

Peatland Plant Community Changes in Annual Production and Composition Through 8-Years of Warming Manipulations Under Ambient and Elevated CO₂ Atmospheres

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Key Points:

- Sustained warming enhanced the growth of woody plant species from newly available nutrient supplies
- Peatland plant community composition changed due to the decline or loss of sensitive species with warming
- Elevated CO₂ responses developed over time but were likely masked initially by nutrient and water-supply limitations

We commit to making these data available to the public upon publication via the U.S. Department of Energy Oak Ridge National Laboratory SPRUCE project data repository. This manuscript has been authored in part by UT-Battelle, LLC under Contract No. DE-AC05-00OR22725 with the U.S. Department of Energy. The United States Government retains and the

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Abstract The Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment has operated five whole-ecosystem warming manipulations (+0, +2.25, +4.5, +6.75 and +9 °C) with paired ambient and elevated CO₂ atmospheres (eCO₂, +500 ppm) for 8 full calendar years (since August 2015). We tracked shrub-layer vegetation responses to the treatments using annual destructive plot sampling. Tree (*Picea* and *Larix*) responses were assessed annually using nondestructive dimensional analyses and allometric conversions. Shrub community changes were assessed for key ericaceous shrubs (*Rhododendron*, *Chamaedaphne*, *Kalmia*), two *Vaccinium* species (*V. angustifolium*, *V. oxycoccos*), graminoid species (mostly *Eriophorum*), and one common forb (*Maianthemum trifolium*), plus minor understory species. We tracked annual aboveground net primary production (ANPP) for vascular plant species in gC m⁻² y⁻¹ and overall stand contribution in dry mass. We observed a linear increase in shrub-layer aboveground biomass accumulation with warming over time due primarily to an increase in ericaceous shrub abundance. Cumulative biomass increases across the shrub community showed overall positive responses to eCO₂ after 8 years. Community composition also changed with warming, with increases in woody shrub density, and the reduction or loss of forbs. The tree community showed minimal initial responses to warming early in the treatments, but since 2020, has shown significant increases in ANPP and individual tree growth with warming. The main driver of change in the vascular plant community was temperature, with less-pronounced effects of eCO₂ evident. These results indicate an overall increase in ANPP with warming from both the tree and shrub-layers of peatland vegetation.

Plain Language Summary We conducted a long-term, manipulative experiment of a raised bog peatland ecosystem to understand changes in plant community composition and function to a wide range of warming treatments (up to +9°C) with and without elevated CO₂ atmospheres. This paper summarizes community composition and growth responses of vascular plants (i.e., trees, graminoids, shrubs and forbs) following 8 years of treatments. Woody shrubs dominant in the understory responded positively to warming early in the study and sustained that response through time. With time, a positive response to elevated CO₂ treatments was also observed. Forb species declined under the warmest temperature treatments. Established tree species were slow to reveal a positive response to warming, but such responses without obvious benefit from elevated CO₂ were apparent after 8 years of treatment. Increased growth of shrubs and trees were

66 attributed to nutrients made available to rooted plants from accelerated decomposition of peat
67 soils and new litter contributions from the death of sensitive plant species.

68

1 Introduction

Arctic and boreal peatlands formed in regions with cool, wet climates where annual rates of primary productivity are greater than rates of ecosystem respiration. Over millennia, this has led to a significant store of belowground organic carbon (Yu et al. 2010). It is estimated that one third of the global pool of soil organic carbon (C) is stored in peatlands (Gorham 2009, Tarnocai et al. 2009). As rapid warming changes the climate of the north, rates of C cycling are expected to change dramatically (Dise 2009; Antala et al. 2022). Climate warming is expected to extend the growing season and could thus increase vegetation growth in high latitudes if other conditions (e.g., water) are not limiting. Understanding how different boreal plant species will respond to warming and atmospheric change (i.e., elevated CO₂; eCO₂) is important for estimating the C balance of these northern ecosystems. For example, using multiple replicates of small mesocosms (0.025 m³) of poor-fen peatland communities in a greenhouse-based warming study, Dieleman et al. (2015) found nonlinear declines in *Sphagnum* spp. and increases in *Carex* spp. with warming, with potential cascading impacts on ecosystem function. In addition, modeling studies (e.g., Heijmans et al. 2008) also clearly point to long-term climate change effects on bog vegetation and C dynamics.

Other previous warming experiments were short term and focused on impacts of leaf-level gas exchange. Bronson and Gower (2010) found that ecosystem warming up to +5 °C did not affect *Picea mariana* photosynthesis or aboveground autotrophic respiration. Way et al. (2008a and 2008b) demonstrated that *P. mariana* seedlings had a thermal optimum for photosynthesis (T_{optA}) that increased with growing temperature above which increased temperature would reduce net C uptake, and presumably growth. T_{optA} of mature *P. mariana* and *Larix laricina* also increased with whole-ecosystem warming, but only partially, by ~0.3 °C per 1 °C of warming (Dusenge et al. 2023). Even so, photosynthetic capacity of *P. mariana* and *L. laricina* increased with warming (Dusenge et al. 2024). However, Kirschbaum (2011) and Körner (2003) demonstrated that there is not a clear translation from photosynthesis to growth for several reasons, including temperature impacts on respiration or drought limitations to growth. Furthermore, Dang et al. (2020) found that eCO₂ stimulated photosynthesis in *P. mariana* seedlings, but that did not translate to increased biomass or growth. Multi-year eCO₂ treatments on mature *P. mariana* and

100 *L. laricina* trees led to downregulation of photosynthesis (Dusenge et al. 2024), which also could
101 buffer any eCO₂ benefit to growth.

102 The composition of vegetation communities also plays an important role in determining the C
103 balance of peatlands as either sinks or sources of C to the atmosphere. For example, shifts from
104 dominance by graminoid species to woody plants, or changes in the relative abundance of
105 vascular plants versus *Sphagnum* mosses has been shown to substantially alter rates of C
106 sequestration in peatlands (Potvin et al. 2015, Norby et al. 2019, Hanson et al. 2020a). While
107 these studies suggest that climate change will affect peatland vegetation communities, many of
108 these studies are limited in spatial and/or temporal scope. Ecosystem-scale, climate-change
109 experiments that allow for feedbacks between plant communities and biogeochemical and
110 hydrological cycles are needed to fully understand potential impacts of warming and eCO₂ on
111 peatland C cycling.

112 The Spruce and Peatland Responses Under Changing Environments experiment (SPRUCES;
113 Hanson et al. 2017) was initiated to track peatland C-cycle responses to a broad range of
114 warming by eCO₂ manipulations over a decade. A key response variable for future warming in
115 peatlands and other ecosystems is how primary producers (trees, shrubs, forbs, and mosses) will
116 respond to warming and changing atmospheric conditions. The SPRUCES experiment provides a
117 unique opportunity to study *in-situ* vegetation growth responses to multi-year, whole-ecosystem
118 warming and eCO₂ treatments in a nutrient-poor, boreal peatland. Warming treatments were
119 hypothesized to yield initial negative growth responses for all plant species due to lack of
120 nutrient availability in the ecosystem and enhanced C use for physiological processes, but this
121 would be reversed if there is a warming-induced release of nutrients from enhanced
122 decomposition rates that could be used to build long-lived vegetation C stocks. The eCO₂
123 treatments were expected to enhance growth of vegetation (de Graaff et al. 2006; Norby et al.
124 2010) due to increased nitrogen use efficiency (Leakey et al. 2009) and to maintain enhanced
125 growth during drier periods due to increased water use efficiency (Walker et al. 2020).

