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Influences of the moss layer and environmental drivers on the active layer depth and soil temperature in a wet sedge Arctic tundra ecosystem

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Abstract

Permafrost soils contain approximately twice the amount of carbon as the atmosphere and this carbon could be released with Arctic warming, further impacting climate. Mosses are major component of Arctic tundra ecosystems, but the environmental drivers controlling heat penetration though the moss layer and into the soil and permafrost are still debated, especially at fine spatial scales where microtopography impacts both vegetation and soil moisture. This study measured soil temperature profiles (1–15 cm), summer thaw depth, water table depth, soil moisture, and moss thickness at a fine spatial scale (2 m) together with meteorological variables to identify the most important controls on the development of the thaw depth during two Arctic summers. We found a negative relationship between the green moss thickness (up to 3 cm) and the soil temperatures at 15 cm, suggesting that mosses insulated the soil even at high volumetric water contents (>70%) in the top 5 cm. A drier top (2–3 cm) green moss layer better insulated deep (15 cm) soil layers by reducing soil thermal conductivity, even if the moss layers immediately below the top layer were saturated. The thickness of the top green moss layer had the strongest relationships with deeper soil temperatures, suggesting that the top layer had the most relevant role in regulating heat transfer into deeper soils. Further drying of the top green moss layer could better insulate the soil and prevent permafrost thawing, representing a negative feedback on climate warming, but damage or loss of the moss layer due to drought or fire could reduce its insulating effects and release carbon stored in the permafrost, representing a positive feedback to climate warming.

1. Introduction

Northern high-latitude ecosystems are characterized by the presence of permafrost, a soil layer that remains frozen for at least two consecutive years (Permafrost Subcommittee 1988). The active layer is the soil directly above the permafrost that thaws during the summer (Permafrost Subcommittee 1988). The depth of this active layer is affected by solar radiation and by soil moisture, which increases the thermal conductivity and heat penetration into deeper soil layers (Permafrost Subcommittee 1988, Schuur *et al* 2015, Fisher *et al* 2016, Dafflon *et al* 2017, Williams *et al* 2020). Globally, permafrost and the active layer currently store an estimated 15 gigatons of carbon (Koven *et al* 2011, Hugelius *et al* 2014, Schurr 2019). Climate warming threatens the stability of this sequestered carbon (Schuur *et al* 2008, Schaphoff *et al* 2013, Miner *et al* 2022). The release of the vast amount of carbon stored in high-latitude soils could affect global climate through positive feedbacks in which increased atmospheric carbon may degrade permafrost and further increase greenhouse emissions (Davidson and Janssens 2006, Schuur *et al* 2008). Despite the potential release of substantial carbon stored in Arctic soils, the overall control that mosses and other environmental drivers have on permafrost degradation is still not fully understood (Luo *et al* 2016, Fisher *et al* 2018). Past studies have established general relationships between the moss layer and changes in belowground thermal conditions (Gornall *et al* 2007, Bueno *et al* 2016, Porada *et al* 2016, Park *et al* 2018, Hrbáček *et al* 2020), but there are still uncertainties on the complex interactions among the environmental drivers and the moss layer in controlling the active layer depth (Grunberg *et al* 2020). The environmental and vegetation controls on active layer depth, especially soil moisture and moss cover, can vary on small (1–10 m) spatial scales due to microtopography (Zona *et al* 2011a, Wilkman *et al* 2018), but such fine-scale variability has not been fully characterized across permafrost dominated ecosystems. The Arctic continues to experience increases in temperature and precipitation and an increase in soil moisture, which can increase permafrost degradation and greenhouse gas emissions (Beringer *et al* 2005, Hayashi *et al* 2007, Blok *et al* 2011, van Huissteden and Dolman 2012, Schaefer *et al* 2014, Boisvert and Strove 2015, Fujinami *et al* 2016, Park *et al* 2018b, Hrbáček *et al* 2020, Miner *et al* 2021). Land surface feedbacks on permafrost thawing and carbon release are still poorly constrained and require a better understanding of the interactions between active layer thermal states and their environmental drivers (Elmendorf *et al* 2012, Khani *et al* 2023). Thaw depth and soil temperature are major controls on greenhouse gas emissions in the Arctic (Zona *et al* 2009, 2011a, Wilkman *et al* 2018), so understanding controls on thaw depth and soil temperature can help refine predictions of future carbon loss from Arctic ecosystems. Given the large carbon store of permafrost soils (Hugelius *et al* 2014), it is critical to improve understanding of the environmental and vegetation controls on active layer development.

Mosses compromise approximately 40% of the biomass in the Arctic sedge tundra biome and exist in dense 'mats' (Euskirchen *et al* 2009). Mosses play a critical role in regulating thaw depths by reducing the heat penetration belowground when dry or increasing it when wet (Beringer *et al* 2005, Hayashi *et al* 2007, Blok *et al* 2010, 2011, Park *et al* 2018b, Hrbáček *et al* 2020). The insulating properties of mosses result from their unique adaptation to desiccation that allows them to survive desiccation (Blok *et al* 2011, Park *et al* 2018b). Insulation by dry mosses reduces soil temperatures and results in a shallower active layer depth (van der Wal *et al* 2001, Blok *et al* 2011, Park *et al* 2018b). Contrawise, a wet moss layer is associated with higher heat conduction in the soil and a deeper active layer depth (Hayashi *et al* 2007, Park *et al* 2018b, Hrbáček *et al* 2020).

The relative importance of different processes affecting soil temperature, active layer depth, and the heat conductivity (Clayton *et al* 2021), should be identified for dominant ecosystem types and moisture regimes across the Arctic. In wetter soils, more of the available energy at the surface goes to latent heat for evaporation, as opposed to sensible heat that warms soils and deepens the active layer. Wetter soils also have a higher heat conductivity, which increases heat penetration into deeper soil layers and increases the active layer depth (Clayton *et al* 2021). Moss cover may have significant impacts on both moisture content and heat fluxes (Soudzilovskaia *et al* 2013, Hrbáček *et al* 2020), but the dual impacts of moss characteristics and moisture content on temperature profiles and active layer depths has not been adequately documented, especially at fine spatial scales where microtopography impacts both moss and moisture. There is a linear relationship between thermal conductivity and moisture content in mosses (O'Donnel *et al* 2009). Organic horizons typically have lower thermal conductivity than mineral soils, which is also influenced by moisture content, in addition to bulk density and water phase (O'Donnell *et al* 2009).

