

# SHRUBS IN THE COLD

INTERACTIONS  
BETWEEN  
VEGETATION  
PERMAFROST  
AND CLIMATE IN  
SIBERIAN TUNDRA

**DAAN BLOK**

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Interactions between vegetation, permafrost  
and climate in Siberian tundra

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# **Shrubs in the cold**

Interactions between vegetation, permafrost  
and climate in Siberian tundra

Daan Blok

## **Thesis**

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**Dirt Floor**

Well the mist shall be your blanket  
While the moss shall ease your head  
As the future is soon forgotten  
As the dirt shall be your bed

*Chris Whitley*



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# 1. General introduction

## *Arctic climate change*

During the last decades, temperatures worldwide have increased. In the scientific community, consensus exists that a large part of this temperature rise is due to anthropogenic greenhouse gas emissions from the burning of fossil fuel (IPCC, 2007). Of all places on Earth, the Arctic region is experiencing the most dramatic increase in temperature (IPCC, 2007). Climatic changes in the Arctic environment may have major impacts on the global climate through feedbacks involving changes in surface properties and soil-atmosphere carbon fluxes (ACIA, 2004). It is estimated that approximately a third of all terrestrial carbon is currently locked away in the year-round frozen permafrost soils of the Arctic (McGuire *et al.*, 2009). The permafrost soils of northeast Siberia, where the studies presented in this thesis were performed (Fig. 1.1), are especially rich in easily decomposable organic remains called *yedoma*. These yedoma deposits were formed during the Pleistocene, when tundra-steppe landscapes predominated in the Arctic (Zimov, 2006). Although the Siberian yedoma permafrost soil is believed to hold most terrestrial carbon of any land mass on Earth (Zimov *et al.*, 2006), it is studied little. Concern exists that higher air temperatures may lead to an increase in permafrost thaw and will be accompanied by an increase in soil carbon release to the atmosphere through decomposition of organic matter (Walker, 2007; Hartley *et al.*, 2008; Schuur *et al.*, 2009). This concern is supported by a soil warming experiment in which an increase in summer soil temperature and permafrost thaw depth was accompanied by a doubling of annual respiratory CO<sub>2</sub> losses to the atmosphere (Natali *et al.*, 2011).

Naturally, the Earth's surface is warmed by the absorption of short-wave radiation from the sun. In turn, the Earth's surface is cooled by the emission of long-wave radiation back to the atmosphere and thus balances the absorbed short-wave solar radiation. A portion of the emitted long-wave radiation is absorbed in the atmosphere by greenhouse gases and is re-emitted back to Earth, leading to surface warming (Bonan, 2008a). This re-emission of long-wave radiation by greenhouse gases is what causes the greenhouse effect and will be enhanced by increasing anthropogenic greenhouse gas emissions. The net balance of incoming and outgoing short- and long-wave radiation is also referred to as the *net radiation* ( $R_n$ ). This is the energy that is involved in the exchange of energy and water between soil and atmosphere and is fractionated in three pathways (Fig. 1.2): (i) evapotranspiration of water by plants and soil, also referred to as the *latent heat flux* ( $LE$ ), (ii) vertical heat transport through the air, also referred to as the *sensible heat flux* ( $H$ ), and (iii) heat transfer to the ground, also referred to as the *ground heat flux* ( $G$ ). The partitioning of net radiation into these three fluxes is dependent on, and can be altered by, changes in soil moisture, vegetation cover and local climate (Bonan, 2008a).

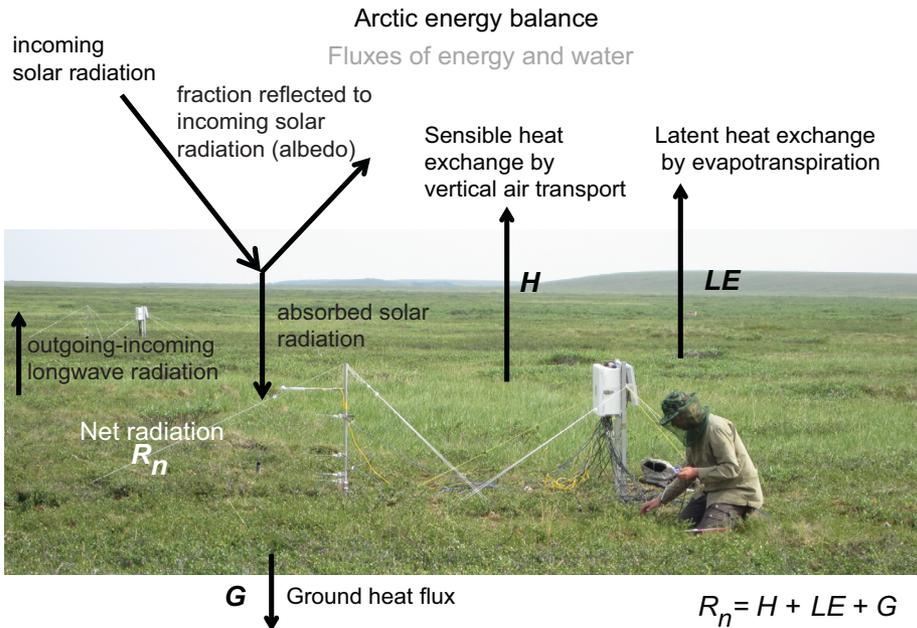
### ***Feedbacks to Arctic warming***

The reason that the Arctic is so responsive to changes in climate is because of the radiative forcing feedbacks involved with changes in snow, ice and vegetation cover (Forster *et al.*, 2007). The proportion of incoming solar radiation that is reflected back to the atmosphere at the Earth's surface is termed *albedo*. For most part of the year, the Arctic is snow-covered and reflects most of the incoming solar radiation, resulting in a high surface albedo and low air temperatures. During springtime, the daylight period at high latitudes increases, melting snow and ice and thus exposing the underlying soil, water and vegetation. As a result, the surface albedo is drastically reduced and the Arctic warms up rapidly during the brief growing season with nearly continuous daylight. An increase of the snow- and ice-free period can feedback to regional warming by *e.g.* reducing the built-up of Arctic sea ice, resulting in an even more rapid melt the next year, thus further decreasing the surface albedo and warming the Arctic (Serreze & Francis, 2006; Bhatt *et al.*, 2010).



**Figure 1.1** Map of the permafrost extent in the Northern Hemisphere, with the asterisk indicating the location of the research site in the Kytalyk nature reserve in Northeast Siberia, Russia. Map adapted from Hugo Ahlenius, UNEP/GRID-Arendal, Global Outlook for Ice and Snow (Brown *et al.*, 1997).

Another major radiative forcing feedback can result from changes in Arctic vegetation cover and concomitant changes in land surface albedo. Vegetation grows at the interface between soil and atmosphere and for a large part determines the exchange of water and energy, thus influencing the local climate. With increasing air temperatures, vegetation changes in the Arctic may result in biome shifts, such as a northwards expansion of boreal forests into tundra areas (Beck *et al.*, 2011). With an increase in canopy density from sparsely vegetated barren tundra in the high-Arctic



**Figure 1.2** Simplified diagram of the energy balance of the Earth's surface in the Arctic tundra and the involved energy and water fluxes with corresponding acronyms.

tundra towards tall boreal forests in the low-Arctic, the surface albedo is reduced (Eugster *et al.*, 2000; Thompson *et al.*, 2004; Beringer *et al.*, 2005). The decline in albedo by a conversion from short-statured vegetation to tall boreal forest is believed to have a large warming potential that may counteract the effect of greater carbon sequestration in woody biomass on atmospheric heating (Anderson *et al.*, 2011). Changes in Arctic species composition may thus feedback positively to further vegetation changes by altering the regional climate (Bonan, 2008b).

### ***Shrub expansion in the Arctic***

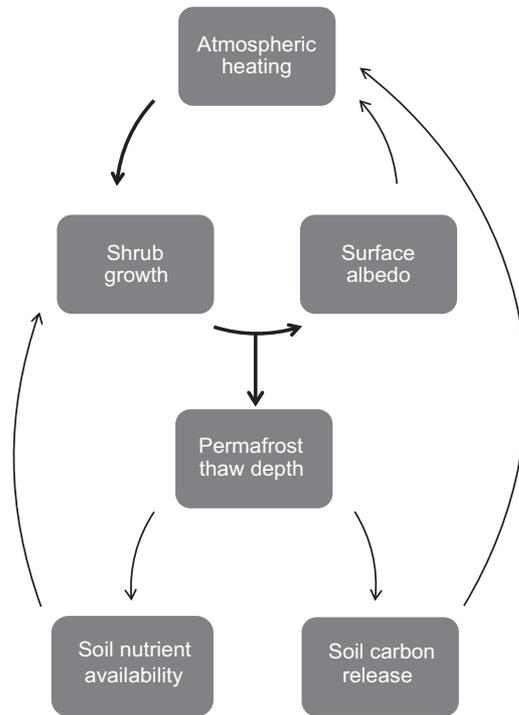
The Arctic tundra environment is characterized by a vegetation mixture of low-statured shrubs, graminoids, forbs, lichens and mosses. Tree growth is not possible because of the severe climate, short growing season and presence of permafrost (Hobbie & Chapin, 1998a). Even though precipitation in the tundra is generally very low, it is a wet environment because of the low annual evapotranspiration. One of the most prominent vegetation changes that are expected with climate warming is an expansion of deciduous shrubs (ACIA, 2004). In many experimental plot-scale warming studies conducted in the Arctic region, deciduous shrub species benefitted most of all species groups from higher air temperatures by increasing their biomass, often at the cost of moss and lichen biomass (Hobbie & Chapin, 1998b; Walker *et al.*, 2006). However, other plot-scale warming studies indicate that herbaceous

species may also benefit from higher air temperatures (Arft *et al.*, 1999). Apart from temperature, nutrients may also be severely limiting for plant growth in tundra environments (Shaver & Chapin, 1980). This is shown by, for example, the amplified growth response of deciduous shrubs in experiments in which warmed plots also received fertilization with nitrogen (N) and phosphorous (P), causing deciduous shrubs to dominate over all other growth forms (Shaver *et al.*, 2001; Bret-Harte *et al.*, 2008). However, this strong growth response was due to one specific deciduous shrub species, *Betula nana* (dwarf birch), and was not a common trait of all deciduous shrubs (Shaver *et al.*, 2001). When *Betula nana* was absent in plots, deciduous shrubs and graminoids performed equally (Bret-Harte *et al.*, 2008). It is suggested that the strong growth response of *Betula nana* is due to this species' high potential growth rate, allowing it to produce many new long shoots and forming a dense canopy under relatively low N investment, similar to the growth strategy of *Molinia* in heather communities under high N supply (Berendse, 1994a). As a result, other species may become overgrown and get outcompeted by light limitation (Bret-Harte *et al.*, 2001; Shaver *et al.*, 2001).

Evidence exists for an ongoing spread of shrubs in Alaska, as shown by comparative repeated aerial photography of current tundra landscapes with landscapes photographed 50 years ago. In most locations, an increase in shrub cover was detected and was accompanied by a rise in air temperature (Sturm *et al.*, 2001b; Tape *et al.*, 2006). Furthermore, remote sensing studies show a greening over much of the Arctic tundra during the last three decades (Myneni *et al.*, 1997; Bunn *et al.*, 2007; Goetz *et al.*, 2007), which is related to an increase in photosynthetic biomass (Jia *et al.*, 2009). Most of the observed greening is attributed to an increase in cover and biomass of deciduous shrubs (Walker *et al.*, 2003a; Tape *et al.*, 2006). This is supported by observations of increased shrub growth in undisturbed control plots during the course of several long-term warming experiments in which ambient temperature rose as well (Chapin *et al.*, 1995; Olofsson *et al.*, 2009), further suggesting that shrubs have already started to increase their growth rate in response to climate warming.

### ***Feedbacks to shrub expansion***

An increase in deciduous shrub cover in Arctic tundra may amplify regional atmospheric heating by reducing the summer surface albedo (Sturm *et al.*, 2005a) and may lead to further shrub growth, thus creating a positive feedback loop (Chapin *et al.*, 2005) (Fig. 1.3). Although forcing feedbacks to climate warming brought on by vegetation changes are currently limited in magnitude in comparison with the forcing exerted by an increase in the snow-free season length (Euskirchen *et al.*, 2009), it is expected that rates of vegetation changes will increase and become a more important forcing feedback in the future (Chapin *et al.*, 2005). Apart from the summer albedo feedback, shrubs may increase their expansion rate by capturing



**Figure 1.3** Schematic overview of summer processes that are related to shrub expansion and their associated feedbacks to climate, with bold arrows indicating the processes studied in this thesis.

wind-blown snow and locally increasing snow height around shrub patches during winter (Sturm *et al.*, 2001a). By increasing snow height around them, shrubs insulate the underneath permafrost soil from the severe cold air. Higher winter soil temperatures may increase microbial decomposition below shrubs (Schimel *et al.*, 2004) and increase nutrient availability during springtime, facilitating further shrub growth (Sturm *et al.*, 2005b). During the last decades, most of the rise in Arctic air temperatures took place during winter (ACIA, 2004) and may therefore have contributed to the recent shrub expansion. However, it is uncertain whether nutrients from increased winter decomposition become available for shrubs during the growing season (Sturm *et al.*, 2005b), since nutrients may be washed away by spring snowmelt. Furthermore, winter-mineralized nitrate may be reduced by denitrifying microbes and thus becomes unavailable.

In contrast to the knowledge that exists on the influence of Arctic shrubs on winter soil conditions, little is known on the effect of shrubs on soil conditions during the growing season in summer. As noted previously, an increase in shrub cover may decrease the summer albedo and thereby trap more energy into the ecosystem (Sturm *et al.*, 2005a) (Fig. 1.3). At the same time, shrubs may increase soil

shading and therefore might reduce summer soil temperatures (Sturm *et al.*, 2005b) and decrease the extent to which the permafrost top-soil thaws during summer. Furthermore, an increase in shrub cover is expected to lead to a reduction in moss biomass (Walker *et al.*, 2006) and consequently may lead to a loss of permafrost insulation, thereby potentially leading to an increase in permafrost thaw. What is the net result of these contrasting effects on summer soil temperature and permafrost thaw?

### **Research aims and thesis outline**

In this thesis I investigate the relationship between vegetation, climate, and summer permafrost thaw in the Siberian tundra with special emphasis on the deciduous shrub *Betula nana*. I use a combination of field experiments, dendrochronology, and remote sensing to answer these three main research questions:

- (i) What is the effect of changes in *Betula nana* cover on summer permafrost thaw depth?
- (ii) What are the main climate drivers for deciduous shrub growth?
- (iii) Can changes in deciduous shrub cover feedback to the regional climate by altering the surface albedo?
- (iv) What is the effect of changes in moss cover below deciduous shrubs on soil heat flux and evapotranspiration?

In the first experiment described in this thesis, I investigate how changes in fractional cover of the most dominant deciduous shrub species in our research area, *Betula nana*, affect summer permafrost thaw depth (**chapter 2**). To test this, I selected twenty ten meter-diameter plots in a tundra site with continuous permafrost (permafrost is present under all vegetated surfaces) in northeast Siberia (Fig. 1.1) and removed all *Betula nana* shrubs from half of the plots. Apart from measuring differences in permafrost thaw depth between plots with and without *Betula nana*, I measured differences in net radiation and determined how much of this net radiation was dissipated as soil heat flux. Measured differences in active layer depth between plot types could thus be validated by measuring differences in soil heat flux, necessary to create differences in permafrost thaw depth.

Next, I investigate the growth response of two Arctic deciduous shrub species to climate over the last six decades by measuring the width of annual growth rings and constructing growth chronologies (**chapter 3**). Although deciduous shrubs are considered by many to benefit from increasing air temperatures by increasing their growth, little is known about their long-term species-specific growth response to climate. In this chapter I investigate the growth response of two deciduous shrub species with contrasting growth forms (low-statured *Betula nana* shrubs and tall-statured *Salix pulchra* (tealeaf willow) shrubs) to climate by correlating ring-width

chronologies with meteorological station data (temperature and precipitation) to determine those climate parameters that are decisive for shrub growth.

In **chapter 4**, the relations between shrub cover, summer temperature, vegetation greenness and surface albedo is investigated by using both field measurements and satellite products. There is evidence that the observed increases in Arctic greenness are related to an increase in surface temperature (Raynolds *et al.*, 2008), but it is unknown how changes in tundra greenness affect the summer albedo on a regional scale. As noted previously, an increase in shrub cover may decrease summer albedo and thereby result in atmospheric heating, driving a further shrub growth increase (Chapin *et al.*, 2005). In this chapter I investigate how deciduous shrub cover is related to summer vegetation greenness and albedo by using field data. Furthermore, I relate satellite products of regional annual summer maximum vegetation greenness and minimum surface albedo to annual summer temperature and compared relationships between these variables among different vegetation and climate zones for four low-Arctic tundra areas across the Arctic.

With increasing deciduous shrub cover, moss growth is expected to be reduced by increased shading by the shrub canopy (Euskirchen *et al.*, 2009). Changes in moss cover may affect the exchange of energy between soil and atmosphere since mosses have a high insulating capacity (O'Donnell *et al.*, 2009) and thus may buffer the underlying permafrost from changes in air temperature. Furthermore, mosses are believed to be very important in tundra water exchange since mosses do not possess stomata or a root system and thus may evaporate water freely. However, the role of mosses in these important ecosystem processes is studied little. In **chapter 5**, the effects of moss cover on both understory evapotranspiration and ground heat flux are investigated by removing patches of moss in plots with high and low *Betula nana* cover. Thus, I could assess the influence of both moss and shrub cover on understory water and heat fluxes in a tundra ecosystem.

In **chapter 6**, the relationship between summer permafrost thaw depth and vegetation characteristics are investigated by measuring vegetation and soil variables along transects at our field site in NE-Siberia. Measurements points along the transects covered most of the variation in vegetation types at the research site, ranging from wet sedge pools to mixtures of relatively dry graminoid tussocks, deciduous and evergreen shrubs, and forbs. I cluster transect sample points on basis of their vegetation composition using ordination techniques and thus create vegetation classes. Differences in vegetation and soil variables between vegetation classes are investigated and related to differences in permafrost thaw depth between vegetation classes.

I conclude this thesis by synthesizing the results presented in chapters 2-5 and discuss the major findings in a broader context (**chapter 7**). Finally, I give recommendations for future research directions based on insights that have emerged from this thesis.



## **2. 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 controls 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 relation 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.

## 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 due to climate warming. However, vegetation cover and soil properties play an important role in protecting permafrost from degradation because of atmospheric warming (Walker *et al.*, 2003b; Yi *et al.*, 2007). A north-south transect study in Alaskan tundra showed little 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.*, 2003b). 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, 1998b). 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 feedback to further regional warming (Chapin *et al.*, 2005) and may 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.*, 2003b; Yi *et al.*, 2007). Although the effects of shrubs on soil processes in the winter have been studied (Sturm *et al.*, 2001a; Sturm *et al.*, 2005b; 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, due to 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 northeast 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 2.1). 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 *Eriophorum vaginatum* is the dominant graminoid, with abundant shrubs of *B. nana*, *Salix pulchra* and *Ledum palustre*. In both sites 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 2.2).

### *Experimental design*

Observational studies that compare permafrost thawing depth and energy exchange between different ecosystems 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 July 11<sup>th</sup>, 2007 and August 3<sup>rd</sup>, 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 by 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 x 5 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 ( $R_n$ ), ground heat flux ( $G$ ) and soil temperature ( $T_s$ ) were measured simultaneously in one plot pair. We chose to relocate our two energy balance systems every three 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 7 of the 10 plot pairs (3 pairs in the ridge site, 4 pairs in the lake bed site) because of time constraints.

For the ground heat flux measurements, per plot three soil heat flux plates (HFPO1, Hukseflux, The Netherlands) and one self-calibrating heat flux plate (HFPO1SC, Hukseflux, The Netherlands) 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 by 20 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, 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  $G_s$  was calculated using the profile integration method (van Boxtel, 1986), by calculating the heat flux from changes in temperature over time interval  $\Delta t$  measured by the thermistors buried at 2 and 5 cm:

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

where  $C_s$  is the volumetric heat capacity of the soil,  $\Delta T_i$  is the change in soil temperature measured by sensor  $i$  during the time interval  $\Delta t$ , and  $\Delta z_i$  is the thickness of the soil layer for which the temperature change  $\Delta T_i$  is representative. A constant  $C_s$  value of  $2.5 \cdot 10^6 \text{ J m}^{-3} \text{ K}^{-1}$  was used. This is a typical  $C_s$  value reported for water-saturated peat and moss soils (Beringer *et al.*, 2001). Total  $G$  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., The Netherlands). All measurements were made at 2-second intervals. 10-minute-averages and standard deviation data were calculated and stored by a datalogger (CR1000, Campbell Scientific, UK) wired to a multiplexer (AM 16/32, Campbell Scientific, UK). Averages of 30 minutes 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 statistical analyses were performed using SPSS for Windows v.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 2.1). In 2008, only *B. nana* cover differed between control and removal plots ( $p < 0.05$ ; Table 2.1), as we intended.

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. 2.1). 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. 2.2, Table 2.3). 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 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. 2.2). The ALT was greater in the plots located on the ridge than in the plots located on the former lakebed ( $p < 0.01$ , Table 2.3). *B. nana* shrubs had a higher cover (Table 2.1) and were taller (Table 2.2) 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. 2.3), 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 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

**Table 2.1** Plant species cover, determined using point intercept measurements, in summer 2007, before *Betula nana* removal, and in summer 2008, after *B. nana* removal. Data are means  $\pm$  SE ( $n = 5$  plots) per location (former lakebed and ridge) and treatment (control: no *B. nana* removed, removal: *B. nana* removed). All data are in percentage of the total number of grid points within the circular 10-m diameter plots. Significant differences ( $*p < 0.05$ ) in vegetation cover between plots with different treatments within each location for both years are indicated.

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

*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., *Claonia* sp., *Cladonia* sp., *Stereocaulon* sp. and *Thamnolia vermicularis*.

**Table 2.2** Vegetation characteristics and snow depth in the control and removal plots, measured in 2008. Data are mean values  $\pm$  SE ( $n = 5$  plots). Significant differences ( $*p < 0.05$ ) between plots with different treatments within each location are indicated.

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

**Table 2.3** Results of a repeated measures ANOVA, testing the effects of location and treatment on the seasonal development of the active layer thickness (ALT) in 2008.

<i>Between-subject effects</i>	Type III sum of squares	df	F	Sig.
Location	1044.7	1	33.2	< 0.001
Treatment	232.0	1	7.4	0.015
Location*Treatment	7.8	1	0.3	0.625
Error	503.7	16		
<i>Within-subject effects</i>				
Time	5197.9	6	267.1	< 0.001
Time*Location	288.5	6	14.8	< 0.001
Time*Treatment	62.0	6	3.2	0.007
Time*Location*Treatment	16.7	6	0.9	0.530
Error	311.3	96		

plots were generally greater in 2008 than in 2007 ( $p < 0.05$ ), especially in the lakebed plots (Fig. 2.3). No significant differences between control and *B. nana* removal plots were measured in moss layer thickness or snow depth (Table 2.2).

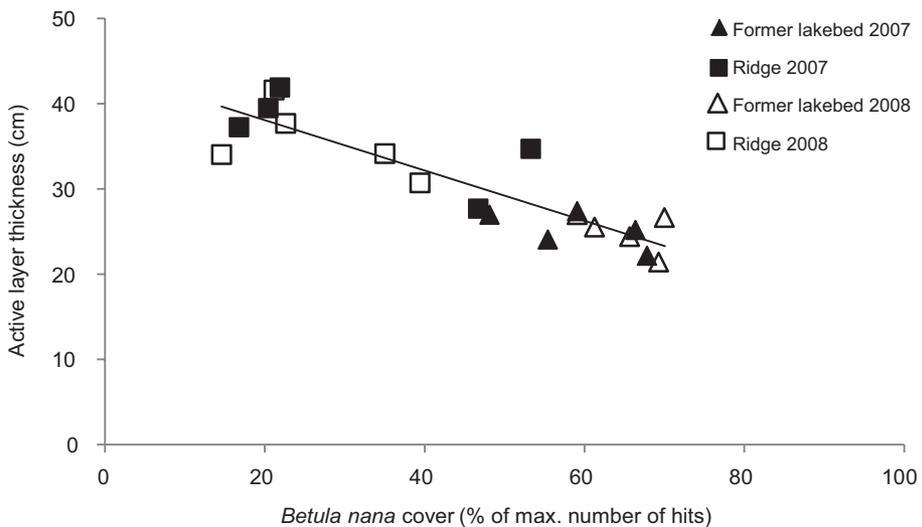
The differences in ALT (Fig. 2.4A) within pairs of control and *B. nana* removal plots were correlated positively with differences in  $G$  (Fig. 2.4B) within plot pairs (Spearman correlation  $\rho = 0.82$ ,  $p < 0.05$ ,  $n = 7$ ). Only the third measured plot pair showed a difference in  $G$  (higher 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. 2.4B). A particularly large difference in ALT was found in the last plot pair measured during the 2008 growing season (Fig. 2.4A).

The average ground heat flux fraction of net radiation ( $G/R_n$ ) was on average 12% and differed by up to 8% within plot pairs (data not shown). The  $R_n$  values were higher in control plots in the former lakebed than in the *B. nana* removal plots (Fig. 2.4C). In contrast,  $R_n$  values of the control and *B. nana* removal plots on the ridge terrain did not show clear differences between treatments (Fig. 2.4C).

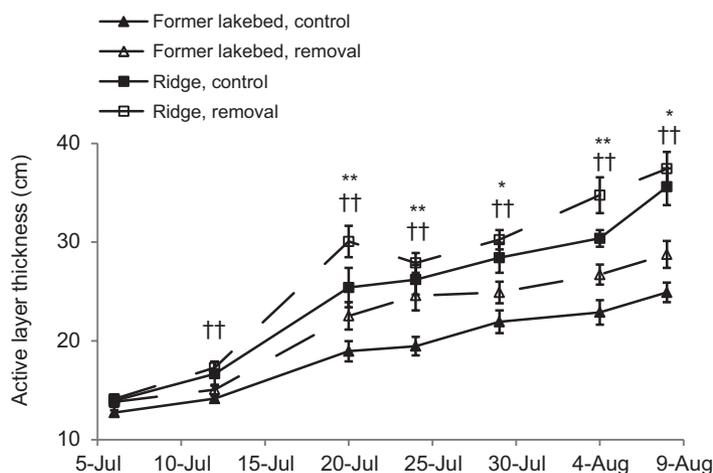
## Discussion

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 due to *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



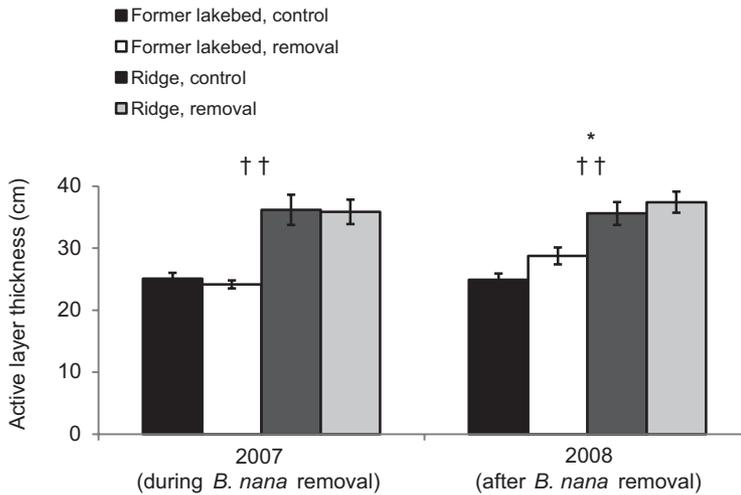
**Figure 2.1** Active layer thickness (ALT) plotted against *B. nana* cover for control plots at the two sites in 2007 and 2008. Measurements of ALT were made on August 7, 2007 and on August 8, 2008. Cover of *B. nana* was measured during the summer of 2007 and again a year later during summer 2008. A linear regression line is fitted to the data ( $r^2 = 0.80$ ;  $ALT = 41.70 - 0.21 * B. nana \text{ cover } (\%)$ ), based on the parameter estimates of the ANCOVA model (see Methods), which includes the effects of year and site.



**Figure 2.2** 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 2.3.

water flow conducted soil heat fluxes away from the permafrost (McFadden, 1998), or because the shrubs were removed from a small area ( $1 \text{ m}^2$ ) (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 ( $178\text{--}388 \text{ g dry } B. \text{ nana } \text{ m}^{-2}$ ), were larger than the *B. nana* biomass removed from Alaskan tundra sites ( $53\text{--}127 \text{ g dry } B. \text{ nana } \text{ m}^{-2}$ ) (Hobbie & Chapin, 1998b; 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

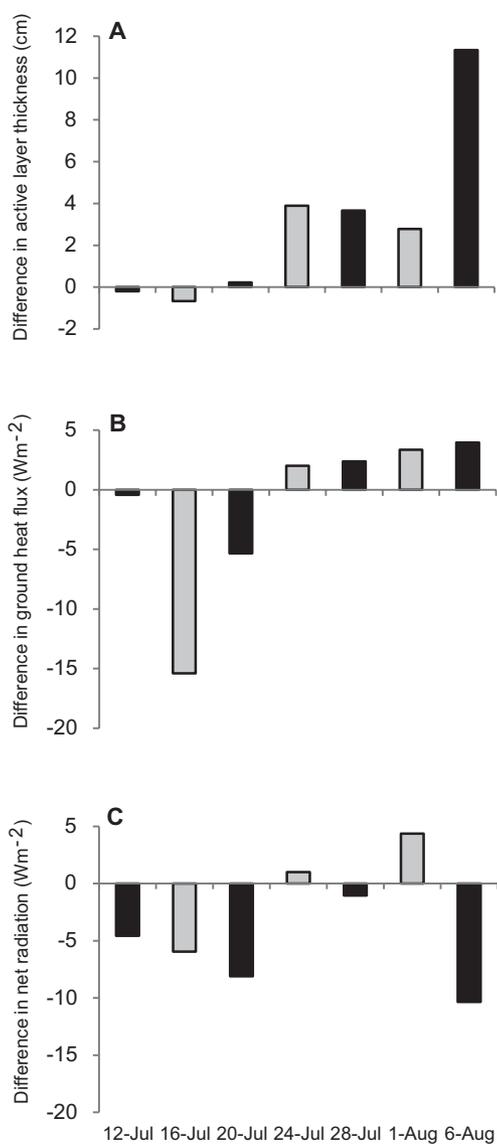


**Figure 2.3** Comparison of active layer thickness (ALT) between control and removal plots during August 7, 2007 and August 8, 2008. The effect of treatment ( $*p < 0.05$ ) and the effect of location ( $††p < 0.01$ ) on ALT are shown for both years. Data are mean values ( $n = 5$  plots)  $\pm$  SE.

