \sum_i \Delta z_i \Delta T_i,$$

where C_s is the volumetric heat capacity of the soil, ΔT_i is the change in soil temperature measured by sensor i during the time interval Δt , and Δz_i is the thickness of the soil layer for which the temperature change ΔT_i is representative. A constant C_s value of $2.5 \times 10^6 \text{ J m}^{-3} \text{ K}^{-1}$ was used. This is a typical C_s value reported for

water-saturated peat and moss soils (Beringer *et al.*, 2001). Total Q_g was calculated using the combination approach (Fuchs & Tanner, 1968), whereby the flux measured by the heat flux plates is summed with the heat flux storage in the soil layer above the heat flux plates. Net radiation was measured at approximately 85 cm above the moss surface using a CNR2 net radiometer (Kipp and Zonen B.V., Delft, the Netherlands). All measurements were made at 2 s intervals. 10 minute averages and standard deviation data were calculated and stored by a datalogger (CR1000; Campbell Scientific) wired to a multiplexer (AM 16/32; Campbell Scientific). Averages of 30 min were calculated for all fluxes.

Data analysis

The effect of *B. nana* removal on ALT in 2008 was analyzed using a repeated measures analysis of variance (ANOVA) with site (lakebed, ridge) and treatment (control, removal) as between-subject factors. Two-way ANOVA was used to test for differences in vegetation composition (cover for each species), vegetation height, moss layer thickness and snow depth between locations and treatments. We used an analysis of covariance (ANCOVA) model to test for the effect of *B. nana* cover on ALT in 10 control plots with natural *B. nana* cover, taking the effect of the two locations into account. The input sequence of the explanatory variables in the model was: 'year' and 'site' as fixed factors and then '*B. nana* cover' as covariable. A regression line, derived from the parameter estimates of the ANCOVA model, was fitted to the data.

All data were tested for normal distribution and equality of variance. The micrometeorological data were checked for outliers by plotting all data and visually inspecting the data for outliers. Daily average fluxes were then calculated. Differences in fluxes between control and removal plots were calculated by subtracting daily average fluxes measured in a removal plot with daily average fluxes measured in the paired control plot. All statistic analysis were made using SPSS for Windows (15.0).

Results

Before *B. nana* removal in 2007, there were no significant differences in plant species cover between control and removal plots within each of the two sites. The sites mainly differed from each other in *B. nana* and evergreen shrub cover ($P < 0.05$; Table 1). In 2008, only *B. nana* cover differed between control and removal plots ($P < 0.05$; Table 1), as we intended.

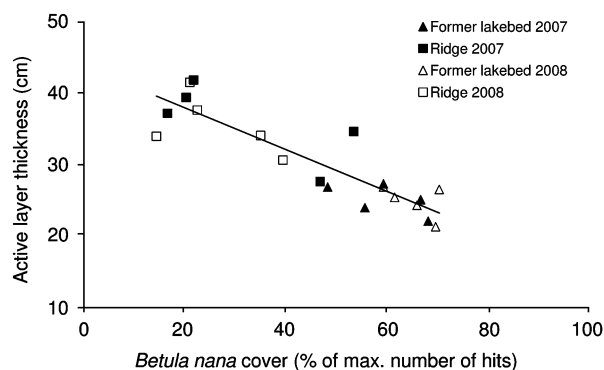


Fig. 1 Active layer thickness (ALT) plotted against *Betula nana* cover for control plots at the two sites in 2007 and 2008. Measurements of ALT were made on August 7, 2007 and on August 8, 2008. Cover of *B. nana* was measured during the summer of 2007 and again a year later during summer 2008. A linear regression line is fitted to the data [$r_2 = 0.80$; ALT = $41.70 - 0.21 \times B. nana$ cover (%)], based on the parameter estimates of the ANCOVA model (see 'Materials and methods'), which includes the effects of year and site.