126 Prior publications (Norby et al. 2019; 2023) from the SPRUCES experiment have characterized
127 the loss of *Sphagnum* spp. productivity and presence in proportion to the sustained warming
128 treatments. Initial and early SPRUCES shrub-layer vegetation responses to the warming

treatments were summarized by McPartland et al. (2020) and showed warming-induced increases in aboveground shrub community growth and the loss of some sensitive species while Malhotra et al. (2020) documented increases in shrub root productivity. Warming treatments at SPRUCE also resulted in species-specific hydraulic stress, with *P. mariana* and *Rhododendron* more conservative in their water use (potentially at the expense of C uptake) than *L. laricina* and *Chamaedaphne* (Warren et al. 2021), which could lead to differential growth rates of the co-occurring species. Hanson et al. (2020) also calculated C budgets for SPRUCE using vascular plant vegetation response data for the first three years of the experiment and found a linear relationship of increasing C loss from the ecosystem proportionate to warming temperature treatments. Increased nutrient availability was documented by Iversen et al. (2021) based on increased ammonium and phosphate bound to cation and anion exchange resins deployed throughout the peat profile.

This paper extends the shrub-layer vegetation response assessment through 8 full years of warming and eCO₂ treatments and adds comparable data for the tree community responses that have developed through time. The key questions addressed are:

- How has the vascular plant community composition changed with time in response to warming and eCO₂?
- Does aboveground net primary production (ANPP) vary with warming levels?
- Are there changes in standing dry mass and ANPP associated with elevated CO₂ and are there any interactions between temperature and eCO₂?
- What vascular plant species benefit or decline from warming?

The results presented here provide insights into the responses of prevalent primary producers in raised-bog ecosystems to warming, and provide key information on long-term changes in C additions to the C balance of ecosystems faced with unprecedented warming. Such data are needed for predictions of long-term ecosystem responses to climate change because the experimentally manipulated levels of warming provide data where the historical record lacks quantitative information.

2 Materials and Methods

2.1 SPRUCE Experiment

The SPRUCE experiment is located on the S1 bog at the Marcell Experimental Forest in northern Minnesota, USA (47.506 N, -93.453 W; Kolka et al. 2011). Mean annual temperature for 1961–2019 is 3.5 °C, and mean annual precipitation is $787 \pm \text{SD of } 104 \text{ mm}$ (Sebestyen et al. 2011). The peatland soil is the Greenwood series, a Typic Haplohemist (<http://websoilsurvey.nrcs.usda.gov>), with average peat depths to the Wisconsin glacial-age lakebed of 2 to 3 m (Parsekian et al. 2012), and deep peat age from 5,100 –11,100 cal BP (Slater et al. 2012; McFarlane et al. 2018).

The S1 bog is an ombrotrophic peatland with a perched water table (Verry et al. 2011), with trees approximately 5–8 m in height. The open canopy is dominated by *Picea mariana* (Mill.) B.S.P. (black spruce), and secondarily by *Larix laricina* (Du Roi) K. Koch (eastern tamarack or larch). Trees of the S1 bog were harvested in strip cuts in 1969 and 1974 to assess natural regeneration of *P. mariana*. All regeneration following the strip-cut events occurred through natural vegetative processes and seeding events (three to four successful events since the two strip cuts). After 48 years of regrowth in the strips used for SPRUCE (i.e., 1974 cuts), the tree-layer of the SPRUCE plots is still largely represented by an open canopy. The understory is dominated by the evergreen shrubs *Rhododendron groenlandicum* (Oeder) Kron & Judd (Labrador tea) and *Chamaedaphne calyculata* (L.) Moench. (leatherleaf), and a bryophyte layer dominated by *Sphagnum* spp. Other species present in this paper include: *Maianthemum trifolium* (L.) Sloboda, *Kalmia polifolia* Wangenh., *Vaccinium oxycoccos* L., *Vaccinium angustifolium* Aiton, and a variety of graminoid species (especially *Eriophorum* spp.). The SPRUCE site also has a dominant nonvascular, bryophyte layer made up of various *Sphagnum* species, the treatment response of which has been documented elsewhere (Norby et al. 2019, Carrell et al. 2019 & 2022, Petro et al. 2023).

The SPRUCE experiment assesses peatland responses to whole-ecosystem warming with or without eCO₂ additions applied within 10 open-top octagonal enclosures (height = 7 m; diameter = 12.8 m; area = 114.8 m²) located on the S1 bog (Figure 1). The temperature treatments, applied continuously since late 2015 with very few interruptions, include deep-peat heating that uses

183 heating elements extending ~3 m into the peat (Hanson et al. 2017) combined with air warming
184 achieved by blowing heated air 1 m above the peat surface to warm the enclosed air space
185 (Hanson et al. 2017). The SPRUCE target differential temperature treatments are +0, +2.25,
186 +4.5, +6.75, and +9 °C with two plots at each temperature treatment. The chambered zero-
187 energy-added plot (+0 °C, ambient CO₂) was chosen to provide the reference temperature for the
188 other treatments in the regression design. One plot for each temperature treatment receives eCO₂
189 by injecting pure CO₂ to a target concentration of +500 ppm during the growing season (Hanson
190 et al. 2017). Deep-peat heating was initiated in June 2014, air warming started in August 2015,
191 and eCO₂ began in June 2016 (Hanson et al. 2017).



Figure 1. A montage of photos showing the SPRUCE experimental site from drone images, plot-level photos, and LIDAR imagery, and the tree and shrub-level vegetation that this paper describes.

Two “ambient” plots (reference conditions, without constructed enclosures), tend to run about 1.6 °C cooler than the “control” plots (constructed enclosures, but no added warming), but this temperature differential is dependent on radiation inputs and snow cover (Hanson et al. 2017). Each enclosure is hydrologically isolated from the rest of the bog by an octagonal sheet-pile corral, driven 3–4 m through the peat into the underlying ancient lake sediments. Outflow pipes allow for passive lateral drainage from each enclosure (Sebestyen & Griffiths, 2016).

Data presented here cover vegetation growth through the first 8 years where elevated temperatures and eCO₂ treatments were applied in combination (2016 through 2023).

Late-season changes in surface water content and water table depths driven by the temperature treatments (with minimal impacts from eCO₂) were seen in some years (especially 2021; Hanson

et al. 2020b) but not all years due to winter recharge and commonly abundant growing season precipitation inputs.

2.2 Shrub-layer Biomass and Growth Assessments

All designated permanent plots used in the SPRUCE study were sampled annually including the 10 SPRUCE treatment plots and ambient plots, the latter measured as a reference for non-warming impacts of the enclosures (Hanson et al. 2018a). Subplots within each enclosure, and in the two ‘ambient’ (non-enclosure) plots, were destructively harvested on an annual basis at the peak of ANPP in the middle of August. The size of a subplot was not always consistent. In 2016, 2017, and 2021, two 0.25 m² subplots per enclosure/ambient plot were sampled. In 2018, four 0.25 m² plots were sampled, in 2019, a single 1.15 m² circular plot was sampled, 2020 and 2022 samples were not collected due to COVID restrictions, and in 2023, three 0.4 m² plots were sampled. In general, subplots were located within each enclosure/plot boundary and away from established instrumentation and permanent vegetation plots used for community change assessments (McPartland et al. 2020).

