ARCTIC VEGETATION CHANGE DRIVEN BY WATER TABLES AND SOIL NITROGEN IN A THAWING PERMAFROST TUNDRA

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ABSTRACT

ARCTIC VEGETATION CHANGE DRIVEN BY WATER TABLES AND SOIL NITROGEN IN A THAWING PERMAFROST TUNDRA

STEPHANIE KADEJ

High-latitude ecosystems are experiencing rapid change due to climate warming, with temperatures rising up to 4 times faster than the global average. The magnitude of carbon(C) stored in these perennially frozen soils, known as permafrost, is nearly 3 times that of the atmosphere with the potential for release as warming leaves these soils vulnerable to thaw and microbial decomposition. Arctic vegetation has the potential to offset C release from permafrost soils because deepening of the active layer releases previously unavailable nutrients for plant uptake. This study investigated changes in productivity and species composition in the Carbon in Permafrost Experimental Heating Research project (CiPEHR) located in moist acidic tundra underlain by permafrost. Direct biomass measurements collected in 2022 were compared across Air and/or Soil warming treatments and plant functional types. Measurements of plant community composition, collected between 2009-2021, using the point-intercept method, were used to analyze changes in species composition over time. Changes in biomass were related to environmental variables such as water table and active layer depth, etc. collected over the course of the experiment. After 14 years, plot trajectories diverged and created environmental gradients. Soil warming led to higher overall species composition change over time, resulting in higher deciduous shrub biomass, while reducing graminoid and non-vascular species biomass. These changes were largely driven by increasing water tables, thaw depths, and the interaction of water tables and soil nitrogen availability. This suggests heterogeneity in soil moisture and soil nitrogen as an increasingly important drivers of vegetation change.

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PREFACE

This thesis was written and formatted as a manuscript to be submitted for publication in an academic journal. The intended submission is for Environmental Research Letters, to be submitted in 2023.

INTRODUCTION

High-latitude ecosystems are experiencing rapid change due to climate warming with temperatures rising up to 4 times faster than the global average (Rantanen et al., 2022; Schuur et al., 2022; Arctic Report Card 2021). The magnitude of carbon(C) stored in these perennially frozen soils(permafrost) is approximately 2-3 times that of the atmosphere (Schuur et. al., 2022; 2015; Hugelius et al., 2014). The climate warming leaves these frozen soils vulnerable to thaw and subsequent microbial decomposition leading to potential carbon release. Tundra ecosystems historically have nutrient poor soils and slow rates of cycling due to low temperatures and short growing seasons (Shaver et al., 1992; Chapin et al., 1995). However, this is expected to change as warming and permafrost thaw deepens the seasonally thawed active layer releasing large amounts of deep soil nitrogen for plant and microbial uptake (Salmon et al., 2016; 2018). The resulting increase in plant biomass and productivity has the potential to partially offset C release from thawed permafrost soils (Salmon et al., 2014). However, the magnitude of this offset is difficult to estimate due to varying spatial and temporal responses of permafrost thaw to atmospheric warming and the ability of plants to access newly available nutrients (Jorgenson et al., 2013).

The rate and form of permafrost thaw is highly dependent on ground-ice content with 20% of the Arctic landscape containing high ground ice content (Olefeldt et al., 2016). These soils are vulnerable to abrupt thaw which is characterized by collapse (subsidence) of the surface soil layer shifting soil hydrology dynamics ultimately increasing the rate of the permafrost carbon feedback (Rodenhizer et al., 2020; 2022). Abrupt thaw can also act as a disturbance to plant communities, such as in cases where subsided soils accumulate water and drown vegetation whereas nearby elevated areas become drier leading to drought conditions (Osterkamp 2009).

There are many types of thermokarst terrain that that differ is size, rate of change, and severity of disturbance to the ecosystem, but thermokarst features produced by non-patterned gradual subsidence often have little erosion (Jorgenson & Osterkamp, 2005; Kokelj & Jorgenson, 2013).

The changes in microtopography due to heterogenous subsidence can alter local soil hydrology, affecting plants mainly through drought, ponding conditions, or by altering nutrient cycling. Changes in local soil hydrology can alter microbial activity, and the mineralization and transport of nitrogen (Harms and Ludwig, 2016; Harms et al., 2014). So, while plant productivity has generally increased under climate warming (Berner et al., 2020), there is high variability in the response of different plant functional types to changing soil conditions such as subsidence and moisture (Campbell et al., 2021; Chapin 1995). Understanding the underlying mechanisms driving this wide range in plant responses will help better explain the cumulative response of the plant community to climate warming.

Arctic tundra vegetation is mainly comprised of vascular plant functional types such as graminoids, dwarf evergreen and deciduous shrubs, as well as non-vascular bryophytes and lichens in the understory. Both long-term remote sensing and field experiments primarily report large increases in dwarf shrub cover and abundance (Myers-Smith et al., 2015; Elmendorf et al., 2012; Sturm et al., 2001), however local-scale studies indicate more heterogeneity in the response of graminoids and dwarf shrubs driven by micro-gradients in soil moisture (Ackerman et al., 2017; Heijmans et al., 2022, Campbell et al., 2021; Naito and Cairns, 2011). Experimental manipulations have observed increased shrub abundance, particularly in deciduous shrubs, under elevated soil temperature and nutrient conditions (Iturrate-Garcia et al., 2020; DeMarco et al., 2014; Chapin 1995). Shrubs have been observed to increase in both in dry and wet soils (Leffler et al., 2016; Ackerman et al., 2017; Naito and Cairns, 2011), but graminoid species, due to their

preference for wetter soils (Heijmans et al., 2022), generally decrease in drying soils (Leffler et al., 2016). As abrupt thaw and subsidence alter local microtopography, the interacting changes in soil hydrology, nutrients and other feedbacks may increase biomass in certain areas, or decrease biomass if conditions become unfavorable to the plant community.

Although Arctic greening (i.e., increases in plant productivity) has been the dominant trend, browning (i.e., decreases in productivity), has been detected with high regional variation across the Arctic landscape (Phoenix and Treharne, 2022; Phoenix and Bjerke, 2016). The heterogenous responses of the plant community to warming is likely due to the heterogeneity of permafrost thaw to climate warming, and as a result there is considerable uncertainty about the rate and magnitude of plant shifts, and if the cumulation of these shifts will increase or decrease the overall productivity of Arctic vegetation to climate warming.

In this study we used a unique long-term permafrost warming manipulation experiment to identify changes in plant biomass, composition, and potential environmental drivers of these changes. This study site is located within the interior of Alaska, and it has experienced both subsidence, and deepening of the active layer, allowing us to investigate the response of the plant community under a variety of soil moisture, subsidence, and thaw conditions. In the initial 5 years of the experiment, plant biomass increased in response to warming and permafrost thaw (Salmon et al., 2016), but subsequent warming and permafrost thaw led to gradients of soil moisture and active layer conditions within treatments (Rodenhizer et al., 2020). Specifically, we sought to determine: 1) the overall effect of 14 years of warming and permafrost thaw on total plant biomass, and plant functional type biomass, 2) the rate and magnitude of species composition change over time, and 3) to understand the impact of changing environmental conditions on plant biomass. We hypothesized 1) soil warming would result in higher overall

plant biomass, specifically within dwarf shrubs, but that there would be high variability in the plant response, 2) the rate and magnitude of plant composition change would increase under soil warming, and 3) differences in biomass between treatments plots is driven by interactions between soil moisture, subsidence, and permafrost thaw.

