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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 are 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.

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 are 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.

Key words: moss; evaporation; ground heat flux; shrub; permafrost; tundra; Arctic; climate change.

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 and others 1995; Wahren and others 2005; Forbes and others 2010; Blok and others 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 and others 1999) or indirectly by increased shading by the shrub canopy and associated leaf litter

(Chapin and others 1995; Hobbie and Chapin 1998; van der Wal and others 2005; Walker and others 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 and others 1993; Man and others 2008) and presumably also by reducing evaporation stress (Busby and others 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 and 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 and others 1998; Beringer and others 2001; McFadden and others 2003; Beringer and others 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 and others 2009). Consequently, mosses can reduce the transfer of energy into the soil and thereby reduce soil temperature (Gornall and others 2007) and facilitate the presence of permafrost (Zimov and others 1995). Thus, a reduction in moss cover may have major implications for permafrost thaw (Gornall and others 2007) and concomitant soil carbon storage (Hollingsworth and others 2008) and release (Zimov and others 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 and others 2011).

Besides their capacity of thermal insulation, mosses may also cool the soil by water evaporation from their surface. Because 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 and others 1992; Lafleur and Schreader 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 and others 2008) and/or sensible heat flux. Furthermore, an increase in vascular plant cover density (for example, shrub encroachment) may also decrease moss evaporation (Heijmans and others 2004b; Beringer and others 2005) and change tundra energy partitioning. Moreover, shrubs decrease the surface albedo by absorbing more solar radiation than shorter-statured tundra vegetation (Sturm and others 2005). This may lead to atmospheric heating and thus result in a further increase in shrub growth, thereby potentially creating a positive feedback loop (Chapin and others 2005).

In summary, mosses are considered to be very important to critical tundra ecosystem processes such as water and energy exchange, but to what 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 and others 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 and others 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 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 and others 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 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 1). The point intercept method that was used to measure plant species cover is described in detail in Blok and others (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 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 aquatilus* ssp. *stans*, henceforth called ''graminoid'')

Table 1. Plant Species Cover, Determined Using Point Intercept Measurements During Summer 2009, in Experimental Plots with a Dense or a Thin *Betula nana* Canopy

Plot type	Dense *Betula nana* canopy	Thin *Betula nana* canopy
Growth form/species		
Deciduous shrub	75.5 ± 3.6**	48.9 ± 6.3
Betula nana	72.3 ± 2.5***	42.3 ± 2.9
Salix spp.	3.2 ± 1.3	5.8 ± 3.0
Vaccinium uliginosum	0.0 ± 0.0	0.7 ± 0.7
Evergreen shrub	8.8 ± 2.3	13.1 ± 10.7
Ledum palustre	0.4 ± 0.3	0.1 ± 0.1
Vaccinium vitis-idea	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

*Also shown are leaf area index values of the vascular vegetation, determined using a SunScan canopy analysis system. 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 chamaemorous, Saxifraga punctata and Valeriana capitata. Moss species include: Aulacomnium turgidum, Dicranum polysetum, Hylocomium splendens, Polytrichium sp. Ptilidium ciliare, Rhitidium rugosum and Tomenthypnum nitens. Lichen species include: Cetraria sp., Cladina sp., Cladonia sp., Sterocaulon sp. and Thamnolia vermicularis. Date are means ± SE (n = 5 plots) per plot type. All data are in percentage of the total number of grid points within the circular 10 m diameter plots. Significant differences in plant species cover and leaf area index between plot types are shown *P < 0.05, **P < 0.01, ***P < 0.001.*

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 (Figure 1). Aboveground graminoid biomass was
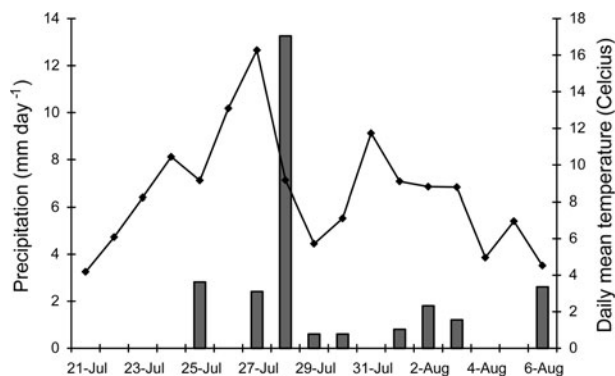
Figure 1. Photograph of a plot with a thin *Betula nana* canopy. Visible are four lysimeters with the following treatments: intact moss and graminoid, intact moss with graminoid removed, intact graminoid with moss removed, moss and graminoid removed. The diameter of the lysimeters is 16.3 cm.