In early years, distinct hummock and hollow sampling squares were collected, but in later years, unsampled hollow areas became unavailable due to prior sampling or instrument installations. For this paper, subsampled areas were summed for an average representation of each ambient or treatment plot.

During destructive harvests, all vegetation within each subplot above the peatland moss layer was clipped at the surface of the moss and placed in plastic bags for transport to a laboratory for sorting. Post-collection sorting included the separation by species or species group followed by a separation of the tissues into current-year vs. older tissues and finally into foliage and woody stem pools. The cumulative dry mass of current-year growth for leaf and stem tissues together is interpreted as the shrub-layer ANPP for the designated plot.

Collected shrub-layer materials were stored in a chest freezer until they could be dried. Dry mass of each species and tissue pool was obtained after oven drying at 70 °C to uniform mass (i.e., several days). Actual C content for species and tissue types (leaves or stems) ranged from 46% to

53%, but this plot-level, ecosystem-scale assessment assumed all tissues to have 48% C (Phillips et al. 2013 and 2021).

2.3 Tree Community Assessments of Annual Growth

In this paper, we combine both traditional, manual tree-growth measurements and terrestrial laser scanning (TLS) data to provide a comprehensive analysis of the response of *P. mariana* and *L. laricina* growth to the SPRUCE treatments over 8 years of the experiment (2016-2023; Hanson et al. 2018b).

In 2011 and 2012, all trees in each enclosure or ambient plot taller than 1.5 m in height were marked with a unique identifier on a metal tag, and the tree's species was noted. Then, a laser-leveling system (Spectra LL400) was used on a tripod throughout the bog (referenced to a 1.3 m measurement pole anchored in the hollow areas) to identify the location of the diameter at breast height (DBH) measurement for each tree. In subsequent years, colored wax pen markings on the trees were used to allow personnel to return to the same measurement height independent of snow depth each year. In winter of each year (2016-2023), circumference measurements of all tagged trees were obtained with a steel DBH tape at the marked DBH location to the nearest 0.1 cm. Tree height measurements were obtained with a clinometer in 2011 and 2012 to the nearest meter, and crown diameters were estimated to the nearest 0.1 m with a graded measurement stick made from PVC pipe. After the enclosure walls were added (2015), the clinometer could no longer be used, so tree height measurements were made with a measurement pole.

Beginning in 2015, TLS of the experimental plots and two ambient plots have enabled height assessments for most trees at an annual resolution (Graham et al. 2019). Periodic height measurements by tape or height pole supplement these data. Tree height together with circumference at DBH are the key inputs to the allometric equations used for tree mass assessment.

Calculation of Tree Mass via Allometric Relationships - DBH was calculated from measured tree circumference (cm) as: $\text{Calc DBH} = \text{Tree Circumference} / 3.1415$. Calculated tree basal area (Calc BA) in m^2 was obtained from measured tree circumference (cm) as: $\text{Calc BA} = (((\text{Tree Circumference}/100)/ 3.1415)/2)^2 * 3.1415$. Finally, calculated basal area at DBH times height

DBH_BA*H) in m^3 was determined to be linear related to total tree aboveground dry mass and is the basis of the subsequent allometric equation.

Individual tree dry mass (kg tree^{-1}) was derived from allometric data for *P. mariana* and *L. laricina* trees harvested from the S1 bog primarily before treatments began (Hanson et al. 2012). Additional harvests of trees outside of the experimental plots and re-evaluation of the allometric relationships were done in 2021. With the addition of new data, the following allometric equation was applied to estimate dry mass for each measured tree:

$$\text{Dry_Mass}_{2021} = [\text{DBH_BA*H}] * 534697 / 1000$$

Determination of Tree ANPP - Tree ANPP data for total tree mass increments in $\text{gC m}^{-2} \text{y}^{-1}$ include all tree species (*P. mariana* and *L. laricina*) contributing to each treatment plot (114.8 m^2 of ground area). Mass estimates from the allometric equations were multiplied by 0.48 (48% C) to obtain units for ANPP. Annual ANPP was determined to be the sum of the difference in mass of all plot trees over an annual cycle plus the mass of a single cohort of foliage for each species. The annual cohort for *P. mariana* was assumed to be one of an average of 5 needle cohorts on the tree. Tree ANPP data are presented in both absolute $\text{gC m}^{-2} \text{y}^{-1}$ and normalized forms that account for plot-to-plot variation during plot selection and randomization prior to the start of the experiment. Normalization was performed by dividing each year's annual ANPP values by the 2014-2015 pretreatment ANPP for the respective plot (Fraction y^{-1}).

To explore variation within and between the two tree species' responses to experimental treatments, mean individual cumulative tree growth from 2016 through 2023 for each species was normalized to their respective initial growth rates as a fractional change where mean cumulative growth over 8 years in grams dry matter (d.m.) tree^{-1} was divided by the initial mean dry mass for individual trees.

2.4 Data Presentation and Statistical Approach

We use simple and multiple linear regression approaches to compare warming and eCO_2 responses in this paper. Other nonlinear regression approaches were also considered but they did not produce a better fit to the data (i.e., goodness of fit judged by AIC criterion). Reference temperature treatments for each year were selected as the mean annual aboveground

temperatures (MAT) measured at 2 m above the bog surface (Hanson et al. 2016). The eCO₂ treatment is applied at +500 ppm as a step change to determine if such effects compensate for C loss driven by warming responses. Multilinear regressions were based on Year (time), MAT, eCO₂, and interaction terms supported by the available degrees of freedom. Regression analyses were run with XLSTAT Premium Version 2024.2.2 (Addinsoft) and detailed results are provided in the supplemental materials tables. Simple or multiple linear regression analyses are described and interpreted as significant based on p-values less than ≤ 0.05 , but some with higher p values are described as a developing trend. Data from ambient plots not included in the full SPRUCE manipulation are included in Figures 2, 4, 5, 6, and 7 to show that they extend in a logical manner from the treatment data, but they are not included in the regression analyses trends with respect to MAT.

Community dry matter composition by species was also assessed using non-metric multidimensional scaling plots (NMDS; Clark 1993) with the vegan package in R and ggplot2 to make the associated graphic. R Code for this analysis is provided in the supplemental materials.

3. Results

3.1 Shrub and Tree Community Composition

Community composition of the shrub-layer vegetation, as characterized by total standing dry mass, has changed over 8 years of treatment manipulations (Figure 2; Table 1). *Kalmia*, *V. oxycoccos*, and *M. trifolium* have essentially disappeared from the warmer plots ($> +4.5$ °C). *Rhododendron* and *Chamaedaphne* have maintained or increased their presence in the community and *V. angustifolium* are clearly increasing in the warmest plots. There has also been some foliar herbivory in *Rhododendron* and *Chamaedaphne* from leaf roller moths (*Acleris* spp.), with greater herbivory observed in the warmer plots (Sue Eggert, unpublished). Data for two ambient plots (labeled as the -2 nominal treatment in Figure 2) are included as a reference and show a similar temporal trend to the two control plots (treatment = 0 in Figure 2).