MATERIALS AND METHODS

Study Site

The Carbon in Permafrost Experimental Heating Research (CiPEHR) project study site is located in the Eight Mile Lake (EML) watershed in Healy, Alaska outside of Denali National Park (Schuur et al., 2009). The site is underlain by permafrost and classified as moist acidic tundra, dominated by the tussock-forming sedge *Eriophorum vaginatum*. Other dominant species include deciduous shrubs: *Betula nana*, *Vaccinium* uliginosum, *Rubus chamaemorus*, and evergreen shrubs: *Rhododendrum subarcticum*, *Empetrum nigrum,* and *Vaccinium vitis-idaea* (Salmon et al., 2016; Schuur et al., 2007). The mean annual temperature is −0.94°C with a growing season (May–September) average temperature of 11.91°C. (Mauritz et al., 2017).

CiPEHR was established in 2008 using snow fences and open top chambers (OTCs, 0.36 m2 x 0.5 m) to experimentally warm and degrade permafrost in order study ecosystem C responses to rising temperatures (Natali et al., 2012). Six snow fences (1.5 x 8 m) were set up during the winter months in three replicate blocks with two fences per block (n = 6 snow fences). Snow fences allow prevailing wind to blow snow and build up on the leeward side, insulating the ground and warming the soil. Snow was removed every April to prevent additional water input and delayed snow melt. At each snow fence, eight 0.36 m^2 plots were separated into four on the control side, and four on the soil warming side of the fence. Additionally, two plots on each side

received air warming via OTCs during the growing season for a total of 48 plots with treatment combinations: Control, Air, Soil, and Air + Soil warming (Natali et al., 2012).

Aboveground Plant Biomass Direct Measurements

In 2022 when the experiment concluded, aboveground live plant biomass was estimated by destructively harvesting a subset of each plot and scaling the weighed biomass to a meter. A 10 x 40 cm quadrat frame was placed in the center of each plot and a serrated knife was used to remove the section of plants and soil to an average soil depth of 25 cm. Upon removal, the length, width, and depth of the soil quadrat were recorded. Quadrats were transported to the University of Alaska Fairbanks, where each quadrat was sorted to plant species and tissue type. For each quadrat, the top 0-5 cm moss/soil was removed to separate living biomass from the remaining soil mass. Sedge species were sorted into specific tissue types: leaf (including leaf base), and stem; Shrub species were sorted to leaf and stem tissues. Nonvascular plants were sorted into mosses and lichens (Table 1). Only living green tissue was included, and dead tissue was measured as litter. Once plants were sorted, each sample was dried for 24 hours at 60 °C and weighed separately.

Indirect Measurements of Plant Species Composition Over Time

For measurement years between 2009-2021 (n = 7 years), aboveground plant species composition was measured using a non-destructive point-intercept method with a 60 x 60 cm PVC frame that had a grid size of 7 x 7 cm (Schuur et al., 2007). The frame was suspended above the canopy and at each of the 49 intersecting grid points, a 1 mm diameter metal rod was dropped vertically through the plant canopy. The species identity and tissue type (leaf, stem, or flower) was recorded for every plant that touched the rod, recorded as a “hit” and average hits per point were calculated for each species in a plot. Previous studies at this site applied

allometric equations to estimate biomass non-destructively (Salmon et al., 2016; Schuur et al., 2007). However, given the direct biomass measurement in this study we used the average hits per point data to analyze species composition changes over time, rather than biomass.

Environmental Monitoring

Meteorological variables were measured continuously using a HOBO Onset station (Bourne, MA, USA). Air temperature was measured year-round at a 2 m height, and rainfall was measured during the growing season. In cases of missing data, variables were gap-filled using eddy and meteorological tower data from an adjacent permafrost thaw gradient monitoring site 1 km away (Schuur et al., 2021). Air temperatures were measured within the OTCs intermittently using shaded thermistors. OTC air temperatures were gap-filled using plot-level linear models relating OTC air temperatures to HOBO ambient air temperatures (Rodenhizer et al., 2020). Soil temperatures were measured at depth (5,10,20, and 40 cm) using constantan-copper thermocouples.

Thaw depth, defined as the distance from the top of the soil/moss surface to the top of the frozen layer, was measured 1-2 times a week at each plot by inserting a metal probe into the ground (3 mm diameter) until it stopped at the frozen layer. Active layer thickness (ALT) was measured as the end of season (mid-September) maximum thaw depth (Mauritz et al., 2017; Natali & Schuur, 2012). As the experiment progressed. longer probes were used in areas of deeper thaw where the shorter probes could not reach. To measure ground subsidence, surface elevation was measured at 2 m intervals in a 30 x 30 m grid at each experimental block using a Trimble high-precision differential GPS. Measurements were taken towards the end of the growing season (August) for the years 2009, 2011, and 2015-2020 (Rodenhizer et al., 2020). Elevation values were interpolated using ordinary kriging to create a continuous elevation

surface for each year and subsidence was calculated as the difference in elevation relative to 2009 (Rodenhizer et al., 2020). Plot-level subsidence was gap-filled in years without measurements using linear interpolation.

Soil hydrology was measured with soil moisture (VWC, GWC) and water table depth. Soil moisture was measured with depth integrated probes from 0 - 20 cm in the soil profile (Campbell Scientific CS616, Logan, UT, USA). Water table depth, the depth from the soil surface to the top of the perched water table, was measured within a PVC well three times a week.

To estimate growing season nitrogen availability, four ion-exchange resin probes (2 Anion, 2 Cation PRS probes, Western Ag Innovations) were placed in each plot at a depth of 15 cm. Probes were placed in June and removed in September before compiling the resins within each plot for analysis. PRS probes measure a variety of additional soil ions (e.g., phosphate, sulphate, potassium) however for this study we focused on the ammonium and nitrate availability in the soil.

Statistical Analysis

In this analysis, plant biomass measurements from the 2022 destructive harvest were used to assess treatment effects after 14 years of warming, while point-intercept measurements were used to understand plant community composition trends over time. To analyze the response of total plant biomass as well as grouped by plant functional type to the warming treatments, linear mixed effect models were run in R using the LME4 package (Bates et al., 2015). Air warming, Soil warming, and the interaction of Air and Soil warming were included in the models as categorical fixed effects. To account for the experimental design and high variability in

environmental conditions between blocks driven by spatial heterogeneity, the random effects of fence nested in block were used across all models.

Control plots served as the reference for the warming treatments and so they are included in model intercept values. For both total biomass and plant functional type (PFT's) biomass analyses, destructive harvest measurements from 2022 were used; PFT's were run individually separated into sedges, evergreen shrubs, deciduous shrubs, mosses, and lichens. Fixed effect coefficients represent the difference in biomass response to warming relative to the control plots.