To further understanding of the controls on the development of the active layer and the implications for the stability of the carbon stored in the permafrost, this study investigated a range of environmental drivers and vegetation characteristics, including solar radiation, soil moisture, air and soil temperatures, and the thickness and moisture content of the moss mat (green and total layer) at fine spatial scales (∼2 m) in a micro-topographically variable polygonal tundra ecosystem. The goal of this research was to quantify the magnitudes and interactions of the biotic and abiotic controls on soil temperature and thaw depth across a range of microtopographic positions in a drained lakes ecosystem. We expected thicker mosses would be associated with shallower depth of thaw and lower belowground temperatures, due to moss insulation of the soil. We anticipated higher volumetric water content (VWC) to be associated with deeper depth of thaw and increased belowground temperatures given an increase in heat conduction with higher soil moisture. We tested these hypotheses using data collected during two intensive field campaigns that documented moss cover, soil thermal profiles, photosynthetic active radiation (PAR), air temperature, and moisture conditions at high spatial resolution during the Arctic summer.

2. Methods

2.1. Study sites

The sites of this research are near Utqiaġvik, Alaska (formerly known as Barrow), which is the largest town in the Alaskan North Slope Borough. Our team has maintained several micrometeorological and eddy covariance towers in Utqiaġvik over the last decades (Zona *et al* 2016). This research was conducted near two of these eddy covariance towers, which were in operation from 2005–2009 (figure 1, the US-Ben (North), and US-Bec (Central) sites, established during the Biocomplexity Experiment, see Zona *et al* 2009, 2012). Data on meteorological drivers (PAR, air temperature, local surface and subsurface soil temperature, relative humidity, wind speed, and net radiation) were measured continuously at another nearby tower (US-Bes) that has been operational since 2005. US-Ben and US-Bec are 662 meters and 356 meters from US-Bes respectively, so we assume that the meteorological data collected at US-Bes were representative of the US-Ben and US-Bec sites. The locations of the towers are: 71.2809N, −156.5965W (US-Bes); 71.28316N, −156.60342W (US-Bec); and 71.28628N, −156.60424W (US-Ben) respectively (Zona *et al* 2009).

The sites are located in a drained lake basin ecosystem characterized by mosses, lichens, and graminoids including *Luzula nivalis, Luzula confusa, Eriophorum russeolum, Carex aquatilis*, and *Poa arctica* (see Davidson *et al* 2016 for more details) with patches of water and partially- to fully-submerged patches of vegetation. The region is characterized by a mix of high center and low center polygons; the middle of the low center polygons is often submerged with ponds of varying sizes. The microtopography results in different environmental conditions at the ∼1 m scale (Zona *et al* 2011a, Wilkman *et al* 2018). Access to US-Bes, US-Bec, and US-Ben sites was facilitated by the establishment of boardwalks during the Biocomplexity experiment in summer 2005 (Zona *et al* 2009). These boardwalks allowed sampling across the sites while limiting disturbance. The soil temperature data were collected every two meters in both US-Ben and US-Bec across 124 m transects that parallel historical water table data collection (Zona *et al* 2012), for a total of 62 plots in US-Ben and 62 in US-Bec.

2.2. Vegetation and environmental controls

Data on soil temperature, soil moisture, and moss cover were collected at 2 m intervals along two 124 m transects at US-Bec and US-Ben (figure 1) from an existing boardwalk to minimize disturbances to the tundra from walking during sampling, which in these waterlogged ecosystems can be very severe. The transects included a range of microtopographic features representative of drained lake ecosystems, including low-center polygons and polygon rims (figure 1, Zona *et al* 2011a, Wilkman *et al* 2018). In each plot we recorded the thickness of the total moss layer and the thickness of the green moss layer. Vegetation in the region is composed primarily of graminoids as the dominant vascular plant group and mosses such as *Sphagnum sp.* and *Drepanocladus sp.* (Davidson *et al* 2016, Zona *et al* 2011b, Peterson 2022 personal communication). Mosses at most of the plots were dominated by *Sphagnum* sp. ($n = 55$) or some combination of predominantly *Sphagnum sp., Drepanocladus sp.,* and other unidentified mosses (defined as 'Mixed' plots, $n = 46$) and a limited number of plots with only *Drepanocladus* sp. ($n = 21$). Only two plots did not have any living moss present, and were classified as 'Mostly decomposed mosses'. Data on the dominant moss genus and moss layer thickness (both total and green) were collected once during the week of 6 July 2021 ($n = 124$), in small (5 cm × 5 cm) sections. The 5 × 5 cm sections were carefully removed using a serrated knife, trying to limit damage to surrounding vegetation. The thickness of the entire moss layer and green moss layer were measured with a ruler, and the samples were reinserted into the holes created by sampling. This data collection was repeated for the second field season during the week of 8 July 2022 in a subset of the plots ($n = 20$ in Summer 2022 vs $n = 124$ in Summer 2021). Fewer samples were collected in 2022 to reduce disturbance to the sites. Measured moss thicknesses in the two years were similar and highly correlated ($R^2 = 92\%$, p-value < 0.001, 2022 moss thickness (cm) = 1.01967 * 2021 moss thickness (cm) + 0.228). In each of the 124 plots we recorded air temperature (5 cm above the surface), and moss and soil temperature profiles every cm from 1 cm below the surface (the top of the moss layer), down to 20 cm below the surface, on a weekly basis using type T thermocouples connected to a CR3000 datalogger (Campbell Scientific, Logan, UT, USA). At the beginning of our sampling, most locations had permafrost shallower than 20 cm; this prevented insertion of the probe to 20 cm, so we used 15 cm as a consistent maximum depth of the soil temperature measurements. The 21 thermocouples were attached to a fiberglass probe, which facilitated insertion in the moss layer and soil (figure 1). Temperature profiles were measured at each point for approximately 3 min after the readings stabilized (1–2 min). We also collected instantaneous measurements of