Figure 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.

removed by cutting the leaves flush with the moss layer using a pair of scissors, leaving the below-ground graminoid parts intact. Care was taken that the surface of the moss layer within the lysimeters was 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.

Lysimeters were weighed every evening on an electronic weighing scale (1 g precision) for a period of 2 weeks (between July 22nd and August 6th 2009) and evapotranspiration was calculated as mm water day^{-1} by determining weight loss. Daily evapotranspiration rates were corrected for water inputs by precipitation, recorded by an electronic rain gauge (Figure 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 h (Table 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 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 and others 2007). Water vapor flux measurements were made at 10 Hz intervals and calculated following the Euroflux methodology (Aubinet and others 2000) and gap-filled by 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 (T)-specific latent heat of vaporization (L_T) value between ±2440 and 2500 kJ kg^{-1} water and was calculated by the following equation (Rogers and Yau 1989):

$$L_T(°C): 6.14 \times 10^{-5}T^3 + 1.59 \times 10^{-3}T^2 - 2.36\,T + 2500.79$$

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.

Table 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)

Species group	Plot type	Lysimeter treatment		
		Graminoid + Moss	Graminoid removal	Moss removal
Moss	Dense *B. nana*	475 ± 40	447 ± 40	
	Thin *B. nana*	544 ± 88	464 ± 52	
Graminoid	Dense *B. nana*	19 ± 8		35 ± 11
	Thin *B. nana*	37 ± 10		38 ± 7

All values are in g dry plant biomass m^{-2} ± SE (n = 5 plots). No significant differences in graminoid and moss biomass were observed between lysimeter treatments and plot types (P > 0.05).
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.

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 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 and others 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 (HFP01, 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 × 25 cm. The removed green moss biomass was dried at 70°C for 48 h 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 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 and others (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 m² within the plots for the lower short- and long-wave 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, because this fraction is less sensitive to changes in weather conditions than the absolute ground heat flux values. All measurements were made at 2-s 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 min 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* canopy) as explanatory variables and

plot as random variable. Measurement time (lysimeters were weighed on 13 dates between July 22nd and August 6th 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 and 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 (Figure 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^{-1} and tundra evapotranspiration rates ranging between 0.7 and 1.7 mm day^{-1}. We measured a relatively large variability in daily average understory evapotranspiration (intact graminoid and moss treatment), which was closely linked to daily variations in
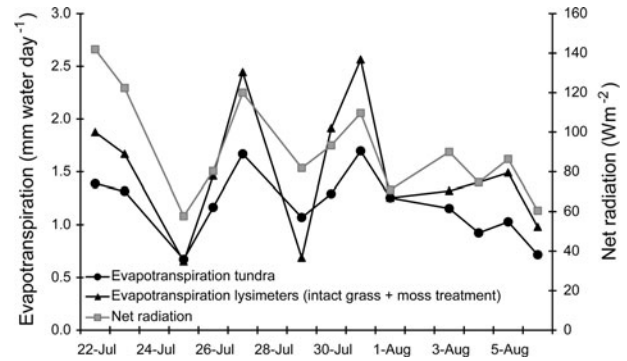
Figure 3. The *black line* and *triangles* represent daily average evapotranspiration rates measured by lysimeters with intact graminoid and moss vegetation ($n = 10$ lysimeters). The *black line* and *circles* represent daily average tundra evapotranspiration, measured by eddy covariance technique. 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 24th, July 28th and August 2nd, and therefore evapotranspiration rates for these dates were averaged with evapotranspiration rates of the following day.

net radiation ($r = 0.74$, $P < 0.01$, $n = 13$ days; Figure 3), as was previously observed for moss evaporation in an Alaskan boreal forest (Heijmans and others 2004a).
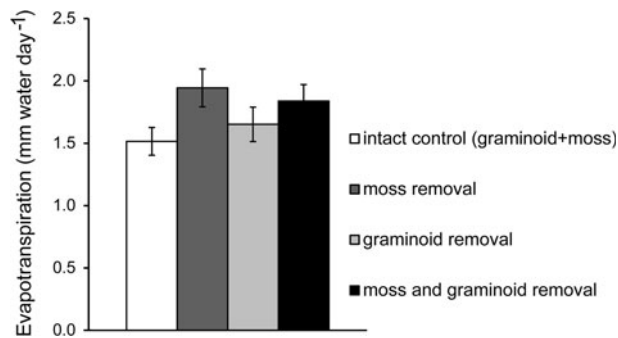
Rates of evapotranspiration differed significantly between lysimeter treatments, but were not affected by *B. nana* canopy density (Table 3). Two lysimeter treatment groups could thus be distinguished on basis of their evapotranspiration rates: lysimeters with and without a green moss layer ($P < 0.001$, $n = 20$). Overall, removal of the green