Point-intercept measurements were used to analyze plant species composition change over time. Point-intercept data was transformed to average "hits" per point, and a matrix of species hits per plot for each year was applied to a Bray-Curtis dissimilarity analysis in R using the vegan package (Oksanen et al., 2013). Plot dissimilarities for each year compared to 2009 were extracted, and then average treatment dissimilarity was calculated for each year. Bray-Curtis dissimilarity index values range from zero, indicating no dissimilarity (community composition is identical) to one, indicating high dissimilarity in that plot relative to 2009. While data presented represents dissimilarities measured relative to 2009, the 2010 dissimilarity values were used to analyze treatment effects as 2009 values were all zero.

To understand the underlying environmental variables influencing plant biomass across treatments, linear mixed effect models were run using the same nested random effect structure used previously. However, continuous environmental variables, rather than categorical treatments, were used as fixed effects. Akaike Information Criterion (AIC) model selection was done using the MuMIn package to justify inclusion of fixed effects (lme4, Bates, Machler, Bolker, & Walker, 2015). Initial models tested the additive and multiplicative effects of environmental variables (soil temperatures at 5 and 10 cm, volumetric water content, subsidence,

active layer thickness, water table depth, growing season soil nutrient availability) and via model selection these variables were reduced to active layer thickness, water table depth, and soil nitrogen availability. Fixed effect terms and their interactions were tested throughout this process and results presented here reflect the most parsimonious models.

RESULTS

Diverging Trajectories

By 2022 treatment plots had undergone dramatic change resulting in a gradient of plot soil conditions within and across treatments (Figure 1). All plots thawed and became wetter, and even resulted in surface water ponding and plant mortality in two of the warming plots. These changes were driven by heterogenous distribution of ground-ice and the differential effect on ground subsidence across treatments and through time as the ice was lost (Rodenhizer et al., 2023;2020; Taylor et al., 2021). After 14 years of warming, Soil warmed plots had higher soil temperatures and more permafrost degradation leading to wetter soils than in Control or Air warming plots, reflected in the depth-to-water-table values closer to zero (water is near/at soil surface due to soil subsidence) (Figure 1). At this stage of the experiment, individual study quadrats each had unique thaw and moisture trajectories based on both treatments and regional climate change acting on underlying soil/ice heterogeneity. To account for differential environmental outcomes for plots within treatments, continuous environmental variables at the plot level were used to analyze environmental drivers of plant productivity. This statistical approach improved upon the analysis as determined by experimental treatments alone.

Growing Season Soil Nitrogen Availability

In 2022 growing season revealed higher N availability in the top 15 cm of soils under warming conditions (Figure 2). Control plots had the lowest soil N available at 10.5 ± 0.7

µg/cm2. While treatment means were not statistically different, LMM analysis using the study's nested experimental design revealed Air warming increased soil N availability by 1.99 µg/cm2 (P = 0.079, Table S1), while Soil warming effects raised soil N by 2.14 µg/cm2 (p = 0.059, Table S1). However, the interaction of Air and Soil warming effects did not further increase soil N, rather it decreased soil N by 1.68 µg/cm2, although this effect was not significant (p = 0.287, Table S1). The wide range in plot soil N within treatments parallels the divergence of other environmental plot conditions described in Figure 1. The two warming plots that were flooded (no plants) had the highest N at 22.6 µg/cm2, however the remaining plots still varied from 18.3 down to 6.8 µg/cm2.

Changes in Plant Biomass

After 14 years of experimental manipulation, Soil warming had 906 ± 112.8 g/m^2 total aboveground plant biomass and had 123.9 g/m^2 or 15.8 % more aboveground biomass relative to Control plots (Figure 3, P = 0.30, Table 2). Air + Soil warming had similar total biomass at 913 ± 111.0 g/m^2, which resulted in a 16.7 %, and 20.5 % higher biomass relative to Control and Air warming plots, respectively, While Soil warming effects analyzed as a treatment difference were not significantly higher than Control, the plot-level variability in the plant response to warming paralleled the wide variability in plot soil conditions. At the same time, treatment effects were detected across plant functional types (PFT), where Soil warming significantly increased deciduous shrub biomass (Figure 4, P = 0.023, Table 3) by 254.4 g/m^2. This translates to 174.8% higher deciduous shrub biomass under Soil warmed conditions, particularly driven by increases in the species *Betula nana, and Vaccinium uliginosum*. Air warming had negligible effects on total biomass, but effects tended to differ between deciduous and evergreen shrubs. Air warming stimulated deciduous shrubs and increased biomass by 29% but decreased evergreen shrubs by

nearly 70% relative to Control plots, although these results were weakly significant for the evergreen decrease only (p=0.09). Soil warming generally stimulated deciduous shrubs, but with the interaction of Air warming, the deciduous shrub biomass was 32% less than Soil warming alone and was non-significantly higher than Control (P = 0.367, Table 3). In contrast, Air + Soil warming interacted significantly on evergreen shrub biomass, indicating that Air and Soil warming work together to increase shrub biomass, than just Air or Soil warming alone. (P = 0.049, Table 3). Treatment effects were not detected for non-vascular species, and one Air + Soil plot with very high moss biomass (> 800 g/m2) was removed to best visualize the data. While non-vascular biomass is low relative to vascular plants, the occurrence of high moss biomass is present across treatments, primarily in plots with low *E. vaginatum* biomass.

Species Composition

Over time, the plant community composition diverged in response to both changes in ambient conditions and as a result of experimental warming (Figure 5). Increasing dissimilarity (Bray-Curtis Index) represents xsthe change in species composition within plots relative to the beginning of the experiment in 2009. Soil warming had the greatest impact on plant composition change on average increasing plot dissimilarity by 0.261 which translates to an 8% greater dissimilarity in community composition relative to Control plots (P < 0.001, Table 4). Increasing plot dissimilarities were largely driven by shifts in species-specific abundances. Very little plant succession including new species (such as trees) were observed during 13 years of warming despite rapid environmental changes occurring in the plots. This suggests that plant succession due to warming may require even longer time scales beyond what was represented in the experiment. Near total plant mortality occurred in 2 of 48 experimental warming plots, as a result of subsidence and flooding, driving the plot dissimilarity index to nearly 1.0. When these plots

were removed from the analysis, Soil warming effects remained highly significant. Air warming effects on species composition changes did not significantly differ from ambient warming in the Control plots, despite higher midday temperatures in the OTCs. The addition of Air + Soil warming did not significantly differ from Soil warming alone suggesting plants may be responding more to belowground environmental changes rather than warming air temperatures alone.

Environmental Analysis

We evaluated the response of the destructively harvested aboveground biomass to multiple continuous environmental variables, which revealed that the fixed effects of active layer thickness (ALT), growing season N availability, water table depth (WTD), and the interaction for the latter were the most parsimonious AIC model (Table 5). We determined continuous environmental variables, instead of treatment categories, were better predictors due to the wide response of plots within and across treatments.