*B. nana* removal on ALT in the long term, since 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  $G$  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  $G/R_n$  values in the control plots were 10% in the former lakebed and 15% in the ridge site. These values are similar to  $G/R_n$  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  $G/R_n$  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). Since 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.*, 2004b).



**Figure 2.4** Differences in: (A) active layer thickness, (B) ground heat flux, (C) net radiation within each of 7 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; grey 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.

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  $R_n$  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  $R_n$  into  $G$  more than offsets the increase in  $R_n$  in plots with higher *B. nana* cover. The greater  $R_n$  values in plots with a high shrub cover and concomitant reduction in the partitioning of  $R_n$  into  $G$  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 non-vascular 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 to 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, since 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.*, 2005b). 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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### **3. What are the main climate drivers for shrub growth in Northeastern Siberian tundra?**

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## Abstract

Deciduous shrubs are expected to rapidly expand in the Arctic during the coming decades due to climate warming. A transition towards more shrub-dominated tundra may have large implications for the regional surface energy balance, permafrost stability and carbon storage capacity, with consequences for the global climate system. However, little information is available on the natural long-term shrub growth response to climatic variability. Our aim was to determine the climate factor and time period that are most important to annual shrub growth in our research site in NE-Siberia. Therefore, we determined annual radial growth rates in *Salix pulchra* and *Betula nana* shrubs by measuring ring widths. We constructed shrub ring width chronologies and compared growth rates to regional climate and remotely sensed greenness data. Early summer temperature was the most important factor influencing ring width of *S. pulchra* (Pearson's  $r = 0.73$ ,  $p < 0.001$ ) and *B. nana* (Pearson's  $r = 0.46$ ,  $p < 0.001$ ). No effect of winter precipitation on shrub growth was observed. In contrast, summer precipitation of the previous year correlated positively with *B. nana* ring width (Pearson's  $r = 0.42$ ,  $p < 0.01$ ), suggesting that wet summers facilitate shrub growth in the following growing season. *S. pulchra* ring width correlated positively with peak summer NDVI, despite the small coverage of *S. pulchra* shrubs ( $< 5\%$  surface cover) in our research area. We provide the first climate-growth study on shrubs for Northeast Siberia, the largest tundra region in the world. We show that two deciduous shrub species with markedly different growth forms have a similar growth response to changes in climate. The obtained shrub growth response to climate variability in the past increases our understanding of the mechanisms underlying current shrub expansion, which is required to predict future climate-driven tundra vegetation shifts.

## Introduction

Climate change scenarios predict increasing air temperatures for the next decades, with most warming occurring at high latitudes (IPCC, 2007). Northern ecosystems will be greatly impacted by climate changes through alterations of the surface energy balance, permafrost thaw and changes in vegetation (ACIA, 2004). Vegetation changes have multiple feedbacks to the regional climate system through changes in the surface albedo, soil moisture exchange and the soil carbon balance (McGuire *et al.*, 2006; Wookey *et al.*, 2009). Of all plant functional types, deciduous shrubs are among the most responsive to changes in temperature by increasing their growth, as shown by many experimental warming studies across the Arctic (Chapin *et al.*, 1995; Hobbie & Chapin, 1998b; Walker *et al.*, 2006).

Evidence for shrub expansion exists for sites in Alaska (Sturm *et al.*, 2001b; Tape *et al.*, 2006) and a recent increase in shrub biomass is measured at multiple sites across the Arctic (Chapin *et al.*, 1995; Hudson & Henry, 2009; Olofsson *et al.*, 2009). On a larger scale, circumpolar greening (Normalized Difference Vegetation Index, NDVI) trends suggest that shrub expansion is a widespread phenomenon across the Arctic (Goetz *et al.*, 2005; Tape *et al.*, 2006; Jia *et al.*, 2009). During warmer periods in the Holocene shrubs were much more abundant than today (Bigelow *et al.*, 2003; Müller *et al.*, 2009), indicating the potential for shrub expansion in the Arctic under current climate change scenarios (ACIA, 2004; IPCC, 2007).

Summer air temperature is known to be a crucial factor for bud-break timing in deciduous Arctic shrubs (Pop *et al.*, 2000) and for radial growth of boreal tree species from Siberia, like *Larix* spp. (larch) (Hughes *et al.*, 1999). However, little is known so far on how shrub growth rates are affected by seasonal changes in precipitation and temperature across the Arctic. Currently, the only study assessing the growth response of deciduous shrubs to climate variability in the Russian Arctic is from *Salix lanata* shrubs from W-Siberia, indicating a strong positive relationship between radial growth and summer temperature (Forbes *et al.*, 2010). Other research on climate-growth relationships of Arctic shrubs include studies on dwarf shrubs from the extreme barren Arctic zone (Rayback & Henry, 2006; Schmidt *et al.*, 2006; Rozema *et al.*, 2009) and shrubs from alpine environments (Bär *et al.*, 2008).

Apart from summer temperature, winter precipitation may also influence tree growth through its effect on the start of cambial activity (Vaganov *et al.*, 1999; Kirilyanov *et al.*, 2003). Furthermore, it is suggested that snow cover may play a crucial role in shrub expansion by causing an increase of winter soil temperatures due to the insulating properties of snow (Sturm *et al.*, 2001a). Changes in snow cover thus can have implications for rates of soil organic matter turnover during the winter-spring period (Schimel *et al.*, 2004; Sturm *et al.*, 2005a; Borner *et al.*, 2008). On a larger timescale, pollen-reconstructions suggest that the areal extent of shrub tundra can be reduced by a decrease in winter precipitation (Bigelow *et al.*,

2003) because this exposes the shrubs more to the harsh Arctic winter conditions. However, negative relationships between snow fall and shrub growth rates have also been reported. For example, snow precipitation has been shown to correlate negatively with the radial growth of *Salix arctica* shrubs in Greenland (Schmidt *et al.*, 2010).

Our general aim was to determine those climate factors that are most important for annual shrub growth and the periods when these factors are most influential in our research site in NE-Siberia. Therefore, we determined annual growth rates in *Betula nana* and *Salix pulchra* shrubs by measuring ring widths. *S. pulchra* and *B. nana* are two of the most widespread Arctic deciduous shrub species with a circumpolar distribution (Hultén, 1968), but to our knowledge have not been used before for dendroclimatological analysis. Both species can be attributed to the same plant functional group, deciduous shrubs (Chapin *et al.*, 1996), but have a clear distinction in growth strategy (Bret-Harte *et al.*, 2002) and hence may respond differently to climate factors and environmental changes. Our specific research questions were:

- (i) how does radial growth of two deciduous Arctic shrub species respond to variation in the most important climate factors, temperature and precipitation?
- (ii) what is the difference in summer *versus* winter climate effects on shrub growth?
- (iii) can inter-annual shrub growth variability be tracked by remotely sensed NDVI data?

## Materials and methods

### *Sampling strategy*

During the summer of 2008 and 2009 samples of *B. nana* and *S. pulchra* shrubs (50 individuals per species) were collected in the Kytalyk nature reserve, (70°49`N, 147°28`E), located approximately 30 km NW from Chokurdakh in the Indigirka lowlands in northeast Siberia, Russia (van der Molen *et al.*, 2007; Blok *et al.*, 2010). Height and micro topography were noted for each sampled shrub. The vegetation cover in the research site consists of a mixture of graminoids, forbs, mosses and shrubs and is classified as vegetation unit G4 (tussock-sedge, dwarf-shrub, moss tundra) at the Circumpolar Arctic Vegetation Map (Walker *et al.*, 2005). *S. pulchra* and *B. nana* shrubs cover approximately 5% and 20% of the research area, respectively (unpublished results). *S. pulchra* grows erect and up to 3m tall, with few branches, whereas *B. nana* grows decumbent and low-statured, with a height up to 30 cm and develops many branches. *B. nana* can greatly increase its number of branches under warming treatments (Bret-Harte *et al.*, 2001) and become rapidly dominant

(Bret-Harte *et al.*, 2008), whereas *S. pulchra* is not known to possess this plasticity in architectural morphology (Bret-Harte *et al.*, 2002). *S. pulchra* grows in relatively wet patches along rivers and lakes, whereas *B. nana* grows more upland on slightly elevated and relatively dry patches. Studies on reindeer grazing effects on vegetation responses in the Arctic indicate that shrub growth rates may be heavily impacted by grazers (Olofsson *et al.*, 2009), but no signs of grazing damage on shrubs or their wood anatomy were observed in our research area. Shrubs were cut well below the moss layer, below the root-shoot transition zone, to ensure that samples contain the oldest, first formed parts of the shrubs. Samples were air-dried before shipment to the lab for analysis.

#### *Dendrochronological analysis*

In the lab, thin sections (20-30  $\mu\text{m}$ ) were prepared from two or more samples along the main stem axis of each shrub (base section and section(s) after first branch node) within each shrub individual using a GSL1 sledge microtome (MICROT L, Schenkung Dapples, Zürich, Switzerland). Missing rings are a common phenomenon in dwarf shrubs and can cause significant dating problems (Kolishchuk, 1990). The use of the serial sectioning method greatly reduces dating errors due to very narrow, eccentric, false or discontinuous growth rings in Arctic shrubs (Woodcock & Bradley, 1994; Bär *et al.*, 2006; Büntgen & Schweingruber, 2010). The thin sections were stained with a safranin/astra blue mixture to enhance contrast between wood tissues, which greatly improves the detection and ability to accurately measure tree rings. After staining, samples were dehydrated by rinsing them subsequently with mixtures of 50%, 96% and 100% alcohol. Dehydrated samples were adhered to a microscope slide with Canada balsam, dissolved in xylol, and covered with a cover glass. The cover glass was pressed firmly to the microscope slide to ensure all air bubbles were removed from the sample. The prepared microscope slides were pressed onto a metal plate using a magnet and put in an oven at 60°C overnight to dry. Dried samples were removed of balsam residue using a razorblade.

Ring-widths were measured from each thin section along at least 2 radii using a LINTAB 4 tree-ring measurement device (RINNTECH, Heidelberg, Germany) with a measurement precision of 0.01 mm, connected to a Leica MS5 stereomicroscope (40x magnification) and software (Time Series Analysis Program (TSAP) v.3.6). TSAP software was used to visually inspect and crossdate ring-width series. Crossdated ring-width series of samples from the same stem height were averaged and compared to those from another height within the same individual to check for missing or wedging rings. Eventually, mean ring-width series were calculated for each shrub. For individual *S. pulchra* shrubs, ring-width series were calculated from measurements taken from samples of two heights (base section, section after first branch node) as chronologies from these series yielded the highest

correlation with climate variables. For *B. nana* shrubs, chronologies calculated from the ring-width series of the base section of each shrub contained the strongest climate signal (data not shown). However, also for *B. nana*, the serial sectioning method (measuring ring-widths at multiple heights) was applied (Kolishchuk, 1990) to check for missing rings and crossdating errors (Bär *et al.*, 2006; Hallinger *et al.*, 2010). No individuals with consistently missing rings along the whole shrub were encountered in our samples. The mean ring-width series of all shrub individuals of the two species were visually inspected and cross-dated using a variety of statistical checks (GLK, GSK, TVBP (modified t-values), and COFECHA software (Holmes, 1983; Grissino-Mayer, 2001)). Only individuals that could be accurately crossdated were included in the final chronologies of the two shrub species. Per shrub species, 19 individuals were included in the final chronologies. The two shrub chronologies were evaluated by three statistical checks: the mean correlation strength between each individual and the mean chronology ( $r$ ); the mean sensitivity (MS), which is the percentage change from each ring to the next (Fritts, 1976); and the expressed population signal (EPS), which is the relationship between a finite sample chronology with a hypothetical perfect chronology with infinite replication (Wigley *et al.*, 1984).

ARSTAN v6.05 standardization software was used to perform a double-detrending procedure to remove age-related growth trends and to remove autocorrelative growth between the previous year and the next. First, a negative exponential curve or linear regression curve was fitted through the raw data, after which a 32-year cubic smoothing spline was fitted through the resulting indices, which preserves 50% of the variance at a wave-length of 32 years (Cook & Peters, 1981). After detrending and standardization procedures, standard chronologies (STD) and residuals chronologies (RES) were obtained (Table 3.1). The RES chronology is the same as the STD chronology but without the influence of growth from the previous year on the growth of the next year (Cook *et al.*, 1990). We compared RES chronologies of *B. nana* and *S. pulchra* shrubs developed in this study with RES chronologies (<http://www.ncdc.noaa.gov/paleo/treering.html>) from *Larix* spp. tree samples collected by F.H. Schweingruber and with a RES chronology from W-Siberia developed by Forbes *et al.*, 2010.

#### *Instrumental climate data*

Climate data from the closest meteorological station (WMO station 21946), located in Chokurdakh at 30 km from the research site and second closest meteorological station (WMO station 24266), located in Verkhoyansk at 660 km from the research site, were used to compare against our shrub chronologies (<http://climexp.knmi.nl/>). Raw daily precipitation and temperature data for the period 1944-2006 were available (Klein Tank *et al.*, 2002). Snow melt data were available for the period 1992-2006. An often applied procedure to identify climate signals in ring-width data

is by using monthly average climate data, but this is a rather coarse time interval to explore the climate-growth relationship during the short Arctic summer. Instead, we performed pentad analyses (Hughes *et al.*, 1999; Vaganov *et al.*, 1999; Kirilyanov *et al.*, 2003; Panyushkina *et al.*, 2003) to assess the period of the maximal growth response to temperature for both *S. pulchra* and *B. nana* shrubs. A pentad is the average temperature during a period of 5 consecutive days. By applying a flexible shifting time-window analysis, pentads with significant relation to the RES shrub chronologies were averaged to find the period of maximum correlation between the shrub chronologies and temperature.

Vegetation summer greenness in our research area was evaluated with Normalized Difference Vegetation Index (NDVI) data, measured by the Advanced Very High Resolution Radiometer (AVHRR) satellites. NDVI records have been shown to be a good measure for tundra plant productivity and correspond with variations in summer warmth (Goetz *et al.*, 2007; Raynolds *et al.*, 2008). NDVI data for the period 1981-2006 were obtained from the Global Inventory Modeling and Mapping Studies (GIMMS) dataset (<http://glcf.umd.edu/data/gimms/>) (Tucker *et al.*, 2005). We analyzed biweekly NDVI data of the Arctic growing season period (June-August) and correlated NDVI data against the RES shrub chronologies. The spatial resolution of the GIMMS NDVI-record was 8 km. We calculated average biweekly NDVI values for multiple spatial scales: a) Research shrub sampling site (1 pixel, 16 km<sup>2</sup>); b) research area including sampling site (4 pixels, 64 km<sup>2</sup>); Kytalyk nature reserve (420 pixels, 6720 km<sup>2</sup>).

### *Data analysis*

Pearson's correlation coefficients  $r$  were calculated to find the climate variable (precipitation, temperature) and period to which shrub growth is most sensitive. A correction for multiple testing was applied by using the false discovery rate procedure to control for type I errors (Verhoeven *et al.*, 2005). A linear regression analysis was performed with peak growing season NDVI of the research area (average NDVI values of four pixels with a spatial resolution of 8km) as a function of summer temperature for the period 1981 to 2006 (Chokurdakh weather station data). Linear regression was performed to explain similarities between the shrub chronologies developed in this study and chronologies developed from regional *Larix* spp. trees, with the Pearson's  $r$  values between shrub and *Larix* spp. RES chronologies as dependent variable and geographical variables as explanatory variables. Data were ln- or square root-transformed where needed to achieve normal distribution. All statistical analyses were performed using SPSS for windows v.17.0.

## Results

Residual (RES) chronologies were established for the two shrub species, with the *S. pulchra* chronology showing higher inter-series correlation than the *B. nana* series (Table 3.1). The large variability in ring width between *B. nana* individuals resulted in relatively low EPS values (0.58 – 0.83), especially in the early part of the *B. nana* RES chronology (1948-1970). *B. nana* and *S. pulchra* RES chronologies correlated significantly with each other ( $r = 0.44$ ,  $p < 0.001$ ,  $n = 59$  years).

We calculated which climate factor (temperature or precipitation) and seasonal period was most important for annual growth of *B. nana* and *S. pulchra*. Significant correlations with radial growth rates were detected only for summer climate variables. No correlation of winter precipitation or winter temperature with shrub growth was detected (Table 3.2). Both deciduous shrub species were most responsive to average summer temperatures of the same time window: the period immediately following snowmelt (June 17<sup>th</sup> – July 19<sup>th</sup>) (Fig. 3.1). The *S. pulchra* chronology showed a high correlation with early summer temperature ( $r = 0.73$ ,  $p < 0.01$ , Table 3.2), similar to correlation strengths found between summer temperature and regional *Larix* spp. chronologies (Hughes *et al.*, 1999; Kirilyanov *et al.*, 2003). Besides early-summer temperature, summer precipitation (June - August) of the year preceding ring formation had a positive influence on the radial growth of *B. nana* ( $r = 0.42$ ,  $p < 0.01$ , Table 3.2). Analysis of long-term summer temperature data from the meteorological station in Chokurdakh for the period 1948-2006 showed a slight positive trend (trend line slope =  $0.014^{\circ}\text{C yr}^{-1}$ , Fig. 3.2), comparable with observations on summer temperature trends from W-Siberia by Forbes *et al.*, (2010). Average yearly winter precipitation (October-April) and standard deviation in our research site during 1948-2006 was  $87 \pm 28$  mm, with a positive trend ( $0.12$  mm  $\text{yr}^{-1}$ ). The *S. pulchra* RES chronology also correlated with early summer temperature data from the second closest meteorological station, located in Verkhoyansk at approximately 660 km southwest from the research site ( $r = 0.49$ ,  $p < 0.01$ ).

We tested to what spatial extent our shrub chronologies may be representative by comparing them to a tree-ring network that covers our research region with a relatively high spatial density, in contrast to the sparse meteorological data available for this region. *B. nana* and *S. pulchra* RES chronologies showed significant correlations with respectively, four and seven out of the 20 *Larix* spp. chronologies from North Yakutia. The *S. pulchra* chronology correlated best with the regional North Yakutia chronology ( $r = 0.78$ ,  $p < 0.01$ ), whereas the *B. nana* chronology correlated best with the Bilibina chronology ( $r = 0.47$ ,  $p < 0.05$ ), constructed from samples located at 880 km from our research site (Table 3.3). For *S. pulchra*, similarities with the other chronologies were explained by latitude and longitude, as shown by the results of a multiple linear regression test (Table 3.4). For *B. nana*, longitude explained most of the similarity with the tree-ring chronologies,

**Table 3.1** Statistics of *Salix pulchra* and *Betula nana* ring-width residual chronologies.

	mean series length (years)	mean ring width (mm)	n	r	EPS	MS
<i>Salix pulchra</i>	48 (10)	0.21 (0.14)	19	0.62	0.83 - 0.97	0.48
<i>Betula nana</i>	46 (16)	0.11 (0.08)	19	0.31	0.58 - 0.90	0.44

n: number of shrub individuals used to construct the final chronology. r: mean correlation of each series with the mean master chronology derived from all series. EPS: expressed population signal, indicates the representativeness of the sample size for a theoretical sample size with an infinite number of shrub individuals (Wigley et al., 1984). MS: mean sensitivity, the mean relative change in ring-width from one year to the next (Fritts, 1976). Values between brackets are standard deviations from the mean.

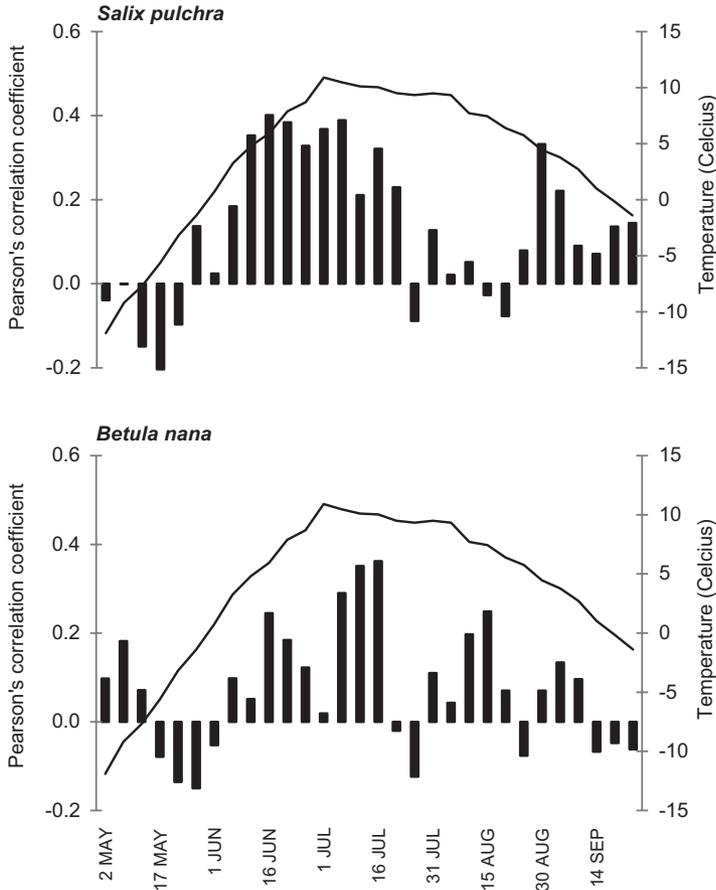
**Table 3.2** Pearson's correlation coefficients between shrub residual chronologies (*Salix pulchra* and *Betula nana*) and local climate variables temperature and precipitation (cumulative), derived from the meteorological station in Chokurdakh, for the period 1948-2006.

Climate variables	Pearson's correlation coefficient	
	<i>Salix pulchra</i>	<i>Betula nana</i>
<b>Summer</b>		
Growing days (temperature > 5°C)	0.42 **	0.21
Summer temperature (Jun-Aug)	0.52 **	0.32
Summer precipitation (Jun-Aug)	0.03	0.06
Early summer temperature (Jun 17th-Jul 19th)	0.73 **	0.46 **
Previous year's summer temperature (Jun-Aug)	-0.22	-0.16
Previous year's summer precipitation (Jun-Aug)	0.16	0.42 **
<b>Winter/Spring</b>		
Snowmelt date	-0.22	0.10
Winter temperature (Oct-Apr)	-0.10	-0.07
Winter precipitation (Oct-Apr)	0.08	0.00
Spring temperature (Mar-May)	-0.11	-0.08
Spring precipitation (Mar-May)	-0.08	-0.05

Growing days: yearly number of days with mean daily temperatures above 5°C. Snow melt date: day of year when snow has melted (snowmelt data available for period 1992 – 2006). Asterisks indicate the adjusted significance levels of the correlations, corrected for multiple testing: \*\* $p < 0.01$

followed by elevation. Up to 57% of the variation in similarities of the shrub chronologies with the *Larix* spp. chronologies could be explained by geographical parameters.

The *S. pulchra* RES chronology showed a positive relationship with peak growing season NDVI (2<sup>nd</sup> half of July) values of the research site area ( $r = 0.43$ ,  $p < 0.05$ , Fig. 3.3), despite the small percentage cover of *S. pulchra* shrubs in



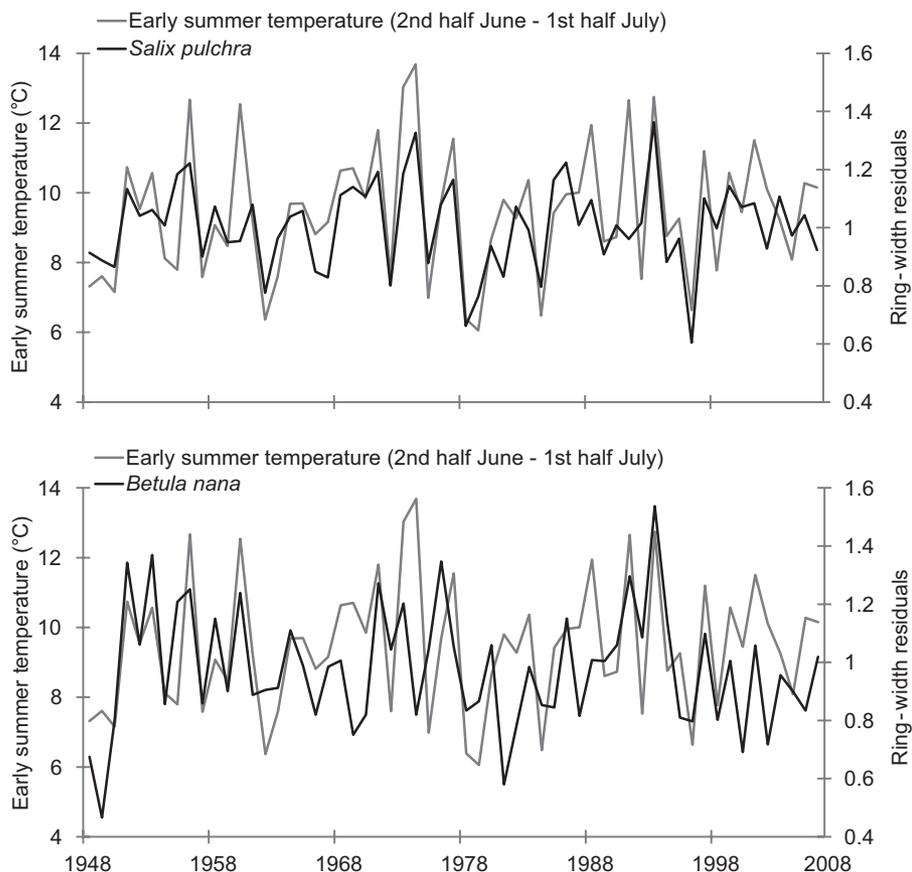
**Figure 3.1** The vertical bars show Pearson’s correlation coefficients between the mean average temperature of 5-day periods (pentads) measured at the Chokurdakh meteorological station for the period 1948-2006, and the residual chronologies of *Salix pulchra* and *Betula nana*. The continuous line shows average daily temperature data for the period 1948-2006 from the meteorological station in Chokurdakh.

the research area ( $< 5\%$  *S. pulchra* cover, results not shown). No correlation of *S. pulchra* growth with biweekly NDVI values from other periods during the growing season was found (data not shown). The *B. nana* RES chronology did not correspond significantly with summer NDVI. No discernable trend in peak growing season NDVI during the available data span (1981 - 2006) was observed in our research area ( $y = 0.0026x + 0.6724$ ). Inter-annual peak growing season NDVI variability could be partially explained by early summer temperature (June 17<sup>th</sup> – July 19<sup>th</sup>) ( $R^2 = 0.42, p < 0.01$ ).

**Table 3-3** Summary of Pearson's correlation coefficients between the residual chronologies developed in this study (*Salix pulchra* and *Betula nana*) and 20 residual chronologies developed from tree-ring width data from sites in N-Yakutia, and one residual chronology developed from *Salix lanata* shrubs from W-Siberia over the common time span 1947-1990.

Site name	<i>Salix pulchra</i>	<i>Betula nana</i>	Latitude	Longitude	Elevation (m)	Species	Distance to site (km)	Source
Chokurdakh	0.74**	0.40*	70.17	148.03	50	<i>Larix dahurica</i>	75	1
North Yakutia	0.78**	0.37	69.30	147.00	80	<i>Larix dahurica</i>	170	2
Allagea River	0.33	0.02	68.27	147.35	140	<i>Larix dahurica</i>	284	1
Andryushkine	0.65**	0.42**	69.17	154.46	50	<i>Larix dahurica</i>	323	1
Ayandina River	0.30	0.26	68.25	143.10	45	<i>Larix dahurica</i>	332	1
Batagay	0.49**	0.04	70.15	138.10	80	<i>Larix dahurica</i>	356	1
Zhaschiviersk	0.08	0.17	67.27	142.37	100	<i>Larix sibirica</i>	444	1
Srednie-Kolymsk	0.06	0.13	67.15	153.42	50	<i>Larix dahurica</i>	472	1
Omoloya	0.59**	0.37	70.57	132.59	20	<i>Larix dahurica</i>	547	1
Tirekhjakh River	0.05	-0.01	67.37	137.28	350	<i>Larix dahurica</i>	556	1
Rossocha River	0.05	0.36	65.09	149.26	300	<i>Larix dahurica</i>	642	1
Cherskij	0.41*	0.40*	68.48	163.03	300	<i>Larix dahurica</i>	654	1
Nulegeler River	0.51**	0.10	71.13	127.26	40	<i>Larix dahurica</i>	731	1
Ust-Nera	0.00	0.20	64.32	143.07	600	<i>Larix dahurica</i>	746	1
Verchoyansk	0.36	-0.15	67.50	130.50	750	<i>Larix dahurica</i>	763	1
Shaguchan River	0.17	0.08	63.35	148.17	1000	<i>Larix dahurica</i>	832	1
Seimchan River	0.02	0.06	63.31	151.43	450	<i>Larix dahurica</i>	853	1
Uel Siktjach	0.07	-0.01	69.17	125.20	130	<i>Larix dahurica</i>	862	1
Bilibina	0.33	0.47*	67.28	167.40	450	<i>Larix dahurica</i>	880	1
Balshoia Anui	0.17	0.20	66.13	165.25	500	<i>Larix dahurica</i>	889	1
Nenets Autonomous Okrug	-0.01	0.19	68.40	58.30	40	<i>Salix lanata</i>	3131	3

Asterisks indicate the adjusted significance levels of the correlations, corrected for multiple testing: \* $p < 0.05$ ; \*\* $p < 0.01$ . Data sources: 1:F.H. Schweingruber (<http://www.wsl.ch/dendro/dendro/db.html>); 2:Hughes et al., 1999 (<http://www.ncdc.noaa.gov/paleo/treering.html>); 3:Forbes et al., 2010



**Figure 3.2** The black lines show *Salix pulchra* and *Betula nana* residual ring-width chronologies. The grey lines show the mean summer temperature (June 17<sup>th</sup> – July 19<sup>th</sup>) for the period 1948-2006.