Table 3. Results of 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 2-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 × graminoid removal	1	0.838	0.367
Plot type × moss removal	1	0.029	0.866
Graminoid removal × moss removal	1	1.646	0.209
Plot type × graminoid removal × moss removal	1	2.162	0.151

moss layer increased evaporative losses by 19% in comparison to lysimeters with an intact green moss layer (Figure 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 *and others* 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 understory evaporation (green moss evaporation and organic soil evaporation) due to a reduced vapour 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 and others 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 (Figure 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 ($n = 3$ temperature loggers per

lysimeter treatment per plot type; data not shown), with daily average soil temperatures ranging between 5 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 (Table 3). This may have been caused by the relatively small amount of aboveground graminoid biomass in the lysimeters (Table 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 and others 2004b; Beringer and others 2005), but we found no significant effect of plot type (dense or thin *B. nana* canopy density) on understory evapotranspiration in our experiment (Table 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 ($P > 0.05$; data not shown).

Our values of understory evapotranspiration are comparable with moss understory evapotranspiration rates measured in an Alaskan open bog location (Heijmans and others 2004b), tundra ecosystem evapotranspiration in Alaska (McFadden and others 2003) and Siberia (Boike and others 2008), and with boreal peatland evapotranspiration in Finland (Wu and others 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 (Figure 3). At the study site the *B. nana* shrub canopy is only 10–20 cm tall, which makes it likely that the

Figure 4. Comparison of daily average evapotranspiration rates between lysimeter treatments during the summer of 2009 (average of 13 measurement dates between July 22nd and August 6th). 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) ± SE. Significances of treatment effects of moss removal and graminoid removal on evapotranspiration are given in Table 3.

understory contributes greatly to whole-ecosystem evapotranspiration. However, our values of understory evapotranspiration may not be representative for average tundra understory evapotranspiration, because 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 ± 55 and 526 ± 40 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 and Chapin 1991; Hobbie and others 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 and others (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 (Figure 5). These values are similar to values reported for other tundra sites in Alaska (McFadden and others 1998; Eugster and others 2000; Beringer and others 2005) and Siberia (Boike and others 2008). No interaction between moss removal and *B. nana* canopy density was observed.
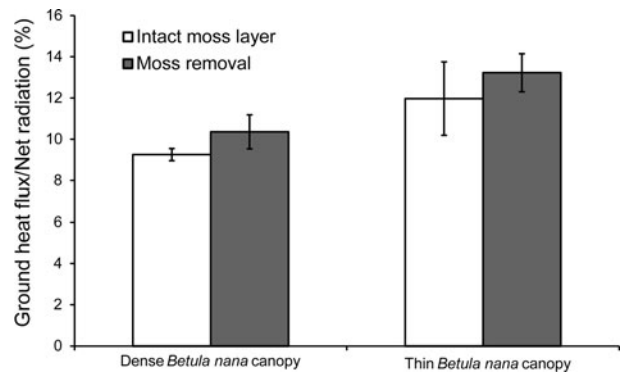
Figure 5. Comparison of average ground heat flux fractions of net radiation. The fraction ground heat flux of net radiation was measured in five plot pairs, with each plot pair consisting of a plot with a dense *Betula nana* cover and a plot with a thin *B. nana* canopy. *White bars* represent measurements 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 5-day period measurement means ($n = 5$ plot pairs) $\pm$ SE. Significances of treatment effects of *Betula nana* canopy density and moss removal on ground heat flux partitioning are presented in the ''Results and Discussion'' section.

On average, net radiation was 7 W m^{-2} higher in plots with a dense *B. nana* canopy (110 ± 10 W m^{-2}) compared to plots with a thin *B. nana* canopy (104 ± 7 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). With a denser *B. nana* canopy, leaf area index increased (Table 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 and others 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 and others 2004; Tape and others

2006; Olofsson and others 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 (Figure 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-h basis (data not shown). The average amplitude between daily minimum and maximum ground heat flux increased from 25.1 W m^{-2} for patches with moss cover to 28.0 W m^{-2} 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^{-2} for patches with moss cover to 32.3 W m^{-2} for patches without moss cover.

Evapotranspiration Versus 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^{-2}. In terms of absolute energy flux differences, removal of the green moss tissue caused an increase in latent heat (8.8 W m^{-2}) that was much larger than the corresponding increase in ground heat flux (1.3 W m^{-2}). 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 soil evaporation and thereby compensated for the warming effect from a reduction in surface albedo, resulting in an overall small surface warming (Rocha and Shaver 2011). 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 and 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 and others 2009) and therefore may decrease the ground heat flux (Beringer and others 2001). Moisture conditions of the moss tissue thus likely determine whether mosses may achieve soil cooling during summer in the 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, because we observed lower ground heat flux fractions in plots with denser *B. 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.

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