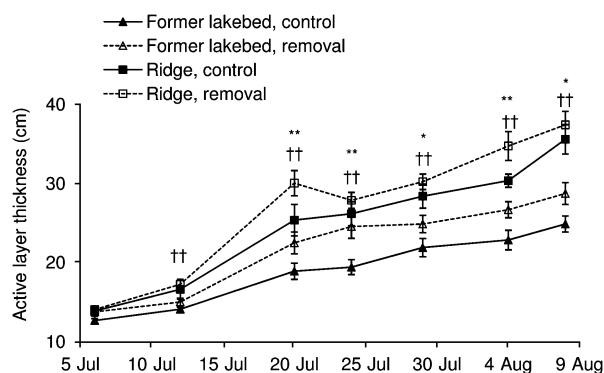


Fig. 2 Seasonal development of the active layer thickness (ALT) measured during summer 2008. Differences between the means of the treatment groups (* $P < 0.05$; ** $P < 0.01$) and differences between means of the locations († $P < 0.05$; †† $P < 0.01$) are shown for each date. Data are mean values ($n=5$ plots) \pm SE. Statistical results are presented in Table 3.

In the undisturbed control plots with varying natural *B. nana* cover, ALT decreased with increasing *B. nana* cover, thus showing a negative correlation between *B. nana* cover and ALT (Fig. 1). This relationship was significant ($P < 0.01$) also after accounting for the effects of year ($P > 0.05$) and site ($P < 0.01$).

Experimental *B. nana* removal had increased ALT significantly by an average of 9% at the end of the 2008 growing season, compared with the control plots (Fig. 2, Table 3). Differences in ALT emerged between the control and *B. nana* removal plots during the 2008 growing season. In early July, no differences in ALT were measured. The critical period for the development

Table 3 Results of repeated measures ANOVA, testing the effects of location and treatment on the seasonal development of the active layer thickness in 2008

	Type III sum of squares	df	F	Significance
Between-subject effects				
Location	1044.7	1	33.2	<0.001
Treatment	232.0	1	7.4	0.015
Location \times treatment	7.8	1	0.3	0.625
Error	503.7	16		
Within-subject effects				
Time	5197.9	6	267.1	<0.001
Time \times location	288.5	6	14.8	<0.001
Time \times treatment	62.0	6	3.2	0.007
Time \times location \times treatment	16.7	6	0.9	0.530
Error	311.3	96		

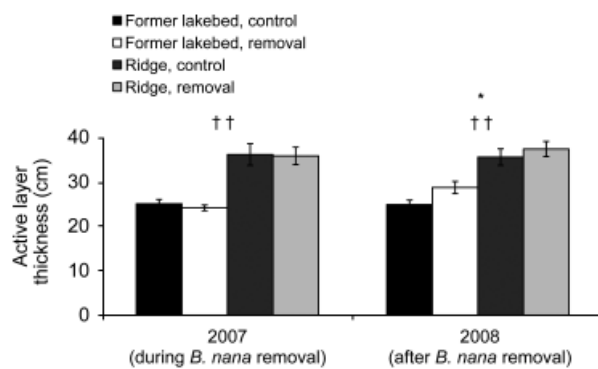


Fig. 3 Comparison of active layer thickness (ALT) between control and removal plots during August 7, 2007 and August 8, 2008. The effect of treatment (* $P < 0.05$) and the effect of location (†† $P < 0.01$) on ALT are shown for both years. Data are mean values ($n = 5$ plots) \pm SE.

of differences in ALT between control and *B. nana* removal plots seems have been from July 12 to July 20, 2008: during these 8 warm days, the ALT increased faster in the removal plots than in the control plots. The resulting differences persisted throughout August, but differences did not increase further (Fig. 2). The ALT was greater in the plots located on the ridge than in the plots located on the former lakebed ($P < 0.01$, Table 3). *B. nana* shrubs had a higher cover (Table 1) and were taller (Table 2) in the former lakebed plots than in the ridge plots.