## Discussion

We show that it is possible to construct ring-width chronologies from Arctic shrub species with markedly different growth forms. The *B. nana* RES chronology was used for climate-growth analysis for the time period 1948-2006, despite the low EPS values in the early part of the chronology due to the limited sample size and high variability in radial growth between *B. nana* individuals. The serial sectioning method allowed us to accurately cross-date ring-width series within and between *B. nana* individuals. Correct measurement and crossdating is independently verified by comparison with regional *Larix* spp. tree-ring chronologies. Some dendroclimatological studies on Arctic *Salix* spp. shrubs do not observe a clear temperature effect on shrub growth (Schmidt *et al.*, 2006; Zalatan & Gajewski,

**Table 3.4** Statistics of multiple regression models explaining the similarities of the shrub chronologies from this study to the regional *Larix* spp. tree ring-width chronologies shown in table 3.3

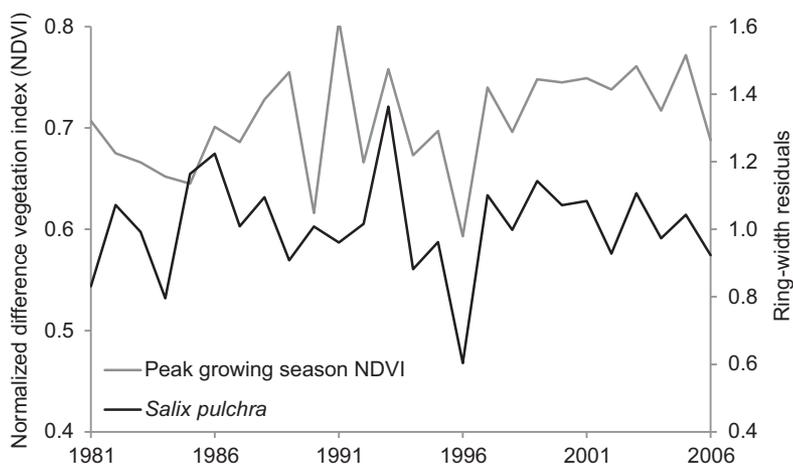
	model parameters (partial correlation)	residuals df	F	model R <sup>2</sup>	adjusted model R <sup>2</sup>	p-value
<i>Salix pulchra</i>	latitude (0.78)	17	13.44	0.61	0.57	0.001
	longitude (0.45)					
<i>Betula nana</i>	longitude (0.73)	17	11.24	0.57	0.52	0.001
	elevation (-0.60)					

The following explanatory variables were given as input to the regression models: distance from our research site, latitude, longitude and altitude of research sites. Non-significant parameters were deleted one at a time from the model. The dependent variables for the two regression models were the Pearson's correlation coefficients of the shrub residual chronologies (*Salix pulchra* and *Betula nana*) with the *Larix* spp. residual chronologies.

2009), highlighting the importance to study multiple shrub species at many sites across the Arctic to assess the implications of climate changes on Arctic shrub growth rates.

Shrub growth in our research site in NE-Siberia was found to be highly sensitive to early summer temperatures, as also observed for boreal tree growth in our research region (Hughes *et al.*, 1999; Vaganov *et al.*, 1999; Kirilyanov *et al.*, 2003; Sidorova *et al.*, 2010). The temperature during the period immediately following snowmelt (mid-June to mid-July) mainly determines radial growth for both *B. nana* and *S. pulchra*, in agreement with observations on controls on bud break timing for these shrub species (Pop *et al.*, 2000). The lower correlation coefficient of *B. nana* radial growth to early summer temperature may be due to its specific growth strategy: under favorable growing conditions, *B. nana* is known to increase its growth mainly by producing many long shoots instead of producing mostly short shoots (Bret-Harte *et al.*, 2001; Bret-Harte *et al.*, 2002), which may result in a shift in growth allocation from radial growth of the older stems to vertical growth of the newly formed shoots. This growth strategy, together with the low-statured growth form of *B. nana*, with its many branches, may result in a reduced sensitivity of its radial growth to temperature. In comparison, *S. pulchra* is unable to greatly increase its vertical stem growth under favorable growing conditions (Bret-Harte *et al.*, 2002). Nevertheless, the time window of maximum growth sensitivity to temperature was found to be identical for *B. nana* and *S. pulchra* shrubs, showing that shrubs with markedly different growth forms can show a similar radial growth response.

No effect of summer precipitation on *B. nana* and *S. pulchra* growth was observed, which is consistent with a study on *Larix* spp. growth in N-Yakutia (Briffa *et al.*, 2008; Sidorova *et al.*, 2010). However, summer precipitation of the



**Figure 3.3** The grey line shows peak growing season (2nd half July) greenness (NDVI) values for the Kytalyk research area in NE-Siberia. NDVI was calculated as the average of four pixels, with each pixel giving a NDVI value for an area measuring 8 by 8 km. The black line shows the *Salix pulchra* residual chronology.

year preceding ring formation shows a positive correlation with *B. nana* growth, suggesting that its growth may be partly water-limited. As *B. nana* grows on relatively well-drained soils, it depends on precipitation for sufficient water supply, especially during late summer. A higher amount of precipitation during this period may alleviate drought stress and promote leaf bud development as well as assimilate storage and thus favor next year's growth. Wahren *et al.*, (2005) observed in their Alaskan research site that deciduous shrub cover increased with increasing summer precipitation. They suggest that increased summer precipitation may result in a deeper active layer, which stimulates organic matter decomposition and possibly increases soil nitrogen availability that favors shrub growth. In comparison to *B. nana* shrubs, *S. pulchra* growth did not correspond with summer precipitation, most likely because *S. pulchra* grows at wetter micro sites than *B. nana* and is therefore less susceptible to temporarily dry conditions as a consequence of changes in summer precipitation.

Changes in snow depth may increase shrub growth via increased soil temperatures in shrub patches: their protruding branches capture drifting snow and thus increase the thickness of the snow layer in shrub-rich areas (Sturm *et al.*, 2001a). A thicker snow pack has been observed to lead to increased winter mineralization (Schimel *et al.*, 2004). A thicker snowpack may also increase the active layer depth and soil nutrient concentrations during the spring season (Nowinski *et al.*, 2010), which may favor further shrub growth and could thus create a positive feedback loop (Sturm *et al.*, 2005b; Hallinger *et al.*, 2010). In contrast, an increase in winter

precipitation may also delay the onset of cambial activity as shown in *Larix* spp. trees in the Eurasian sub-Arctic (Vaganov *et al.*, 1999; Kirilyanov *et al.*, 2003). In this study we did not observe a correlation between shrub growth and winter precipitation for neither *B. nana* nor *S. pulchra*. This does not necessarily exclude a potential effect of local snow cover on shrub growth as winter precipitation is only one of several parameters (*e.g.* sublimation, wind dispersal, vegetation, local precipitation patterns, topography, aspect) affecting local snow height and associated soil thermal conditions (Yang *et al.*, 2005). A deeper snow pack, associated with taller shrubs, can alter the duration of the snow melt period (Pomeroy *et al.*, 2006).

In Greenland, a negative correlation has been observed between early spring snow cover extent and radial growth for *Salix arctica* shrubs (Schmidt *et al.*, 2006). Nevertheless, the net effect of deeper snow on snow melt timing may be limited, because protruding shrub branches through the snow decrease the spring albedo, leading to increased absorption of solar radiation and higher snow melt rates (Sturm *et al.*, 2005a). We observed no correlation of radial shrub growth with snow melt timing but we did observe a positive correlation with growing season length for *S. pulchra*. The relatively small number of years with snow melt data compared to the number of years with growing season length data may explain the difference in correlation strength with *S. pulchra* radial growth.

Our *S. pulchra* chronology correlated with *Larix* spp. tree chronologies from up to 880 km away from our research site, indicating that year-to-year growing conditions in the Siberian far east are similar for large territories (Vaganov & Kirilyanov, 2009). Similarities with *Larix* spp. chronologies were not explained by distance from our research site, but by latitude and longitude (*S. pulchra*) or longitude and elevation (*B. nana*). This suggests that climate-growth reconstructions from shrubs may be representative for large areas, but that these areas are restricted to climate zones defined by elevational and latitudinal boundaries.

Our *B. nana* chronology did not show a significant correlation with summer NDVI, which could be a result of a potential trade-off in growth allocation in *B. nana* shrubs between radial growth of old branches and vertical growth of newly formed stems. If growth of *B. nana* under favorable growing conditions is allocated relatively more to new shoot meristems and attached leaf buds, this may explain the asynchrony between radial growth of the older stems with the NDVI signal. In contrast to *B. nana*, *S. pulchra* radial growth did show a significant correlation with summer NDVI, despite the low cover of *S. pulchra* in our research area. The only other Siberian dendroclimatological study, using *Salix lanata* shrubs, shows a much higher correspondence with summer NDVI (Forbes *et al.*, 2010). Correspondingly, in this study area the relative cover of shrubs was also much higher (> 20% cover of *Salix* spp., in comparison to the approximate 5% *Salix* spp. cover in our research site), probably resulting in a greater proportion of NDVI being explained by radial growth of *Salix* spp. Nevertheless, our results confirm that *Salix* spp. shrubs may be

successfully used to track peak-growing season greening trends over a longer time period than the available satellite record.

Climate warming scenarios predict increases in summer temperature and summer precipitation in the Arctic (IPCC, 2007) that will impact future Arctic vegetation growth. One of the most prominent climate-induced vegetation changes is expected to be an increase in shrub growth. An increase in shrub cover can have important consequences for the Arctic ecosystem including changes in the surface energy balance (Eugster *et al.*, 2000; Chapin *et al.*, 2005; Euskirchen *et al.*, 2009), soil organic matter turnover rates (Weintraub & Schimel, 2003; Weintraub & Schimel, 2005) and tundra fire regimes (Racine *et al.*, 2004; Higuera *et al.*, 2008; Lantz *et al.*, 2010). Furthermore, a higher shrub cover may lead to increased soil shading, thereby reducing the energy input into the soil, reducing summer permafrost thaw (Blok *et al.*, 2010) and lower tundra soil carbon release during summer (I.H. Myers-Smith & D.S. Hik, unpublished manuscript). Our study area lies within the largest tundra zone in the world. Nevertheless, as of yet, no climate-growth studies on shrubs exist for this region.

We constructed growth chronologies of two widespread Arctic deciduous shrub species (*Betula nana* and *Salix pulchra*) that have not been used before in dendroclimatology. We show that deciduous shrub species with markedly different growth forms have a similar growth response to changes in climate. We provide the first climate-growth study on shrubs for East-Siberia, the largest tundra region in the world. The obtained shrub growth response to climate variability in the past increases our understanding of the mechanisms underlying current shrub expansion, which is required to predict future climate-driven tundra vegetation shifts. Our results indicate that the main climate drivers for shrub growth in our research area in NE-Siberia are early summer temperature and summer precipitation.

### **Acknowledgements**

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## **4. Arctic vegetation response to summer climate: relation between shrub cover, NDVI, surface albedo and temperature**

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## **Abstract**

Recently observed Arctic greening trends from normalized difference vegetation index (NDVI) data suggest that shrub growth is increasing in response to increasing summer temperature. An increase in shrub cover is expected to decrease summer albedo and thus positively feedback to climate warming. However, it is unknown how albedo and NDVI are affected by shrub cover and inter-annual variations in summer climate. Here, we examined the relationship between deciduous shrub cover, NDVI and albedo using field data that was collected in a tundra site in NE-Siberia. Field data showed that NDVI increased and albedo decreased with increasing deciduous shrub cover. We then selected four Arctic tundra regions and compiled annual growing season maximum NDVI and minimum albedo maps from MODIS satellite data (2000-2010) and related these satellite products to tundra vegetation type and regional summer climate. We observed that maximum NDVI was greatest in shrub tundra and that inter-annual variation was negatively related to summer minimum albedo but showed no consistent relationship with summer temperature. Furthermore, shrub tundra showed higher albedo values than wetland and barren tundra, indicating that a northwards expansion of shrub tundra may not lead to a decrease in summer albedo when shrub tundra replaces current high-Arctic tundra vegetation. Instead, our field data suggest that a decrease in summer albedo can be expected when higher temperatures lead to increased shrub growth within low-Arctic shrub and graminoid tundra.

## Introduction

Climate change is expected to have great impacts on the Arctic tundra ecosystem (ACIA, 2004). Changes in temperature, precipitation and growing season length are likely to have great effects on future vegetation development in the Arctic and may result in ecosystem feedbacks that may lead to further climatic changes (Wookey et al., 2009). For example, changes in vegetation may influence the local climate and change the regional water and energy balance (Eugster et al., 2000).

As evidence for increasing Arctic vegetation growth, greening trends have been observed in multiple high-latitude regions during the last decades, based on the satellite-inferred normalized difference vegetation index (NDVI) (Bunn *et al.*, 2007; Jia *et al.*, 2009; Walker *et al.*, 2009). NDVI records have been shown to be a good measure for plant productivity (Tucker & Sellers, 1986) and for the Arctic region NDVI has been shown to spatially correspond with variations in summer warmth (Raynolds et al., 2008). Changes in NDVI may indicate a response of Arctic tundra vegetation productivity and/or vegetation composition to increases in temperature. Most of the high-latitude areas with a significant positive trend in NDVI are restricted to tundra areas, in contrast to many boreal areas that show browning over the last decades (Bunn & Goetz, 2006).

Within Arctic vegetation types, deciduous shrub species such as dwarf birch (*Betula nana*) are expected to respond most to changes in temperature (Walker *et al.*, 2006; Euskirchen *et al.*, 2009). Photographic and satellite data suggest that shrubs are at least partly responsible for the recent greening trends (Tape et al., 2006). Recently, dendrochronological studies showed that radial growth of several willow (*Salix* spp.) shrub species in Siberia is positively related to local peak-summer NDVI and summer temperature (Forbes *et al.*, 2010; Blok *et al.*, 2011), providing support for a linkage between increased shrub growth, tundra greening and increasing air temperature.

Along with an increase in NDVI, shrub expansion may lead to a higher absorption of shortwave solar radiation, thereby decreasing the summer surface albedo and potentially leading to additional local atmospheric heating (Chapin *et al.*, 2005; Euskirchen *et al.*, 2009). Indeed, a negative correlation between shrub cover and summer albedo has been observed in Alaskan shrub tundra (Beringer *et al.*, 2005; Sturm *et al.*, 2005a). However, it remains unclear how spatial and temporal differences in summer albedo are related to summer climate and vegetation composition at a larger spatial scale. Our hypotheses were that summer albedo is negatively related to summer NDVI and that summer NDVI increases and summer albedo decreases with increasing summer temperature and shrub fractional cover.

To test these hypotheses, we

(i) examined the relationship between deciduous shrub cover, NDVI and albedo using data from a field campaign in a low-Arctic tundra site in NE-Siberia

(ii) evaluated recent (2000-2010) trends and correlations in satellite-derived peak-growing season NDVI and minimum albedo with climate station data of four low-Arctic regions in Yakutia (E-Siberia), Nunavut (Canada), Yamal (W-Siberia) and the North Slope of Alaska.

## Materials and methods

### Field measurements

#### *Site description*

Field measurements were made in a low Arctic tundra site in the Kytalyk nature reserve (70°49`N, 147°28`E) in the Indigirka lowlands in northeast Siberia, Russia. The vegetation at the research site consists of a mixture of graminoids, forbs, mosses and shrubs and is classified as a mixture of vegetation classes G4 (tussock-sedge, dwarf-shrub, moss tundra) and S2 (low-shrub tundra) on the circumpolar Arctic vegetation map (CAVM) (Walker et al., 2005). Vegetation height ranges between 2 m for willow shrubs located along lake margins and river banks to a few cm for dry lichen-dominated patches. Measurements of NDVI, albedo, leaf area index (LAI) and plant species cover were made in 20 experimental 10 m-diameter plots during summer 2008 and 2009. Half of these plots were located in *Betula nana*-dominated patches lying in the bed of a former thermokarst lake, hereafter referred to as lakebed plots. The *B. nana*-dominated patches in this former lake area are alternated by wet sedge depressions with *Eriophorum angustifolium*, *Carex aquatilis* and *Sphagnum* mosses. The other half of the plots were located on top of a Pleistocene river terrace, hereafter referred to as ridge plots. Vegetation in these ridge plots consisted of a mixture of *Eriophorum vaginatum* tussocks, evergreen shrubs (*Ledum palustre*, *Vaccinium vitis-idea*, *Cassiope tetragona*) and deciduous dwarf shrubs (*Betula nana*, *Salix pulchra*, *Salix glauca*, *Vaccinium uliginosum*). Vegetation height was approximately 10 cm in plots in the ridge location and 15 cm in the lakebed plots. Plots were selected pairwise on the basis of similarity in vegetation cover before removal treatment. In one plot of each plot pair (5 lakebed and 5 ridge plots), all *Betula nana* was removed during summer 2007 (Blok et al., 2010). Since summer 2007, some regrowth of *B. nana* had occurred, albeit significant differences in *B. nana* fractional cover remained during summer 2008 and 2009, the period in which measurements presented in this paper were made. Two plot types could thus be distinguished: plots with dense *B. nana* fractional cover (control plots) and plots with thin *B. nana* fractional cover (removal plots), with lower *B. nana* fractional cover in the ridge plots relative to the lakebed plots.

*Spectral reflectance measurements and NDVI calculation*

Vegetation spectral reflectance measurements were made during July 2008 using a field spectrometer (ASD Field Spec Classic FR, Analytical Spectral Devices Inc., Boulder, CO), with a spectral range between 350 nm to 2500 nm. Reflectance of the vegetation was measured from a distance of 1 m above the vegetation (from nadir) in all 20 plots, replicated 20 times per plot. The mean reflectance was calculated for each plot by averaging the 20 replicates. Wavelengths affected by atmospheric water vapor (350-399 nm, 1361-1409 nm, 1801-1959 nm, 2401-2500 nm) were excluded from further analysis. The mean reflectance per plot was spectrally resampled to the MODerate resolution Imaging Spectroradiometer (MODIS) satellite response function using ENVI v4.5 software (ITT Visual Information Solutions, Boulder, CO). NDVI values for each plot were calculated using resampled red (band 1, 620-670 nm) and near infrared (band 2, 841-876 nm) field spectrometer reflectance according to equation 4.1:

$$(4.1) \quad \text{NDVI} = (R_{\text{NIR}} - R_{\text{red}}) / (R_{\text{NIR}} + R_{\text{red}})$$

in which  $R_{\text{NIR}}$  = near-infrared reflectance and  $R_{\text{red}}$  = red reflectance. NDVI values were compared against plant species fractional cover in the plots as recorded by point intercept.

*Fractional cover, albedo and leaf area index measurements*

Species fractional cover was measured in all plots using the point intercept method. A description of the method and plant fractional cover data for summer 2008 and 2009 are given in table 2.1 and in table 5.1, respectively.

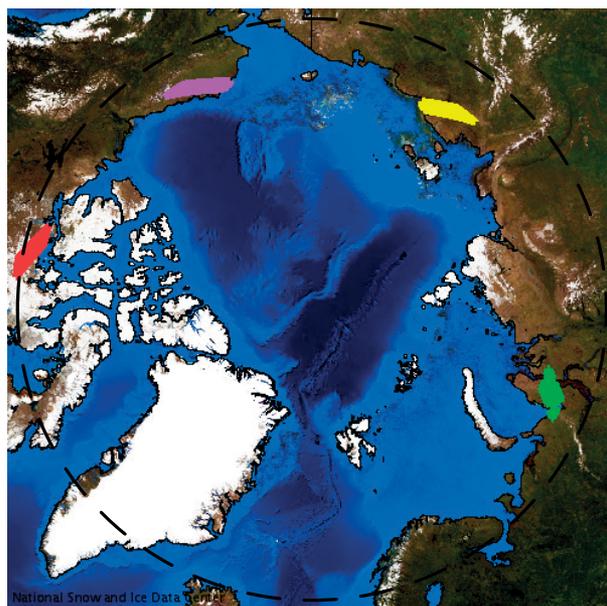
Albedo in the 10 lakebed plots was measured during July 2009 from net shortwave radiation ( $SW_{\text{net}}$ ) measurements using two systems, each consisting of a CRN2 net radiometer (Kipp & Zonen B.V., Delft, The Netherlands) connected to a CR1000 datalogger (Campbell Scientific, Shepshed, UK). The radiometers were mounted at 85 cm height above the vegetation in all 10 plots in the former lakebed area (5 plot pairs, each pair consisting of one control plot and one removal plot). Measurements were made simultaneously in one plot pair at a time for 5-6 full days after which systems were installed into the next plot pair. Ten-minute  $SW_{\text{net}}$  records were averaged to 30-minute values. Incoming shortwave radiation ( $SW_{\text{in}}$ ) was measured continuously by a CM7b shortwave albedometer (Kipp & Zonen B.V., Delft, The Netherlands) mounted on a meteorological tower at 4.5 m height (van der Molen et al., 2007). Midday average albedo (13:00h to 16:00h) was calculated from 30-minute average  $SW_{\text{net}}$  (measured at the experimental plots) and  $SW_{\text{in}}$  data (measured at the meteorological tower) using equation 4.2:

$$(4.2) \quad \text{albedo} = (SW_{in} - SW_{net})/SW_{in}$$

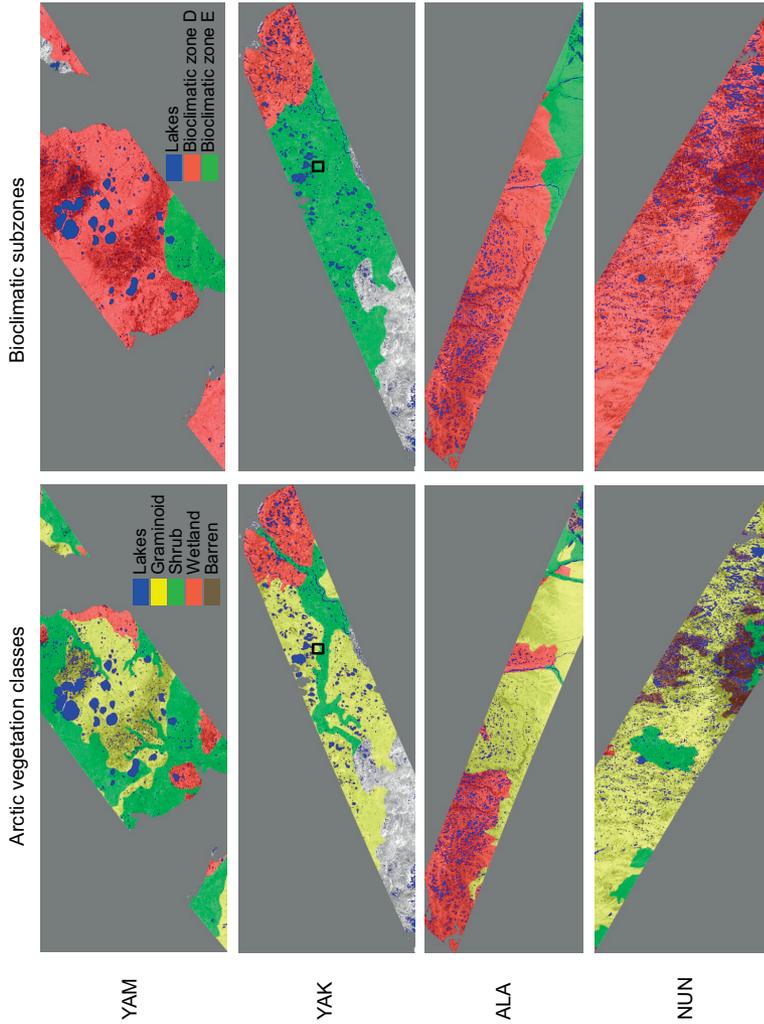
Leaf area index (LAI) was measured at 20 random points in each plot on 31 July 2009 using a SunScan canopy analysis system (SS1, Delta-T Devices, Cambridge, UK).

#### *Statistical analysis of field measurements*

Pearson's correlation coefficients ( $r$ ) were calculated between NDVI, albedo, LAI and *Betula nana* fractional cover, as measured in the experimental plots. Multiple linear regression analysis was used to assess how much of the variation in NDVI, albedo and LAI in the plots is explained by fractional cover of the dominant plant species and plant functional types. A step-wise model input sequence was used, whereby only significant plant species or functional types were added to the model. A mixed model analysis was used to determine differences in surface albedo between control and removal plots in the lakebed. Because surface albedo was measured pairwise in one control and one removal plot at a time, factor "pair" was included in the model as a random factor to take into account potential differences in surface



**Figure 4.1** Map showing the Arctic region in Lambert Azimuthal Equal-Area projection with the black dashed line depicting the Arctic Circle. Research areas are highlighted by the following colours: yellow (Indigirka lowlands, Yakutia, E-Siberia), bright green (Yamal peninsula, W-Siberia), red (Nunavut, Canada) and purple (North Slope, Alaska). Map background is derived from the National Snow and Ice Data Center (NSIDC) Atlas of the Cryosphere ([http://nsidc.org/data/atlas/atlas\\_info.html](http://nsidc.org/data/atlas/atlas_info.html)), Boulder, Colorado, USA (Maurer, 2007).



**Figure 4.2** Overview of the four research regions (YAM: Yamal, W-Siberia, YAK: Yakutia, E-Siberia, ALA: North Slope, Alaska, NUN: Nunavut, Canada) used in this study. Areas are shown in latitude/longitude grids, reprojected from the original sinusoidal projection. The images on the left side show vegetation classification maps based on the Circumpolar Arctic Vegetation Map (CAVM Team, 2003) with red: wetlands, green: shrub tundra, yellow: graminoid tundra, brown: barren tundra. The images on the right show the research areas with bioclimatic subzones classification based on summer warmth index (SWI) (CAVM Team, 2003) with red: subzone D (SWI 12-20 °C), green: subzone E (SWI 20-35 °C). All classification maps are projected onto 250-m resolution MODIS maxNDVI composite maps. The grey areas in the YAK maps do not fall into the Arctic zone and are excluded from analysis. Blue areas indicate lakes and rivers. The black squares in the YAK maps indicate the location of the Kytalyk research site where field measurements were made.

albedo between plot pairs caused by weather conditions. All data were checked for homogeneity of variance and normal distribution and natural-log transformed where necessary. Note that in graphs the non-transformed raw data are shown for better interpretation but in statistical analysis transformed data were used when necessary to meet assumptions of normality. SPSS v.17.0 was used for all statistical analysis.

## **Satellite and meteorological data**

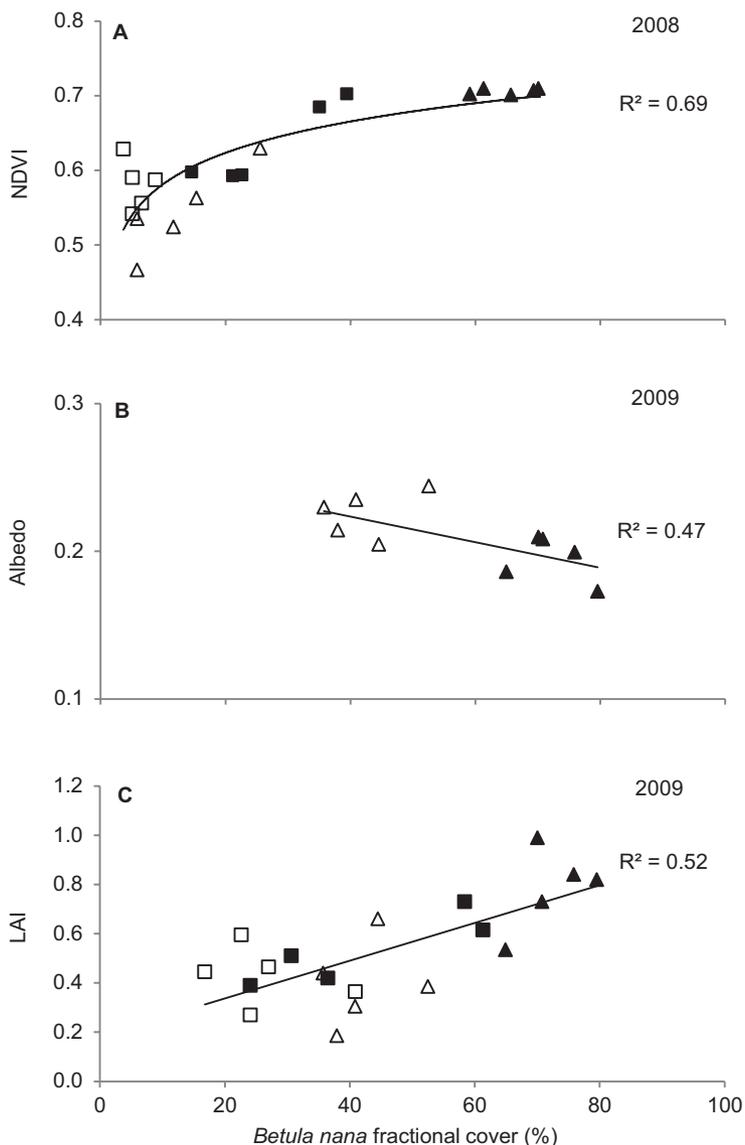
### *NDVI and albedo data*

For analyzing the relationship of annual growing season maximum NDVI, minimum albedo and meteorological station data, we selected a 200 by 200 km area in Yakutia, NE-Siberia centered on the coordinates of our field site (70°49`N, 147°28`E), along with three other low Arctic tundra areas that can be characterized as regions of plain landscapes (CAVM Team, 2003) . The other three similar-sized areas are located in the North Slope of Alaska (center pixel at 70°0`N, 154°0`W), in the Yamal peninsula, NW-Siberia (center pixel at 69°3`N, 70°0`E) and in the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada (center pixel at 67°0`N, 101°3`W) (Fig. 4.1). Hereafter, these regions will be referred to as YAK, ALA, YAM and NUN, respectively. All four areas are located within bioclimatic subzones D (summer warmth index (SWI) 12-20 °C) and E (SWI 20-35 °C) and are all characterized by a vegetation consisting of a mixture of the CAVM vegetation classes barren tundra, graminoid tundra, shrub tundra and wetlands (Fig. 4.2). Substrate soil chemistry is characterized in most part as slightly acidic to circumneutral (pH 5.5-7) for all four areas (Walker et al., 2005).