The water table depth values reported here are the depth to the top of the perched water table from the ground surface in cm, therefore a decreasing water table depth is indicative of increasing soil moisture conditions closer to the ground surface, while increasing WTD is indicative of drier soils. Drier soils (increasing WTD) resulted in a 25.9 g/m^2 decrease in total biomass per cm of water table depth ($P = 0.014$, Table 5). This would suggest wetter soils lead to higher plant biomass, which was generally true with the exception of two warming plots that flooded due to rapid permafrost thaw and subsidence (Figures S1, S2). The remaining 46 experimental plots experienced more gradual increases in WTD and ALT.

Growing season N availability alone was negatively related to biomass ($P = 0.001$, Figure S3), and this is likely due to high N demand in high biomass plots decreasing soil N availability,

along with other environmental soil drivers. However, LMM results revealed significant interaction effects between soil N availability and WTD. This suggests that in the presence of soil N, drier soils may still stimulate plants, increasing aboveground biomass by 2.51 g/m^2 for every $\mu g/cm^2$ of N and cm of increasing WTD. Increasing ALT was the final major predictor of aboveground biomass, leading to a 2.42 g/m^2 increase in biomass for every cm of ALT change. The effects of ALT, and interactions between WTD and soil N availability, support the hypothesis that permafrost thaw and soil moisture conditions are major environmental drivers of biomass change, with the mechanism of soil N availability playing a role.

DISCUSSION

This study investigated the changes in Arctic tundra vegetation after over a decade of experimental warming to identify the major shifts in plant biomass and composition, and the underlying environmental drivers of these changes. These results showed that tundra vegetation has undergone significant shifts in both plant functional type biomass and species composition, with notable increases shrub biomass to warming. These changes are consistent with previous studies at this site and the broader Arctic that have reported increasing shrub abundance due to climate warming (Schuur et al., 2007; Mekonnen et al., 2021, Tape et al., 2006). While it is known that deeper permafrost thaw releases more nutrients stimulating plant productivity (Salmon et al., 2016;2018), this study highlights the increasing importance of changing soil moisture and interactions with permafrost thaw and soil nutrients in driving plant biomass.

Diverging Environmental Trajectories associated with Experimental Warming

As a result of experimental warming interacting with the underlying heterogeneous tundra ecosystem, individual plot trajectories diverged creating a gradient of unique thaw and soil moisture conditions across plots within treatments (Figure 1; Rodenhizer et al., 2023). There

was a wide variability of ALT ranging from 0.85 m in Control to over 2.6 m in Soil warmed plots. Growing season WTD ranged from 33 cm below to over 11 cm above the soil/moss surface. While no treatment was applied, Control plots still experienced ambient climate warming conditions (Schuur et al. 2021); this warming is reflected in the deepening ALT in Controls over time (Figure 1). All plots experienced some degree of subsidence due to ground ice loss, and all but two plots became wetter as a result (Rodenhizer et al., 2023; 2020). Plots that remained dry experienced high variability in WTD during the growing season, while wetter plots maintained a shallow WTD and/or resulting in ponding (Rodenhizer et al., 2023). Importantly, the divergent changes in environmental conditions are not unique to this experiment, as nearly 20% of the Arctic landscape is vulnerable to rapid thaw and subsidence (Olefeldt et al., 2016). The formation of wet, subsided sites near drier, elevated sites has shown to alter plant productivity (Osterkamp, 2009), and early research at a nearby permafrost monitoring site suggested subsidence as a driver of plant composition change (Schuur et al., 2007).

Plant Biomass Differences Associated with Experimental Warming

Effects within experimental treatments were detected at the plant functional type (PFT) level, where Soil warming increased shrub biomass, predominantly in deciduous taxa (Figure 3). Deciduous shrubs, specifically *Betula nana,* and *Vaccinium uliginosum,* responded strongly to Soil warming treatments. The combination of Air and Soil warming seemed to maintain evergreen shrub biomass, specifically *Rhododendron subarcticum*, suggesting that evergreen shrubs could potentially benefit under future climate warming as well although both the Air and Soil warming treatments alone had lower mean evergreen biomass. Previous studies have shown increasing shrub biomass under warming conditions (Natali et al., 2012; Schuur et al., 2007). Other experimental manipulations have shown increases in deciduous shrubs (Sistla et al., 2013;

Van Wijk et al., 2004; Walker et al., 2006; Chapin et al., 1995), and remote sensing studies agree on increasing shrub abundance in the Arctic tundra region over the last two decades (Myers-Smith and Hick, 2018; Myers-Smith et al., 2020; Berner et al., 2020). A similar experimental warming study using snow fences and OTC's at Toolik, Lake, Alaska in moist non-acidic tussock tundra found increasing abundance of deciduous shrub *Betula nana* but decreasing abundance of the sedge *E. vaginatum* in Soil warmed sites after 20 years (Leffler et al., 2016). In this study, Soil warming effects on graminoid biomass as a categorical treatment were not significant, however the Soil warming treatment did increase ALT, WTD (Figure 1), and soil N availability, which were the direct factors found to drive that biomass response (Table 5). Increases in graminoids along with shrubs have been reported all around the Arctic in response to climate warming (Heijmans et al., 2022; Elmendorf et al., 2012, Bjorkman et al., 2020), often at the expense of mosses and lichens that become shaded out (Bjorkman et al., 2020). In the initial 5 years of experimental warming at this site, we found increasing aboveground biomass response to Soil warming, driven by *E. vaginatum* (Salmon et al., 2014). However, this trend was not maintained, as after 14 years of warming sedges had a lower average biomass. Decreases in *E. vaginatum* abundance were attributed to drying soils in experimentally warmed sites at Toolik, but despite wetter conditions induced by warming in this study, sedge biomass was still lower especially compared to deciduous shrubs. This suggests despite temporarily wetter conditions, graminoids will not be able to outcompete shrubs under future climate warming.

Furthermore, low relative biomass of non-vascular plants suggests this functional group will decrease in response to warming. Earlier studies at this site suggested mosses would lose productivity under Air warming, but Soil warming could benefit certain moss species (Deane-Coe et al., 2014). However, after 14 years of warming, non-vascular species primarily decreased

in Soil, and Air + Soil warming treatments, with the exception of one Soil warming plot that had >30 g of moss collected in the plot sub-sample. Non-vascular die off has been attributed to competition from shrubs and graminoids, which results in the mosses being shaded out (Bjorkman, et al 2020).

Long-term Experimental Warming Leads to Greater Plant Composition Change

Experimental Soil warming lead to greater and more rapid community composition change over time (Figure 4), even while ALT and WTD trajectories diverged in both Control and Soil warming treatments (Table 4). Air warming did not have a significant impact on community composition relative to the Control. This suggests that even while some Control and Air warming plots paralleled Soil warming plots with deep thaw and wet soils, increasing winter soil temperatures via higher snowpack ultimately had a greater effect on the plant community composition change (Table 4). The shift in Control plots can be attributed to regional climate warming driving species competition, This composition change is reflected in the disappearance of non-vascular plants, decreasing Sedges and Evergreen shrubs, with a concurrent increase of deciduous shrubs to warming (Figure X).