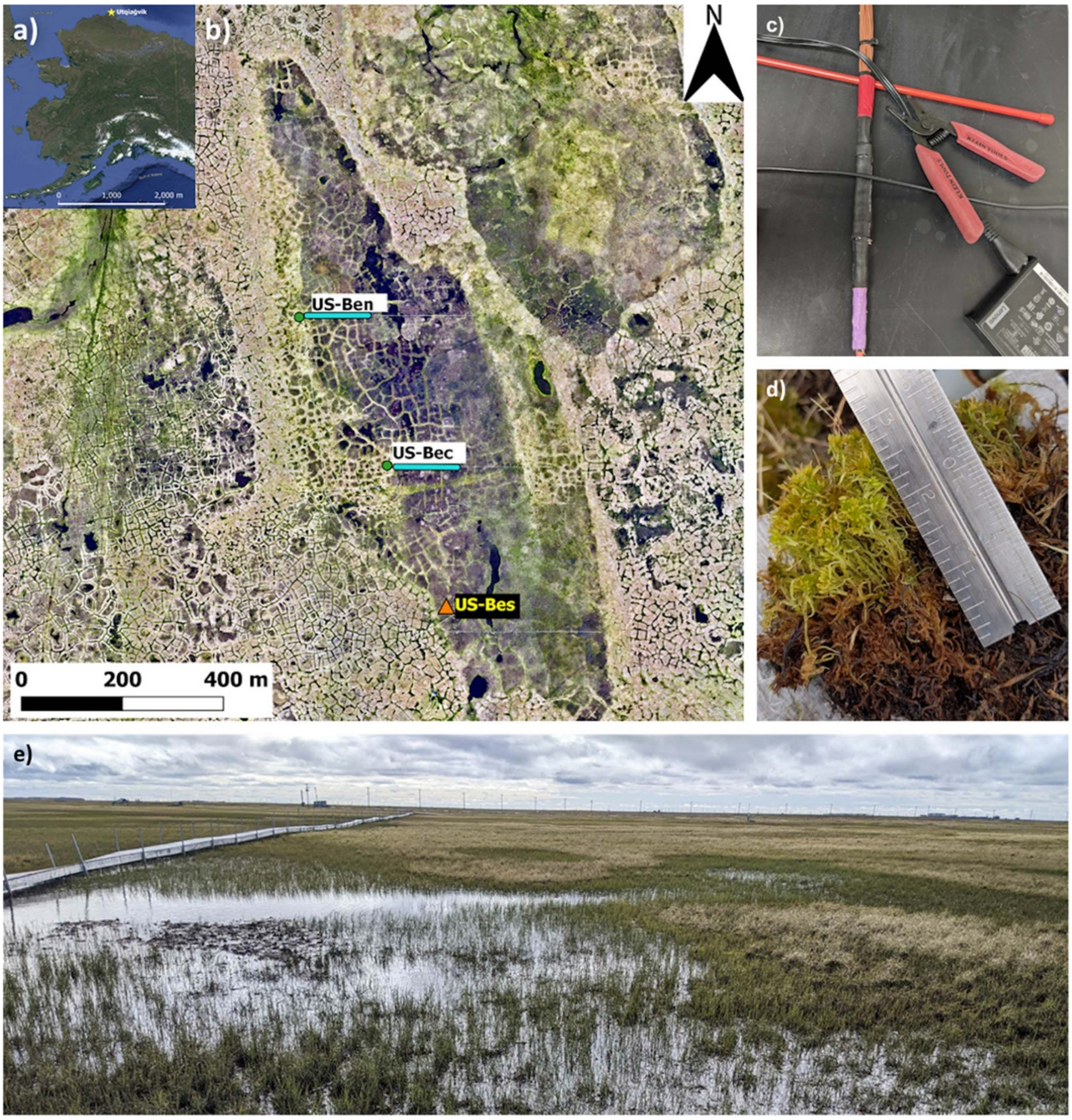

Figure 1. Study site: (a) map of Alaska showing the general location of Utqiaġvik (Google Earth Pro Copernicus/Landsat satellite imagery, 2023). (b) A high-resolution orthorectified camera imagery mosaic acquired by the National Ecological Observatory Network (NEON) Airborne Observation Platform (AOP) highlighting the US-Ben and US-Bec transects (highlighted in blue) and the US-Bes tower site. (c) A soil probes including 21 thermocouples for belowground and air temperature recordings. (d) A cross section of the moss layer, showing the thickness of the total (lowest brown point to uppermost green point) moss layer thickness and green moss layer. (e) A photograph noting the waterlogged conditions of the research sites.

moss/soil water content (VWC) weekly in the first 5 cm of the moss or soil layer using a FieldScout TDR300 (Spectrum Technologies, Aurora, IL, USA) and 5 cm rods. The FieldScout was calibrated using local water samples to account for nutrients that may influence conductivity. Thaw depth was collected weekly in each of the sampling plots by inserting a metal probe with 1 cm markings until it reached the frozen soil layer (Zona *et al* 2009). Water table depth below the surface was measured in perforated PVC pipes previously installed in each plot (Zona *et al* 2009, 2012). The ground surface was defined as the top of the green moss layer, consistent with previous studies from this area (Zona *et al* 2009, 2012, Wilkman *et al* 2018). Data on moss temperature moss water content, thaw depth, and water table level were collected weekly over 4 weeks in 2021 (8th July–28th July) and 4 weeks in 2022 (23rd June–14th July). We attempted to collect the measurements consistently at the same time of the day (midmorning to early afternoon). Based on long-term data over the last 20 years from our sites, the soil temperature and VWC in July 2021 and 2022 were similar to the long-term average (Zona *et al* 2014). Elevation at each plot along the transects and at the US-Ben and US-Bec stations was taken from Zona *et al* (2012), allowing us to quantify the microtopographic influence on soil moisture, soil temperature profiles, vegetation, and active layer development.