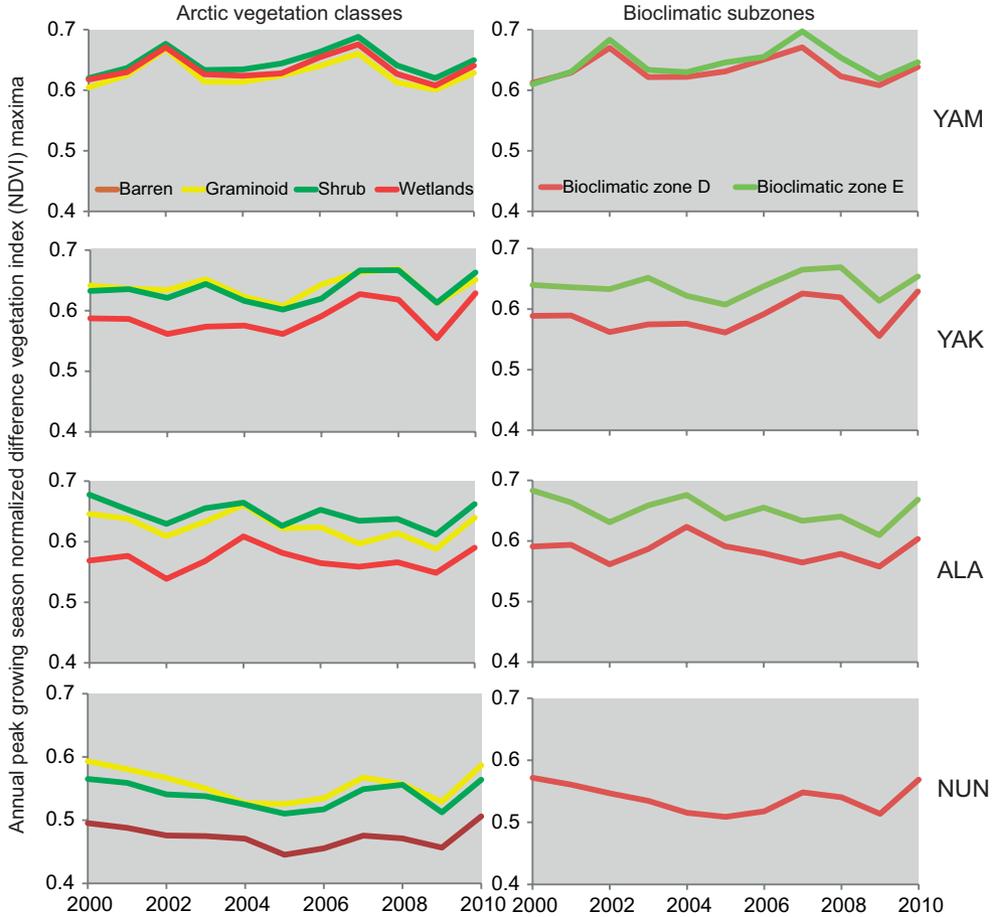
MODIS albedo, NDVI, and land cover data were obtained from the Oak Ridge National Laboratory (ORNL) Distributed Active Archive Center (DAAC) for biogeochemical dynamics using the MODIS subsetting tool (<http://daac.ornl.gov/MODIS/modis.shtml>), accessed January and February 2011. Sinusoidal projected NDVI and albedo Collection 5 data subset grids were acquired for the four low-Arctic tundra areas (Fig. 4.1) for the period 2000-2010. We used MODIS NDVI product MOD13Q1 (250 m spatial resolution, 16-days composites produced every 16 days) to compile annual maximum NDVI (maxNDVI) maps by selecting the maximum NDVI from the 16-days composites for each pixel (Holben, 1986).

We used the MODIS shortwave white-sky albedo (WSA) product MCD43A3 (500 m spatial resolution, 16-days composites produced every 8 days) that is quality-filtered by the subsetting tool. We constructed annual peak growing season minimum WSA (minWSA) maps by selecting the minimum WSA value between day of year (DOY) 193 and 225 for each pixel. This period (DOY 193-225: 12th July – 13th August) corresponded with the period when maxNDVI was reached at the peak of the growing season.

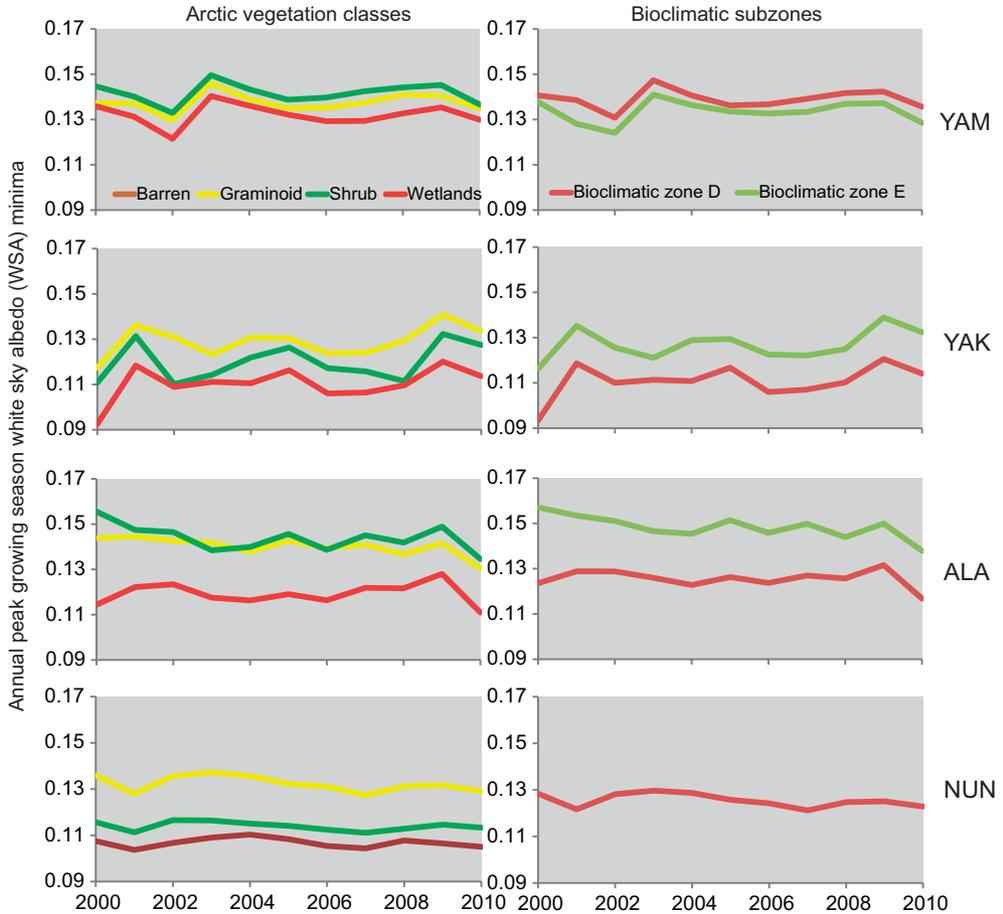
## Relation between shrub cover, NDVI and albedo



**Figure 4.3** Graphs showing A) normalized difference vegetation index (NDVI), B) surface albedo and C) leaf area index (LAI) plotted against *Betula nana* fractional cover, measured in 20 plots located in the Kytalyk nature reserve in NE-Siberia. Albedo (only lakebed plots) and LAI were measured during summer 2009 and NDVI was measured during summer 2008. *B. nana* fractional cover was measured during both summers by point intercept. Closed symbols indicate control plots with dense *B. nana* canopies and open symbols indicate removal plots with thin *B. nana* canopies. Squares represent plots at the ridge site; triangles represent plots at the lakebed site. Black lines indicate logarithmic (A) and linear (B, C) regression lines with coefficient of determination ( $r^2$ ) values.



**Figure 4.4** Regional annual normalized difference vegetation index maxima (maxNDVI) per Arctic vegetation class and bioclimatic subzone. The images on the left show maxNDVI values per Arctic vegetation class (red: wetlands, green: shrub tundra, yellow: graminoid tundra, brown: barren tundra) and the images on the right show regional maxNDVI values per bioclimatic subzone (green: subzone E, summer warmth index 20-35 °C), red: subzone D, summer warmth index 12-20 °C).



**Figure 4.5** Regional annual white sky albedo minima (minWSA) per Arctic vegetation class and bioclimatic subzone. The images on the left show minWSA values per Arctic vegetation class (red: wetlands, green: shrub tundra, yellow: graminoid tundra, brown: barren tundra) and the images on the right show annual minWSA values per bioclimatic subzone (green: subzone E, summer warmth index 20-35 °C), red: subzone D, summer warmth index 12-20 °C).

We used the 2005 MODIS land cover type 1 product MCD12Q1 (500 m spatial resolution) to mask out water body pixels, restricting further analysis to mostly vegetated pixels. Annual maxNDVI and peak growing season minWSA values were spatially averaged per vegetation class and bioclimatic subzone by projecting the circumpolar Arctic vegetation map and bioclimatic class descriptions (<http://www.geobotany.uaf.edu/cavm/>) onto the maxNDVI and minWSA layers. Only maxNDVI and minWSA data were analyzed that contained a representative number of pixels per vegetation class and bioclimatic subzone. This resulted in the exclusion of barren tundra in ALA and wetland tundra in NUN for further analysis.

#### *Meteorological station data*

Raw daily temperature data were obtained for all regions from regional meteorological stations. Meteorological station data were used instead of gridded satellite-derived temperature data, to ensure that completely independent data sets were compared against each other. We compared and combined two independent meteorological station records for areas without a centrally located meteorological station to provide an approximation of average regional climate. Only meteorological station data with a full data record (no missing days) were used in this study. As a result of this quality criterion, meteorological stations which were located closest to a research area but lacking a full data record were excluded from analysis. Instead, meteorological station data were then used from the second-closest station that could provide a full temperature data record (Table 4.1). Annual summer warmth index (SWI) values were calculated for each region as the annual sum of mean monthly temperatures above zero degrees Celsius.

#### *Statistical analysis of satellite and meteorological data*

Satellite-derived annual maxNDVI and minWSA were analyzed for trends over the available MODIS data period, 2000-2010. Regression slopes in maxNDVI, minWSA and monthly air temperature were calculated per region as well as per Arctic vegetation class and bioclimatic subzone. Linear mixed models were used to analyze how much of the inter-annual variation in maxNDVI and minWSA can be explained by variations in summer climate and to analyze how interannual variations in maxNDVI and minWSA were related to one-another. Hereto, data from all regions were combined with region specified as random factor. Pearson correlation coefficients  $r$  were calculated between annual peak-growing season maxNDVI, minWSA, and meteorological temperature data to analyze relationships between these variables. A correction for multiple testing was applied by using the false discovery rate procedure to control for type I errors for correlations with monthly temperature data (Verhoeven et al., 2005).

## Results

### *Field data: relation between shrub fractional cover, NDVI and albedo*

NDVI was positively related to *Betula nana* fractional cover ( $r^2 = 0.69$ ,  $p < 0.001$ ,  $n = 20$  plots), with highest NDVI values being measured in lakebed control plots and lowest NDVI values in lakebed removal plots (Fig. 4.3a). Larger differences in NDVI between control and removal plots were measured in the lakebed than in the ridge location because *B. nana* grows less dense in the ridge location and thus the removal effect was smaller in the ridge than in the lakebed. Together, *B. nana*, graminoid and moss fractional cover explained 82.7% of the variation in NDVI, as shown by multiple regression analysis (data not shown). NDVI values saturated at *B. nana* fractional cover values above 40%. Control and removal plots in the lakebed area differed significantly in surface albedo ( $p < 0.05$ ,  $n = 5$  plot pairs, Fig. 4.3b), with higher albedo values being measured in plots with a thin *B. nana* canopy. *B. nana* fractional cover explained 46.5% of the variation in albedo between plots. Fractional cover of species other than *B. nana* did not significantly improve the regression model explaining variation in albedo (not shown). LAI was positively related to *B. nana* fractional cover ( $r^2 = 0.52$ ,  $p < 0.001$ ,  $n = 20$  plots, Fig 4.3c), but showed no significant relationship with albedo.

### Satellite data

#### *NDVI and albedo relations with tundra vegetation class and bioclimatic subzone*

Annual maxNDVI values were found to be greatest in areas classified as shrub tundra, closely followed by graminoid tundra. Lowest maxNDVI values were observed in barren tundra (Fig. 4.4). In all areas we observed a large difference in annual maxNDVI between vegetation classes, except for Yamal (YAM), where no clear difference in maxNDVI between vegetation classes was observed. Neither did maxNDVI values differ much between bioclimatic subzones for the YAM area, in contrast to the two other Arctic regions with both bioclimatic subzones, Yakutia (YAK) and Alaska (ALA). There, we did see large differences in maxNDVI between bioclimatic subzones, with southern tundra areas showing consistently higher maxNDVI values than northern tundra areas.

Annual growing season minWSA generally followed the same pattern in differences between Arctic vegetation classes and bioclimatic subzones as maxNDVI, with the exception of graminoid tundra showing considerably higher minWSA values than the other Arctic vegetation classes for YAK and NUN. Lowest minWSA values were observed in barren and wetland tundra areas (Fig. 4.5), which is most likely due to the relative great proportion of water and bare soil in these areas. Unexpectedly, highest minWSA values were observed in the warmest bioclimatic subzones, which also had the highest maxNDVI.

**Table 4.1** List of meteorological station data used to compare against maxNDVI and minWSA for the period 2000-2010. Indicated are station names (WMO meteorological station numbers), coordinates, elevation and data sources.

Research area	Station name (WMO)	Station coordinates (lat, lon)	Station elevation (m)	Source
Yamal, W-Siberia (YAM)	Amderma (23022)	69°45'N, 61°42'E	49	1
	Berezovo (23631)	63°55'N, 65°3'E	32	1
Yakutia, E-Siberia (YAK)	Chokurdakh (21946)	70°37'N, 147°52'E	61	2
North Slope, Alaska (ALA)	Barrow (70026)	71°17'N, 156°37'W	4	1
Nunavut, Canada (NUN)	Imnaviat Creek	68°37'N, 149°18'W	930	3
	Cambridge Bay Airport (71925)	69°6'N, 105°7'W	27	1

1. National Climatic Data Center (NCDC), <http://www.ncdc.noaa.gov/>

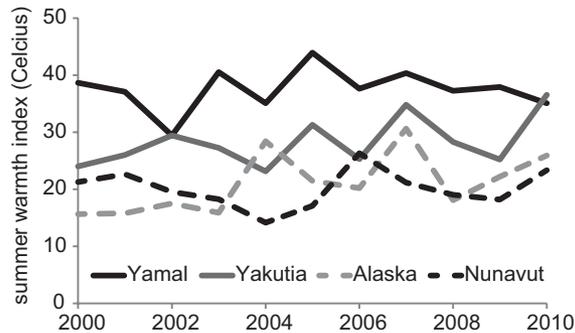
2. KNMI explorer, <http://climexp.knmi.nl/> (Klein Tank et al., 2002)

3. Natural Resources Conservation Service (NRCS), SNOTEL site 968, <http://www.wcc.nrcs.usda.gov>

**Table 4.2** Pearson's correlation coefficients of annual mean peak-growing season maximum normalized difference vegetation index (maxNDVI) and minimum white sky albedo (minWSA) per Arctic region with summer warmth index and mean summer monthly temperatures derived from meteorological stations listed in table 4.1. Asterisks indicate the significance levels of the correlations: # $p < 0.10$ , \* $p < 0.05$

	maxNDVI				minWSA			
	YAM	YAK	ALA	NUN	YAM	YAK	ALA	NUN
minWSA	-0.65*	-0.39	-0.62*	-0.23				
Summer warmth index	-0.30	0.47	0.10	0.43	0.53	0.10	-0.36	-0.56
<b>Monthly temperature</b>								
May	-0.03	0.72#	-0.15	0.09	-0.13	-0.07	-0.26	-0.15
June	0.31	-0.24	0.48	0.02	0.21	-0.03	-0.38	-0.30
July	0.13	0.27	-0.25	0.79*	0.10	0.30	-0.42	-0.52
August	-0.46	0.44	0.25	-0.05	0.72#	-0.14	-0.32	-0.26

A significant negative relationship between inter-annual variation in regional average growing season maxNDVI and minWSA ( $p < 0.01$ ) was observed when data from all regions were analyzed together using a mixed-model analysis. However, when data were analyzed separately per region, significant relations between maxNDVI and minWSA were observed only for ALA and YAM (Table 4.2).



**Figure 4.6** Shown are regional annual summer warmth index (SWI) values derived from temperature data from meteorological stations listed in table 1; grey line (Yakutia, E-Siberia), black line (Yamal peninsula, W-Siberia), dashed black line (Nunavut, Canada) and dashed grey line (North Slope, Alaska).

#### *Correlations with temperature*

When regional summer temperature and NDVI data were analyzed together, mixed-model results showed that variations in July temperature tended to correlate positively with maxNDVI ( $p = 0.066$ ). However, when data were analyzed separately per region, large differences in correspondence of maxNDVI and minWSA with monthly air temperature data were observed, with some regions showing a high correspondence with temperature and other regions showing no correspondence (Table 4.2). For NUN July temperature was most important to annual maxNDVI ( $r = 0.79$ ,  $p < 0.05$ ,  $n = 11$  years) whereas for YAK mean May temperature was most important to annual maxNDVI ( $r = 0.72$ ,  $n = 11$  years). No relationship between maxNDVI and mean monthly temperature was observed for YAM and ALA. Summer warmth index did not correlate significantly with maxNDVI for any region. For inter-annual variations in growing season minWSA there were no significant relations with summer temperature variables.

We did not detect any significant temporal trends in regional average maxNDVI during the period 2000-2010, neither did we detect trends in regional average minWSA for any of the four Arctic regions. In contrast, we did observe an increase in SWI, with positive trends observed for ALA ( $0.91$  SWI  $^{\circ}\text{C year}^{-1}$ ) and YAK ( $0.67$  SWI  $^{\circ}\text{C year}^{-1}$ ) (Fig. 4.6).

## **Discussion**

### *NDVI*

Previously, NDVI has been found to be a good measure for shrub photosynthetic biomass in Alaskan tundra (Kushida et al., 2009). Likewise, we observed a clear positive correlation between *B. nana* leaf fractional cover and NDVI in our

experimental plots. However, our results also indicated that NDVI saturates at *B. nana* fractional cover values above 40%. This NDVI saturation level corresponds closely to the saturation level of NDVI with biomass found by van Wijk and Williams (2005). Both studies therefore support the fact that NDVI may not be useful for detecting future shrub expansion in tundra areas that are already high in green shrub biomass.

Summer NDVI has been shown to spatially correspond with SWI for pan-Arctic vegetation based on satellite data of 1993 and 1995 (Raynolds et al., 2008). Jia et al. (2006) found a high positive temporal-spatial correlation of NDVI with SWI in two transects of the Alaskan North Slope from 1991-2000. We indeed observed greater maxNDVI values at lower Arctic latitudes, suggesting that peak growing season biomass is positively related to summer temperature. Furthermore, NUN showed a strong correspondence between maxNDVI and July temperature. For YAK, maxNDVI was mostly affected by early growing season temperature, suggesting that an increase in growing season length may also influence peak biomass. In contrast, we did not observe any significant temporal correspondence between maxNDVI and SWI inter-annual variation for any of the four regions studied for 2000-2010. Despite positive trends in summer temperature for YAK and ALA during the last decade, no trends in maxNDVI were detected, suggesting that vegetation growth may not linearly respond to changes in temperature. Another explanation for the lack of trends is that a saturation of the NDVI signal may have obscured an increase in plant biomass since maxNDVI values were close to NDVI saturation levels detected in the field. Of all regions studied, YAM showed least inter-annual variation in maxNDVI between vegetation classes and bioclimatic subzones. This may be a result of intensive reindeer grazing and/or other disturbance factors such as landscape erosion, resulting from increased permafrost thaw, affecting tundra vegetation and NDVI (Walker et al., 2009). Furthermore, YAM showed little inter-annual variation in summer temperature during the last decade, which may contribute to the low correspondence of maxNDVI with temperature in this region.

Several studies suggest that observed greening trends across the Arctic are related to an expansion of deciduous shrubs (Sturm *et al.*, 2001b; Jia *et al.*, 2003; Stow *et al.*, 2004; Tape *et al.*, 2006; Stow *et al.*, 2007; Jia *et al.*, 2009). Our analysis of satellite data shows that shrub tundra shows highest maxNDVI values of all vegetation classes, together with graminoid tundra. These results, combined with earlier observations of strong correlations between annual radial shrub growth and summer NDVI during recent decades (Forbes *et al.*, 2010; Blok *et al.*, 2011), support the hypothesis that tundra greening is related to increasing deciduous shrub growth but does not exclude the possibility that this greening may also be related to an increase in graminoid biomass.

### *Albedo*

It has been proposed that an increase in deciduous shrub cover in the Arctic as a response to increasing air temperatures may lead to a decrease in summer surface albedo and cause atmospheric heating, thereby potentially triggering a positive feedback loop leading to a further increase in shrub growth (Chapin et al., 2005). Taking NDVI as a proxy for green biomass and growth, we indeed observed a significant negative relationship between inter-annual variations in peak-growing season maxNDVI and minWSA, which supports the hypothesis that a temperature-driven increase in green biomass may lead to a reduction in summer albedo.

Unexpectedly, values of annual minWSA were on average higher in bioclimatic subzone E than in the cooler bioclimatic subzone D, suggesting that summer albedo does not linearly decrease with increasing summer temperature along a high to low Arctic tundra gradient. Albedo may be influenced more by non-photosynthetic landscape elements (*e.g.* water bodies, plant litter, bare ground) than temperature: towards the south, shrub fractional cover generally increases but fractional cover of water bodies decreases, which may explain the higher albedo values observed in southern tundra with relative high shrub fractional cover.

In line with this observation, we observed that peak growing season minimum albedo values are generally not lower in shrub tundra than in other tundra vegetation zones. For three out of four Arctic areas investigated, lowest albedo values occurred in wetland tundra. Even though we masked out large water bodies, sub-pixel scale inundated areas and soil moisture may have been larger in wetland tundra than in shrub tundra, resulting in a greater absorption of solar radiation by the relatively dark water and soil surface and causing lower albedo values. From the vegetation classification map it is evident that in more northern areas wetlands tend to dominate. Therefore, a northwards shift of shrub tundra, replacing wetland tundra, may not lead to a decrease in summer minimum albedo during the snow- and ice-free season. For the low-Arctic shrub tundra zones, our field data however suggest that a decrease in summer albedo can be expected with increasing shrub growth. Given the high temperature sensitivity of vegetation in the low-Arctic zone (Epstein *et al.*, 2004a), these areas may experience the most rapid vegetation transition towards shrub dominance with increasing temperature, triggering a positive warming feedback through decreasing albedo.

### **Acknowledgments**

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## **5. The cooling capacity of mosses: controls on water and energy fluxes in a Siberian tundra site**

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## **Abstract**

Arctic tundra vegetation composition is expected to undergo rapid changes during the coming decades because of changes in climate. Higher air temperatures generally favor growth of deciduous shrubs, often at the cost of moss growth. Mosses are considered to be very important to critical tundra ecosystem processes involved in water and energy exchange, but very little empirical data is available. Here, we studied the effect of experimental moss removal on both understory evapotranspiration and ground heat flux in plots with either a thin or a dense low shrub canopy in a tundra site with continuous permafrost in Northeast Siberia. Understory evapotranspiration increased with removal of the green moss layer, suggesting that most of the understory evapotranspiration originated from the organic soil layer underlying the green moss layer. Ground heat flux partitioning also increased with green moss removal indicating the strong insulating effect of moss. No significant effect of shrub canopy density on understory evapotranspiration was measured, but ground heat flux partitioning was reduced by a denser shrub canopy. In summary, our results show that mosses may exert strong controls on understory water and heat fluxes. Changes in moss or shrub cover may have important consequences for summer permafrost thaw and concomitant soil carbon release in Arctic tundra ecosystems.

## Introduction

Arctic tundra vegetation composition is expected to undergo rapid changes during the coming decades (ACIA, 2004) because of changes in climate (IPCC, 2007). Higher air temperatures generally favor growth of deciduous shrubs (Chapin *et al.*, 1995; Wahren *et al.*, 2005; Forbes *et al.*, 2010; Blok *et al.*, 2011), potentially at the cost of the understory moss and lichen vegetation. Moss growth may be reduced directly by higher air temperature because of the relative low temperature optima of mosses for photosynthesis (Hobbie *et al.*, 1999) or indirectly by increased shading by the shrub canopy and associated leaf litter (Chapin *et al.*, 1995; Hobbie & Chapin, 1998b; van der Wal *et al.*, 2005; Walker *et al.*, 2006). In contrast to negative effects of canopy density on moss growth, shading of the moss surface has also been found to benefit moss growth by alleviating photo-inhibition of photosynthesis (Murray *et al.*, 1993; Man *et al.*, 2008) and presumably also by reducing evaporation stress (Busby *et al.*, 1978). At the moment, the net effect of canopy density on moss growth and its response to future changes in climate and vascular plant composition is poorly understood.

Changes in moss growth may have important implications for tundra ecosystem processes (Lindo & Gonzalez, 2010). For example, mosses are considered to strongly control the exchange of water and energy between soil and atmosphere in Arctic tundra ecosystems (McFadden *et al.*, 1998; Beringer *et al.*, 2001; McFadden *et al.*, 2003; Beringer *et al.*, 2005). Because of their low thermal conductivity, mosses have a high insulating capacity, especially when they are dry and their tissue contains a large volumetric air fraction (O'Donnell *et al.*, 2009). Consequently, mosses can reduce the transfer of energy into the soil and thereby reduce soil temperature (Gornall *et al.*, 2007) and facilitate the presence of permafrost (Zimov *et al.*, 1995). Thus, a reduction in moss cover may have major implications for permafrost thaw (Gornall *et al.*, 2007) and concomitant soil carbon storage (Hollingsworth *et al.*, 2008) and release (Zimov *et al.*, 2006). Furthermore, mosses can control soil conditions and thereby influence ecosystem properties. In soils with thicker moss-organic mats, organic matter accumulation increases, soil moisture increases and nutrient availability decreases. Mosses may thus control the stand-structure in Arctic ecosystems (Gornall *et al.*, 2011).

Besides their capacity of thermal insulation, mosses may also cool the soil by water evaporation from their surface. Since mosses do not possess stomata to regulate their water transport, moss evaporation under conditions of sufficient soil moisture supply is regarded similar to evaporation of an open water surface (Lafleur, 1990; Lafleur *et al.*, 1992; Lafleur & Schreder, 1994). Evaporation of water from the moss surface results in an energy loss from the soil surface because of the latent heat flux involved with vaporization. Consequently, a reduction in soil moisture concentration under dry conditions may reduce moss evaporation and may lead to

an overall increase in ground heat flux (Boike *et al.*, 2008) and/or sensible heat flux. Furthermore, an increase in vascular plant cover density (*e.g.* shrub encroachment) may also decrease moss evaporation (Heijmans *et al.*, 2004b; Beringer *et al.*, 2005) and change tundra energy partitioning. Moreover, shrubs decrease the surface albedo by absorbing more solar radiation than shorter-statured tundra vegetation (Sturm *et al.*, 2005a). This may lead to atmospheric heating and thus result in a further increase in shrub growth, thereby potentially creating a positive feedback loop (Chapin *et al.*, 2005).

In summary, mosses are considered to be very important to critical tundra ecosystem processes such as water and energy exchange, but to which extent they control these processes is not well known. Here, we experimentally studied for the first time the influence of mosses on both evapotranspiration and ground heat flux in a tundra site in Northeast Siberia. Our research questions were:

- (i) What is the effect of moss cover on ground heat flux and evapotranspiration?
- (ii) What is the effect of shrub canopy density on moss controls on ground heat flux and evapotranspiration?

## Materials and methods

### *Site description*

The experiments in this study were conducted in the Kytalyk nature reserve (70°49`N, 147°28`E), 30 km Northwest of the town Chokurdakh in Northeast Siberia, Russia. The vegetation at the research site consists of a mixture of graminoids, forbs, mosses and shrubs and is classified as vegetation unit G4 (moist tussock-sedge, dwarf-shrub, moss tundra) and S2 (low-shrub tundra) at the Circumpolar Arctic Vegetation Map (Walker *et al.*, 2005). The subsoil is silty clay overlain by 10–15 cm of highly organic soil carpeted with a layer of moss approximately 4–5 cm thick. Regional climate data (Chokurdakh weather station (WMO station 21946, <http://climexp.knmi.nl/>), 1948–2006) show mean annual air temperatures of -13.9 °C and average July temperatures of 10.5 °C. The mean annual precipitation is 205 mm, most of which falls during the summer months, with July being the wettest month with an average precipitation of 32 mm (Klein Tank *et al.*, 2002).