Active Layer Thickness, Water Table, and Soil Nitrogen Availability Drive Differences in Plant Biomass

Just as the environmental conditions diverged in response to experimental warming, so did the plant community. After 14 years of warming, the effect of treatments as categorial variables were sometimes, but not always, significant for explaining changes in plant biomass (Figure 2, Figure 3, Table 2) due to high variability in environmental conditions within treatments. However, analyzing underlying environmental conditions of each plot revealed that differences in permafrost thaw, water, and soil N availability drove the biomass response to

experimental warming (Table 5). When soil N availability was removed from models, ALT and WTD became the major drivers (results not shown). In this reduced model, drying soils (increasing WTD) significantly decreased plant biomass, and the presence of interactions with permafrost and soil N suggests that changing soil moisture conditions in the Arctic may become an increasingly important driver of biomass change. Soil N availability interacted significantly with WTD, but not with ALT. This suggests that soil moisture plays a major role in the ability of plants to utilize increased soil N. The interaction effects suggest that while drying Arctic soils may reduce plant productivity, deepening of the active layer and subsequent release of N into the soil could offset the negative effects of drying soils. These significant environmental predictors of biomass after 14 years of experimental warming support the hypothesis that changes in water table, thaw, driven by subsidence at our site, were the major drivers of biomass change.

Soil N availability generally increased with higher water tables, with highest N availability in the thermokarst pond, which drove the negative correlation between resin N and biomass. However, there was also high resin N detected in drier plots as well increasing soil N availability does not necessarily translate to higher plant biomass, as changing soil moisture conditions with permafrost thaw have shown to alter soil N cycling and transport (Xu et al., 2021; Harms et al., 2012;2019), and plant nutrient uptake (Semenchuk et al., 2015; Chapin and Shaver, 1981). Previous studies at this site observed changes in plant canopy N in response to changes in water table and active layer (Jasinski et al., 2022), providing earlier evidence of the important implications of changing water tables on plants and soil N availability at our site. Resin N has showed similar responses in previous studies done at this site where canopy N and soil resin N had opposing trends (Natali et al., 2012). The reoccurrence of this soil N and

biomass mismatch at our site suggests N cycling may be significantly altered by the diverging environmental trajectories.

Implications

Current evidence from warming studies (Leffler et al., 2016) show decreasing soil moisture in response to long-term warming, and current climate warming model predict widespread drying in Arctic landscapes (Schuur et al., 2022). However, few studies account for the impacts of subsidence in tussock tundra ecosystems underlain by permafrost This study highlights the impact of subsidence and the cascade of changes on ALT, WTD, and soil N that ultimately drive plant community change. Across the broader Arctic, the expansion of shrubs has been attributed to increases in soil moisture, deepening of the active layer, and increases in soil nutrient availability (Mekonnen et al., 2021). However, this comes at the cost of non-vascular and graminoid species also highlighted in this study. The underlying environmental mechanisms that drive plant biomass differences reveal that while permafrost thaw is releasing nitrogen (Salmon et al., 2014, 2018), the plant community may not be able to take advantage of the increased nutrients if rapid shifts in permafrost thaw, and water tables destabilize plant communities first. As 20% of the Arctic is vulnerable to abrupt permafrost thaw and subsidence (Olefeldt et al., 2016), it is crucial to understand the cumulative impact changing environmental conditions will have on plant productivity and community composition. Unfortunately, the detected increases in shrub biomass with warming are not currently able to offset C release from thawing permafrost soils (Schuur et al., 2021).

TABLES

Plant Functional Type	Species	Control		Air		Soil		Air + Soil	
		Leaf	Stem	Leaf	Stem	Leaf	Stem	Leaf	Stem
Graminoid	Carex bigelowii	2.4 ± 0.8	1.5 ± 0.6	6.6 ± 2.2	10.7 ± 4.4	30.9 ± 11.5	40.9 ± 16.8	5.3 ± 1.8	9.6 ± 4.6
	Eriophorum vaginatum	176.3 ± 45.2	131.8 ± 38.0	124.4 ± 28.9	167.6 ± 47.0	123.6 ± 38.1	85.9 ± 31.4	123.5 ± 37.7	83.5 ± 28.0
Deciduous	Betula nana	0.3 ± 0.3	6.3 ± 4.6	7.1 ± 3.8	21.4 ± 13.4	2.2 ± 1.4	89.8 ± 55.1	13.8 ± 9.4	80.5 ± 46.8
	Rubus chamaemorus	9.4 ± 4.1	6.4 ± 2.3	9.2 ± 2.6	5.2 ± 1.8	13.8 ± 5.4	9.6 ± 3.3	19.4 ± 5.1	12.9 ± 3.1
	Vaccinium uliginosum	13.8 ± 3.2	109.2 ± 22.5	15.1 ± 3.6	130.0 ± 27.6	79.5 ± 44.7	204.8 ± 45.5	30.5 ± 8.1	146.7 ± 34.4
Evergreen	Andromeda polifolia	6.4 ± 3.8	6.6 ± 3.7	7.2 ± 3.9	10.9 ± 4.2	12.2 ± 4.8	18.3 ± 7.2	4.1 ± 1.8	7.6 ± 4.2
	Empetrum nigrum	16.1 ± 5.1	17.0 ± 5.4	12.0 ± 6.2	15.6 ± 7.7	7.0 ± 3.6	11.2 ± 5.9	8.7 ± 6.5	15.8 ± 12.4
	Oxycoccus microcarpus	1.1 ± 1.0	1.5 ± 1.3	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.3 ± 0.2	0.4 ± 0.3
	Rhododendron subarcticum	47.3 ± 10.6	134.0 ± 35.9	21.8 ± 5.1	72.1 ± 12.0	28.4 ± 6.4	116.2 ± 25.2	38.4 ± 6.1	183.2 ± 51.0
	Vaccinium vitis-idaea	14.1 ± 4.2	15.4 ± 4.3	6.5 ± 2.9	6.4 ± 2.2	4.5 ± 1.6	6.2 ± 1.8	6.1 ± 1.4	7.9 ± 1.9
Nonvascular	Moss	54.4 ± 19.2	-	83.8 ± 28.7	-	20.1 ± 8.3	-	37.7 ± 18.0	-
	Lichen	10.7 ± 4.1	-	21.8 ± 9.5	-	0.4 ± 0.3	-	5.7 ± 4.3	-

Table 1. Species-specific tissue biomass provided as 2022 treatment means and standard error. Non-vascular biomass was recorded as “leaf” tissue.