No differences in ALT were observed between the control and *B. nana* removal plots during the summer of 2007 (Fig. 3), the period during which the removal experiment was set up. This suggests that it is unlikely that the differences in ALT observed in 2008 between the control and *B. nana* removal plots resulted from

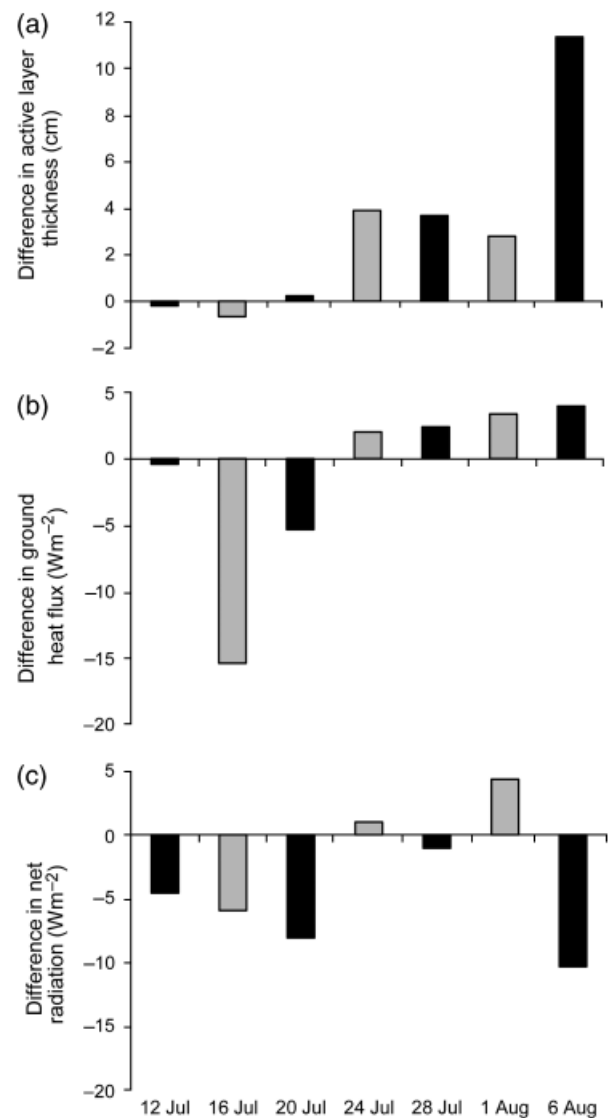


Fig. 4 Differences in: (a) active layer thickness, (b) ground heat flux, (c) net radiation within each of seven plot pairs measured consecutively. Each pair consists of a *Betula nana* removal and a control plot: black bars represent the difference within a plot pair on the former lakebed; gray bars indicate the difference within a plot pair on the ridge. Positive differences indicate a larger value for the *B. nana* removal plot than the paired control plot.

differences in original site conditions. Whereas the ALT values measured in the control plots at the end of the growing season in 2008 were similar to or lower than the ALT values measured in 2007, the ALT values in the *B. nana* removal plots were generally greater in 2008 than in 2007 ($P < 0.05$), especially in the lakebed plots (Fig. 3). No significant differences between control and *B. nana* removal plots were measured in moss layer thickness or snow depth (Table 2).

The differences in ALT (Fig. 4a) within pairs of control and *B. nana* removal plots were correlated

positively with differences in Q_g (Fig. 4b) within plot pairs (Spearman's correlation $\rho = 0.82$, $P < 0.05$, $n = 7$). Only the third measured plot pair showed a difference in Q_g (higher in control plot) between the control and removal plot that was not corresponding with the difference in ALT (lower in *B. nana* removal plot; Fig. 4b). A particularly large difference in ALT was found in the last plot pair measured during the 2008 growing season (Fig. 4a).

The Q_g/Q_n fractions were on average 12% and differed by up to 8% within plot pairs (data not shown). The Q_n values were higher in control plots in the former lakebed than in the *B. nana* removal plots (Fig. 4c). In contrast, Q_n values of the control and *B. nana* removal plots on the ridge terrain did not show clear differences between treatments (Fig. 4c).