### *Overall experimental design*

Our study setup consisted of two complementary experiments: in the first experiment, we studied the influence of moss and graminoid cover on evapotranspiration (henceforth called “evapotranspiration experiment”) and in the second experiment we studied the effect of moss cover on ground heat flux (henceforth called “ground

**Table 5.1** Plant species cover, determined using point intercept measurements during summer 2009, in experimental plots with a dense or a thin *Betula nana* canopy. Also shown are leaf area index values of the vascular vegetation, determined using a SunScan canopy analysis system.

Plot type	Dense <i>B. nana</i> canopy		Thin <i>B. nana</i> canopy	
<b>Growth form/species</b>				
Deciduous shrub	75.5 ± 3.6	**	48.9 ± 6.3	
<i>Betula nana</i>	72.3 ± 2.5	***	42.3 ± 2.9	
<i>Salix</i> spp.	3.2 ± 1.3		5.8 ± 3.0	
<i>Vaccinium uliginosum</i>	0.0 ± 0.0		0.7 ± 0.7	
Evergreen shrub	8.8 ± 2.3		13.1 ± 10.7	
<i>Ledum palustre</i>	0.4 ± 0.3		0.1 ± 0.1	
<i>Vaccinium vitis-idea</i>	8.3 ± 2.2		13.0 ± 10.8	
Graminoid	18.8 ± 1.7	*	33.4 ± 5.9	
Forbs	0.1 ± 0.1		1.3 ± 1.0	
Moss	83.6 ± 2.6		83.6 ± 2.9	
Lichen	26.7 ± 6.6		21.5 ± 3.7	
Total litter	70.8 ± 3.4	***	50.5 ± 0.8	
Leaf area index	0.78 ± 0.07	**	0.40 ± 0.08	

*Salix* species: *Salix pulchra*, *Salix fuscescens* and *Salix glauca*. Graminoid species: *Arctagrostis latifolia*, *Eriophorum vaginatum*, *Carex aquatilis* ssp. *stans*. 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., *Cladina* sp., *Cladonia* sp., *Sterocaulon* sp. and *Thamnolia vermicularis*. Data are means ± SE ( $n = 5$  plots) per plot type. All data are in percentage of the total number of grid points within the circular 10m diameter plots. Significant differences in plant species cover and leaf area index between plot types are shown \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

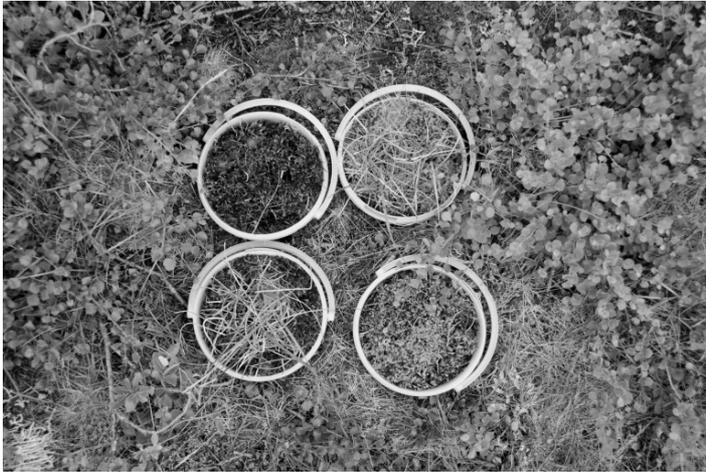
heat flux experiment”). As the measurements of ground heat fluxes by ground heat flux plates probably disturbs evapotranspiration, we conducted two separate experiments to exclude potential confounding effects of one measurement setup affecting the results of the other experiment. Both experiments were conducted in ten circular plots of 10 m diameter during the summer of 2009. A relatively large plot size was chosen to minimize the influence of surrounding vegetation on ground heat fluxes within the plots and to enable measurements to be made of net radiation (net sum of incoming minus outgoing shortwave and longwave radiation) within the plots. Plots were located in the former bed of a drained thermokarst lake. In this area, wet patches dominated by *Eriophorum angustifolium*, *Carex aquatilis*

*ssp. stans* and *Sphagnum* species alternate with slightly elevated patches that are dominated by dwarf birch (*Betula nana*). The plots used in this study were located within these *B. nana*-dominated patches. Plots were selected pairwise on the basis of their similarity in vegetation cover. During the summer of 2007, all *B. nana* was removed from one randomly chosen plot within each plot pair by cutting back all *B. nana* stems flush with the moss layer using a pruning shear (Blok *et al.*, 2010). In 2009, when we conducted the experiments described in this paper, regrowth of *B. nana* had occurred, but differences in *B. nana* canopy density remained (Table 5.1). Two plot types could thus be distinguished: plots with a thin *B. nana* canopy and plots with a dense *B. nana* canopy. Plant species cover in all plots was measured during the summer of 2009 by taking point intercept measurements on a grid (Table 5.1). The point intercept method that was used to measure plant species cover is described in detail in Blok *et al.*, 2010. Leaf area index of the vascular vegetation in plots was measured at approximately two cm above the moss layer during summer 2009 using a SunScan canopy analysis system (SS1, Delta-T Devices, Cambridge, UK) (Table 5.1).

## Evapotranspiration experiment

### *Lysimeter evapotranspiration*

We measured understory evapotranspiration using lysimeters that were created by placing vegetation columns with moss (non-*Sphagnum* moss, with dominant moss species *Aulacomnium palustre* and *Aulacomnium turgidum*) and sedge vegetation (*Carex aquatilis ssp. stans*, henceforth called “graminoid”) inside plastic buckets with a closed bottom and a height of 15.6 cm and a diameter of 16.3 cm. Vegetation and attached soil columns were cut from moist sedge-tundra patches that occur in between the plots to exclude the possibility of differences in moss conditions prior to the start of the experiment that may have been caused by the shrub removal treatment during summer 2007. Four of these filled lysimeters were installed per plot (5 plots with dense *B. nana* canopy, 5 plots with thin *B. nana* canopy), with a moss removal and graminoid removal treatment being applied in a full factorial setup in each plot, resulting in four lysimeter treatment groups: control treatment consisting of intact graminoid and moss vegetation, moss removal and leaving graminoid vegetation intact, graminoid removal and leaving moss vegetation intact, graminoid and moss removal. The top 2-3 cm of green moss tissue was removed by hand-plucking the green tissue until the red-brown organic layer underneath became visible (Fig. 5.1). Aboveground graminoid biomass was removed by cutting the leaves flush with the moss layer using a pair of scissors, leaving the belowground graminoid parts intact. Care was taken that the surface of the moss layer within the lysimeters was at level with the surrounding moss layer in the plots. Soil and plant material that was cut from within the plots to facilitate placement of the lysimeters in the ground was deposited outside of the plots.



**Figure 5.1** Photograph of a plot with a thin *Betula nana* canopy. Visible are four lysimeters with the following treatments: intact moss and graminoid, intact moss with graminoid removed, intact graminoid with moss removed, moss and graminoid removed. The diameter of the lysimeters is 16.3 cm.

Lysimeters were weighed every evening on an electronic weighing scale (1 gram precision) for a period of two weeks (between July 22<sup>nd</sup> and August 6<sup>th</sup> 2009) and evapotranspiration was calculated as mm water day<sup>-1</sup> by determining weight loss. Water inputs from precipitation, recorded by an electronic rain gauge, were deducted from calculated evapotranspiration rates (Fig. 5.2). To determine the relation between soil temperature and moss evaporation, we installed temperature loggers that recorded temperature hourly (SL52T, Signatrol Ltd, Gloucestershire, UK) at a depth of 2 cm below the moss surface in half (20) of the lysimeters. At the end of the experiment, plant dry weight in the lysimeters was determined by removing all green biomass and drying it at 70 °C for 48 hours (Table 5.2). Volumetric green moss water content was determined from the difference between fresh and dry weight. Moss biomass was not determined per species, but the identities of the dominant moss species in the lysimeters were noted (Table 5.2).

#### *Eddy covariance evapotranspiration*

Daily evaporative losses as measured by lysimeters were compared with larger-scale whole-ecosystem evapotranspiration rates measured as latent heat flux ( $W\ m^{-2}$ ) by eddy covariance instrumentation (R3-50 ultrasonic anemometer, Gill Instruments, Lymington, UK; Li-7500 infra-red gas analyzer, Licor, Lincoln, NE, USA), installed at a measurement height of 4.7 m above the moss surface (van der Molen *et al.*, 2007). Latent heat flux measurements were made at 10Hz intervals and calculated following the Euroflux methodology (Aubinet *et al.*, 2000) and gap filled using linear interpolation. The eddy covariance instrumentation was located at a distance

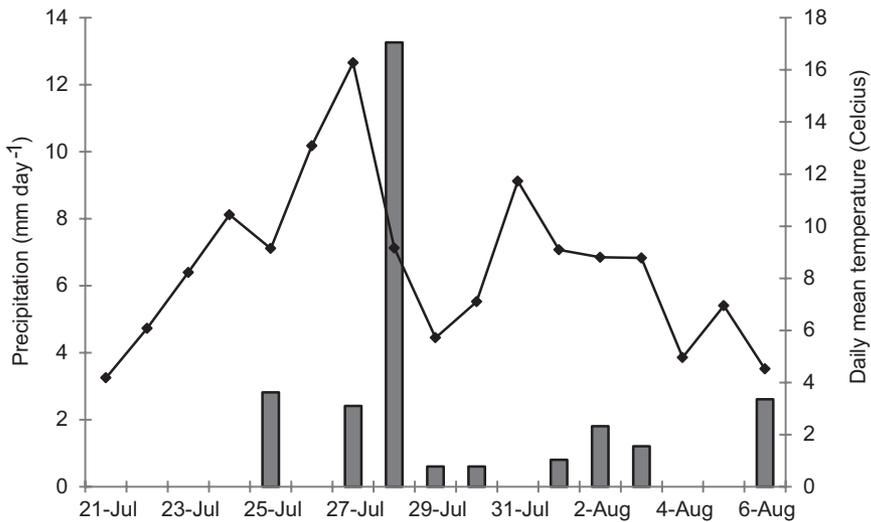
of 200-300 m from our experimental plots. The half-hourly latent heat flux values measured by eddy covariance were converted to evapotranspiration rates by dividing latent heat fluxes by an air temperature-specific latent heat of vaporization ( $L_p$ ) value between  $\pm 2440$  and  $2500 \text{ kJ kg}^{-1}$  water and was calculated by the following equation (Rogers and Yau, 1989):

$$L_p (\text{°C}): 6.14 \cdot 10^{-5} T^3 + 1.59 \cdot 10^{-3} T^2 - 2.36 T + 2500.79$$

Half-hourly evapotranspiration values were then summed to daily evapotranspiration values. Net radiation was measured by a net radiometer (Q7, Campbell Scientific, Logan, UT, USA, type) and air temperature was measured by a type-E chromel-constantan thermocouple (made at the Free University Amsterdam, The Netherlands), both variables being measured at the same height as the eddy covariance instrumentation.

### Ground heat flux experiment

Ground heat flux, net radiation, soil temperature and soil moisture were measured simultaneously in one plot pair at a time, with each plot pair consisting of a plot with dense *B. nana* canopy and a plot with thin *B. nana* canopy (Table 5.1). Measurements were made in each plot pair for 5 consecutive days, after which the instrumentation was removed and installed in another plot pair. The two flux instrumentation systems were alternately placed in plots with dense or thin *B. nana* canopy to avoid any potential measurement bias caused by differences and/or inaccuracies in instrumentation (Eugster *et al.*, 1997). All 5 plot pairs were measured during July and early August 2009. Soil moisture was measured in each plot by two ML2x theta-probes (Delta-T Devices, Cambridge, UK). For the ground heat flux measurements, per plot six ground heat flux plates (HFPO1, Hukseflux, Delft, the Netherlands) were inserted in the soil at a depth of 8 cm: using a sharp knife, soil columns with a surface area of approximately 20 by 20 cm were cut out. An incision was made horizontally into one side of the soil pits and the 8 cm-diameter heat flux plates were inserted, ensuring they were in good contact with the soil. The ground heat flux plates contain a thermopile sensor that measures the temperature gradient over the plate and generates a voltage output from which the ground heat flux is calculated. For half of the six heat flux plates per plot, the live green moss tissue was removed from the soil directly above the heat flux plates for an area measuring 25 x 25 cm. The removed green moss biomass was dried at 70 °C for 48 hours and dry weight was determined. Above each ground heat flux plate, thermistors (T107, Campbell Scientific, UK) were installed at depths of 2 and 5 cm below the top of the moss surface to measure soil temperature and calculate the ground heat storage in the soil layer above the ground heat flux plates. For ground heat flux plates that were placed in soils from which moss was removed, only one thermistor was installed above the



**Figure 5.2** The black squares represent daily average temperature and the grey bars represent daily sums of precipitation during the summer of 2009, when the evapotranspiration experiment was conducted. Temperature and precipitation data were recorded by the meteorological station at the research site.

flux plate, at a depth of 5 cm below the original top level of the moss layer. Total ground heat flux was calculated by summing the ground heat flux measured by the heat flux plates at 8 cm depth with the ground heat storage in the soil layer above the ground heat flux plates, as described in detail in Blok *et al.*, 2010. Net radiation was measured in each plot at approximately 85 cm above the moss surface using a CNR2 net radiometer (Kipp & Zonen B.V., Delft, the Netherlands), covering an area of approximately 32 m<sup>2</sup> within the plots for the lower short- and longwave radiation sensors that have a viewing angle of 150°. The fraction ground heat flux of net radiation (the proportion of net available energy in the ecosystem that is used to heat the ground) was calculated and analyzed from net radiation and ground heat flux data, since this fraction is less sensitive to changes in weather conditions than the absolute ground heat flux values. All measurements were made at 2-second intervals. Ten-minute-averages and standard deviation data were calculated and stored by a datalogger (CR1000, Campbell Scientific, UK), wired to a multiplexer (AM 16/32, Campbell Scientific, UK). Averages for 30 minutes were calculated for all fluxes.

#### *Data analysis*

Lysimeter evapotranspiration data were analyzed by a mixed-model with lysimeter treatment (moss and graminoid removal) and plot type (dense or thin *B. nana*

**Table 5.2** Aboveground plant dry biomass in lysimeters during the evapotranspiration experiment, shown separately per species group (moss, graminoid), plot type (dense or thin *Betula nana* canopy density) and lysimeter treatment (intact graminoid and moss, intact moss with graminoid removed, intact graminoid with moss removed). All values are in g dry plant biomass m<sup>-2</sup> ± SE (*n* = 5 plots). No significant differences in graminoid and moss biomass were observed between lysimeter treatments and plot types (*p* > 0.05).

Species group	Plot type	Lysimeter treatment		
		Graminoid+Moss	Graminoid removal	Moss removal
Moss	dense <i>B. nana</i>	475 ± 40	447 ± 40	
	thin <i>B. nana</i>	544 ± 88	464 ± 52	
Graminoid	dense <i>B. nana</i>	19 ± 8		35 ± 11
	thin <i>B. nana</i>	37 ± 10		38 ± 7

Moss species include *Aulacomnium palustre*, *Aulacomnium turgidum*, *Dicranum spp.*, *Polytrichum strictum*, *Ptidilium ciliare*, *Sanionia unicata*, *Tomentypnum nitens* and some *Sphagnum spec.* *Carex aquatilis ssp. stans* was the only graminoid species present inside the lysimeters.

**Table 5.3** Results of a mixed-model analysis, testing the effects of lysimeter treatments (graminoid removal, moss removal) and plot type (dense or thin *Betula nana* canopy) on evapotranspiration during a two-week period during the summer of 2009.

Explanatory variables	df	F	Sig.
Plot type	1	0.142	0.709
Graminoid removal	1	0.226	0.638
Moss removal	1	16.385	<0.001
Plot type x graminoid removal	1	0.838	0.367
Plot type x moss removal	1	0.029	0.866
Graminoid removal x moss removal	1	1.646	0.209
Plot type x graminoid removal x moss removal	1	2.162	0.151

canopy) as explanatory variables and plot as random variable. Measurement time (lysimeters were weighed on 13 dates between July 22<sup>nd</sup> and August 6<sup>th</sup> 2009) was indicated as a repeated variable, to avoid temporal pseudo-replication. Daily lysimeter evapotranspiration rates were compared to daily net radiation, air temperature and daily tundra evapotranspiration by calculating Pearson's correlation coefficients (*r*). Analyses of evapotranspiration data were performed using SPSS 17.0 for Windows.

Mixed-model analyses were performed on five-daily average ground heat flux fractions of net radiation, taking into account the spatial split-plot design: each

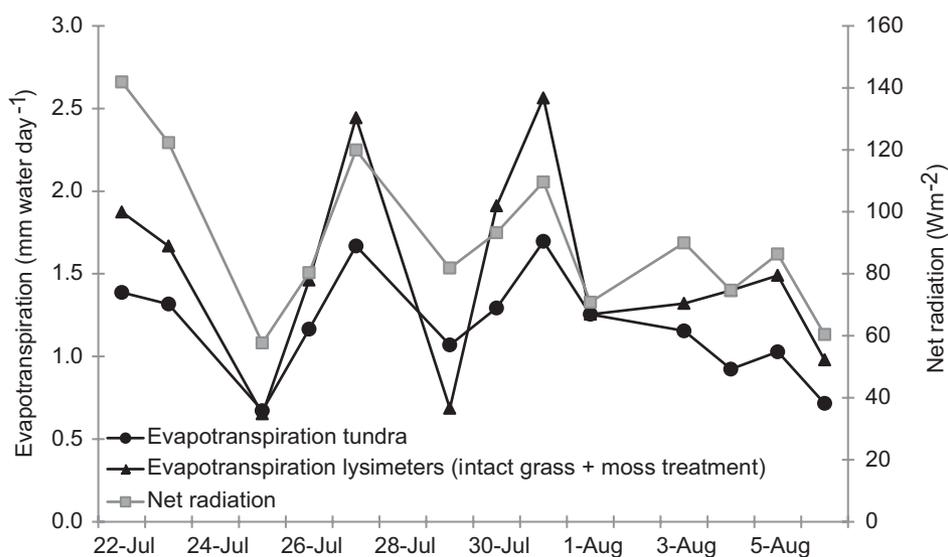
of the in total five plot pairs consisted of a plot with a thin *B. nana* canopy and a plot with a dense *B. nana* canopy, with ground heat fluxes being measured at six locations at a time within each plot, both in soils with and without a moss layer (resulting in three subplots per moss treatment per plot). Using this analysis, both the plot pairing and the spatial pseudo-replication of multiple ground heat flux measurements per plot type per moss treatment were taken into account. Different models with and without one of the two explanatory variables included (plot type, moss removal), were compared against each other for model-fit using chi-square tests of independence. Explanatory variables were considered to have a significant effect on the fraction ground heat flux of net radiation when model fits differed by  $p < 0.05$  from each other (Crawley, 2007). Mixed model analyses of ground heat flux fractions were performed using R v. 2.11.1. (R Development Core Team, 2008), using lme4 package for mixed-model analysis (Bates & Maechler, 2009).

## Results and Discussion

### Evapotranspiration experiment

Understory evapotranspiration rates as measured by the lysimeters were compared with daily tundra evapotranspiration, as measured by eddy covariance (Fig. 5.3). A strong correlation was found between daily average understory evapotranspiration measured by lysimeters (intact graminoid and moss treatment) and tundra evapotranspiration measured by eddy covariance ( $r = 0.92$ ,  $p < 0.001$ ,  $n = 13$  days), with understory evapotranspiration rates ranging between 0.7 and 2.4 mm day<sup>-1</sup> and tundra evapotranspiration rates ranging between 0.7 and 1.7 mm day<sup>-1</sup>. We measured a relative large variability in daily average understory evapotranspiration (intact graminoid and moss treatment), which was closely linked to daily variations in net radiation ( $r = 0.74$ ,  $p < 0.01$ ,  $n = 13$  days; Fig. 5.3), as was previously observed for moss evaporation in an Alaskan boreal forest (Heijmans *et al.*, 2004a).

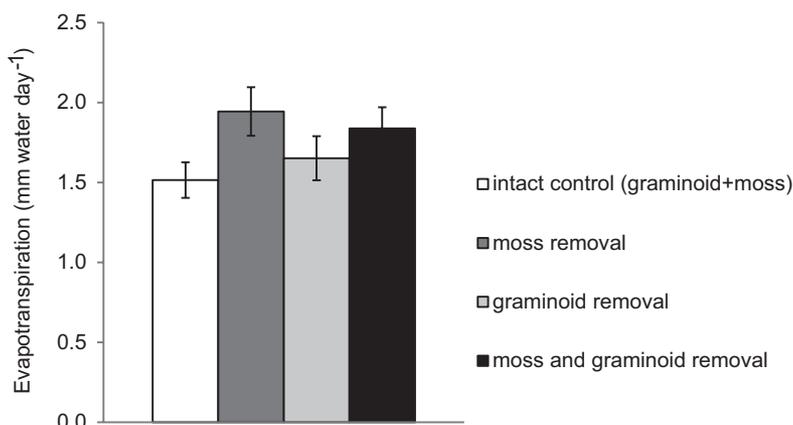
Rates of evapotranspiration differed significantly between lysimeter treatments, but were not affected by *B. nana* canopy density (Table 5.3). Two lysimeter treatment groups could thus be distinguished on basis of their evapotranspiration rates: lysimeters with and without a green moss layer ( $p < 0.001$ ,  $n = 20$ ). Overall, removal of the green moss layer increased evaporative losses by 19% in comparison to lysimeters with an intact green moss layer (Fig. 5.4). Apparently the live green moss layer acted as a barrier for water exchange from the underlying red-brown organic layer with the atmosphere. This suggests that mosses may suppress understory evapotranspiration, even though they lack stomatal control and are considered to evaporate freely (McFadden *et al.*, 2003). The effect of moss removal on understory evapotranspiration may be driven by several processes. First, the sheltering of the organic layer by an intact green moss layer may have limited total



**Figure 5.3** The black line and triangles represent daily average evapotranspiration rates measured by lysimeters with intact graminoid and moss vegetation ( $n = 10$  lysimeters). Black line and circles represent daily average tundra evapotranspiration, measured by eddy covariance technique. The grey line and squares represent daily average tundra net radiation, as measured by a radiometer on the eddy covariance tower. Note that lysimeters were not weighed on July 24<sup>th</sup>, July 28<sup>th</sup> and August 2<sup>nd</sup> and therefore evapotranspiration rates for these dates were averaged with evapotranspiration rates of the following day.

understory evaporation (green moss evaporation and organic soil evaporation) due to a reduced vapor pressure gradient between the lower moss layer and the air, thereby mainly reducing evaporation of the lower organic soil layer. Second, green moss evaporation may have been limited by soil water supply from the organic soil (Douma *et al.*, 2007), although the frequent precipitation events ensured that the top green moss layer remained moist throughout the experiment. Finally, the relatively dark surface of the remaining organic soil layer in lysimeters from which the green moss tissue was removed (Fig. 5.1) could have decreased the surface albedo and may have caused an increase in energy available for evaporation.

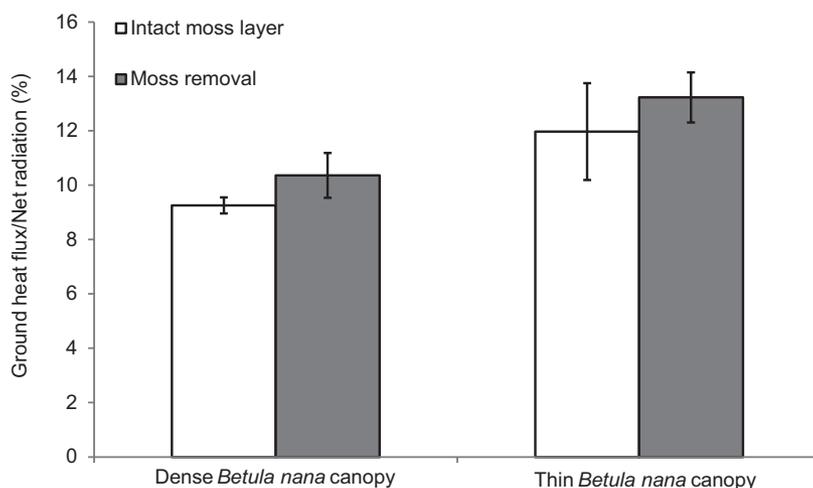
No significant differences in soil temperature were measured at 2 cm depth between lysimeter treatments and between plot types ( $p > 0.05$ ,  $n = 3$  temperature loggers per lysimeter treatment per plot type; data not shown), with daily average soil temperatures ranging between 5°C and 16°C. The observed increase in evaporation with moss removal may have dissipated the potential surplus in absorbed solar energy away from the red-brown organic surface, thereby preventing soil warming. Graminoid clipping did not significantly affect evapotranspiration in our lysimeters



**Figure 5.4** Comparison of daily average evapotranspiration rates between lysimeter treatments during the summer of 2009 (average of 13 measurement dates between July 22<sup>nd</sup> and August 6<sup>th</sup>). Lysimeter treatments consisted of four treatment groups: white bar: intact graminoid and moss vegetation, dark grey bar: graminoid with moss removed, light grey bar: moss with graminoid removed, and black bar: moss and graminoid removed. Data are mean values ( $n = 10$  lysimeters)  $\pm$  SE. Different symbols indicate the significant effect of the moss removal treatment ( $p < 0.001$ ; Table 5.3).

(Table 5.3). This may have been caused by the relatively small amount of aboveground graminoid biomass in the lysimeters (Table 5.2). However, it may also have been caused by their contrasting potential effects on evapotranspiration: on the one hand, graminoids may increase evapotranspiration by transpiration through the graminoid leaf stomata and on the other hand, graminoids may decrease understory evapotranspiration through shading and sheltering of the moss surface, thereby reducing moss evaporation.

Previous studies showed that an increase in canopy density may decrease moss evaporation (Heijmans *et al.*, 2004b; Beringer *et al.*, 2005), but we found no significant effect of plot type (dense or thin *B. nana* canopy density) on understory evapotranspiration in our experiment (Table 5.3). This may have been caused by the cloudy summer conditions during the course of our experiment which may have limited canopy shading effects. We used rainfall data from an electronic rain gauge standing in an open location without canopy sheltering for determining evapotranspiration in the lysimeters. It is possible that lysimeters in plots with different canopy densities have received a slightly different amount of rainfall due to potential differences in rain interception by the shrub canopy. However, when only days without precipitation events were taken into account, an effect of canopy density on understory evapotranspiration could still not be detected ( $p >$



**Figure 5.5** Comparison of average ground heat flux fractions of net radiation. The fraction ground heat flux of net radiation was measured in five plot pairs, with each plot pair consisting of a plot with a dense *Betula nana* cover and a plot with a thin *B. nana* canopy. White bars represent measurements within plot patches with an intact green moss layer and grey bars represent measurements in plot patches from which the green moss layer was removed. Data are averages of five-day period measurement means ( $n = 5$  plot pairs)  $\pm$  SE. Asterisks indicate significant ( $p < 0.05$ ) effects of moss removal and *B. nana* canopy density on the ground heat flux fractions of net radiation.

0.05; data not shown). Our values of understory evapotranspiration are comparable with moss understory evapotranspiration rates measured in an Alaskan open bog location (Heijmans *et al.*, 2004b), tundra ecosystem evapotranspiration in Alaska (McFadden *et al.*, 2003) and Siberia (Boike *et al.*, 2008), and with boreal peatland evapotranspiration in Finland (Wu *et al.*, 2010). On average, understory evapotranspiration as measured by lysimeters with intact graminoids and mosses exceeded tundra evapotranspiration by 26%, especially during sunny days with relatively high amounts of incoming solar radiation (Fig. 5.3). At the study site the *B. nana* shrub canopy is only 10-20 cm tall, which makes it likely that the understory contributes greatly to whole-ecosystem evapotranspiration. However, our values of understory evapotranspiration may not be representative for average tundra understory evapotranspiration, since moss moisture levels in our lysimeters were relatively high throughout the experiment. Volumetric green moss water content in the lysimeters was on average 67% at the start of the experiment (moss removal treatments) and 80% at the end of the experiment (intact moss layer treatments). Therefore, moss evaporation in our lysimeters presumably was not water-limited during relative warm periods, which may be in contrast to a potential limited understory evapotranspiration in most parts of the tundra within the eddy

covariance tower footprint. Nevertheless, daily patterns in evapotranspiration measured by lysimeter and eddy covariance corresponded well and give confidence to our lysimeter method for measuring daily understory evapotranspiration.

### Ground heat flux experiment

Moss biomass did not differ between plots with dense or thin *B. nana* canopies ( $p > 0.05$ ). The average green dry moss biomass that was removed from plots with a dense *B. nana* canopy was  $561 \pm 55 \text{ g m}^{-2}$  and  $526 \pm 40 \text{ g m}^{-2}$  for plots with a thin *B. nana* canopy. These values are within the range of green moss biomass values reported for shrub tundra in Toolik Lake, Alaska (Shaver & Chapin, 1991; Hobbie *et al.*, 1999). The portion of available energy in the ecosystem (incoming - outgoing radiation) that was partitioned into soil heating (fraction ground heat flux of net radiation) was on average 11.1% higher in patches without a green moss layer compared to patches with an intact moss layer ( $\chi^2 = 3.85, p < 0.05$ ). This difference is likely caused by the insulation provided by the porous uppermost green moss layer, thereby reducing the thermal heat transfer between air and soil. This insulating effect of mosses was also found by Gornall *et al.* (2007) and Van der Wal and Brooker (2004), who recorded lower temperatures under thick moss mats than under shallow moss mats. On average, daily values of fractionation of net radiation into ground heat flux were 9.8% for plots with dense *B. nana* canopy and 12.6% for plots with thin *B. nana* canopy (Fig. 5.5). These values are similar to values reported for other tundra sites in Alaska (McFadden *et al.*, 1998; Eugster *et al.*, 2000; Beringer *et al.*, 2005) and Siberia (Boike *et al.*, 2008). No interaction between moss removal and *B. nana* canopy density was observed.