	Treatment		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	782.14	593.28 – 971.00	**<0.001**
Air [Y]	-24.62	-264.50 – 215.27	0.837
Soil [Y]	123.88	-116.00 – 363.76	0.303
Air [Y] × Soil [Y]	31.32	-307.93 – 370.57	0.853
Random Effects			
σ2	84653.81		
τ_{00} fence.lme:block.lme	10147.20		
τ_{00} block.lme	0.00		
ICC	0.11		
$N_{\text{fence.lme}}$	6		
$N_{\text{block.lme}}$	3		
Observations	48		
Marginal R2 / Conditional R2	0.051 / 0.152		

Table 2. Linear mixed effects model results for treatment effects on total biomass after 14 years of experimental warming

	Sedges			Deciduous Shrubs			Evergreen Shrubs			Mosses			Lichens		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	312.03	164.32 – 459.74	**<0.001**	145.48	-14.61 – 305.57	0.074	259.50	166.80 – 352.20	**<0.001**	54.47	-27.55 – 136.49	0.187	10.67	-1.65 – 22.99	0.088
Air [Y]	-1.19	-210.08 – 207.71	0.991	42.70	-174.78 – 260.17	0.694	-106.56	-229.71 – 16.60	0.088	29.34	-86.65 – 145.34	0.612	11.09	-6.33 – 28.51	0.206
Soil [Y]	-30.70	-239.59 – 178.19	0.768	254.35	36.88 – 471.82	**0.023**	-55.15	-178.30 – 68.01	0.371	-34.33	-150.32 – 81.67	0.553	-10.29	-27.72 – 7.13	0.239
Air [Y] × Soil [Y]	-58.20	-353.62 – 237.22	0.693	-138.76	-446.31 – 168.80	0.367	174.69	0.53 – 348.86	**0.049**	59.33	-104.71 – 223.37	0.469	-5.74	-30.38 – 18.90	0.640

Table 3. Linear mixed effects model results for treatment effects on plant functional type biomass after 14 years of experimental warming. Bolded values indicate statistical significance at $p < 0.05$.

	Dissimilarity		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.29	0.22 – 0.37	**<0.001**
Air [Y]	0.01	-0.03 – 0.04	0.620
Soil [Y]	0.08	0.04 – 0.11	**<0.001**
Air [Y] × Soil [Y]	-0.01	-0.06 – 0.04	0.701
Random Effects			
σ2	0.01		
τ_{00} year.lme	0.01		
τ_{00} fence.lme:block.lme	0.00		
τ_{00} block.lme	0.00		
ICC	0.42		
$N_{\text{fence.lme}}$	6		
$N_{\text{block.lme}}$	3		
$N_{\text{year.lme}}$	6		
Observations	288		
Marginal R2 / Conditional R2	0.063 / 0.457		

Table 4. Linear mixed effects model results for Bray-Curtis plot dissimilarity as a result of experimental warming. Plot dissimilarity is measured as the difference in species composition (matrix of species average hits per point) relative to the plot species composition difference in 2009 Control plots served as the reference and estimates are included in the intercept.

	biomass		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	1126.95	611.04 – 1642.86	**<0.001**
alt	2.42	0.06 – 4.78	**0.045**
totalN	-52.64	-82.09 – -23.18	**0.001**
wtd mean	-25.99	-46.47 – -5.51	**0.014**
totalN × wtd mean	2.51	0.97 – 4.05	**0.002**
Random Effects			
σ2	67977.18		
τ_{00} fence.lme:block.lme	0.00		
τ_{00} block.lme	0.00		
$N_{fence.lme}$	6		
$N_{block.lme}$	3		
Observations	48		
Marginal R2 / Conditional R2	0.311 / 0.311		

Table 5. Linear mixed effect model results testing the effects of active layer thickness, growing season water table depth, soil N availability, and the interactive effects on destructively harvested biomass after 14 years of experimental warming.

Supplemental Tables

	Treatment		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	10.53	8.54 – 12.52	**<0.001**
Air [Y]	1.99	-0.24 – 4.22	0.079
Soil [Y]	2.14	-0.09 – 4.37	0.059
Air [Y] × Soil [Y]	-1.68	-4.84 – 1.47	0.287
Random Effects			
σ2	7.32		
τ_{00} fence.lme:block.lme	0.89		
τ_{00} block.lme	0.63		
ICC	0.17		
$N_{\text{fence.lme}}$	6		
$N_{\text{block.lme}}$	3		
Observations	48		
Marginal R2 / Conditional R2	0.097 / 0.253		

Supplemental Figure 1. Linear Mixed Effects Model results for Air and Soil warming treatment effects on growing season soil N extracted from the top 15 cm of the soil profile.

FIGURES

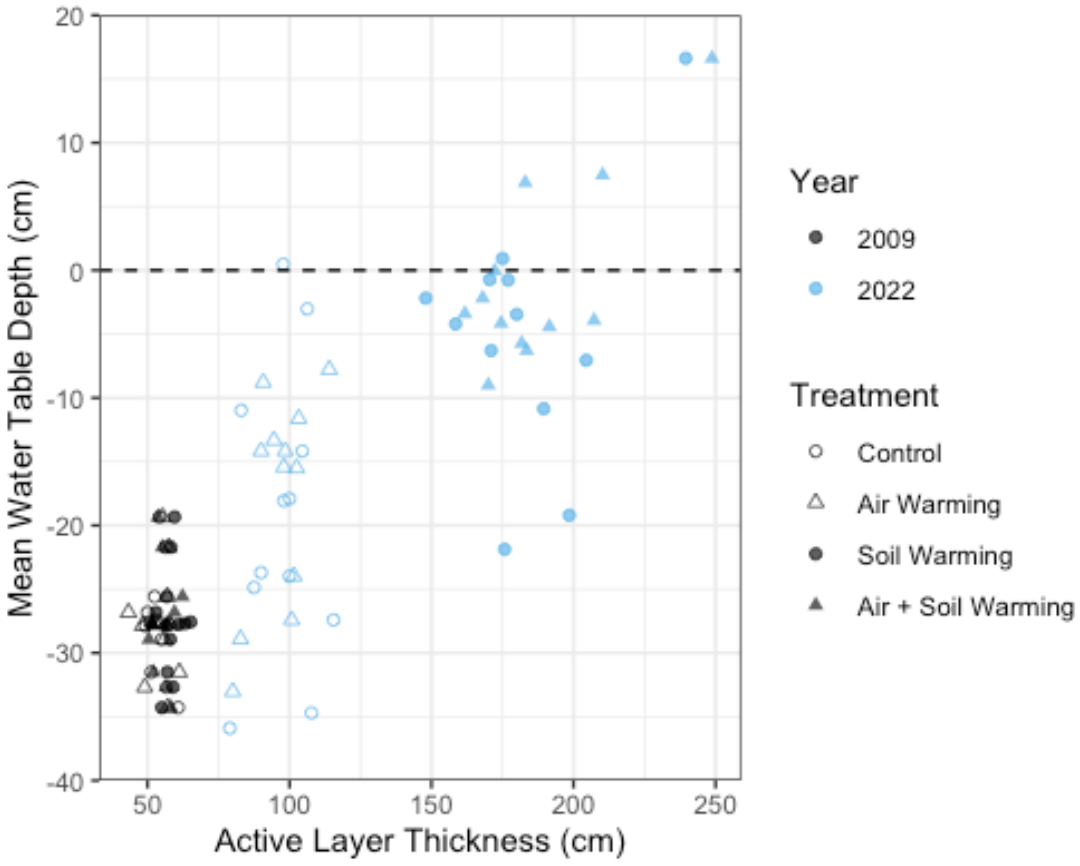


Figure 1. Mean growing season water table depth and active layer thickness of plots across treatments at the start and end of the experiment The black horizontal dashed line represents the soil surface, and points above this line indicate plots that have very high soil moisture, with water ponding above the ground surface.