Discussion

Our observations in undisturbed vegetation showed that *B. nana* cover was inversely correlated with ALT. From observations of plant cover and ALT in natural vegetation gradients it remains unclear what is cause and effect, and differences in microclimate or hydrology may obscure a direct relationship. By removing the deciduous shrub *B. nana*, we were able to demonstrate empirically, for the first time, that *B. nana* significantly reduces ALT. As the *B. nana* removal was associated with a decrease in total biomass, we cannot separate the *B. nana* effect from a simple biomass removal effect. However, under multiple scenarios of climate change it is expected that tundra biomass will increase, mainly because of *B. nana* (Euskirchen *et al.*, 2009) and combined with the observed negative relationship in natural vegetation, our experimental results suggest that increased shrub biomass may slow down the expected future increase in permafrost thaw with climate warming.

Similar findings were observed in a model study, where permafrost thaw was found to be less under a shrub canopy than under unvegetated ground (Yi *et al.*, 2007). The few other experimental studies on the influence of shrub cover on permafrost thaw have not shown any effect of shrub removal on ALT, either because lateral subsurface water flow conducted soil heat fluxes away from the permafrost (McFadden, 1998), or because the shrubs were removed from a small area (1 m²) (Hobbie *et al.*, 1999). Our large plot size seems to have diminished the influence of the surrounding intact vegetation. Also, the amounts of biomass we removed (178–388 g dry *B. nana* m⁻²), were larger than the *B. nana* biomass removed from Alaskan tundra sites (53–127 g dry *B. nana* m⁻²) (Hobbie & Chapin, 1998; Shaver *et al.*, 2001; Bret-Harte *et al.*, 2004). The larger

amount of *B. nana* biomass removed in our experiment compared with the other studies could partly account for differences in treatment effect on ALT.

In 2008, no differences in ALT were apparent between the control and *B. nana* removal plots at the start of the growing season, but differences did emerge later. This indicates that the differences in ALT we observed are primarily attributable to summer processes. Permafrost temperatures, however, are influenced by changes in mean annual conditions (Serreze *et al.*, 2000): for example, shrubs trap snow, and the resulting thicker insulating snow layer in shrub-dense areas means that the permafrost temperatures in these areas are higher (Sturm *et al.*, 2001a). Our data on snow depth in early May 2008, however, did not show any differences in snow depth between the control and *B. nana* removal plots. This might be because our plots were not large enough to result in differences in snow trapping. The removal of *B. nana* did not lead to changes in moss thickness or moss cover either. Such changes could mask the direct effects of *B. nana* removal and potentially alter the effects of *B. nana* removal on ALT in the long term, because mosses have a high insulative value (Beringer *et al.*, 2001).

The large difference in ALT measured in the last plot pair in 2008 probably results from the difference in energy that accumulated during the growing season and was available to thaw the permafrost. The largest difference in Q_g between a control and a removal plot was measured during the warmest period of the 2008 growing season. However, seasonal changes in the fractionation of the energy balance components cannot be followed consistently since we changed measurement location (plot pair) every 3 days throughout the growing season.

The mean daily Q_g/Q_n values in the control plots were 10% in the former lakebed and 15% in the ridge site. These values are similar to Q_g/Q_n values reported from other moist tundra sites (Eugster *et al.*, 2000; Thompson *et al.*, 2004; Beringer *et al.*, 2005; Boike *et al.*, 2008). The most probable explanation for the increase in Q_g/Q_n in *B. nana* removal plots *vis-à-vis* their paired control plots is the reduction in the shading of the soil surface by the canopy. An alternative explanation is a decrease in the latent heat flux fraction of the *B. nana* removal plots. The removal of the *B. nana* shrubs greatly reduced the total leaf area, diminishing the transpiration capacity of the vegetation. However, the total evapotranspiration of the tundra also includes evaporation from moss (Beringer *et al.*, 2005). As mosses do not actively transpire water because they lack stomata, the evaporation from a moss surface is greatly influenced by the microclimate (Heijmans *et al.*, 2004). The removal of *B. nana* shrubs increased the amount of radiation

reaching the more exposed moss surface, thereby probably increasing moss evaporation, which may have offset the reduced shrub transpiration.