An NMDS analysis of community species contributions to dry matter (Figure 3) further highlights the increase in *V. angustifolium*, *Rhododendron*, and *Chamaedaphne* with warming and through time.

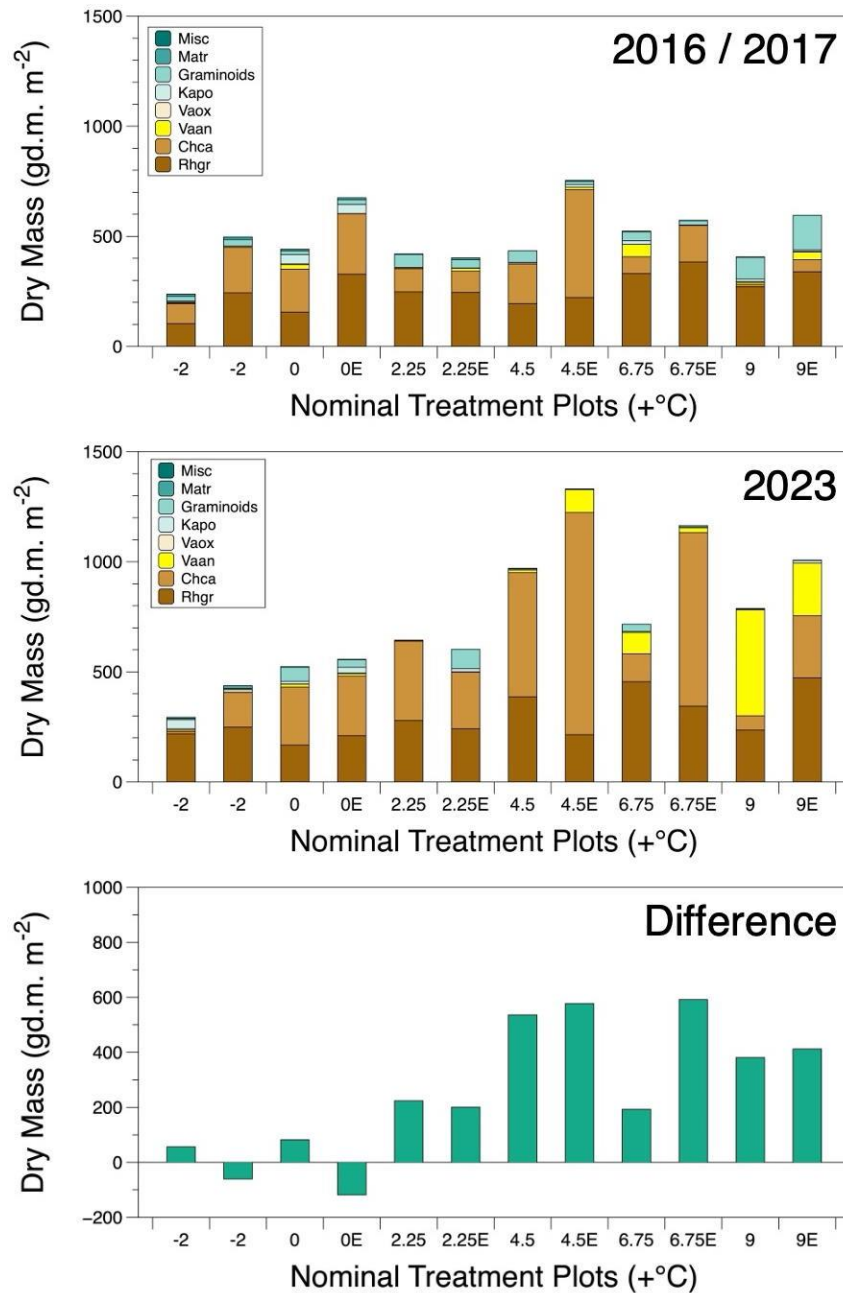


Figure 2. Shrub community composition by dry mass contribution per unit ground area (total foliage plus stem mass) at the beginning of SPRUCE (mean of 2016 and 2017, 1 m² total sample; top graph), in 2023 (1.2 m² sampled; middle graph), and the shrub dry mass difference developed over 8 years of SPRUCE treatment manipulations (bottom graph). Individual species contributions to the 8-year difference in dry mass are shown in Table 1. Matr = *Maianthemum trifolium*; Kapo = *Kalmia polifolia*; Vaox = *Vaccinium oxycoccus*; Vaan = *Vaccinium angustifolium*; Chca = *Chamaedaphne calyculata*; Rhgr = *Rhododendron groenlandicum*; Misc = miscellaneous (e.g., *Betula* seedlings). For nominal temperature levels, -2 represents ambient reference plots that run approximately 2°C cooler than the actual no-energy-added controls (+0°C) and “E” designates the eCO₂ plot data.

Table 1. Cumulative 8-year difference in dry mass by plots and treatments (difference between 2016/2017 and 2023), where positive values indicate an increase in dry mass over the 8-year period. Species abbreviations are as shown in Figure 2 except “Gram” equals Graminoids. Ambient and elevated CO₂ treatments are Amb and Elev, respectively.

			Contributing Species Mass Difference (g dry matter m ⁻²)								
Plot #	Temp Treat. (°C)	CO ₂ Treat.	Rhgr	Chca	Vaan	Vaox	Kapo	Gram	Matr	Misc	8-year Difference
7	-2	Amb	114.8	-79.2	2.1	3.6	35.3	-16.5	-3.8	0.0	56.4
21	-2	Amb	5.7	-50.0	1.2	11.3	-3.6	-25.5	0.4	0.0	-60.4
6	0	Amb	11.8	68.4	-8.5	-1.7	-30.1	47.1	-5.0	0.0	82.0
19	0	Elev	-117.7	-3.4	10.0	2.2	-15.0	12.4	-6.5	0.0	-118.1
20	2.25	Amb	31.3	255.2	0.0	-1.0	-3.8	-56.7	-1.3	0.0	223.8
11	2.25	Elev	-3.7	160.4	-10.8	-1.2	13.8	50.1	-7.6	0.0	201.0
13	4.5	Amb	192.3	383.2	10.9	-1.1	-0.2	-48.9	-0.1	0.0	536.1
4	4.5	Elev	-7.6	519.3	94.1	-0.4	-11.2	-11.8	-4.7	0.0	577.6
8	6.75	Amb	124.2	51.0	39.3	-0.2	-10.8	-7.7	-2.8	0.0	192.9
16	6.75	Elev	-39.3	622.8	20.3	-0.7	4.4	-13.9	-1.9	0.0	591.7
17	9	Amb	-35.4	54.5	471.8	-3.6	-8.0	-95.7	-2.5	0.0	381.2
10	9	Elev	133.5	227.8	203.7	-2.9	5.4	-154.9	-0.2	0.0	412.3