On average, net radiation was  $7 \text{ W m}^{-2}$  higher in plots with a dense *B. nana* canopy ( $110 \pm 10 \text{ W m}^{-2}$ ) compared to plots with a thin *B. nana* canopy ( $104 \pm 7 \text{ W m}^{-2}$ ). The higher net radiation values measured in plots with dense *B. nana* cover are probably caused by the higher absorbance of solar radiation by the greater leaf area, leading to a lower surface albedo in plots with higher *B. nana* canopy density. This increase in net radiation did not result in significantly higher absolute ground heat flux values in plots with a dense *B. nana* canopy ( $p > 0.05$ ; data not shown). Instead, the partitioning of net radiation into ground heat flux was smaller in plots with a dense *B. nana* canopy compared to plots with a thin *B. nana* canopy ( $\chi^2 = 4.41, p < 0.05$ ; Figure 5.5). With a denser *B. nana* canopy, leaf area index increased (Table 5.1), which reduced the amount of solar radiation penetrating to the moss and soil surface. This is in agreement with our previous study which showed that an increase in shrub canopy density may reduce ground heat flux and lead to a decrease in summer permafrost thaw (Blok *et al.*, 2010). No interaction between shrub canopy density and moss removal was observed ( $p > 0.05$ ). Model studies and field data show that Arctic vegetation composition may change during the coming decades,

with shrubs increasing and mosses decreasing with climate warming (Epstein *et al.*, 2004b; Tape *et al.*, 2006; Olofsson *et al.*, 2009). Our results show that a decrease in moss cover may increase partitioning of net radiation into ground heat flux through loss of soil insulation, but that this increase in ground heat flux fractionation may be compensated by an increase in shrub canopy density and concomitant soil shading which may lead to soil cooling (Fig. 5.5). It is thus uncertain how future vegetation changes will influence soil thermal conditions and thawing of permafrost in Arctic ecosystems.

Changes in storage and release of heat in the upper soil layer above the heat flux plates only contributed about 0.5% to the total ground heat flux on a 24-hour basis (data not shown). The average amplitude between daily minimum and maximum ground heat flux increased from 25.1 W m<sup>-2</sup> for patches with moss cover to 28.0 W m<sup>-2</sup> for patches without moss cover in dense *B. nana* canopy plots. For plots with a thin *B. nana* canopy, the amplitude between daily minimum and maximum ground heat flux values increased from 28.3 W m<sup>-2</sup> for patches with moss cover to 32.3 W m<sup>-2</sup> for patches without moss cover.

### **Evapotranspiration vs. ground heat flux**

Daily evaporative water loss as measured by the lysimeters is equivalent to a latent heat flux which can be expressed in W m<sup>-2</sup>. In terms of absolute energy flux differences, removal of the green moss tissue caused an increase in latent heat (8.8 W m<sup>-2</sup>) that was much larger than the corresponding increase in ground heat flux (1.3 W m<sup>-2</sup>). The increase in ground heat flux with moss removal was most likely due to an increase in soil thermal conductivity but was partly compensated by an increase in understory evapotranspiration with moss removal. This corresponds with energy exchange measurements from a burned site in Alaska, where a fire-induced decrease in moss cover increased understory evapotranspiration and thereby compensated for the warming effect from a reduction in surface albedo, resulting in an overall small surface warming (Rocha & Shaver, 2011b). During evapotranspiration, energy is conducted from the soil surface to the air and creates a negative soil heat flux, thereby cooling the soil. Nevertheless, the moss removal treatment resulted in an overall greater partitioning of net radiation into ground heat flux, suggesting that the insulating effect of the green moss layer was of greater influence on the partitioning of net radiation into ground heat flux than the reduction of understory evapotranspiration by the green moss layer.

Weather conditions during the course of our experiments were relatively cool and wet. The frequent precipitation events ensured that the moss layer remained moist, so understory evapotranspiration was probably not limited by insufficient moisture supply (Admiral & Lafleur, 2007). Under drier summer conditions, moss evaporation may have been reduced, which could have increased the fractionation of net radiation into ground heat flux. In contrast, the insulating effect of mosses is

greater when the moss layer is dry and contains a relatively large air fraction, which decreases the moss thermal conductivity (O'Donnell *et al.*, 2009) and therefore may decrease the ground heat flux (Beringer *et al.*, 2001). Moisture conditions of the moss tissue thus likely determine whether mosses may achieve soil cooling during summer in most part by thermal insulation or by evaporation.

## Conclusions

Understory evapotranspiration increased with removal of the green moss layer, suggesting that most of the understory evaporation originated from the denser moss-organic layer underlying the green moss layer. Partitioning of net radiation into ground heat flux also increased with green moss removal, which may indicate that soil heat losses by increased understory evapotranspiration were smaller than the increase in soil heat input by a reduction in soil insulation with moss removal. Furthermore, our results suggest that this increase in ground heat flux partitioning with moss removal may be partly compensated by an increase in soil shading by a denser shrub canopy, since we observed lower ground heat flux fractions in plots with denser *Betula nana* cover. In summary, our results show that mosses may exert strong controls on understory water and heat fluxes in Arctic tundra ecosystems and suggest that changes in moss cover may have important consequences for summer permafrost thaw and the tundra soil carbon balance.

## Acknowledgments

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## **6. Summer permafrost thaw depth related to vegetation composition in a Siberian tundra site**

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## **Abstract**

The Arctic is expected to experience severe climatic changes during the coming decades. With increasing air temperature, tundra ecosystems are expected to shift towards more shrub-dominated vegetation, potentially at the cost of lichen and moss vegetation. Arctic vegetation can greatly affect summer permafrost thaw depth through soil insulation by mosses and soil shading by the canopy. Here, we determined the relationship between vegetation composition and summer permafrost thaw depth by measuring vegetation and soil characteristics along transects in a low-Arctic tundra site in NE-Siberia with continuous permafrost. We clustered transect sample points on basis of their vegetation composition using ordination techniques and could thus distinguish four distinct vegetation classes, subsequently increasing in soil moisture: dry tussock evergreen shrub, moist deciduous shrub, moist *Sphagnum*-sedge and wet sedge pools. Shallowest permafrost thaw depth was measured in deciduous shrub vegetation dominated by *Betula nana* with high leaf area index and deepest permafrost thaw was measured in wet sedge vegetation dominated by *Eriophorum angustifolium*. Furthermore, permafrost thaw depth showed a significant inverse relationship with *B. nana* cover. With denser *B. nana* canopies, the amount of solar radiation penetrating to the soil surface is reduced, thereby lowering permafrost thaw depth. These results suggest that an expansion of deciduous shrubs may partly buffer against the effects of climate warming on permafrost thaw.

## Introduction

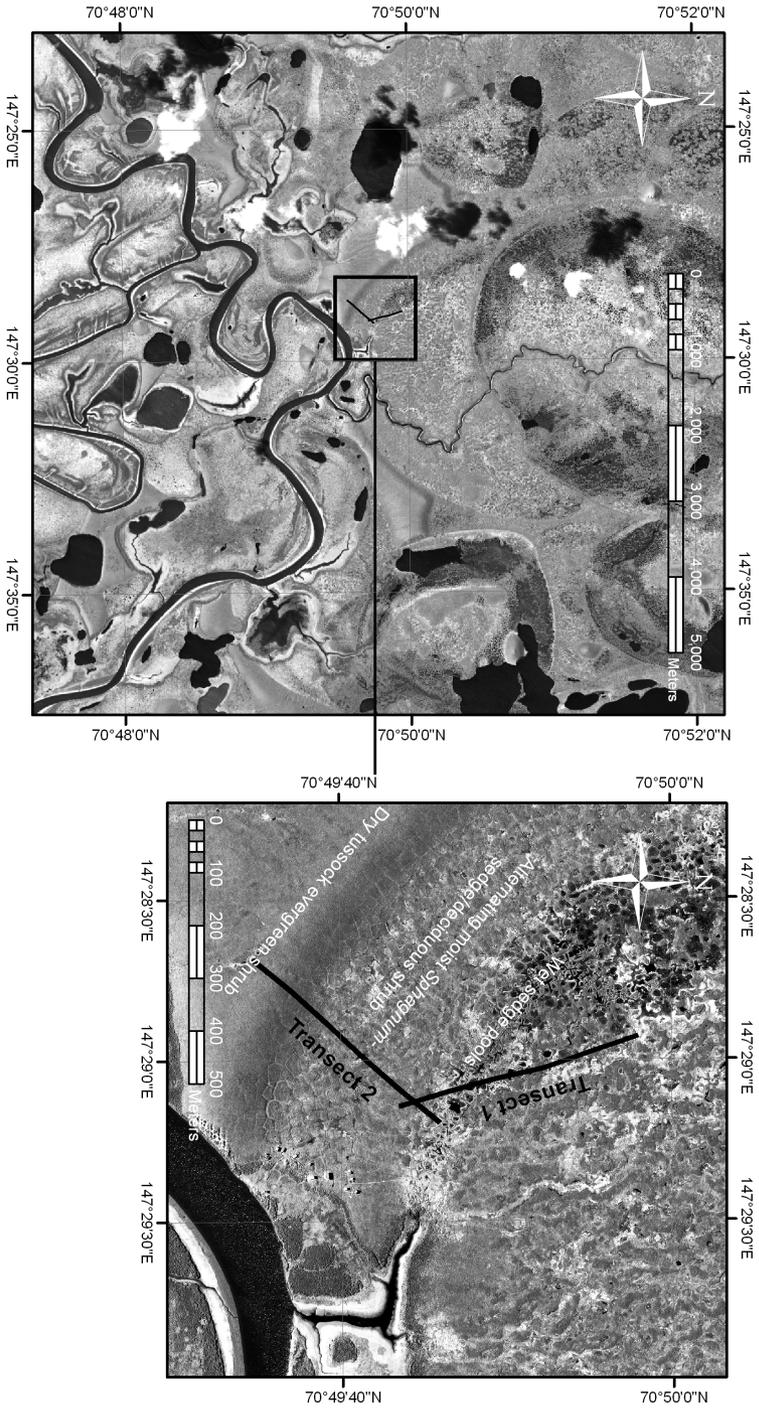
The Arctic region is expected to experience severe changes in climate during the coming decades (IPCC, 2007) that will likely have great impacts on high-latitude ecosystems (ACIA, 2004, Post *et al.*, 2009). Climatic changes may impact the exchange of water and energy in tundra ecosystems, with consequences for permafrost thaw depth (Romanovsky *et al.*, 2010) and concomitant soil carbon release to the atmosphere (Dorrepaal *et al.*, 2009, Schuur *et al.*, 2009, Zimov *et al.*, 2009). With increasing air temperatures, the tundra ecosystem is expected to shift towards more shrub-dominated vegetation, potentially at the cost of lichen and mosses (Walker *et al.*, 2006). Arctic vegetation may have great effects on summer permafrost thaw depth (Anisimov *et al.*, 2002) through insulation of the underlying permafrost by mosses (Gornall *et al.*, 2007) and soil shading by the shrub canopy (Blok *et al.*, 2010). Both soil insulation and soil shading reduce the fractionation of solar radiation into ground heat flux and thus reduce the amount of energy available for permafrost thaw. Strong relations between vegetation composition and permafrost thaw depth have been observed. For example, a large-scale observational study in Alaska showed strong differences in permafrost thaw depth, also referred to as the active layer thickness (ALT), between vegetation types along a gradient from shrub-dominated to barren tundra (Nelson *et al.*, 1997). However, not just vegetation composition changes along these vegetation gradients, but regional climate as well. This complicates the evaluation of the direct effects of vegetation composition on ALT since air temperature and vegetation are both crucial factors determining ALT (Anisimov *et al.*, 1997, Zhang & Stamnes, 1998, Anisimov *et al.*, 2002). For example, higher air temperatures from northern to southern tundra may promote an increase in vegetation biomass and thereby obscure the effect of air temperature on ALT through an increase in permafrost insulation by vegetation (Walker *et al.*, 2003b).

Here, we determined the relationship between vascular and non-vascular plant species composition and ALT along transects in a Northeastern Siberian tundra site under similar climate. We used ordination techniques to cluster transect sample points into classes on basis of their vegetation composition. Furthermore, we evaluated how ALT was related to the variables leaf area index (LAI), moss thickness, vegetation height and organic layer thickness, and compared differences between vegetation classes.

## Materials & methods

### *Site description and measurements*

Measurements were made in a low-Arctic tundra site within the Kytalyk nature reserve in NE-Siberia, Russia (70°49`N, 147°28`E). The research site is located on the North bank of the Berelekh (Yelon) River, a tributary of the Indigirka River,



**Figure 6.1** GeoEye satellite image of the Kyratyk research site in the Indigirka lowlands in NE-Siberia taken on August 19, 2010. Indicated in the subset image are the two transects, vegetation classes (dry tussock evergreen, moist deciduous shrub, moist *Sphagnum*-sedge and wet sedge pools), and a 500-m scale bar. In the lower right corner of the subset image a tributary of the Indigirka river, the Berelekh (Yelon) river, is visible. Coordinates are in latitude/longitude in the WGS84 (World Geodetic System) coordinate system.

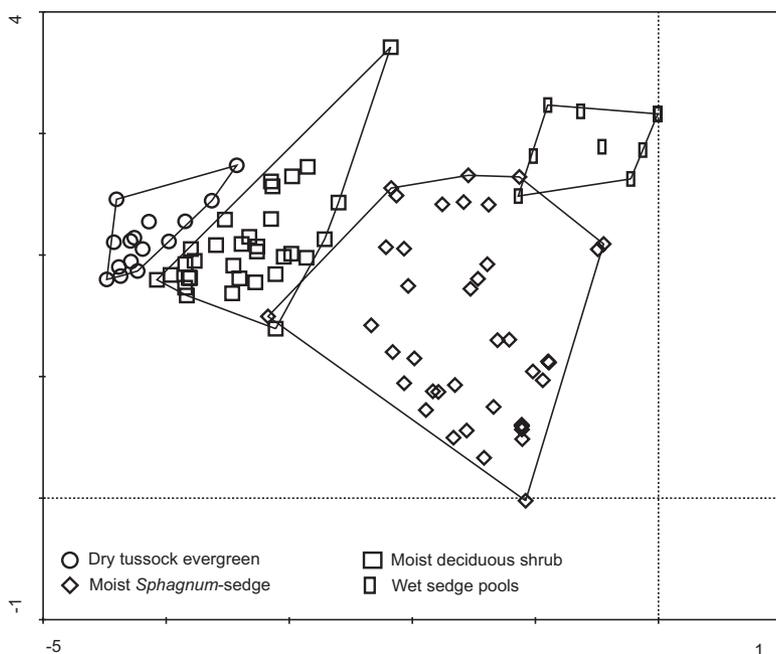
approximately 30 km NW of the town Chokurdakh. The vegetation at the research site consists of a mixture of graminoids, forbs, mosses and shrubs and is classified by vegetation classes G4 (tussock-sedge, dwarf-shrub, moss tundra) and S2 (low-shrub tundra) on the circumpolar Arctic vegetation map (CAVM) (Walker *et al.*, 2005). The subsoil is silt clay overlain by 10–15 cm of highly organic soil, carpeted with an approximately 4–5 cm thick moss layer. Regional climate data (Chokurdakh weather station (WMO station 21946), <http://climexp.knmi.nl/>, 1948–2006) show mean annual air temperatures of  $-13.9^{\circ}\text{C}$  and average July temperatures of  $10.5^{\circ}\text{C}$ . Mean annual precipitation is 205 mm, most of which falls during the summer months. July is the wettest month with an average precipitation of 32 mm (Klein Tank *et al.*, 2002).

On 29 and 30 July 2009, plant species cover, ALT, LAI, moss layer thickness, vegetation height and organic layer thickness (only transect 2) were measured every 10 meters along two perpendicular 500-m linear transects. Latitudinal and longitudinal coordinates were recorded every 10 transect points using a GPS and were projected onto a high-resolution satellite image (Fig. 6.1). This resulted in a total of 100 measurement points varying in vegetation composition from mixtures of *Eriophorum vaginatum*, *Betula nana* and *Ledum palustre* shrubs to *Betula nana*-dominated patches and wet sedge pools. At every measurement point, a vegetation description was made and plant species fractional cover was estimated of an area measuring approximately 50 by 50 cm. Within these 50 by 50 cm areas, ALT was measured randomly 3 times by inserting a blunt metal probe into the soil. ALT was defined as the distance between the top of the moss layer and the permafrost table. LAI of vascular vegetation was measured using a SunScan canopy analysis system (SS1, Delta-T Devices, Cambridge, UK), held at the top of the moss surface. Moss layer thickness was measured at every transect sample point by cutting a 5 by 5 cm column using a sharp knife and measuring the thickness of the green moss layer with a tape measure. These 5 by 5 cm moss samples were individually labeled and packed for shipment to the laboratory in Yakutsk, Russia, where moss and lichen species were identified (Supplement 1b). For moss species, nomenclature followed Savicz-Lyubitskaya & Smirnova, 1970, Ignatov & Ignatova, 2003, 2004, Ignatov *et al.*, 2006 and Potemkin & Sofronova, 2009. For lichen species, nomenclature followed Kopaczewskaja *et al.*, 1971, Blum *et al.*, 1975, Golubkova *et al.*, 1978 and Golubkova *et al.*, 1996. Vegetation height was measured at every transect point as the distance between the canopy and the top of the moss layer. Organic layer thickness was measured (only for transect 2) by pushing a soil profiler of approximately 2 cm diameter to the permafrost table and extracting a soil column. A sharp knife was used to cut a clean soil profile, after which the organic layer thickness was measured using a tape measure. Although we did not measure soil moisture in our transects, soil moisture data were collected at our research site during a field campaign in 2008 in locations with similar vegetation as in our transects (supplement 2). Samples of

the top-5 cm organic soil layer were collected at 36 points within a vicinity of 1 km of our transects and vegetation cover was noted for each sample point. Soil moisture was gravimetrically determined, after which soil moisture data were clustered according to the vegetation classes presented in figure 6.2.

### *Vegetation classification and ordination*

Transect sample points were clustered into classes according to their vascular plant species cover and presence of moss and lichen species using two-way indicator species analysis (TWINSPAN) for Windows v2.3 (Hill & Šmilauer, 2005). Nine division cut levels were set in TWINSPAN, at 1, 2, 5, 10, 15, 20, 40, 60 and 70% species fractional cover. For non-vascular moss and lichen species, only presence data was available and species presence was indicated as 1% cover. The minimum group size for division was set at 4; all other settings were left at default. Detrended correspondence analysis (DCA) was performed on vascular plant species cover data from transect sample points on basis of their taxonomic composition and were plotted in multidimensional space using CANOCO for Windows v4.55 (ter Braak & Šmilauer, 2002). Envelopes were drawn around transect sample point classes identified by TWINSPAN to visualise taxonomic differences between vegetation classes.



**Figure 6.2** Ordination of transect sample points ( $n = 100$ ) by detrended correspondence analysis (DCA) of vascular plant species cover data. Envelopes are drawn around clusters of transect sample points identified by two-way indicator species analysis (TWINSPAN).

### *Statistical analysis*

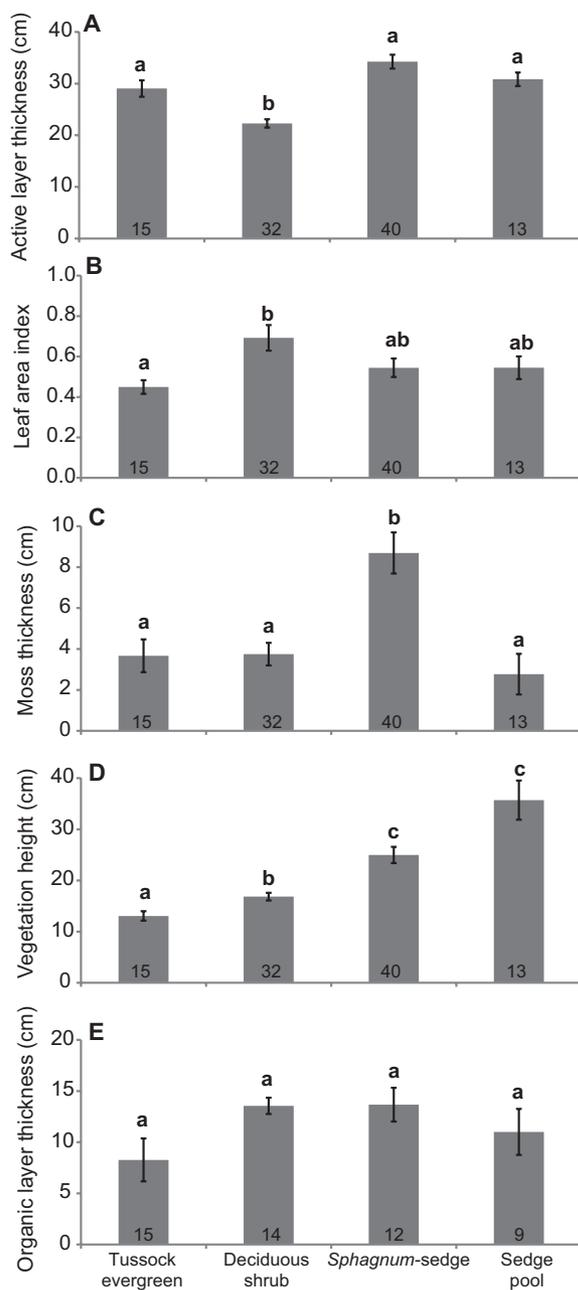
Mean values of variables ALT, LAI, moss layer thickness, vegetation height and organic layer thickness were calculated per TWINSPAN vegetation class. Analysis of variance (ANOVA) tests were performed to test for significant differences between vegetation classes. Since assumptions of equal sample sizes and equal variances among vegetation classes were not met, Games-Howell post-hoc tests were performed to determine which vegetation classes differed significantly from each other.

Cover of dominant vascular plant species within plant functional groups (supplement 1a; dry graminoid: *Eriophorum vaginatum*, deciduous shrub: *Betula nana*, evergreen shrub: *Ledum palustre*, wet graminoid: *Carex aquatilis*) were plotted against ALT to test for linear relationships and Pearson correlation coefficient ( $r$ ) values were calculated between species cover and ALT. Data were square-root transformed where necessary to meet assumptions of normal distribution and variance. ANOVA and regression analyses were performed using SPSS for Windows v17.0.

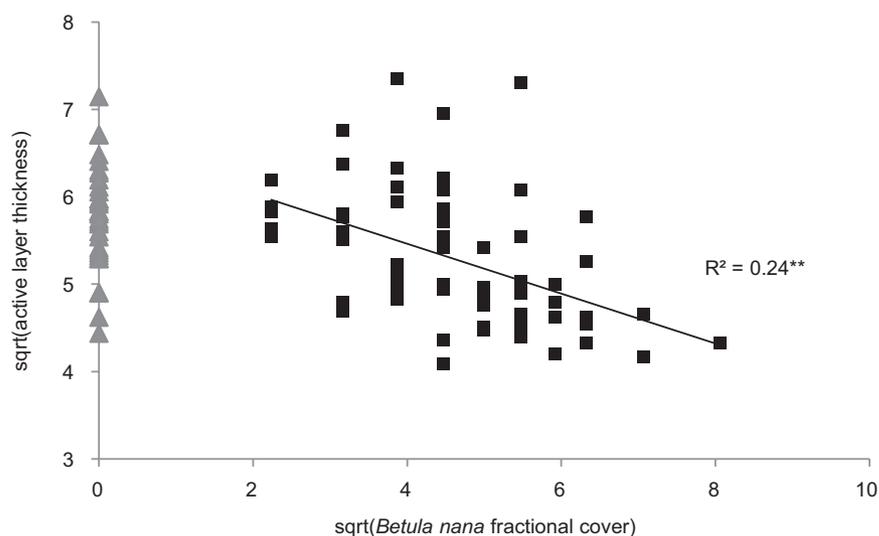
Canonical correspondence analyses (CCA) were performed using CANOCO for Windows v4.55 (ter Braak & Šmilauer, 2002) to analyse how patterns in species composition were related to variables ALT, LAI, vegetation height and moss thickness. All measured variables were selected as model input except for organic layer thickness, since data for this factor were only available for transect 2. Focus scaling was selected to inter-species distances with bi-plot scaling used to visualize CCA results. Significances of canonical axes were evaluated using Monte Carlo permutation tests (499 runs). CCA analyses were conducted separately for response variables vascular (supplement 1a) and non-vascular (supplement 1b) vegetation data since qualitative (non-vascular species presence) and quantitative (vascular species cover) data cannot be analysed simultaneously using unimodal ordination methods such as CCA (Lepš & Šmilauer, 2003).

## **Results**

We clustered transect sample points on basis of their vegetation composition using TWINSPAN. Only the first two divisions of the TWINSPAN output were used, resulting in a total of four distinct vegetation classes, subsequently increasing in soil moisture along a gradient from (Fig. 6.2, supplement 2): dry tussock evergreen (*Ledum palustre*, *Eriophorum vaginatum*, *Salix glauca*, *Vaccinium uliginosum*, *Dactylina arctica*, *Dicranum elongatum*), moist deciduous shrub (*Betula nana*, *Salix pulchra*, *Arctagrostis latifolia*, *Aulacomnium palustre*), moist *Sphagnum*-sedge (*Sphagnum* spp., *Carex aquatilis*, *Comarum palustre*, *Salix fuscescens*) and wet sedge pools (*Eriophorum angustifolium*).



**Figure 6.3** Shown are mean values per vegetation class, with A) active layer thickness, B) leaf area index, C) moss thickness, D) vegetation height, and E) organic layer thickness (transect 2). Standard error bars are shown with superscripts indicating significant differences between vegetation classes ( $p < 0.05$ ). Numbers in bars indicate the number of transect sample points ( $n$ ) per vegetation class.



**Figure 6.4** Square-root transformed active layer thickness (ALT) values plotted against *Betula nana* fractional cover. The regression line is plotted through transect data points (black squares) containing *Betula nana* cover ( $n = 68$ ). The asterisk indicates the significance level of the relationship between *B. nana* and ALT: \*\* $p < 0.001$ . Grey triangles depict transect data points ( $n = 32$ ) without *B. nana* cover.

ALT varied between 16 and 53 cm, with shallowest ALT measured in transect points within the deciduous shrub class (Fig. 6.3A). ALT in this class differed significantly from values recorded in the other vegetation classes ( $p < 0.05$ ). For LAI, only dry tussock evergreen differed from moist deciduous shrub, with lower LAI values measured in the former class (Fig. 6.3B). Moss thickness did not differ between vegetation classes, except for the moist *Sphagnum*-sedge class having a significantly thicker moss layer compared to the other classes (Fig. 6.3C). This is due to the thick *Sphagnum* carpets present in this class, in contrast to the relatively thin moss layers in the evergreen and deciduous-shrub dominated classes. In the wet sedge pool class, a moss layer was absent in several transect points, resulting in an on average thin moss layer. Vegetation height increased along with soil moisture, with lowest vegetation being measured in the dry tussock evergreen class and tallest vegetation in the wet sedge class (Fig. 6.3D). Organic layer thickness data were only available for transect 2 and did not significantly differ between vegetation classes (Fig. 6.3E). Of all dominant plant species, only *Betula nana* and *Eriophorum vaginatum* showed a significant relationship with ALT, with the former species showing a negative relationship ( $r = -0.49$ ,  $p < 0.001$ ,  $n = 68$  transect points, Fig 6.4) and the latter species a positive relationship ( $r = 0.70$ ,  $p < 0.001$ ,  $n = 19$  transect points). Results of the CCA revealed that ALT, LAI, moss layer thickness and vegetation height could

explain approximately 18% of the variation in vascular species composition, with vegetation height explaining most variation (supplement 3). Variation in lichen and moss species presence could be explained for approximately 6% (supplement 4), with moss thickness contributing most to explained variation.

## Discussion

Our observation of significantly lower ALT values under deciduous shrub-dominated vegetation agrees with results of an experimental study where removal of the deciduous shrub *Betula nana* lead to an increase in ALT (Blok *et al.*, 2010). Furthermore, in the study presented here we observed a negative relationship between *B. nana* cover and ALT on a landscape scale, confirming that an increase in shrub cover may reduce summer permafrost thaw. The negative relationship between *B. nana* and ALT is most likely explained by an increase in soil shading with increasing shrub canopy density (McFadden *et al.*, 1998), which corresponds with our observation of highest LAI values being measured in the vegetation class dominated by deciduous shrubs. Furthermore, we observed that LAI increased with increasing *Betula nana* cover ( $r = 0.55$ ,  $p < 0.001$ ,  $n = 68$ ). As a result of increased soil shading by a denser shrub canopy, partitioning of net radiation into ground heat flux is reduced and less energy is available for permafrost thaw (Blok *et al.*, 2010).

In contrast to their soil cooling effect, shrubs may increase air temperature by trapping more energy into the ecosystem by reducing the surface albedo (Sturm *et al.*, 2005a, Blok *et al.*, 2010). It has been proposed that this effect may result in a positive feedback to further shrub growth if atmospheric heating leads to greater soil organic matter turnover rates, thereby increasing the nutrient availability for plants (Chapin *et al.*, 2005). Results from this study however suggest that the summer soil shading effect of shrubs predominates over the albedo effect and that an increase in shrub cover may result in summer soil cooling, thereby reducing permafrost thaw depth. The stabilizing effect of shrub vegetation on permafrost is further supported by field data (Gross *et al.*, 1990, Walker *et al.*, 2003b, Walker *et al.*, 2004) and model studies, whereby a succession from barren to tussock shrub tundra was shown to lead to a reduction in permafrost thaw depth (Yi *et al.*, 2007, Jorgenson *et al.*, 2010). It is however not yet proven that a reduction in summer permafrost thaw depth with increasing shrub cover reduces soil nutrient availability during the growing season and if this can eventually restrict shrub growth.