3. Statistical analysis

All statistical analyses were conducted using R version 4.2.0 (R Core Team 2022) using the caret, leaps, and MASS packages (Venables and Ripley 2002, Kuhn, 2015, Lumley and Miller 2022, Posit Team 2022, R Core Team 2022). Stepwise multiple regressions and univariate regressions (both linear and nonlinear) were used to test for and model the relationships between the deepest (minimum given the negative sign) thaw depth (D_{thaw}) or the temperature difference between 1 and 15 cm belowground (dT1_15) and environmental predictors, and to evaluate the collinearity in predictors. Stepwise multiple regressions were conducted to identify the most influential variables, then compared to the results of the univariate analysis, which were not affected by multicollinearity among the environmental drivers. We tested for correlations among predictor variables, which complicates significance tests when included together in the same stepwise regression mo predictor variables that were highly correlated ($-0.65 \geqslant r \geqslant 0.65$ and p-value < 0.05, figure S1) were not included in the stepwise multiple regression models, and we selected the variable with the higher explanatory power in the univariate analysis. Data from both 2021 and 2022 were summarized by the mean, median, or maximum over the entire measurement period for each plot along each transect to avoid issues from pseudoreplication, given that we sampled the same plots multiple times. Before deciding to aggregate the data we tested other statistical methods that are appropriate for a repeated-measure sampling design, but the non-normal distribution of the data complicated use of parametric tests. The predictor variables for maximum D_{thaw} included median water table level, median soil water content, maximum temperature 15 and 1 cm belowground, air temperature at 5 cm aboveground, green moss layer thickness, total moss layer thickness, and median PAR. The predictor variables for maximum belowground temperature (at 1 and 15 cm depth) included median water table level, median moss and soil water content, air temperature at 5 cm aboveground, green moss layer thickness, total moss layer thickness, and median PAR. These variables were expected to have the strongest influence on the heat penetration in the soil, and therefore D_{thaw} and soil temperature. The maximum moss and soil temperatures represent the warmest conditions during the field campaign, while the minimum (most negative) value was used for D_{thaw}, as it represented the deepest thaw, equivalent to the active layer depth in peak/late warm season. The median for each plot was used for the remaining variables (moss and soil moisture, water table, air temperature, and PAR), since medians are less influenced by outliers. Deviation from the mean elevation (dz) was calculated as a simple difference between each elevation point and the mean elevation dT1_15 was calculated as the difference between belowground temperatures at 1 cm and 15 cm. We also tested the influence of dominant moss genus on the relationship between the total and the green moss layer thickness and temperature by testing the significance in the interaction term between dominant moss genus and moss layer thickness in the regression models. We then tested if the environmental drivers included in the statistical analysis were significantly different by dominant moss genus using a non-parametric Kruskal–Wallis test (given their skewed distribution). If the Kruskal–Wallis test was significant we performed a post-hoc Dunn test to identify which group was different, using the dunnTest function in the FSA (Fisheries Stock Assessment package, version 0.9.5) in R. The 'Mostly decomposed mosses' plots were not included in this analysis as they only had $N = 2$.

Thaw depth and soil temperatures were non-linear functions of environmental drivers, so we tested a variety of non-linear regressions, including polynomial and logarithmic regressions (Zona *et al* 2023). We did not find an ecological explanation for the statistical models with the highest explanatory power (third order polynomial models). Therefore, we applied piecewise regressions to test for breakpoints in the regressions, using the segmented package in R (Muggeo 2003, 2008). When a breakpoint was statistically significant ($p < 0.05$), we included separate linear regressions for the two datasets separated by the breakpoint. Akaike information criterion (AIC), R^2, and p-values, were used to evaluate model performance. AIC estimates the prediction error and can be used to rank the overall quality of statistical models; AIC values in tandem with p-values and R^2 values helps in the model selection, with lower AIC associated with less complex and therefore better models (Fisher *et al* 2016, Thompson *et al* 2016, Wang *et al* 2019, Buchwal *et al* 2020). We also used structural equation modeling (SEM) through the Lavaan package in R (Rosseel 2012) to test the interactions between variables and to visualize of how they influence thaw depth and soil temperatures (Park *et al* 2018b, Wilcox *et al* 2019, Buchwal *et al* 2020, Thunberg *et al* 2021). SEM identified the direct and indirect roles and interactions of different environmental drivers, and is appropriate for datasets with collinear predictor variables (Graham 2003). The ability of SEM to test the direct and indirect effects of one variable on another allowed us to evaluate relationship in a complex system such as the ones studied here, where many environmental drivers are related to each other.