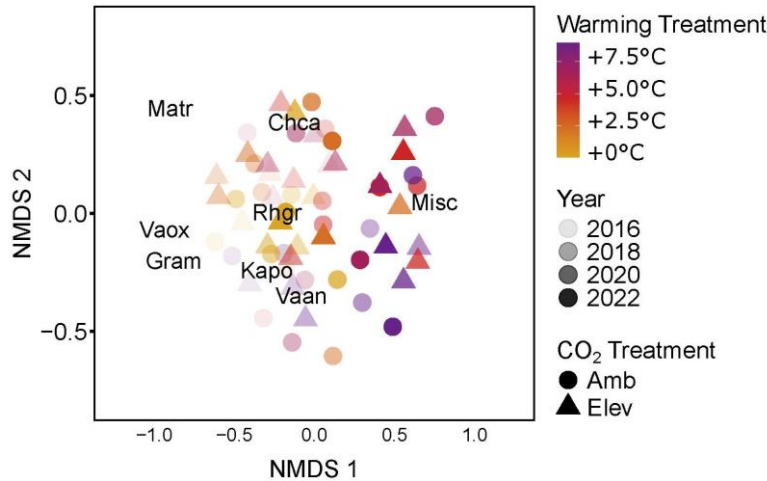


Figure 3. A non-metric multidimensional scaling (NMDS) plot of shrub species dry matter showing a transition in warmer plots through time and with nominal temperature and eCO₂ treatments. The analysis was done on the biomass data for all species in all years sampled (2016, 2017, 2018, 2019, 2021, 2023). Points are one per plot per year and the species text locations indicate the ordination direction associated with each species in the plots. Species abbreviations are as shown in Figure 2. The warmer treatment plots are more purple and early years are more transparent points.

Both tree species (*L. laricina* and *P. mariana*) have maintained their presence across the warming treatments, but mortality of some individuals (mostly *P. mariana*) has developed in the warmest plots over time (Table S9).

3.2 Shrub-layer Community ANPP and Mass

A comparison of total dry mass summed across all shrub-layer species at the beginning of the SPRUCE study (2016-2017) showed no pattern with respect to the initial imposed treatments (Figure 4 upper); however, after 8 years of sustained warming and eCO₂ treatments, warming has resulted in greater standing dry mass of the shrub community and eCO₂ generally increases standing dry mass, especially at the warmer temperature treatments (i.e., +4.5 °C and higher; Figure 4 lower). Treatment differences were the result of changes in the standing woody biomass pool. Foliar production, by itself, was not significantly different across the imposed treatments (Supplemental data Figure S1).

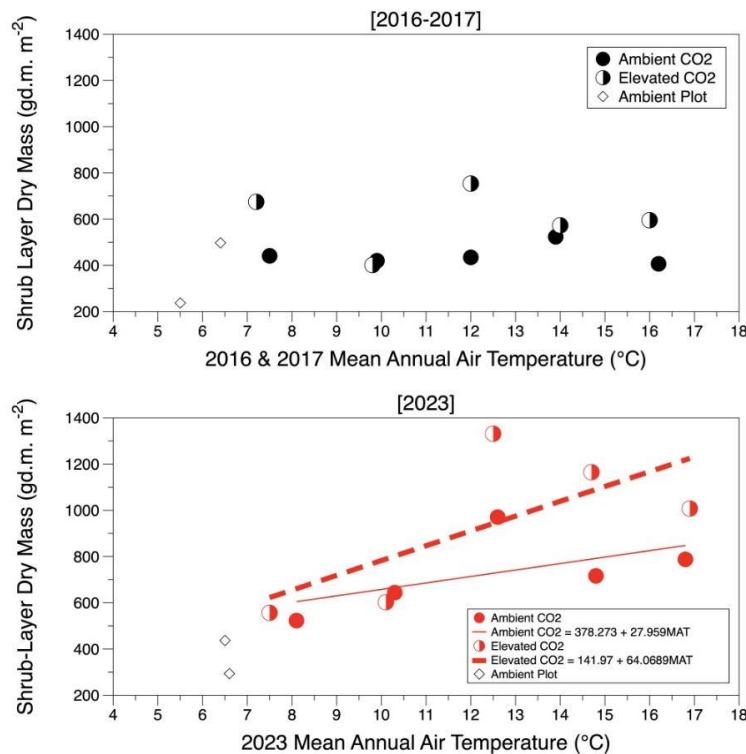


Figure 4. Shrub-layer total aboveground dry mass summed across all species at the beginning of the SPRUCE study (upper graph for a 1 m² sample) and after 8 years of treatments (lower graph for a 1.2 m² sample) plotted against mean annual air temperature (MAT) in each enclosure/plot. Based on AIC values, a second-degree polynomial fit to the 2023 data was not better than the linear fit depicted. Fitted regression coefficients for 2023 are in Table S1. Two ambient plot data points are included in each graph for reference to the treatment data.

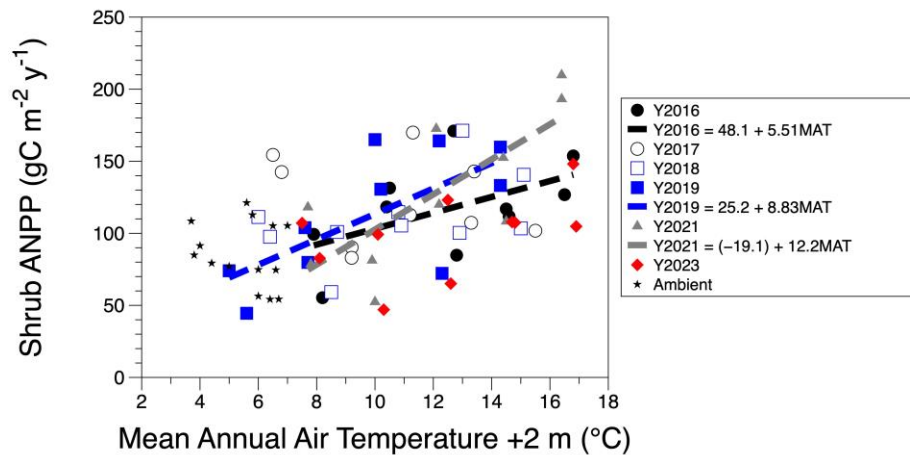


Figure 5. Aboveground net primary production data (ANPP) by year for the peatland shrub community, demonstrating significant positive responses of ANPP to warming (plotted against mean annual air temperature (MAT) in each enclosure/plot). Regression lines are provided for years with significant fitted linear relationships (Table S2). Ambient plot data (stars), not included in the regression calculations, are coplotted for reference.

Annual shrub-layer ANPP showed increases with warming treatments since the early years of the SPRUCE experiment (Figure 5). With 8 full years of treatment, the multiple linear regression of the annual shrub-layer ANPP data for year, temperature, and eCO₂ treatments (Table S3) revealed a significant overall model (Prob. F = <0.0001) with significant responses to mean annual temperature (MAT; Prob. F = <0.0001) and eCO₂ (Prob. F = <0.009). An interaction between temperature and eCO₂ was not significant. The predicted model parameters for temperature and eCO₂ were both positive but the impact of eCO₂ was smaller (Table S3). Within the shrub-layer community, the enhanced growth of ericaceous shrubs (*R. groenlandicum*, *C. calyculata*, and *V. angustifolium*) increased C with warming, while the graminoid species have showed little change (*Eriophorum* spp.), and the ground-hugging forb *M. trifolium* and other miscellaneous species are disappearing with warming, so reducing C storage for the peatland.