Previously, it has been suggested that an increase in tundra graminoid cover may result in summer soil cooling because graminoid vegetation reflects a relative great proportion of incoming solar radiation and thereby increases the surface albedo (Zimov, 2005). In contrast, we observed a positive relationship between cover of one of the dominant graminoid species at our research site, *Eriophorum vaginatum*,

and ALT. However, we also noted an inverse relationship between *Betula nana* and *Eriophorum vaginatum* fractional cover in transect points containing both species ( $r = -0.47, p < 0.05, n = 19$ ), suggesting that the observed positive relation between *Eriophorum vaginatum* and ALT may also be an indirect effect of the competitive balance between these species (Bret-Harte *et al.*, 2008). This is supported by the observation that under favourable growing conditions (high temperature, high nutrient availability), *Betula nana* may outcompete *Eriophorum vaginatum* and become the dominant species (Chapin *et al.*, 1995, Bret-Harte *et al.*, 2008).

Along with changes in canopy shading, a transition from dense shrub towards open sedge vegetation may also be accompanied by an increase in soil moisture. Soil moisture is considered as one of the key parameters that determine the soil thermal conductivity in Arctic soils (Hinzman *et al.*, 1991, O'Donnell *et al.*, 2009) and changes herein thus can have large effects on the permafrost thaw depth (Shiklomanov *et al.*, 2010). With higher soil moisture, soil thermal conductivity increases, facilitating a greater energy flux into the soil, but at the same time also increases the soil heat capacity and thereby requiring a greater heat flux to increase the soil temperature. Thus, the net effect of soil moisture on soil thermal conditions and ALT development is uncertain. Although we did not measure soil moisture in our transects and thus cannot directly distinguish between soil shading effects and soil moisture effects on ALT development, soil moisture data from 2008 showed that soil moisture almost linearly increased from dry tussock evergreen shrub towards wet sedge pools (supplement 2). ALT in our transects however did not linearly increase along this soil moisture gradient and suggests that other effects such as canopy shading may also influence ALT. The soil moisture gradient may similarly explain why moss thickness did not show a relation with ALT. The increase in moss layer thickness was probably accompanied by an increase in soil moisture, as thicker *Sphagnum* moss mats were found in wet habitats, thereby potentially obscuring the insulating effect of moss (Beringer *et al.*, 2001).

To summarize, we show that distinct vegetation classes can be distinguished at our tundra site in NE-Siberia. ALT was significantly lower under *Betula nana*-dominated vegetation than under any other vegetation class. Furthermore, we observed a negative relationship between *Betula nana* cover and ALT, suggesting that a vegetation shift towards greater shrub dominance may partly buffer permafrost against future rising temperatures.

### Acknowledgements

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**Supplement 1a** Vascular plant species acronyms and corresponding full names following Hultén (1968).

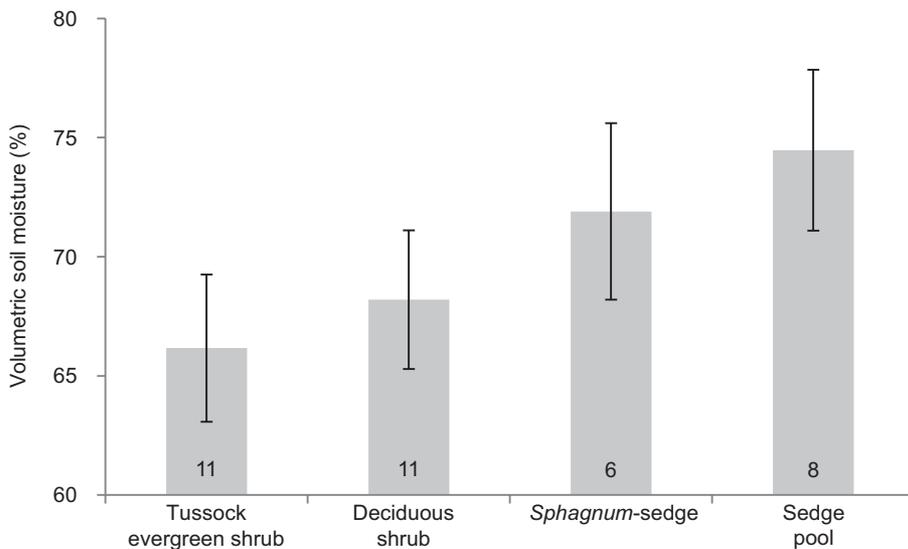
acronym	full species name
<b>Deciduous shrub</b>	
<i>Arc alp</i>	<i>Arctostaphylos alpina</i> (L.) Spreng
<i>Bet nan</i>	<i>Betula nana</i> L.
<i>Sal fus</i>	<i>Salix fuscescens</i> Anderss.
<i>Sal gla</i>	<i>Salix glauca</i> L.
<i>Sal pul</i>	<i>Salix pulchra</i> Cham.
<i>Vac uli</i>	<i>Vaccinium uliginosum</i> L.
<b>Evergreen shrub</b>	
<i>Cas tet</i>	<i>Cassiope tetragona</i> (L.) D. Don
<i>Led pal</i>	<i>Ledum palustre</i> L.
<i>Vac vit</i>	<i>Vaccinium vitis-idaea</i> L.
<b>Dry graminoid</b>	
<i>Arc lat</i>	<i>Arctagrostis latifolia</i> (R. Br.) Griseb.
<i>Car spp</i>	<i>Carex</i> spp.
<i>Eri vag</i>	<i>Eriophorum vaginatum</i> L.
<b>Wet graminoid</b>	
<i>Car aqu</i>	<i>Carex aquatilis</i> Wahlenb.
<i>Ele pal</i>	<i>Eleocharis palustris</i> (L.) Roem & Schult.
<i>Eri ang</i>	<i>Eriophorum angustifolium</i> Honck.
<b>Forbs</b>	
<i>Com pal</i>	<i>Comarum palustre</i> L.
<i>Ped spp</i>	<i>Pedicularis</i> spp.
<i>Pyr rot</i>	<i>Pyrola rotundifolia</i>
<i>Rub cha</i>	<i>Rubus chamaemorus</i> L.
<i>Sax pun</i>	<i>Saxifraga punctata</i> L.
<i>Tof coc</i>	<i>Tofieldia coccinea</i> Richards
<i>Val cap</i>	<i>Valeriana capitata</i> Pall.

**Supplement 1b** Moss species acronyms and their corresponding full names. Nomenclature followed Savicz-Lyubitskaya & Smirnova, 1970, Ignatov & Ignatova, 2003, 2004, Ignatov *et al.*, 2006 and Potemkin & Sofronova, 2009.

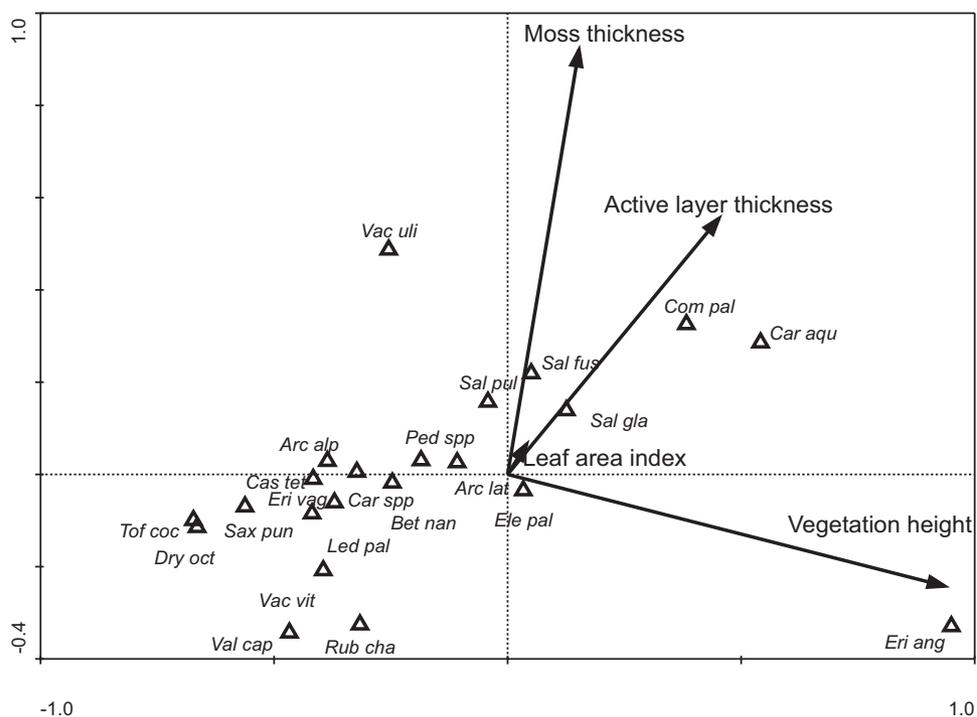
acronym	full species name
<b>Bryophyte</b>	
<i>Aul pal</i>	<i>Aulacomnium palustre</i> (Hedw.) Schwägr.
<i>Aul tur</i>	<i>Aulacomnium turgidum</i> (Wahlenb.) Schwägr.
<i>Dic ang</i>	<i>Dicranum angustum</i> Lindb.
<i>Dic elo</i>	<i>Dicranum elongatum</i> Schleich. ex Schwägr.
<i>Dic fle</i>	<i>Dicranum flexicaule</i> Brid.
<i>Dic lae</i>	<i>Dicranum laevidans</i> R.S. Williams
<i>Ham ver</i>	<i>Hamatocaulis vernicosus</i> (Mitt.) Hedenäs
<i>Hyl spl</i>	<i>Hylocomium splendens</i> var. <i>obtusifolium</i> (Geh.) Paris
<i>Pol hyp</i>	<i>Polytrichum hyperboreum</i> R. Br.
<i>Pol jun</i>	<i>Polytrichum juniperinum</i> Hedw.
<i>Pol str</i>	<i>Polytrichum strictum</i> Brid.
<i>Pti cil</i>	<i>Ptilidium ciliare</i> (L.) Hampe
<i>Rhi pse</i>	<i>Rhizomnium pseudopunctatum</i> (Bruch & Schimp.) T.J. Kop
<i>San uni</i>	<i>Sanionia uncinata</i> (Hedw.) Loeske
<i>Sph aon</i>	<i>Sphagnum aongstroemii</i> Hartm.
<i>Sph bal</i>	<i>Sphagnum balticum</i> (Russow) C.E.O. Jensen
<i>Sph com</i>	<i>Sphagnum compactum</i> Lam. & DC.
<i>Sph rus</i>	<i>Sphagnum russowii</i> Warnst.
<i>Sph squ</i>	<i>Sphagnum squarrosum</i> Crome
<i>Sph sub</i>	<i>Sphagnum subsecundum</i> Nees
<i>Sph ter</i>	<i>Sphagnum teres</i> (Schimp.) Ängstr.
<i>Sphen sax</i>	<i>Sphenolobus saxicola</i> (Schrad.) Steph.
<i>Tom nit</i>	<i>Tomentypnum nitens</i> (Hedw.) Loeske

**Supplement 1b (continued)** Lichen species acronyms and their corresponding full names. Nomenclature followed Kopaczewska *et al.*, 1971, Blum *et al.*, 1975, Golubkova *et al.*, 1978 and Golubkova *et al.*, 1996.

acronym	full species name
<b>Lichen</b>	
<i>Cet isl</i>	<i>Cetraria islandica</i> (L.) Ach.
<i>Cla acu</i>	<i>Cladonia acuminata</i> (Ach.) Norrl.
<i>Cla ama</i>	<i>Cladonia amaurocraea</i> (Flörke) Schaer.
<i>Cla chl</i>	<i>Cladonia chlorophaea</i> (Florke ex Sommerf.) Spreng.
<i>Cla coc</i>	<i>Cladonia coccifera</i> (L.) Willd.
<i>Cla cor</i>	<i>Cladonia cornuta</i> (L.) Hoffm.
<i>Cla def</i>	<i>Cladonia deformis</i> (L.) Hoffm.
<i>Cla fim</i>	<i>Cladonia fimbriata</i> (L.) Fr.
<i>Cla mac</i>	<i>Cladonia macroceras</i> (Delise) Hav.
<i>Dac arc</i>	<i>Dactylina arctica</i> (Hook.) Nyl.
<i>Fla cuc</i>	<i>Flavocetraria cucullata</i> (Bellardi) Karnefelt et Thell
<i>Pel aph</i>	<i>Peltigera aphthosa</i> (L.) Willd.
<i>Pel can</i>	<i>Peltigera canina</i> (L.) Willd.
<i>Pel pol</i>	<i>Peltigera polydactylon</i> (Neck.) Hoffm.

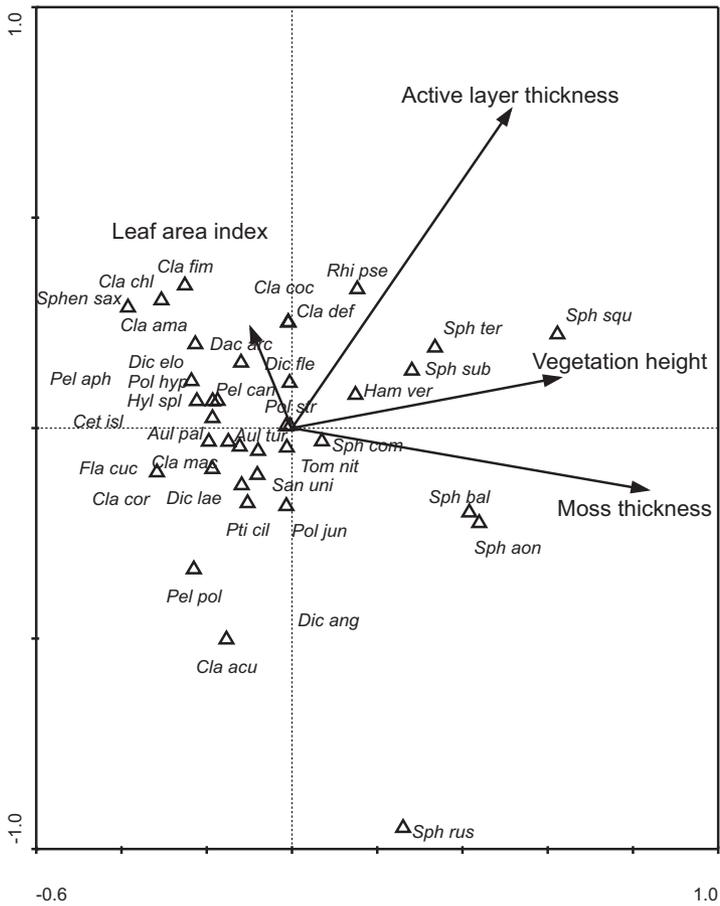


**Supplement 2** Gravimetrically determined mean volumetric soil moisture per vegetation class. Samples of the top-5 cm organic soil layer were collected at the Kytalyk research site during a field campaign in July 2008. Soil samples were collected at 36 points and vegetation cover was noted for each sample point. Samples were clustered into classes on basis of their vegetation composition, similar to the classes shown in figure 6.2. Numbers indicated in bars represent the number of transect sample points ( $n$ ) per vegetation class.



**Supplement 3** Ordination of vascular plant species in sample points ( $n = 100$ ) by canonical correspondence analysis (CCA). Arrows indicate variables active layer thickness, leaf area index, moss thickness and vegetation height. Full names of plant species acronyms are given in supplement 1a.

Summer permafrost thaw depth related to vegetation composition



**Supplement 4** Ordination of non-vascular bryophyte and lichen species in sample points ( $n = 100$ ) by canonical correspondence analysis (CCA). Arrows indicate variables active layer thickness, leaf area index, moss thickness and vegetation height. Full names of plant species acronyms are given in supplement 1a. Full names of moss and lichen species acronyms are given in supplement 1b.



## 7. Synthesis and general discussion

The Arctic region is experiencing rapid changes in climate, with the most prominent change being a rise in air temperature (ACIA, 2004; IPCC, 2007). Vegetation in high-latitude tundra regions is very responsive to changes in climate which may have great implications for the tundra vegetation composition (Bhatt *et al.*, 2010). Of all plant species groups, deciduous shrubs are expected to respond most strongly to higher air temperatures by increasing their growth, possibly at the cost of understory moss and lichen vegetation (Cornelissen *et al.*, 2001; Walker *et al.*, 2006). Climatic and vegetation changes in the Arctic may feedback to the global climate system by changing the tundra soil carbon balance (Sitch *et al.*, 2007). For example, vegetation changes may change the surface albedo and soil insulation and thereby affect the surface energy balance and permafrost thaw depth (McFadden *et al.*, 1998) and concomitant soil carbon release to the atmosphere (McGuire *et al.*, 2009). However, much is unknown about the effect of climate-driven vegetation changes in the tundra ecosystem on soil conditions during summer and the feedback of these vegetation changes to the regional climate. In this thesis, I studied the interaction between vegetation, climate and summer permafrost thaw in the Siberian tundra, with special emphasis on *Betula nana* (dwarf birch), since this deciduous shrub species is known to be especially responsive to environmental changes. As previously stated in the first chapter, the main research questions of my thesis were:

- (i) What is the effect of changes in *Betula nana* cover on summer permafrost thaw depth?
- (ii) What are the main climate drivers for deciduous shrub growth?
- (iii) Can changes in deciduous shrub cover feedback to the regional climate by altering the surface albedo?
- (iv) What is the effect of changes in moss cover below deciduous shrubs on soil heat flux and evapotranspiration?

### *Betula nana* effect on permafrost thaw

An increase in shrub growth with higher air temperatures may amplify regional heating by decreasing the surface albedo (Sturm *et al.*, 2005a), causing atmospheric heating and thus providing a positive feedback to further shrub expansion (Chapin *et al.*, 2005) (Fig. 7.1). As a result, permafrost thaw may increase and lead to an increase in soil carbon release to the atmosphere. It was unknown however if the increase in atmospheric heating and soil warming potential by shrub expansion could be offset by an increase in soil shading with increasing deciduous shrub cover. I studied the net effect of these contrasting effects of shrub expansion on belowground thermodynamics and permafrost thaw depth by performing a shrub

removal experiment in a Siberian tundra site with continuous permafrost. I removed all *Betula nana* shrubs from ten-meter diameter plots and compared permafrost thaw depth and soil heat flux in removed plots with plots with intact *Betula nana* cover (chapter 2). While the surface albedo was indeed reduced by denser *Betula nana* cover, the absolute amount of energy that was conducted to the soil was lower, resulting in an overall reduction in permafrost thaw depth. Apart from the observed increase in permafrost thaw depth with *Betula nana* removal, I found an inverse relationship between *Betula nana* cover and permafrost thaw depth in undisturbed control plots (chapter 2) and in field transects over a broader range of vegetation types (chapter 6). This inverse relationship between increasing shrub cover and decreasing permafrost thaw depth has been proposed before (Callaghan *et al.*, 2004; Sturm *et al.*, 2005b), but has never before been supported by experimental evidence. Based on these results, I could provide an answer to my first research question: a climate-driven vegetation change towards more shrub-dominated tundra is likely to reduce summer permafrost thaw and thus may slow down the increase in permafrost temperature that is expected with climate warming (Fig. 7.1).

#### *Shrub growth response to climate*

Next, I studied whether an increase in shrub growth is likely to occur under climate warming in the Siberian tundra. While experimental plot warming studies generally show a positive growth response of shrubs to temperature (Walker *et al.*, 2006), little was known about the growth response of shrubs to natural climatic variability (Forbes *et al.*, 2010). For the East-Siberian tundra in particular, no previous attempts have been made to relate inter-annual variability in shrub growth to climate. I determined what are the main climate variables that drive growth of two deciduous shrub species with a pan-Arctic distribution, *Betula nana* and *Salix pulchra*, by measuring annual secondary growth and comparing growth rates with meteorological station data (chapter 3). I could thus answer the second research question of my thesis: early summer temperature most strongly determines deciduous shrub growth in NE-Siberian tundra.

#### *Shrub effect on surface albedo*

It is suggested that a pan-Arctic shrub expansion may already be underway, as evidenced by a greening of Arctic tundra areas during the last three decades by Earth-orbiting satellites (Myneni *et al.*, 1997; Tape *et al.*, 2006; Goetz *et al.*, 2007; Jia *et al.*, 2009). There is evidence that the observed increases in Arctic greenness, expressed as NDVI, are related to an increase in surface temperature (Raynolds *et al.*, 2008). However, inter-annual variations in summer tundra greenness were not yet linked to variations in summer albedo. In chapter 4, I show from field data that *Betula nana* cover is positively related to summer greenness, but negatively related to summer albedo. On a larger scale, I show from satellite data that summer

greenness is greatest in shrub tundra areas compared to all other tundra vegetation types and that inter-annual variations in summer greenness are negatively related to summer albedo, confirming the relationships observed in the field. At the same time, satellite data show that a widespread shrub expansion does not necessarily lead to a reduction in summer albedo for all tundra areas, as vegetation zones that are currently classified as barren and wetland tundra (Walker *et al.*, 2005) show lower summer albedo minima values than shrub tundra areas. Therefore, a shrub expansion in these vegetation zones will not lead to a reduction in summer surface albedo and atmospheric heating. Instead, a lowering of the surface albedo may be expected with shrub expansion within low-Arctic graminoid and shrub tundra vegetation zones (chapter 4).

#### *Soil cooling by mosses*

With increasing air temperature, deciduous shrub growth generally increases, often at the cost of moss and lichen growth by light limitation (Hobbie *et al.*, 1999; Cornelissen *et al.*, 2001; Aerts *et al.*, 2006; Bret-Harte *et al.*, 2008). A decrease in moss cover may increase summer permafrost thaw, since mosses are known for their insulating capacity and may buffer permafrost soil against warming (Gornall *et al.*, 2007; O'Donnell *et al.*, 2009). In chapter 5, I show that soil heat flux indeed increases with moss removal, even though the concomitant increase in understory evaporation with moss removal may partly compensate for the loss of soil insulation and reduce the impact of the reduction in moss biomass on soil heat flux. This corresponds with observations made in a burned tundra site in Alaska, where fire resulted in a reduced moss cover but did not lead to a large increase in soil heat flux because of the cooling effect of increased soil evaporation (Rocha & Shaver, 2011b), possibly as a consequence of a reduction in surface albedo after fire. Thus, a reduction in moss cover may not necessarily lead to an increase in permafrost thaw. Furthermore, if rising air temperatures lead to a denser shrub cover, the concomitant increase in soil shading might compensate for the reduction in soil insulation by reduced moss cover, thereby lowering the soil heat flux and permafrost thaw depth (chapter 5).

### **Shrub expansion feedbacks to climate**

#### *Soil cooling versus atmospheric heating*

Together, the results presented in chapters 2-4 suggest that a temperature-driven increase in shrub growth may reduce the surface albedo, but at the same time may lead to an overall reduction in summer permafrost thaw through an increase in soil shading and concomitant reduction in ground heat flux. A decrease in surface albedo by a denser shrub cover, with relatively fewer energy being allocated to ground heat fluxes must result in a greater dissipation of energy into sensible and latent heat fluxes, thus leading to atmospheric heating (Chapin *et al.*, 2005). Atmospheric fluxes were not measured in the shrub removal experiment, but the

sum of latent and sensible heat fluxes (also referred to as available energy) can be estimated by deducting ground heat fluxes from net radiation. Both sensible and latent heat fluxes can lead to atmospheric heating, either through convective flows of air and water or through the greenhouse effect exerted by the presence of water vapour particles in the atmosphere. The fractionation of available energy between sensible and latent heat fluxes may change with rising air temperatures by increased stomatal regulation of transpiration, thus potentially shifting the balance towards greater sensible heat fluxes. Furthermore, if rising air temperatures will lead to an increase in shrub growth, the moss understory may receive less light. As a consequence, moss evaporation may be reduced, thus further limiting total tundra evapotranspiration and potentially leading to greater sensible heating. However, the balance of division of available energy into sensible and latent heat fluxes will also likely be dependant on precipitation inputs and therefore complicate predictions on tundra energy partitioning under altered climate conditions.

A model study (Lawrence, 2010) confirms the results of the shrub removal experiment presented in chapter 2, but at the same time shows that the soil warming effect by atmospheric heating from a decrease in surface albedo with a large-scale shrub expansion may exceed the contrasting soil cooling effect of canopy shading. The model results suggest that permafrost thaw depth will increase more in response to rising temperatures when accompanied by an expansion of shrubs due to a decrease in surface albedo (Lawrence, 2010). However, the model does not allow for an increase in shrub canopy density with increasing air temperature and thus cannot account for a negative feedback to soil warming by increasing shrub density and concomitant greater soil shading. Nevertheless, there may be a critical tipping point (Scheffer *et al.*, 2001), where the increase in shrub biomass and concomitant soil cooling by canopy shading may no longer be able to compensate for the increase in atmospheric heating by a lowering of the surface albedo, especially when accompanied by a reduction of insulating moss cover. However, the results presented in this thesis suggest that shrub expansion will lead to summer soil cooling, since I did not find a reduction in moss cover with denser shrub cover. Furthermore, I observed that the reduction in albedo with denser shrub cover was more than offset by a reduction in soil heat flux by increased canopy shading, at least in the short term. In the long term, rising air temperatures may no longer lead to an increase in shrub growth, either through restrictions in shrub height growth determined by the thickness of the winter snow layer or by a limitation in shrub cover density determined by light limitation imposed by self-shading of shrubs. If a rise in air temperature is no longer accompanied by an increase in soil shading by greater shrub growth, permafrost temperatures may rise. This may lead to a collapse of shrub patches when deeper permafrost thaw will result in soil subsidence and wetter soil conditions that are unfavorable for *Betula nana* shrubs. Nevertheless, remote sensing studies show that shrub cover has been increasing during the last decades (*e.g.* Tape *et al.*, 2006; Jia

*et al.*, 2009) and dendrochronological studies on Arctic shrubs (Forbes *et al.*, 2010, Hallinger *et al.*, 2010; chapter 3) do not show a recent decline in growth response to temperature, suggesting that a temperature-induced increase in shrub growth may partly buffer permafrost against rising air temperatures for the coming decades.

### *Shrub effect on fire*

Apart from changing the surface albedo, shrubs may positively feedback to climate warming by increasing the frequency of tundra fire events (shrub-dominated tundra may burn up to once every 144 years, as often as modern boreal forests (Higuera *et al.*, 2008)) and thereby influence the soil carbon balance of Arctic tundra ecosystems (McGuire *et al.*, 2009). Shrubs allocate a relatively large proportion of their biomass to woody stems (Shaver, 1986) and may facilitate tundra fires by providing fuel (Higuera *et al.*, 2008). Apart from releasing carbon from soil organic matter and plant biomass to the atmosphere, fires may also temporarily greatly reduce the surface albedo and lead to surface warming (Haag & Bliss, 1974). Although the surface warming may in large part be offset through surface cooling by increased soil evaporation (Rocha & Shaver, 2011b), a single large fire may result in a massive carbon release to the atmosphere, turning a large tundra area from a net carbon sink into a net carbon source for a few years after fire (Rocha & Shaver, 2011a). Apart from affecting the tundra carbon balance, fires may facilitate an expansion of deciduous shrubs by creating new seedbeds (Racine *et al.*, 2004; Lantz *et al.*, 2010). Furthermore, fire may promote shrub dominance by the relatively high soil nutrient availability after fire (Wein & Bliss, 1973).

## **Will shrubs increase or decrease their expansion rate?**

### *Winter warming versus summer cooling*

In chapter 3, I showed that for both *Betula nana* and *Salix pulchra*, two of the most widely occurring deciduous shrub species with a circumpolar distribution (Hultén, 1968), growth was observed to be very sensitive to fluctuations in early summer temperature (Fig. 7.1). This is in line with several other dendroclimatological studies on the growth response of Arctic deciduous shrubs to interannual variations in temperature using different shrub species (Walker, 1987; Lantz *et al.*, 2009; Forbes *et al.*, 2010) and suggests that deciduous shrubs may share a common positive growth response to temperature, at least for low-Arctic tundra shrubs. However, most of the increase in air temperature that is expected in the Arctic environment for the coming decades is thought to occur during the winter period when shrubs are dormant (ACIA, 2004). Winter temperature increases may not directly lead to an increase in shrub growth, but may promote winter mineralization of organic matter and may lead to an increase in soil nutrient availability next spring (Schimel *et al.*, 2004; Weintraub & Schimel, 2005). As described in the first chapter of this thesis, a positive feedback loop has been proposed that links increases in winter snow depth

and shrub growth: by capturing drifting snow with their protruding branches, shrubs may increase the local snow height, increasing soil winter temperatures and increase winter mineralization and nutrient availability, thus promoting further shrub growth (Sturm *et al.*, 2001a; Hallinger *et al.*, 2010). However, the final step of the snow-shrub hypothesis is not validated by experimental evidence: an increase in winter snow depth may not lead to a positive feedback to further shrub growth if nutrients that are mineralized during winter are washed off with spring snowmelt or if mineralized nitrogen is reduced by denitrifying bacteria and does not become available for shrubs during the growing season (Hobbie & Chapin, 1996; Sturm *et al.*, 2005b). More studies are therefore needed to evaluate the effect of changes in winter soil conditions on shrub growth in Arctic tundra in comparison to the effect of changes in summer soil conditions on shrub growth.