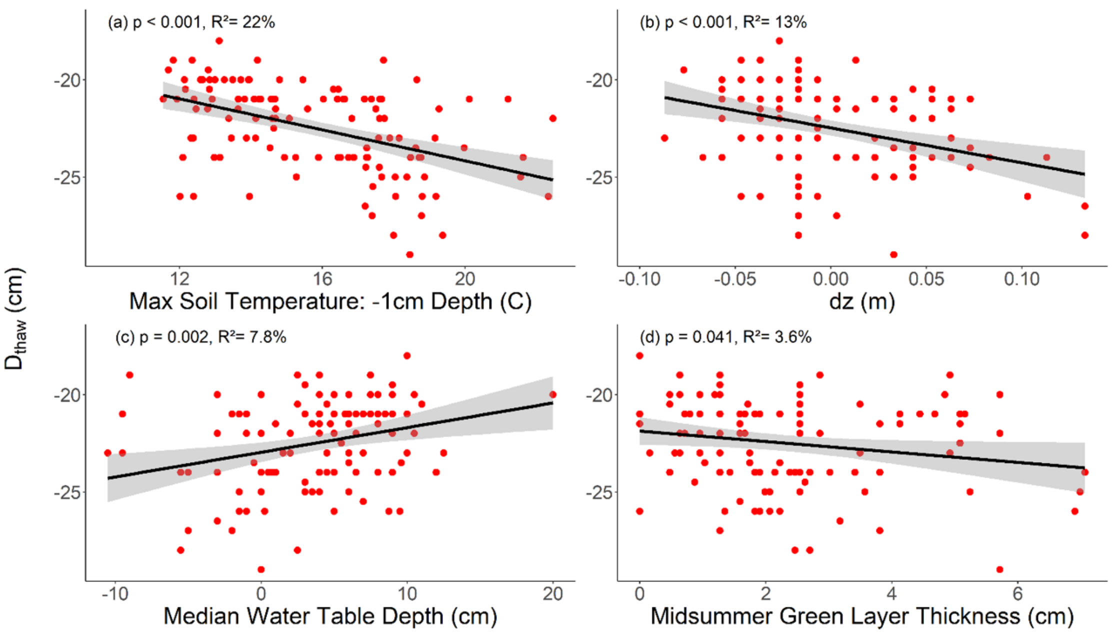

Figure 2. Relationship between the deepest thaw depth (D_{thaw}) and predictor variables for the entire study period (summer 2021 and 2022), for both study sites combined, demonstrating (a) a negative relationship with maximum soil temperature at 1 cm depth (indicated as −1 cm), (b) a negative relationship with the deviation from the mean elevation (dz), (c) a positive relationship with water table level, and (d) a negative relationship with green moss layer thickness.

4. Results

Several of the predictor variables were strongly correlated (table S1, figure S1) and were not included together in the regression models. Thaw depth was best explained by maximum temperature at 1 cm depth in both stepwise ($p<0.001$, $R^2 = 22\%$, AIC = 500, table S2) and univariate regressions (tables S3 and S4). Thaw depth had statistically significant univariate correlations with maximum belowground temperature at 1 cm, deviation from mean elevation (dz), median water table level, and green moss layer thickness (figure 2). For dT1_15, the median water content, D_{thaw}, and dz were significant predictors (p-value < 0.001, $R^2 = 45\%$, AIC = 525, table S5). Similarly, dT1_15 correlated with dz, water content, and green and total moss layer thicknesses (figure 3). For dT1_15, microtopographic position (dz) had the highest explanatory power ($R^2 = 34\%$, figure 3). The addition of soil water content and the deepest D_{thaw} increased the R^2 to 45% (table S3).

Moss layer thickness correlated with several other environmental variables. The green moss layer thickness correlated negatively with D_{thaw} (figure 2, p-value = 0.041, $R^2 = 3.6\%$) and positively with *XX* (figure 3, p-value < 0.001, $R^2 = 21\%$ when the green layer thickness was less than 3.1 cm), with total layer thickness ($p < 0.001$, $R^2 = 7.0\%$) and with dT1_15. The green moss layer thickness (figure 4, $p < 0.001$, $R^2 = 9.7\%$) and total layer thickness ($p = 0.031$, $R^2 = 4.0\%$) correlated positively with the seasonal maximum belowground temperature at 1 cm, but both green moss layer thickness ($p = 0.002$, $R^2 = 7.9\%$) and total moss layer thickness (figure 4, $p = 0.006$, $R^2 = 6.3\%$) correlated negatively with the maximum soil temperature 15 cm belowground dz correlated negatively with D_{thaw} (figure 2, p-value < 0.001, $R^2 = 13\%$) and positively with dT1_15 (figure 3, p-value < 0.001, $R^2 = 34\%$). Green moss layer thickness (p-value < 0.001, $R^2 = 13\%$), and total moss layer thickness (p-value < 0.001, $R^2 = 15\%$) correlated positively with dz.

Belowground water content had a strong negative relationship with dT1_15 when water content was greater than 74.4% (figure 3, p-value < 0.001, $R^2 = 19\%$) and no significant relationship below that threshold. Belowground temperatures at 1 cm were negatively associated with water content past a threshold of 74.3%, with no significant relationship was for soil water content below this threshold, but soil temperature at 15 cm was positively correlated with soil water content past a soil water content of 76.4% (figure 4). Water table level correlated positively with D_{thaw} (figure 2, $p = 0.002$, $R^2 = 7.8\%$). A complete description of the statistics of the stepwise, and the univariate models, and of the breakpoint analyses are included in tables S2–5.

Microtopographic position impacted both belowground temperature and water content. The median belowground temperature at 1 cm was higher (mean ± 95% CI, 17.3 ± 4.3 °C) in high elevation plots