3.3 Tree Community ANPP and Mass

In one early year of the study (2017; Table S4 and S5), tree ANPP showed a linear decline with warming, followed by several years of no clear trend with warming. However, in 2022 and 2023, the tree ANPP pattern reversed, and now exhibits a consistent increase with warming when regressions are performed on individual years of data (Figure 6). These patterns were significant

in absolute growth data, but the early year negative growth reductions were no longer evident in the normalized data set (Table S4 and S5).

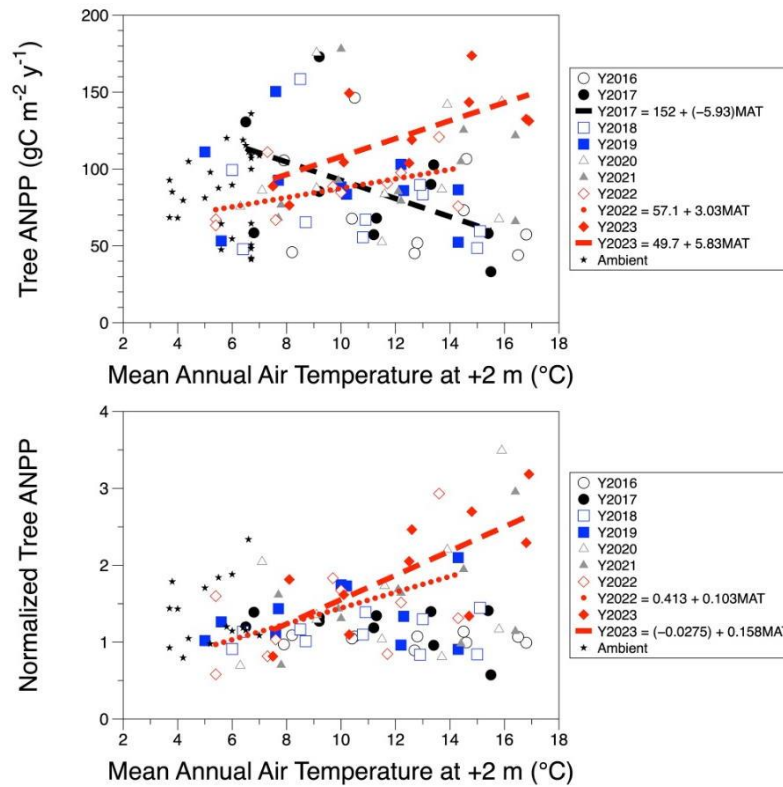


Figure 6. Measured tree aboveground net primary production (ANPP) data (upper graph) and normalized (lower graph) for tree species showing an initial negative or insignificant response that transitioned to a positive response to warming after multiple years of treatment applications. Regression coefficients for absolute data are in Table S4, and for normalized data in Table S5. Tree growth is normalized to 2015 growth rates and plotted as fraction y⁻¹. Ambient plot data (stars), not included in the regression calculations, are coplotted for reference.

Multiple linear regression of the annual tree ANPP data for year, temperature, and eCO₂ treatments (Table S6) revealed a significant overall model (Prob. F = 0.041) with significant responses restricted to year (Prob. F = 0.003) reflecting the increase in overall tree ANPP over time. However, the same multiple linear regression for data normalized to the 2015 initial tree ANPP values (Table S7) provided alternate insights. The tree ANPP normalized data showed a significant overall model (Prob. F = <0.0001) with significant responses for year (Prob. F = <0.0001), mean annual temperature (MAT; Prob. F = <0.0001) and the MAT by eCO₂ interaction (Prob. F = 0.002). Normalization of the tree data was necessary as it accounted for pretreatment plot selection biases that remained after randomization.

The 2016 complement of trees in each plot was established through natural regeneration and 42 years of growth following strip cutting of this bog in the winter of 1974–1975. Unlike the shrub vegetation responses which developed quickly after treatment applications in 2016, it appears that multiple years of sustained treatments have been required for tree physiology and perhaps carbohydrate and nutrient pools to drive a sustained and consistent warming response.

While the previous data on tree species ANPP at the plot level provide one metric for tree community responses, it does not separate or define how the two dominant tree species, *P. mariana* and *L. laricina*, varied in their response to warming. Figure 7 show species-specific changes in growth over the period from 2016 through 2023. Graham (2020) previously conducted an early 3-year analysis of the tree species responses to warming from the SPRUCE manipulations using TLS, contrasting different response metrics including basal area, height, and dry mass. The responses for trees in the early years of the SPRUCE study were inconclusive, however, following 8 full years of warming manipulations, both *L. laricina* and *P. mariana* trees showed a positive response to the warmest treatments (Figure 7, Table S8). Notably, there was greater variability in tree growth and success in the warmest +9 °C plots, reflecting some trees growing at high rates and others stagnant or in decline.

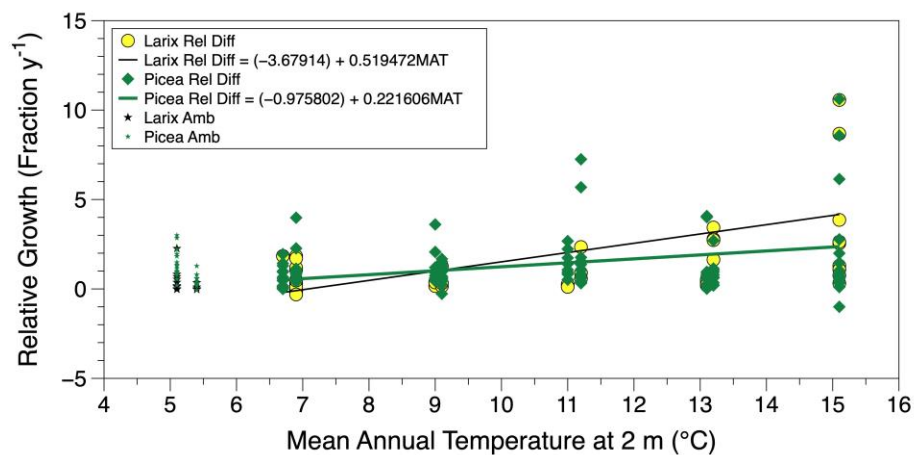


Figure 7. Cumulative mean individual tree mass growth for *Picea mariana* and *Larix laricina* trees from 2016 through 2023 normalized to the tree mass at the beginning of treatments in 2016. Fitted coefficients are in Table S8. MAT = mean annual temperature. Ambient plot data (star symbols), not included in the regression calculations, are coplotted for reference.

Eight years of environmental manipulations represents a challenging length of time over which to draw solid conclusions regarding changes in tree populations given their long lifespans. Nevertheless, SPRUCE experimental data suggest both an increase in extant tree mortality with the extreme level of warming and a trend towards increasing establishment of tree-size individuals (>1.5 m height) with warmer treatments as well (Table S9). We conclude that tree development is derived from seedlings present in 2016. Tree canopy damage and mortality (in some cases) are tied to specific extreme environmental events, which predominantly affected the warmest plots (spring freeze in 2016 – Richardson et al. 2018; heatwave impacts in 2020 and 2024). We hypothesized that tree mortality may be limited by eCO₂-induced increases in assimilated C, increased water use efficiency, or by sustaining maintenance functions or enhanced belowground root development. Conversely, inherent bog nutrient limitations may also remain an impediment to vascular plant function under stressful conditions. Unfortunately, the length of the SPRUCE study and the number of observed plots has not enabled us to draw clear conclusions with respect to mortality or recruitment of *P. mariana* or *L. laricina* in response to eCO₂.