The reason the Q_n values in all the control plots measured in the former lakebed were higher than in their paired *B. nana* removal plots is because the denser and relatively dark shrub canopy has a lower albedo and absorbs more solar radiation than the short tundra vegetation. Despite this, the ALT was smaller in the control plots – probably because the reduced partitioning of Q_n into Q_g more than offsets the increase in Q_n in plots with higher *B. nana* cover. The greater Q_n values in plots with a high shrub cover and concomitant reduction in the partitioning of Q_n into Q_g must thus result in an increase in sensible and latent heat fluxes. This agrees with previously reported findings that higher shrub cover in the Arctic may cause atmospheric heating (Thompson *et al.*, 2004; Chapin *et al.*, 2005), but we have shown that in addition, the increased shrub cover may concomitantly also reduce summer permafrost thaw.

Increased shrub growth has been found to cause a reduction in nonvascular plant biomass (Walker *et al.*, 2006). In our site, however, there were no differences between the removal and control plots in moss cover or moss thickness, and the moss cover was generally high, even in the plots with high *B. nana* cover. The removal of *B. nana* shrubs may have caused disturbances in the removal plots, e.g., by unintentional trampling of the moss layer during *B. nana* removal in 2007. Such disturbance could have contributed to the differences in ALT between treatments, but this seems unlikely, given that no differences in moss cover or moss thickness were measured in 2008. Moreover, the strong inverse correlation between ALT and *B. nana* cover for undisturbed control plots confirms that increased shrub growth may reduce summer permafrost thaw.

Global temperature data show that the mean annual air temperature in northeast Siberia increased by 1.5–2 °C between 2001 and 2007, compared with the 1951–1980 average (Hansen, 2008). This is much higher than the observed 0.5 °C average global surface temperature rise during this period. Permafrost temperature records, however, do not show a general warming trend during the last decade (Brown & Romanovsky, 2008), despite large increases in surface air temperature. Data from several Siberian Arctic permafrost stations do not show a discernible trend between 1991 and 2000 (IPCC, 2007). Our results suggest that an expansion of deciduous shrubs in the Arctic triggered by climate warming may buffer permafrost from warming resulting from higher air temperatures.

This study shows that a vegetation shift from graminoid-dominated tussock tundra towards shrub-dominated tundra can decrease summer permafrost thaw.

This could feedback negatively to global warming, because the lower soil temperatures in summer would slow down soil decomposition and thus the amount of carbon released to the atmosphere. However, it remains unknown how the decomposition rates of organic matter will be altered by a potential expansion of *B. nana*. The relatively recalcitrant leaf litter of deciduous shrubs compared with graminoids could potentially partly offset the accelerated litter turnover rates resulting from higher air temperature (Cornelissen *et al.*, 2007). Evidence to support this finding appeared in a recent meta-analysis, which showed that the leaf litter quality affects decomposition rates much more than changes in climate do (Cornwell *et al.*, 2008).

Our finding that under higher *B. nana* cover there was a decrease in ALT is significant, because it is in this thawed soil layer that microbial decomposition of organic matter takes place. It can therefore be inferred that under shrub canopies, soil nutrient availability may be lower during summer because of the decrease in the soil decomposition rates of soil organic matter and leaf litter. Interestingly, this would suggest that further shrub growth might be slowed, as shrubs are known to benefit most from a relatively high nutrient availability (Chapin *et al.*, 1995; Walker *et al.*, 2006; Bret-Harte *et al.*, 2008). In contrast, winter soil temperatures are known to increase with higher shrub abundance, because snow is trapped by shrub branches (Sturm *et al.*, 2005). It is unknown whether a potential decrease in soil decomposition activity during summer is offset by an increased activity during the winter months.

Failure to fully understand the effect of climate change and related vegetation shifts on permafrost thermodynamics is hampering predictions on future permafrost thaw. We have presented the first experimental evidence that the expansion of deciduous shrubs in the Arctic triggered by climate warming may reduce summer permafrost thaw. This vegetation change may partly offset the permafrost degradation expected to result from the air temperature rise predicted for the coming decades. Continued warming of the Arctic region, however, may overcome the shading effect of the shrubs and cause an increase in permafrost thaw in the long term. Permafrost models currently lack a dynamic vegetation component (Riseborough *et al.*, 2008). Our findings underline the need for such models to take climate-induced vegetation changes into account, in order to accurately predict future permafrost distribution.

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