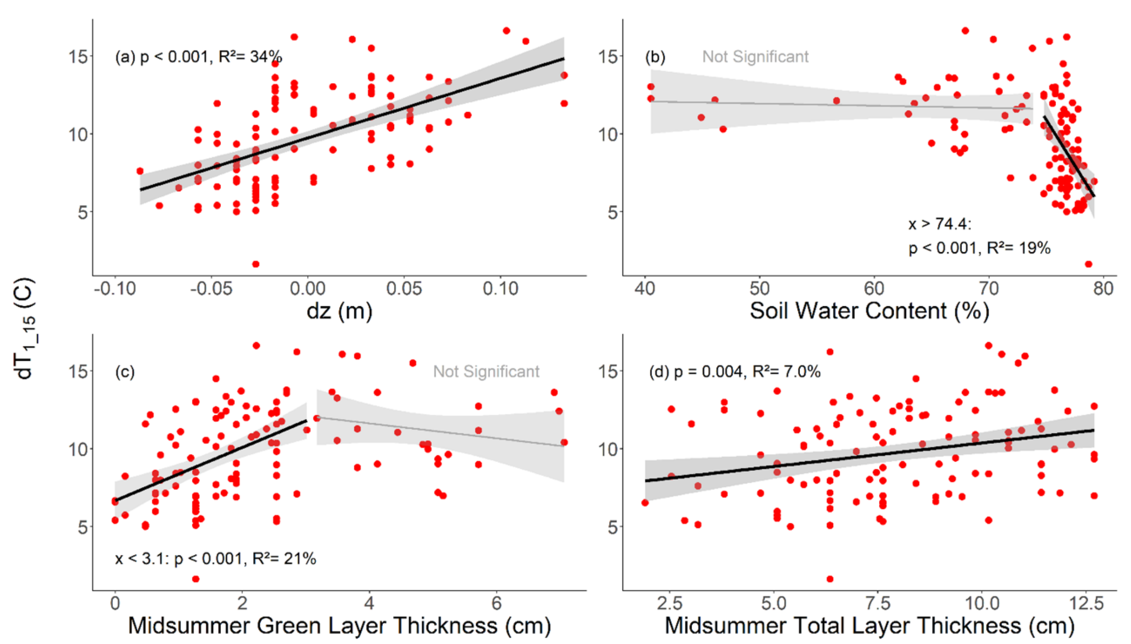

Figure 3. Relationship between the difference between temperature at 1 cm and 15 cm belowground (dT1_15) and predictor variables for the entire sampling period (summer 2021 and 2022) across all the sampling plots, showing (a) a positive relationship with the deviation from the mean elevation (dz) (b) a negative relationship with soil water content for soil water content greater than 74.4%, (c) a positive relationship with the midsummer green moss layer thickness for green moss layer thickness less than 3.15 cm, and (d) a positive relationship with the total moss layer thickness.

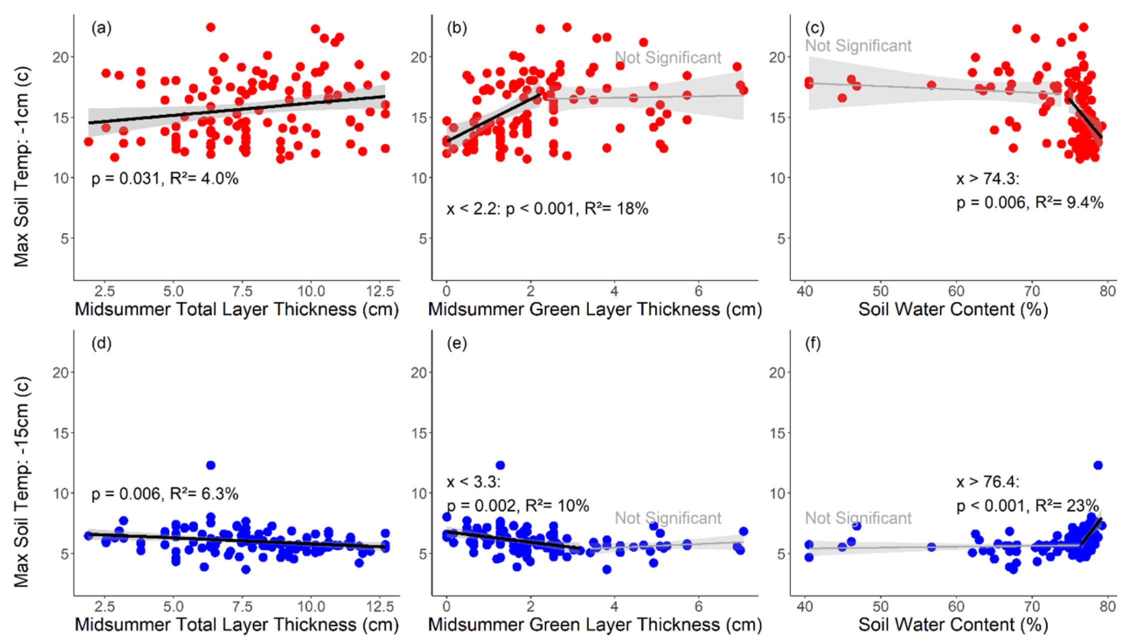

Figure 4. Relationships between maximum belowground temperature at 1 cm or 15 cm and predictor variables for the entire period of measurements (both summer 2021 and 2022), for all sampling plots. Thicker green and total moss layers corresponded to higher temperatures close to the surface (a) and (b), but to lower temperatures at deeper depths (d) and (e). As the soil water content close to the soil surface (average over 0–5 cm) increases, soil temperatures decrease at −1 cm (c) but increase at −15 cm (f).

($dz > 0$), compared with low elevation areas ($dz < 0$, mean ± 95% CI, 14.8 ± 4.9 °C; $p < 0.001$, figure S2). Soil water content was lower in plots above the mean elevation (70.6 ± 17.4%) compared with plots below the mean elevation (74.7 ± 12.8%) ($p = 0.007$).

The dominant moss genus did not significantly affect the relationship between the soil temperature at 15 cm belowground and the total thickness of the moss layer (i.e. the interaction term between dominant moss genus and moss layer thickness was not significant in the linear or polynomial regression with soil temperature). On the other hand, the interaction term between green layer thickness and