3.4 Shrub-layer versus Tree Contributions to ANPP

The SPRUCE study represents a manipulation of an established peatland community into which the trees have regrown since 1975 and for which the tree canopy has not yet fully “closed” in all treatment plots as is true of a nearby reference bog on the Marcell Experimental Forest. The shrub-layer community was fully established at the beginning of SPRUCE treatments and shrub-layer ANPP has remained reasonably consistent over time while showing a positive response to warming. Conversely, the trees continued to increase their basal area and height (data not shown) over the duration of the SPRUCE study and showed increasing numbers with time which adds to their contribution to ANPP. By 2023, tree contributions to ANPP, which lagged that of shrubs in 2016 (Hanson et al. 2020a), now contribute ANPP equal to, if not exceeding, that of the shrub-layer community.

4. Discussion

4.1 Shrub Growth

The results for the shrub-layer community summarized in this paper are a logical extension of the early results published by McPartland et al. (2020). After five years of experimental manipulation of temperature and CO₂ levels at SPRUCE, McPartland et al. (2020) concluded that “a series of changes to the composition, diversity, and productivity of the vascular plant community” were driven by temperature change with only a minor effect of eCO₂ treatments. After 8 years of manipulation, the positive temperature response of shrub-layer ANPP continues to be evident (Figure 5), but we now observe a significant increase in cumulative shrub-layer mass associated with the sustained eCO₂ treatments, with no interaction with warming temperatures (Figure 4, Table S1 and S3). Overall, the increase in ANPP of the shrub-layer was driven by woody shrub species (notably *Vaccinium angustifolium*, *Chamaedaphne calyculata*, *Rhododendron groenlandicum*) rather than graminoids or forbs (Figure 5).

Although the poor-fen mesocosms of Dieleman et al. (2015) and SPRUCE represent different peatland forms and vegetation composition, they both show vegetation community changes with warming and clearly demonstrate the loss of *Sphagnum* cover. *Sphagnum* declines have been described for SPRUCE by Norby et al. (2019, 2023). They attributed the dramatic decline to a combination of factors, including temperature and water limitations, along with increased shade competition from shrubs (Norby et al. 2023).

4.2 Tree Growth

Given that the warmest SPRUCE treatments (+6.75 to +9°C) are consistent with the most severe Intergovernmental Panel on Climate Change (IPCC) predictions for high latitudes in 2100 (Collins et al., 2013; Lee et al. 2021), it is notable that the nearly decadal response for both *P. mariana* and *L. laricina* growth and production is positive to warming. Previous studies measuring the response of C storage to temperature in *P. mariana* and *L. laricina* have been based on large-scale, tree-ring assessments that typically examine the effect of prevailing monthly temperatures on growth, rather than assessing the effect of experimental warming (Brooks et al. 1998; Girardin et al. 2001; ACIA 2005; Juday and Barber 2005; Wilmking and Myers-Smith 2008; Mamet and Kershaw 2011; Nishimura and Laroque 2011; Walker and

Johnstone 2014). Girardin et al. (2016) used a robust dendrochronological analysis to measure the effect of environmental change (warming and water availability) on tree growth in Canada's boreal forest. From their projections, they concluded that future warming would lead to soil water availability and respiration being limiting factors on NPP over the next century. However, they also noted that the response did vary due to other environmental or physiological factors (e.g., CO₂ fertilization, respiration acclimation to high temperature).

The only year we observed a trend for tree ANPP to correlate negatively with temperature was the first year of the study, which we interpret as an indication of an acclimatory transition period after treatments were initiated and when new foliage developed under the prevailing treatments. Subsequent years showed a flat response of *P. mariana* and *L. laricina* ANPP to temperature, potentially indicating that a balance had been achieved between C uptake and release. The increased temperatures certainly increased respiration rates, and initial estimates indicate thermal acclimation of respiration for *L. laricina*, but not *P. mariana* (Dusenge et al. 2021). As trees are long-lived organisms that maintain internal C storage pools that can be used for growth or respiration, changes in growth due to external drivers are expected to develop over multiple years. Since the evergreen *P. mariana* retains five or more foliar cohorts, whole plant acclimation will take longer than for the deciduous *L. laricina* that replaces its needles each year. Hydraulic acclimation of the vascular system in response to greater atmospheric demand (increased vapor pressure deficit) would also be a contributing factor to growth responses over time. That is, tree vigor improves as sequential rings of xylem develop under the experimental conditions to allow greater hydraulic conductivity through the stems to the foliage.

Thermal biochemical acclimation, stored non-structural carbohydrate pools, shifts in whole-plant morphology or allocation, and changes in soil nutrient availability are all feasible mechanisms to account for the tree growth responses reported here and likely each played some role in the integrated growth responses tracked over time in both shrubs and trees. (Figures 4, 5, 6, and 7).

Other research has reported beneficial effects of warming for boreal tree growth (Kauppi et al. 2014) or a lack of response (Girardin et al. 2016; Stefanski et al. 2020). D'Orangeville et al. (2018) found positive responses at low levels of warming (+2 °C) but negative responses with

higher levels of warming. In addition, Reich et al. (2015) showed growth responses to warming to differ spatially and among plant species. Multiple studies of *P. mariana* showed that warming could result in either increased or decreased growth and productivity in North America (Brooks et al. 1998; ACIA 2005; Juday and Barber 2005; Wilmking and Myers-Smith 2008; Grant et al. 2009; Mamet and Kershaw 2011; Nishimura and Laroque 2011; Walker and Johnstone 2014; Girardin et al. 2016). Bronson and Gower (2010) used a multi-year, whole-tree/ecosystem warming (soil and air) experiment to evaluate the effect warming (+5 °C) had on *P. mariana* in upland soils while ensuring that plots with elevated temperatures maintained the same soil moisture as ambient plots using daily irrigation. They found that elevated temperatures alone had no effect on photosynthesis or aboveground respiration in *P. mariana*. Other studies have also found negative correlations between growth and temperature and attribute the decrease in growth to warming-induced limitations in soil water availability (Brooks et al. 1998; Wilmking and Myers-Smith 2008; Walker and Johnstone 2014; Girardin et al. 2015).

4.3 eCO₂ Responses

As boreal ecosystems warm in the future, there will be concurrent increases in atmospheric CO₂. Studies of mature boreal tree growth responses to eCO₂ are rare, but also indicate an interaction with other environmental and edaphic resources. The response of the shrub community to eCO₂ at SPRUCE was slow to develop, but after 8 years now shows a significant response (Figure 4; Table S3 p-value = 0.034), although there was no interaction between the eCO₂ and temperature response.

Other published examples include mature *Larix decidua* growth increases under eCO₂, but primarily for years with early springs after a prior warm growing season (Dawes et al. 2011). Sigurdsson et al. (2013) showed that growth increased in 40-year-old *Picea abies* trees exposed to eCO₂, but only when supplemental nutrients were applied. Similarly, in a nutrient poor peatland, there was no effect of CO₂ on growth for vascular or nonvascular plants (Hoosbeek et al. 2001). The limited available literature on warming and eCO₂ effects for boreal plants highlights the need for assessing the direct effects of warming and CO₂ on growth rates, and the interactive indirect effects that arise.