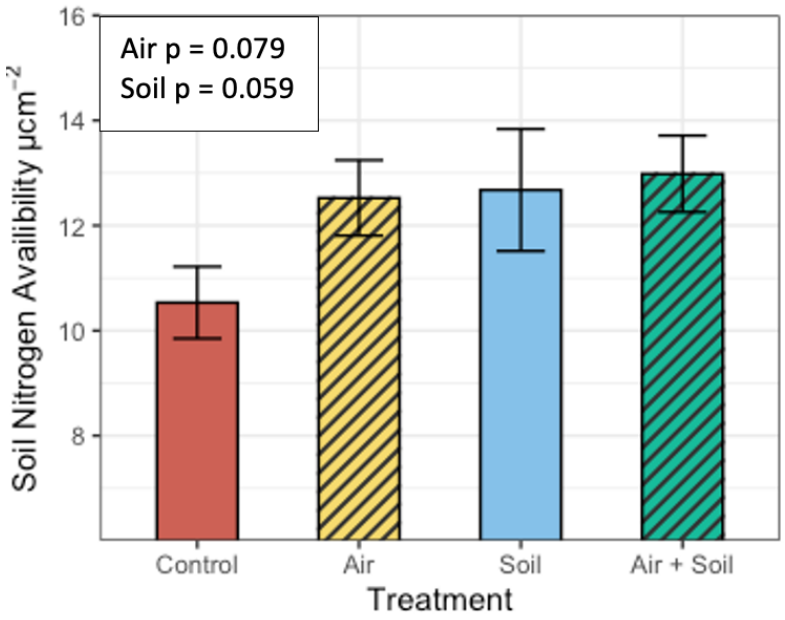


Figure 2. 2022 Growing Season Nitrogen Availability by treatment. Error bars represent standard error based on treatment means.

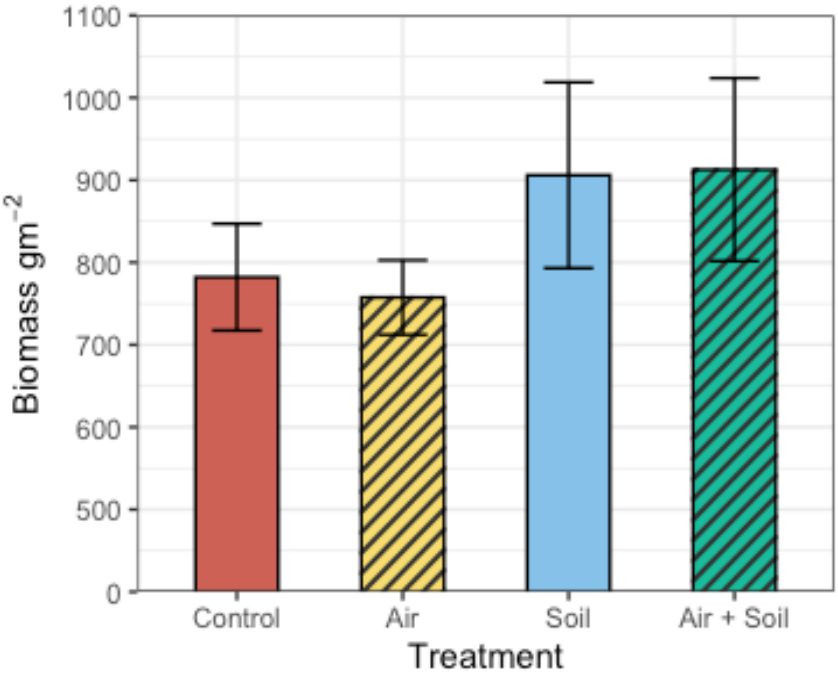


Figure 3. Directly harvested total biomass by treatment after 14 years of experimental warming. Error bars represent standard error based on treatment means.