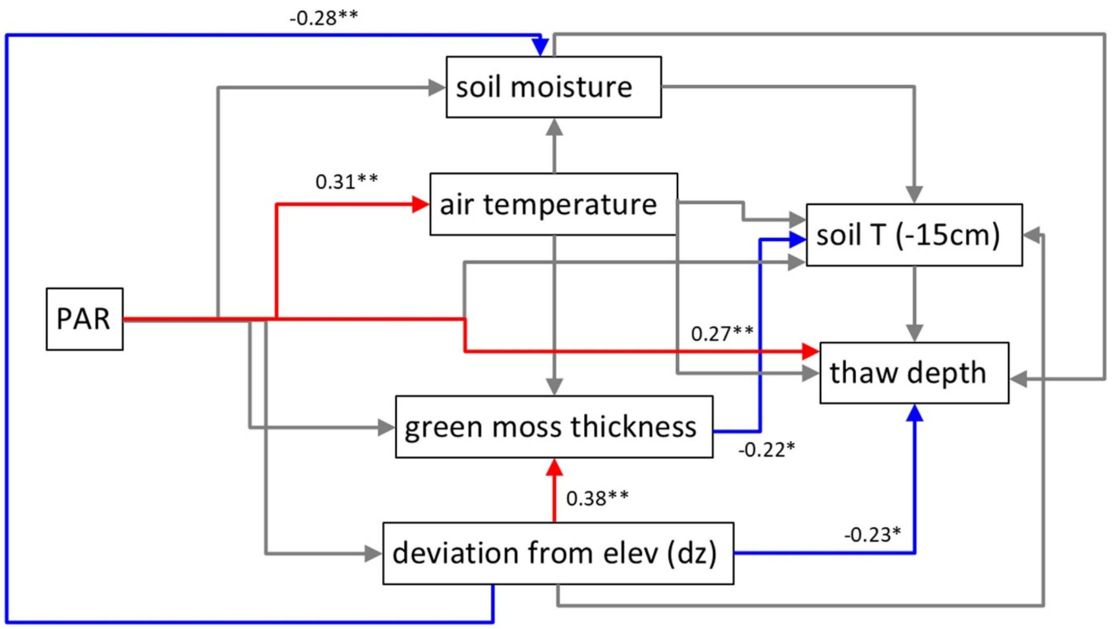

Figure 5. A structural equation model of the relationships included in the regression analyses. The standardized coefficients are included in proximity of the regression lines when significantin either blue (negative), or red (positive), with one asterix for a $p < 0.05$, and two for a $p < 0.001$. The total moss layer.

soil temperature at 15 cm was significant (only the slope of the mixed category was significantly different from the other two (*Sphagnum sp.* and *Drepanocladus sp.* groups)). The mean dz, the total thickness of the moss layer, the thickness of the green layer, and D_{thaw} were not significantly different among the moss genera ($p > 0.05$ in a Kruskal–Wallis test, table S6), while water table level, VWC, and soil temperature at 1 cm and 15 cm depth were significantly different ($p < 0.05$, figure S2, table S6). The Dunn post-hoc test showed that water table depth was different among all the genera groups, while VWC was only different between the mixed and the *Sphagnum* groups, and the belowground temperature at 1 cm and 15 cm depths were only different between the mixed and *Sphagnum* groups (table S6)

The structural equation model provided an overview of the complex relationships among the variables, including their direct and indirect effects. The median PAR was significantly and positively related with median air temperature, and the deepest D_{thaw}, (figure 5). VWC was positively and significantly associated with maximum deepest D_{thaw}, and finally, the green moss layer thickness was negatively related with maximum soil temperature at 15 cm, and dz was positively associated with green layer thickness, and negatively associated with deepest D_{thaw}, and water content (figure 5).

Overall, we find that microtopography governs soil thermal regimes through its impacts on moss thickness and soil moisture: topographic highs are associated with thicker moss layers, lower soil moisture, deeper active layer depth, higher shallow (1 cm) belowground temperatures, lower deeper (15 cm) soil temperatures and a larger thermal gradient (dT1_15) than topographic lows. The relationship between belowground temperatures and moss thickness or soil moisture was highly nonlinear: moss layers had a cooling effect on 15 cm soil temperature, but only up to moss thickness of ∼3 cm. Soil moisture impacted temperatures at 1 cm (negatively) and 15 cm (positively), but only near saturation, where the effect was strong.

5. Discussion

Green moss layer thickness and microtopographic position (dz) exerted the dominant controls on soil temperature profiles and thaw depth. Thicker green moss layers co-occurred with cooler deep (15 cm belowground) soil temperature, which is consistent with moss thermal insulation (Beringer *et al* 2005, Fisher *et al* 2016, Hrbáček *et al* 2020). Thicker mosses insulate the soil (Blok *et al* 2011, Chadburn *et al* 2015, Park *et al* 2018b, Hrbáček *et al* 2020, Heijmans *et al* 2022) as shown by the cooler deeper soil temperature under thicker moss, even with warmer near surface (i.e. 1 cm) belowground temperatures at microtopographic highs. Green moss thickness was higher in higher elevation areas possibly because higher local surface temperature might have stimulated moss growth in these temperature limited ecosystems (Harley *et al* 1989, Bengtsson *et al* 2021). Near-surface (1 cm) belowground temperature was the main control on thaw depth, consistent with previous studies (Schuur *et al* 2015, Dafflon *et al* 2017). Moisture content was also a very important control on belowground temperature, with opposite relationships for the near surface (negative) and deeper soil temperatures (positive). Cooler near surface belowground temperature co-occurred with higher moisture content, which could be explained by higher evaporative cooling of a wetter moss layer (Heijmans *et al* 2004a, 2004b) and by higher thermal conductivity and more rapid heat transfer to lower soil layers. The higher thermal conductivity and heat penetration in wetter soils is a major control on deeper soil temperature and thaw depth (Hinkel *et al* 2001, Hinkel and Nelson 2003, Shiklomanov *et al* 2010, Soudzilovskaia *et al* 2013, Curasi *et al* 2016, Fisher *et al* 2016, Hrbáček *et al* 2020). We observed significant breakpoints in the linear regressions, with different impacts of the top green moss layer (∼2–3 cm) than deeper green moss layers on soil temperatures at 1 cm and 15 cm. This suggests that the top green moss layer has the most relevant role in regulating the heat transfer into deeper soils, which is consistent with the reported significant relationship between moss layer thickness and thaw depth only for the top ∼15–20 cm of the moss layer (Douglas *et al* 2008). The top green moss layer is denser than underlaying moss layers (Zona *et al* 2011b) and has higher water retention capacity because of papillae (Clymo 1970, Dykas 2018), and therefore is more important in regulating the heat penetration into the soil than lower moss layers. The top moss layer is also more influenced by solar radiation, and might be drier than underlying layers due to evaporation, which would reduce the heat conduction into the soil. Commonly-reported VWC measurements average the top 5–10 cm and might miss important differences in moisture content between surficial and underlying moss layers. This highlights the challenges in properly capturing the small-scale variability in the moisture content of the moss layer without destructive sampling (Zona *et al* 2011b). The importance of the top moss green layer on the deeper soil temperature is also confirmed by the SEM which showed a significant and negative relationship between these variables (i.e. cooler deep soils with thicker green moss layers). This result is consistent with the importance of surface conditions for the thermal conductivity of moss and soil (Riseborough *et al* 2013, Clayton *et al* 2021), and with observed exponential relationships between active layer depth and moss thickness and a steeper relationship for shallower moss layers (Fisher *et al* 2016). The green layer of *Sphagnum* has higher water retention capacity than underlaying fibrous and amorphous layers (O'Donnell *et al* 2009). The dominant role of the uppermost moss layer on the thermoregulation of soil might at least partially explain the lack of relationship between the intensity of the moss buffering and the total moss layer thickness reported by previous studies (Hrbáček *et al* 2020), given that the first few cm of the top green layer are the most important for modulating soil temperature. This is also supported by the SEM, which showed that the green moss layer thickness was significant, while the total moss layer thickness was not significant in controlling the deeper soil temperature in a complex model including all the direct and indirect interactions. Therefore, understanding the vulnerability of the topmost portion of the green moss layer to climate change and other disturbances like fire is critical to predict heat conduction into the soil, permafrost degradation, and the fate of the soil carbon stored in the Arctic.