The positive winter feedback effects of increasing shrub cover on spring nutrient availability may be counteracted by negative effects of increasing shrub cover and concomitant increase in soil shading on summer nutrient availability (Callaghan *et al.*, 2004). In chapter 2 I described how increasing shrub cover may lead to a reduction in summer soil heat flux and permafrost thaw. Soil temperature is one of the critical factors determining decomposition rates in Arctic tundra (Hobbie, 1996) and a decrease in permafrost temperatures and thaw depth may lead to a reduction in organic matter turnover and thereby reduce nutrient availability for shrubs during the growing season. Moreover, it has been suggested that the stimulating effect of increased soil temperature on nutrient mineralization is transitory and will not be sustained in the long term (Callaghan *et al.*, 2004) by acclimation of soil biota to temperature (Hartley *et al.*, 1999; Schmidt *et al.*, 1999). It thus remains uncertain what the balance is of winter soil warming and summer soil cooling on overall nutrient availability for shrubs. The balance of these contrasting summer and winter effects of shrubs on soil nutrient availability will determine whether shrubs will increase or decrease their own expansion rate.

### *Shrub effect on nutrient cycling*

The direct effects of temperature on shrub growth may be of less importance than the indirect effects of temperature on shrub growth through changes in organic matter turnover rates and nutrient availability (Chapin, 1983; Hobbie & Chapin, 1998b). This is shown by the generally much stronger positive growth response of deciduous shrubs to fertilization than to temperature (Chapin *et al.*, 1995; Bret-Harte *et al.*, 2001; Shaver *et al.*, 2001; Bret-Harte *et al.*, 2002), but this may also be due to differences in the magnitude of the applied treatment doses. Apart from determining decomposition rates by affecting soil thermal conditions, shrubs may alter decomposition rates of organic matter by their litter input (Berendse, 1994b; Hobbie, 1996; Cornwell *et al.*, 2008). It has been shown that a shift from graminoid- towards shrub-domination in tundra may lead an increase in leaf litter



2010). A potential reduction in summer decomposition rates of soil organic matter with denser shrub cover may also lower soil carbon losses to the atmosphere and thus negatively feedback to global warming (Fig. 7.1) (Cornelissen *et al.*, 2007). However, it has also been reported that an increase in soil respiration with increasing summer temperature may offset the increase in carbon storage by higher plant productivity and thereby lead to a net carbon loss to the atmosphere (Mack *et al.*, 2004). It remains unknown whether shrubs may increase or decrease soil nutrient availability through their effect on soil temperature and organic matter input by their stem and leaf litter. Opposing summer and winter effects of shrubs on soil temperature complicate predictions on their effect on soil nutrient turnover and call for studies investigating the year-round net effect of shrubs on soil nutrient cycling.

#### *Herbivore impacts on shrub growth*

The positive feedback loop between winter snow depth and shrub growth may be intersected by changes in the abundance of plant herbivores. An increase in leaf nutrient concentrations by an increase in soil nutrient availability with higher winter snow depth may attract more plant herbivores and thus increase grazing pressure to shrubs. This has been shown by a snow manipulation experiment in Abisko, Sweden where an increase in winter snow depth resulted in higher *Betula nana* leaf N concentrations and an increase in herbivore damage by moth larvae, thus potentially reducing the spread of *Betula nana* (Torp *et al.*, 2010). In another experiment, reindeer grazing pressure on *Betula nana* shrubs during early spring and late autumn have been shown to counteract the increase in *Betula nana* growth as a result of increasing air temperature (Olofsson *et al.*, 2009). Furthermore, shrub growth may be limited by snow height, as *Salix alaxensis* branches that protruded above the snow line in Alaskan tundra were observed to receive greater grazing pressure from ptarmigan than snow-buried branches (Tape *et al.*, 2010).

#### **Future challenges**

Currently, it is unknown what the limits are of shrub expansion in terms of shrub height, shrub patch density and altitudinal and latitudinal range expansion. Large parts of the tundra may be unsuitable for shrub growth because of high soil moisture or because of nutrient limitation and are thus not likely to become colonized by shrubs in a future warmer climate. Furthermore, the growth response of shrubs to temperature may differ between Arctic climate zones, since allocation of resources under increased air temperature may be attributed more to reproduction in colder high-Arctic areas and more to growth in warmer low-Arctic areas (Arft *et al.*, 1999). It has been suggested that shrub expansion is most likely to occur in southern low-Arctic tundra areas with relatively dense cover of deciduous shrubs, as shrubs in these areas were found to be most responsive to temperature (Walker *et al.*, 2003a; Epstein *et al.*, 2004a). Future research should focus on the mechanisms responsible

for shrub expansion and the importance of summer *versus* winter processes for shrub expansion. Whether an expansion of deciduous shrubs will lead to a net increase or decrease in nutrient availability is likely to determine the rate and limit of future shrub expansion. Experimental studies are needed to evaluate if winter-mineralized nutrients become available for shrubs during the growing season and thus can drive further shrub growth. Furthermore, future research should focus more on linkages between shrub effects on above- and belowground ecosystem processes. What are the implications of changes in shrub abundance for the soil carbon balance (Fig. 7.1)? Will an increase in woody shrub biomass increase or decrease the carbon storage of tundra ecosystems (Fig. 7.1)? More experimental studies are needed to evaluate the role of shrub vegetation in the exchange of water, energy and carbon between soil and atmosphere in Arctic ecosystems because changes in any of these compartments may have large consequences for the regional climate and feed back to the global climate. For reliable predictions on the effects of vegetation changes on the Arctic climate and *vice versa*, it is necessary for climate models to include a more detailed vegetation classification of tundra areas. Furthermore, not only albedo feedbacks through changes in Arctic shrub cover should be included in climate models, but also effects of changes in shrub cover on soil thermal dynamics, permafrost thaw, fire events, soil-atmosphere water, energy and carbon exchange, and soil nutrient availability should be incorporated into climate models as well (Chapin *et al.*, 2008; Ostle *et al.*, 2009; Swann *et al.*, 2010).



## List of symbols and abbreviations [units]

ALT	Active Layer Thickness [cm]
AVHRR	Advanced Very High Resolution Radiometer
CAVM	Circumpolar Arctic Vegetation Map
$C_s$	Volumetric heat capacity [ $\text{J m}^{-3} \text{K}^{-1}$ ]
DOY	Day Of Year
$E$	Evaporation [mm]
EPS	Expressed Population Signal
$ET$	Evapotranspiration [mm]
$G$	Ground heat flux [ $\text{W m}^{-2}$ ]
GIMMS	Global Inventory Modeling and Mapping Studies
$G_s$	Ground heat storage [ $\text{J m}^{-2}$ ]
$H$	Sensible heat flux [ $\text{W m}^{-2}$ ]
LAI	Leaf Area Index
$LE$	Latent heat flux [ $\text{W m}^{-2}$ ]
maxNDVI	Maximum Normalized Difference Vegetation Index
minWSA	Minimum White Sky Albedo
MODIS	Moderate Resolution Imaging Spectroradiometer
MS	Mean Sensitivity
NDVI	Normalized Difference Vegetation Index
ORNL DAAC	Oak Ridge National Laboratory Distributed Active Archive Center
RES	Residual ring-width chronology
$R_n$	Net radiation [ $\text{W m}^{-2}$ ]
$G/R_n$	Proportion ground heat flux of net radiation
$R_{NIR}$	Near-Infrared Reflectance
$R_{red}$	Red reflectance
STD	Standard ring-width chronology
SWI	Summer Warmth Index [ $^{\circ}\text{C}$ ]
$SW_{in}$	Incoming shortwave radiation [ $\text{W m}^{-2}$ ]
$SW_{net}$	Net shortwave radiation [ $\text{W m}^{-2}$ ]
$T_s$	Soil temperature [ $^{\circ}\text{C}$ ]
WMO	World Meteorological Organization
$\Delta T_i$	Change in soil temperature measured by sensor $i$ during the time interval $\Delta t$ [ $^{\circ}\text{C}$ ]
$\Delta z_i$	Thickness of the soil layer for which the temperature change $\Delta T_i$ is representative [m]



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## Summary

The Arctic is experiencing dramatic changes in climate, with the most prominent change being a rise in air temperature. High-latitude tundra regions are very responsive to changes in temperature, which may cause important shifts in tundra vegetation composition. Of all plant species growing in tundra, deciduous shrubs respond most to an increase in temperature by increasing their growth, often at the cost of nonvascular plants. With increasing shrub cover, the surface albedo may be reduced and lead to atmospheric heating by trapping more solar radiation into the Arctic ecosystem. As a result of this warming, the highly organic permafrost soils may thaw deeper and start decomposing, leading to an emission of greenhouse gases carbon dioxide and methane to the atmosphere, thus contributing to global warming. However, much is unknown about the effect of climatic changes on shrub and moss growth in tundra ecosystems and how these vegetation changes may feedback to climate. The main aim of my thesis was to study the interactions between vegetation, climate and summer permafrost thaw in the North-eastern Siberian tundra, with special emphasis on the shrub *Betula nana* (dwarf birch), since this circumpolar occurring deciduous shrub species is known to be especially responsive to environmental changes.

In contrast to their atmospheric heating potential, shrubs may also have a soil cooling effect through canopy shading. I studied the net effect of these contrasting effects of changes in shrub cover on permafrost thaw depth by performing a shrub removal experiment in a Siberian tundra site with continuous permafrost. I removed all *Betula nana* shrubs from ten-meter diameter plots and compared permafrost thaw depth and surface albedo in *Betula nana*-removed plots with plots with intact *Betula nana* cover. While the surface albedo was reduced by denser *Betula nana* cover, the absolute amount of energy that was conducted to the soil was reduced, resulting in an inverse relationship between *Betula nana* cover and permafrost thaw depth in undisturbed control plots. Moreover, *Betula nana* removal increased permafrost thaw depth in comparison with control plots, showing that an expansion of *Betula nana* shrubs with climate warming may buffer permafrost against increasing summer air temperatures.

While experimental plot warming studies generally show a positive growth response of shrubs to temperature, little is known about the growth response of deciduous shrubs to natural climatic variability. For the East-Siberian tundra in particular, no previous attempts have been made to relate inter-annual variability in shrub growth to climate. I investigated the growth response of two pan-Arctic distributed deciduous shrub species with contrasting growth forms (*Betula nana*: low statured, many branches; *Salix pulchra* (tealeaf willow): tall-statured, few branches) to climate by correlating ring-width chronologies with meteorological station data and determined which climate parameters and seasonal period were

most important for shrub growth. I found that early summer temperature is the most important climate driver for growth of both shrub species, correlating very strongly with annual growth ring widths. Furthermore, growth of *Salix pulchra* was significantly related to satellite-derived peak-growing season summer greenness, showing that shrub chronologies may be successfully used to track Arctic summer greenness trends further back in time than the available 30-year satellite record on Arctic summer greening.

There is evidence that the Arctic tundra is greening in response to rising summer air temperatures during the last three decades, potentially as a result of an increase in deciduous shrub growth. However, little is known about linkages between inter-annual variations in tundra summer greenness and surface albedo in relation to changes in shrub cover. Using field data, I showed that *Betula nana* cover was positively related to summer greenness at the research site in NE-Siberia, but negatively related to summer albedo, which confirms the idea that shrub expansion may feedback positively to atmospheric heating. On a larger scale, I showed by analysing satellite data for four tundra regions across the Arctic that summer greenness is greatest in areas classified as shrub tundra. Furthermore, I observed that inter-annual variations in summer greenness are negatively related to variations in summer albedo. At the same time, satellite data show that a widespread shrub expansion may not lead to a reduction in summer albedo for all tundra areas, as vegetation zones that are currently classified as barren and wetland tundra show lower summer minimum albedo values than shrub tundra areas. In these areas, other non-vegetation surface properties such as barren soil and water bodies may also greatly affect the surface albedo.

Climate warming generally favours deciduous shrub growth, but is often accompanied by a reduction in moss and lichen cover. A decrease in moss cover may increase summer permafrost thaw, since mosses are known for their insulating capacity and may buffer permafrost against air warming. However, little empirical data is available on the role of mosses in water and heat exchange in tundra ecosystems. By performing a moss removal experiment in plots with dense and thin *Betula nana* cover, I show that the amount of available energy that is partitioned into soil warming increases with moss removal, but that a concomitant increase in understory evaporation with moss removal may partly compensate for the loss of soil insulation. No significant effect of *Betula nana* canopy density on understory evapotranspiration was measured, but ground heat flux partitioning was reduced by a denser shrub canopy. These results show that changes in moss or shrub cover may have important consequences for summer permafrost thaw.

Finally, I investigated the relationship between summer permafrost thaw depth and vegetation characteristics by measuring vegetation and soil variables along transects in North-eastern Siberian tundra. Transect measurements points covered most of the local variation in vegetation. I clustered transect sample points

on basis of their vegetation composition using ordination techniques and could thus distinguish four vegetation classes, ranging from sedge pools to mixtures of graminoid tussocks, deciduous and evergreen shrubs and forbs. Differences in vegetation and soil variables between vegetation classes were investigated and related to differences in permafrost thaw depth between vegetation classes. Shallowest permafrost thaw was observed in the vegetation class dominated by the deciduous shrub *Betula nana*, with permafrost thaw depth showing a negative relation with *Betula nana* cover, confirming the results from the removal experiment that increasing *Betula nana* cover may reduce summer permafrost thaw depth.

In conclusion, I show that deciduous shrub growth in the Siberian tundra is likely to increase with climate warming and thereby may reduce summer permafrost thaw depth, despite that with increasing shrub cover more solar radiation is trapped into the ecosystem by a reduction of the surface albedo. The results of my thesis suggest it is important to incorporate feedbacks between shrub growth, permafrost thaw and climate in model predictions on the Arctic climate and stability of permafrost in a future warmer world.



## Samenvatting

Het Arctisch gebied ondergaat drastische veranderingen in klimaat, met als belangrijkste verandering een verhoging van de temperatuur. Noordelijk gelegen toendragebieden zijn erg gevoelig voor klimaatsveranderingen en kunnen grote verschuivingen in plantensamenstelling veroorzaken. Van alle plantensoorten die voorkomen in het Arctisch toendragebied reageren bladverliezende struiken het sterkst op temperatuurstijgingen, vaak ten koste van mossen en korstmossen. Het weerkaatsingsvermogen van zonlicht (albedo) van het toendra oppervlak neemt af met een hogere struikbedekking en kan daardoor leiden tot een warmere atmosfeer. Als gevolg van deze luchtopwarming zou de organische permafrostbodem (bodem welke het gehele jaar bevroren is) dieper kunnen ontdooien gedurende de zomer en daardoor meer gaan ontbinden, wat vervolgens kan leiden tot de uitstoot van broeikasgassen methaan en koolstofdioxide. Ten gevolge van het broeikas effect van deze gassen kan het klimaat weer verder opwarmen en dus potentieel een positieve terugkoppeling vormen naar verdere uitbreiding van het stuikareaal. Er is echter nog veel onbekend over de effecten van klimaatsveranderingen op de groei van struiken en mossen in toendra ecosystemen en de mogelijke terugkoppelingen van veranderingen in plantengroei op het klimaat. Het hoofddoel van mijn proefschrift was om de interacties tussen vegetatie, klimaat en permafrostdooi te bestuderen in de Noordoost-Siberische toendra, met speciale aandacht voor de struiksoort *Betula nana* (dwergberk), aangezien deze soort voorkomt in vrijwel het gehele polaire gebied en erg gevoelig is voor milieuveranderingen.

In contrast met hun positieve effect op de luchttemperatuur kunnen struiken ook een verkoelende werking hebben op de bodem via beschaduwing. Ik heb deze contrasterende effecten van struikbedekking op permafrost dooidiepte bestudeerd door een struik-verwijderingsexperiment uit te voeren in een toendra gebied met continue permafrost (permafrost vormt een continue laag onder het oppervlak) in Noordoost-Siberië. In plots van tien meter doorsnede heb ik alle *Betula nana* struiken verwijderd en vervolgens de permafrost dooidiepte in deze plots vergeleken met dooidiepte in plots met intacte *Betula nana* bedekking. Hoewel de albedo (weerkaatsing van zonlicht) lager was in plots met intacte *Betula nana* bedekking, was de absolute hoeveelheid energie die naar de bodem werd geleid lager, resulterend in een inverse relatie tussen permafrost dooidiepte en *Betula nana* bedekking in ongestoorde controle plots. Plots waarin *Betula nana* was verwijderd hadden een grotere permafrost dooidiepte dan plots met intacte *Betula nana* struiken. Dit laat zien dat een verhoging van het stuikareaal als gevolg van temperatuurstijging permafrost zou kunnen beschermen tegen een opwarmend klimaat.

Hoewel experimentele verwarming studies in het algemeen een positieve groeirespons laten zien van struiken is er weinig bekend over de groeirespons van Arctische struiken op natuurlijke klimaat variabiliteit. Voor het Oost-Siberische

gebied was er zelfs nog geen enkele studie gedaan over de relatie tussen natuurlijke klimaat variabiliteit en struikgroei. Ik heb de groeirespons van twee circumpolair voorkomende struiksoorten met contrasterende groeiwijze (*Betula nana*: lage struik, produceert veel takken; *Salix pulchra* (Arctische wilg): hoge struik, produceert weinig takken) op klimaat gemeten door chronologieën van jaarringbreedtes te produceren en deze te vergelijken met temperatuur- en neerslagdata van het meest nabijgelegen meteorologisch station van de afgelopen 60 jaar. Zodoende heb ik bepaald wat de belangrijkste klimaat variabele en tijdsperiode zijn voor groei van deze twee struiksoorten. Ik concludeer dat de vroege zomertemperatuur (2<sup>e</sup> helft Juni - 1<sup>e</sup> helft Juli) het meest bepalend is voor groei van beide soorten, aangezien deze variabele het sterkst gerelateerd was aan de jaarringbreedtes. Verder was groei van *Salix pulchra* significant gerelateerd aan door satelliet waargenomen toendra groenwaarden (maat voor productiviteit van de vegetatie) gedurende de piek van het groeiseizoen. Dit laat zien dat struik chronologieën mogelijk kunnen worden gebruikt om toendra groenwaarden verder terug in de tijd te herleiden dan de beschikbare satelliet dataset van de laatste 30 jaar.

Er zijn aanwijzingen dat de waargenomen vergroening van het Arctisch gebied van de laatste decennia veroorzaakt wordt door een stijging van de zomertemperatuur. Mogelijk is deze vergroening een gevolg van een toename in struikgroei. Er is echter nog weinig bekend over de relatie tussen veranderingen in vergroening, struikgroei, zomertemperatuur en albedo in de toendra. Aan de hand van veldmetingen in een toendragebied in Noordoost Siberië laat ik zien dat bedekking van *Betula nana* positief is gerelateerd aan groenheidswaarden van de vegetatie, en negatief is gerelateerd aan albedo. Dit bevestigt het vermoeden dat een toename in struikgroei kan leiden tot een versnelling van opwarming van de atmosfeer van het Arctisch gebied door meer zonnestraling te absorberen en daarmee de albedo van het aardoppervlak te verlagen. Aan de hand van satelliet waarnemingen van vier regio's verspreid over het Arctisch gebied laat ik zien dat groenwaarden het hoogst zijn in gebieden geclassificeerd als struiktoendra. Verder was de jaarlijkse variatie in groenwaarden negatief gerelateerd aan zomer albedo waarden. Tegelijkertijd laten de satelliet albedo waarnemingen zien dat een wijdverspreide uitbreiding van het struikareaal niet altijd hoeft te leiden tot een verlaging van de albedo, aangezien toendra gebieden geclassificeerd als drasland en kale toendra lagere albedo waarden lieten zien dan struiktoendra. In deze toendragebieden hebben andere variabelen dan vegetatie zoals kale bodem en wateroppervlakten waarschijnlijk ook een grote invloed op de albedo van het aardoppervlak.

Een verhoogde temperatuur heeft over het algemeen een positieve invloed op de groei van Arctische struiken, maar gaat vaak ten koste van de groei van mossen en korstmossen. Een reductie in mos bedekking kan mogelijk leiden tot een diepere permafrostdooi aangezien mossen een sterk isolerend vermogen hebben. Er zijn echter weinig empirische data over de rol van mossen in de uitwisseling

van energie en water tussen bodem en atmosfeer in toendra ecosystemen. Ik laat aan de hand van een mos-verwijderingsexperiment in plots met open en dichte begroeiing van *Betula nana* zien dat er meer energie naar de bodem wordt geleid met verwijdering van de moslaag, maar dat tegelijkertijd de bodemverdamping toeneemt. Deze toename in verdamping compenseert mogelijk ten dele het verlies aan bodem isolatie. Struikdichtheid had geen effect op de bodemverdamping, maar de bodemwarmteflux was wel lager onder een dichter struikdek. Deze resultaten laten zien dat veranderingen in mos en struik bedekking als gevolg van een veranderd klimaat mogelijk belangrijke gevolgen heeft voor de permafrost dooidiepte gedurende de zomer.

Ten slotte heb ik de relatie tussen permafrost dooidiepte en vegetatie bepaald door vegetatie en bodemparameters te meten langs transecten in een toendra gebied in Noordoost Siberië. De meetpunten in de transecten omvatten de meeste variatie in lokale vegetatie. Meetpunten in de transecten werden gegroepeerd op basis van vegetatiesamenstelling met gebruik van ordinatie technieken. Op basis hiervan konden vier vegetatieklassen worden onderscheiden, variërend van natte zegge-vegetatie tot mengsels van grasachtige, kruiden en struiken. Verschillen in bodem- en vegetatievariabelen tussen vegetatieklassen werden geanalyseerd en gerelateerd aan verschillen in permafrost dooidiepte tussen de vegetatieklassen. De dunste dooidieptes werden gemeten in de vegetatieklasse gedomineerd door *Betula nana*. Binnen deze vegetatieklasse werd ook een inverse relatie tussen permafrost dooidiepte en *Betula nana* bedekking gemeten. Dit bevestigt de resultaten van het *Betula nana*-verwijderingsexperiment en laat zien dat een toename in *Betula nana* groei als gevolg van een opwarmend klimaat permafrost kan bufferen tegen een hogere luchttemperatuur.

Samenvattend laat ik zien dat groei van bladverliezende struiken in de Siberische toendra waarschijnlijk toeneemt met een opwarmend klimaat. Een toename in struikoppervlak kan leiden tot een reductie in permafrost dooidiepte, ondanks de hogere absorptie van zonlicht en daarmee verlaging van de oppervlakte-albedo door toendrastruiken. De resultaten van mijn proefschrift wijzen er op dat het belangrijk is om terugkoppelingen tussen struikgroei, permafrostdooi en klimaatsveranderingen mee te nemen in modelvoorspellingen over het Arctisch klimaat en de stabiliteit van permafrost in een toekomstig warmere wereld.



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Zonder de kameraadschap van mede-Darwin aio's was het zeker niet zo gezellig geweest tijdens het Siberische veldwerk. Frans-Jan, wij hebben aardig wat

## Dankwoord

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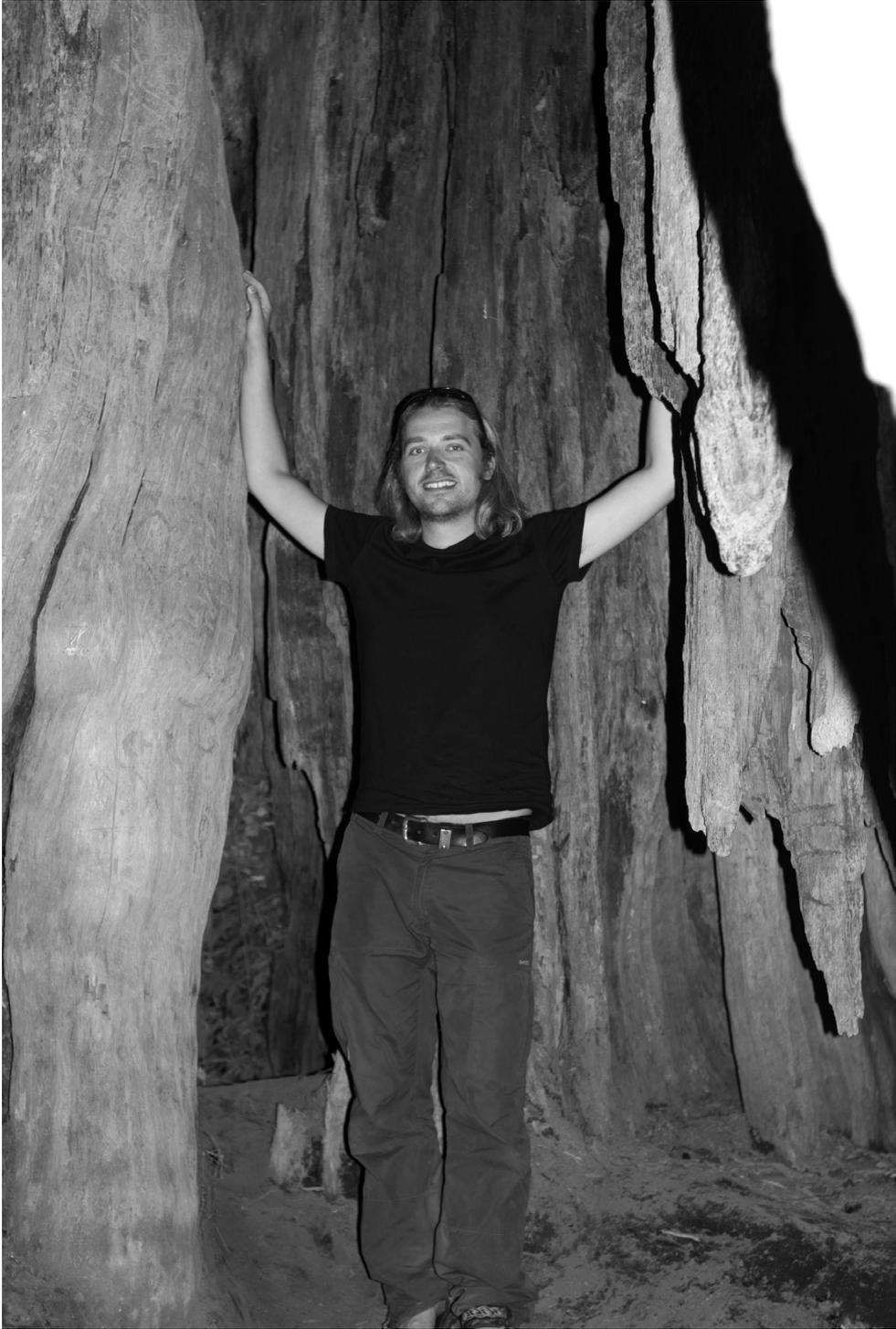
It was great to have met many members of the shrub-hub community in Vienna and San Francisco during EGU/AGU. A special thanks to Isla as enthusiastic driving force of the shrub-hub team. Hopefully we will all meet again soon. I also greatly enjoyed meeting all the participants of the "5<sup>th</sup> international workshop on water, carbon and energy cycles over boreal and arctic regions" held November 2010 in Wageningen. Furthermore, I would like to thank all my fellow Darwin-PhD's: it was great fun to speak to you during the annual Darwin-days in Veldhoven.

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## Curriculum vitae

Daan Blok was born 2 September 1981 in Nijmegen, the Netherlands. After graduating from Kandinsky College in the year 2000, he started to study Biology at Radboud University Nijmegen. During his BSc, he followed the supplementary interdisciplinary Honours Programme. In 2005 he did an internship at the Laboratory for Palaeobotany and Palynology at Utrecht University, reconstructing past atmospheric CO<sub>2</sub> from fossil leaf remains that were deposited in the Netherlands during the early Holocene. For his second internship at the department of Landscape Ecology (UU) in 2006, Daan studied the effects of nitrogen deposition and temperature on N<sub>2</sub>O emissions from an Icelandic wetland. After obtaining his MSc degree Biology in March 2007, he started as a PhD student at the department of Plant Ecology and Nature Conservation at Wageningen University. Daan then spent the next four summers in the Siberian tundra studying the interactions between vegetation, permafrost and climate, resulting in this thesis.

### Publications

Blok D, Heijmans MMPD, Schaepman-Strub G, van Ruijven J, Parmentier FJW, Maximov TC, Berendse F (2011) The cooling capacity of mosses: controls on water and energy fluxes in a Siberian tundra site.

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*Environmental Research Letters*.



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has successfully fulfilled all requirements of the  
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Wageningen, 5 October 2011

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- o PhD Competence Assessment
- o Techniques for Writing and Presenting Scientific Papers
- o PE&RC Introduction Weekend

Oral Presentations

- o Feedbacks of vegetation change to surface energy balance and seasonal thawing of permafrost, IMPETUS 2007 – OSL – APECS – PYRN Training workshop on Permafrost Research Methods, 30 November – 2 December 2007, St. Petersburg, Russia
- o How does shrub growth relate to local climate and what are potential effects of shrub expansion on permafrost thawing, EGU General Assembly, 3 – 7 May 2010, Vienna, Austria
- o Shrub growth response to climate change and feedbacks of vegetation change to permafrost thaw in the Siberian arctic tundra, AGU Fall Meeting, 13 – 17 December 2010, San Francisco, USA
- o Shrub growth response to climate change and feedbacks of vegetation change to permafrost thaw in the Siberian arctic tundra, ESA Annual Meeting, 2 – 6 August, 2010, Pittsburgh, USA

SENSE Coordinator PhD Education and Research

A handwritten signature in black ink, appearing to read "Johan Feenstra", written over a horizontal line.

Mr. Johan Feenstra



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Darwin Center for Biogeosciences

### **Photo information**

- page 116: Arctic Tern (*Sterna paradisaea*)
- page 118: Red-spotted Bluethroat (*Luscinia svecica svecica*)
- page 132: Arctic Redpoll (*Carduelis hornemanni*)
- page 136: Rough-legged Buzzard (*Buteo lagopus*)
- page 140: Red-throated Pipit (*Anthus cervinus*)
- page 146: Sandhill Crane (*Grus canadensis*)
- page 148: Long-tailed Skua (*Stercorarius longicaudus*)
- page 151: Pectoral Sandpiper (*Calidris melanotos*)

All photographs by Daan Blok, except photo on page 11 by Monique Heijmans and photo on page 144 by Annelein Meisner