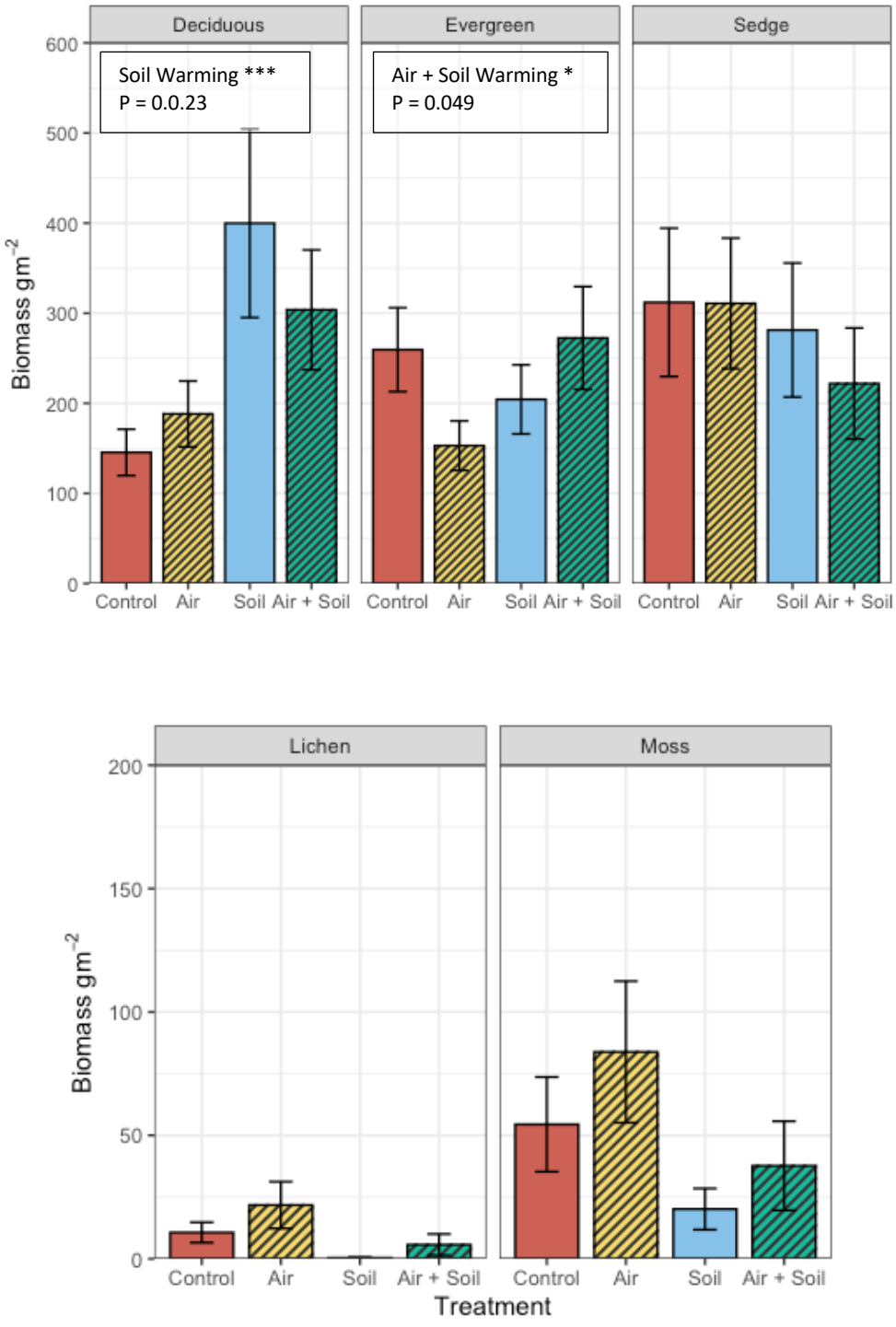


Figure 4. Directly harvested biomass of plant functional types by treatment: Sedges, Deciduous Shrubs, Evergreen shrubs, Mosses, and Lichens after 14 years of warming. Error bars represent standard error based on treatment means.

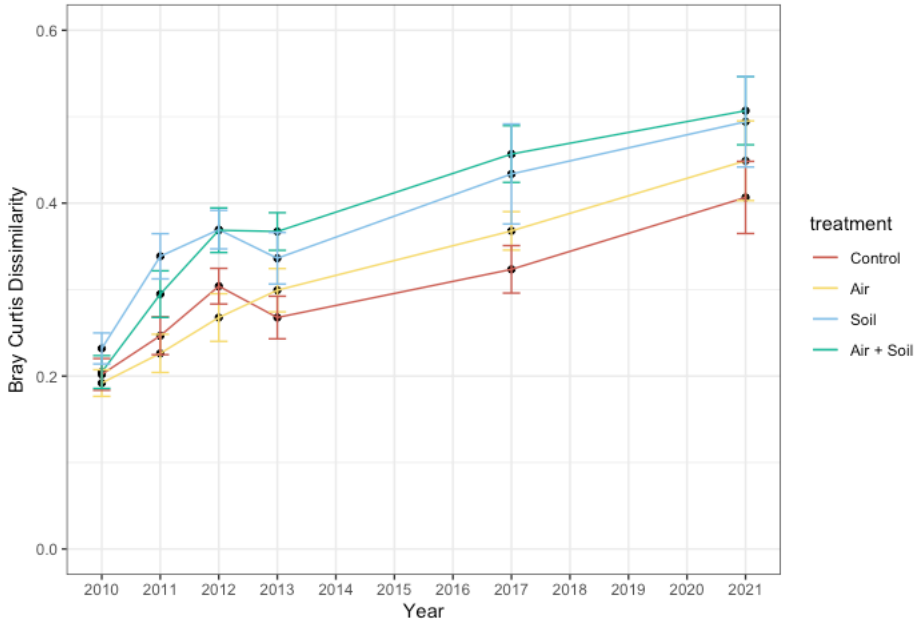
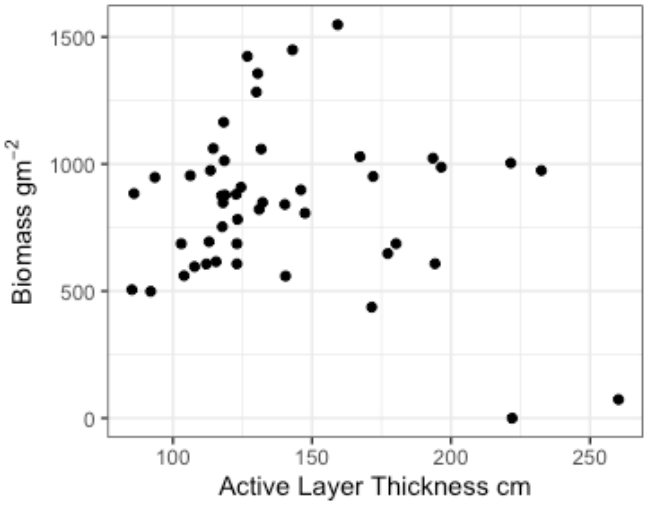
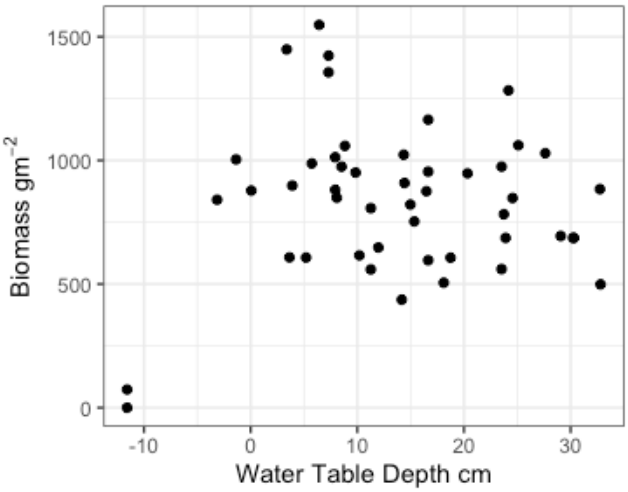


Figure 5. Bray-Curtis dissimilarity for species composition over time by treatment. Plot-level species composition is represented as average hits per point measured non-destructively. Dissimilarity over time measures the difference in composition in each individual plot relative to its composition in 2009. Error bars represent standard error based on annual treatment means.

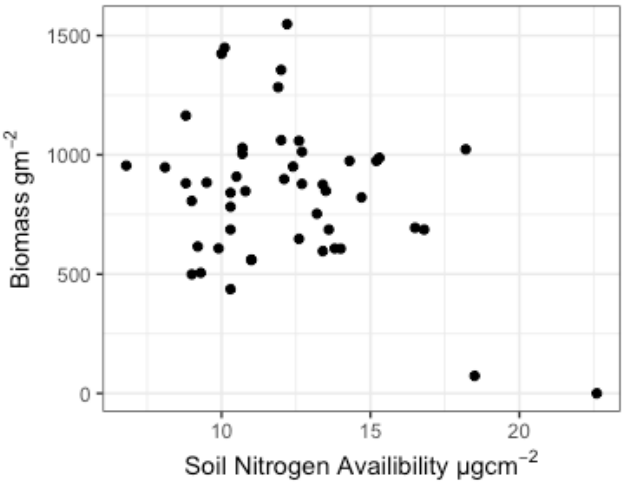
Supplemental Graphs



Supplemental Figure 1. Biomass at different Active layer Thicknesses in 2022. Each point represents an individual plot, with plots at or near zero experiencing flooded soils.



Supplemental Figure 2. Biomass at different Water Table depths. Each point represents an individual plot, with plots at or near zero experiencing flooded soils.



Supplemental Figure 3. Biomass versus Soil Nitrogen availability. Each point represents an individual plot, with plots at or near zero experiencing flooded soils.

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