The lack of a significant relationship between temperatures at 1 and 15 cm belowground and soil moisture until approximately 74.3% and 76.4% respectively, is consistent with the observed exponential relationship between the thermal conductivity and relative moisture content reported for bryophytes and lichen in permafrost ecosystems, with a steeper relationship at higher moisture levels (Porada *et al* 2016). The relationship between d*z* and green moss thickness together with the relationships between green moss thickness and surface temperatures at 15 cm depth confirms that microtopography is critical to modeling the response of these ecosystems to climate change (Zona *et al* 2011a, Wilkman *et al* 2018).

The relationships between soil temperature and thickness of the total moss layer were similar for different genera, which might be related to the overall similar morphology of the mosses in our site. On the other hand, the significant interaction term between the green moss thickness and genus in the regression with soil temperature at 15 cm suggested that water retention might show some difference in different genera in the very top living moss layer. The literature disagrees about the role of moss genus on soil temperature, with some studies showing differences among moss species (Connone *et al* 2006, Cannone and Gugliemin 2009), while others reporting that moss thickness (Soudzilovskaia *et al* 2013) and/or moss water holding capacity were more relevant controls than moss species (Soudzilovskaia *et al* 2013, Hrbáček *et al* 2020).

The SEM supported the dominant role of green moss thickness on deeper soil temperature and the soil insulation by mosses (Fisher *et al* 2016, Hrbáček *et al* 2020, Wang *et al* 2020, Clayton *et al* 2021). Importantly, this analysis showed that air temperature and the deeper soil temperature were not correlated, consistent with the lack of a significant relationship found between active layer depth and growing degree days (Grünberg *et al* 2020). The disconnect between air temperature and deeper soil temperature explains the persistence of permafrost in ecosystems where air temperature has a mean annual average above zero (Jorgenson *et al* 2010). The lack of significant correlations between soil moisture and thaw depth suggests that soil thermal conductivity and latent heat of fusion of soil (Clayton *et al* 2021) might balance each other out in this waterlogged ecosystem. The increased heat conduction to deeper soil layers under a wetter surface moss layer might have been balanced by the larger energy required to thaw the active layer in wetter soils, resulting in shallower thaw depth (Clayton *et al* 2021). Given the complex interaction of these opposing processes, incorporating knowledge on the response of permafrost to atmospheric warming into large-scale model simulations is critical to refine predictions of future permafrost dynamics (Euskirchen *et al* 2006, Nicolsky *et al* 2007, Lawrence *et al* 2008). Forest and tundra fires affect the living top moss layers, increasing permafrost degradation (Swanson *et al* 1996, Myers-Smith *et al* 2008, Jones *et al* 2015, Fisher *et al* 2016, Michaelides *et al* 2019). Mosses might take decades to recover (Chen *et al* 2022), so increased permafrost degradation can contribute substantially to carbon loss into the atmosphere (O'Donnell *et al* 2011, Michaelides *et al* 2019).

6. Conclusion

Microtopography and the thickness of the top moss layer were the main controls on soil temperatures and thaw depths. Microtopography impacts soil thermal regimes indirectly through its impacts on moss and soil moisture. Thicker green moss (up to 3 cm) in topographic highs resulted in cooler deep (15 cm) soil temperatures, suggesting that mosses insulated the soil even in this waterlogged ecosystem. The very top moss layer was likely drier than lower layers due to evaporation, allowing it to insulate deeper soil layers by reducing soil thermal conductivity. The dominant role of moisture on the deeper soil temperature is consistent with the cooler soils under the drier plots. A more accurate measurement of moisture level of this top green layer is difficult without destructive sampling and its importance on heat conduction to deeper soil layers poses a challenge for explaining relationships between moisture (usually measured in the top 5–10 cm) and deeper soil temperatures or active layer depth. SEM of the key environmental drivers showed that air temperature was not correlated to either deeper soil temperature or thaw depth, supporting the importance of soil insulation by the moss layer. Future studies should attempt to capture the influence of snow depth and snow water equivalent on the moisture layer of mosses and evaluate how changes in snow cover can affect thaw depth and soil temperature regimes in Arctic ecosystems. Knowledge of these processes and complex interactions are critical to further our understanding of the response of permafrost to anticipated change in climate.

Data availability statement

The data are freely available to the public at this link: Zona *et al* (2023). Environmental and vegetation control on active layer and soil temperature in an Arctic tundra ecosystem near Utqiaġvik, Alaska, 2021–2022. Arctic Data Center. doi:https://doi.org/10.18739/A2P843X6W.

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Conflict of interest

The authors declare that they have no conflict of interest.

Ethics statement

This research was conducted in accordance with the principles embodied in the Declaration of Helsinki and in accordance with local statutory requirements. All participants gave written informed consent to participate in the study. No human or animal subjects were used in this study.

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