The eCO₂ responses for the established trees (50-years-old in 2024) studied in SPRUCE are not yet significant (Table S6 and S7). Previous studies of boreal or northern temperate tree species found eCO₂ to have positive effects on fertilized *P. mariana* and *L. laricina* seedling growth (Tjoelker et al. 1998) and total biomass in mature *P. abies* (Sigurdsson et al. 2013) when nutrients were added, but no effects without fertilization. In a three-year study of 20-year-old boreal *Pinus sylvestris* exposed to eCO₂ and temperature (Peltola et al. 2002), diameter growth displayed a moderate increase with temperature, but a major increase with eCO₂, especially early in the growing season, a period when nutrients are most available following snowmelt. In a 12-year study of *Populus tremuloides*, eCO₂ treatments increased C and NPP (Talhelm et al. 2014). While there are some similarities between the SPRUCE experiment and these previous studies, a significant difference is that the SPRUCE study system represents a nutrient-poor wetland, and thus we expected to see a limited relationship between growth and eCO₂ due to the lack of available nutrients to support growth.

Future eCO₂ atmospheres have the potential to buffer water stress and increase water use efficiency, and are therefore expected to facilitate growth in the future. Indeed, CO₂ enrichment studies have led to growth increases in temperate forests (e.g., Körner et al. 2005; Norby et al. 2005), although this benefit would be dependent on stand development (Walker et al. 2019) and limited under drying conditions (De Kauwe et al. 2013), nutrient limitations (Finzi et al. 2006; Norby et al. 2010), or due to interactions with warming-induced physiological acclimation (Dusenge et al. 2019; 2024). Further, any increase in net C uptake would not be realized in aboveground biomass, but rather shunted belowground to roots (Iversen 2010) or lost via respiration (e.g., Jiang et al. 2020). In boreal seedlings exposed to eCO₂, there was a reduction in biomass growth for *P. mariana*, but an increase in growth for *L. laricina* (Dusenge et al. 2020).

4.4 The Role of Nutrients in Driving Positive Responses to Warming and Community Change

SPRUCE observations on enhanced nutrient cycling with warming (Iversen et al. 2023) provide a logical explanation for our observations of cumulative increases in shrub and tree vegetation production and mass. When combined with SPRUCE project observations that N and P did not increase in porewater with warming during the first few years of the experiment (Iversen et al.

2023), it is likely that rooted shrubs and trees had access to the nutrients made available from warming-induced decomposition of dying vegetation (*Sphagnum* [Norby et al. 2019, 2023] and *Maianthemum* spp. [this paper]) and peat. Prior to the implementation of SPRUCE treatments, *Sphagnum* made up 57% of the biomass N pool and 46% of the biomass P pool (Salmon et al. 2021). Therefore, we hypothesize that enhanced growth of woody shrub species and trees show improved growth and biomass accumulation with warming because previously limiting nutrients (esp. N and P) have become available through an increased aerobic soil profile, and root expansion and function (Duchesneau et al. 2024). Petro et al. (2023) provide data from SPRUCE to support the transfer of N forms resulting from *Sphagnum* degradation under warming into such available pools. Petro et al. (2023) saw an increase in N availability in shallow peat with warming, but this response was not evident in eCO₂ plots, potentially the result of increased N utilization by the enhanced shrub growth documented in this study. An analysis of the levels of N and P made available from warming and foliar nutrient content is underway to quantitatively evaluate a relationship between vascular plant growth enhancements under warming and the essential elements made available from the turnover of dead species and the consumption of preexisting peat by microbial communities.

In this paper, we observed changes in plant community composition forced by imposed warming treatments. Kastovská et al. (2018) studied the influence of extant vegetation cover on nutrient cycling of peatlands. They found that when ericoid shrubs represented by *Vaccinium myrtillus* were predominant in peatlands, they were associated with lower N and P tissue concentrations and enhanced availability of N and P, and increased decomposition of plant litter. From the SPRUCE data presented in this paper, we hypothesize that enhanced nutrient availability from decomposition is responsible for *V. angustifolium* proliferation in the warmest SPRUCE treatments which seems highly correlated to the data from Kastovská et al. (2018). It remains unclear if the established vegetation studied by Kastovská et al. (2018) are the cause or the result of long-term nutrient cycling processes in the *Picea* swamp forests that they studied.

4.5 Physiological Explanations

Using gas exchange data from the SPRUCE site, Jensen et al. (2019) leveraged a land-surface model parameterized to the site (ELM-SPRUCE) to simulate tree growth responses to the

treatments. These early SPRUCE results suggested that there could be an interaction between temperature and eCO₂ that influences *P. mariana* growth, in which a negative effect of temperature on NPP is reduced in the presence of eCO₂. Indeed, there was some evidence of reduced *Picea* water stress with eCO₂ for the warmest treatments (Warren et al. 2021). Modeled *L. laricina* NPP also decreased with warming and ambient CO₂ but exhibited small increases in NPP with eCO₂ (Jensen et al. 2019), which does not match results from our measurements that show a positive response of *L. laricina* to temperature developing with time (Figure 7). Continued experimental observations through the end of the SPRUCE experiment (2025) will be used to test and improve the ELM-SPRUCE model, and to resolve if the long-term patterns embedded into model assumptions hold.

Species-specific growth responses to temperature observed in this study are supported by other measurements at the SPRUCE site, including foliar N, which increased for both species with warming (Dusenge et al. 2021), sapflow and gas exchange, which indicated greater stomatal limitations for C uptake by *P. mariana* (Warren et al. 2021; Dusenge et al. 2021), and sapflow and water potentials, which indicated more conservative hydraulic behavior by *P. mariana* (Warren et al. 2021). Despite the greater leaf N and greater photosynthetic capacity in both species (Dusenge et al. 2024), only *L. laricina* displayed increased photosynthetic performance (as indicated by photosynthesis measured at 25°C) with warming (Dusenge et al. 2021). In addition, plant water stress was also greater for *L. laricina* than *P. mariana* at SPRUCE (Warren et al. 2021), subjectively observed as some *L. laricina* branch tip dieback in late summer, which concurrently indicates greater potential C uptake by *L. laricina* and further buttresses our observation of increased *L. laricina* growth with warming. Together, these studies suggest that *L. laricina* prioritized C balance and growth, while *P. mariana* prioritized water retention and hydraulic safety in response to warming and the associated increase in vapor pressure deficit, which are conclusions further reflected and integrated by our growth results. A connection between warmer temperatures, water limitations, and a negative growth response of *P. mariana* to temperature has been described in previous studies (Wilmking and Myers-Smith 2008; Walker and Johnstone 2014). Here after 8 years, we only see a positive aboveground growth response.

4.5.1 Precipitation Interactions

Over longer time periods, the effects of warming play out under a shifting precipitation regime, such that if water becomes more limiting, it could interact with warming and result in growth reductions. This would be especially true if water limitations were to occur early in the growing season (e.g., May-June) when active growth is underway (Hanson and Weltzin 2000). The SPRUCE study has provided little opportunity to fully test such dynamics. However, there is some evidence for this at the leaf level at SPRUCE whereby *P. mariana* photosynthesis was reduced under warming treatments due to stomatal responses to drying conditions (Dusenge et al. 2021). Bronson and Gower (2010) found that photosynthesis did not decline with warming in another *P. mariana* warming study with irrigated plots. An ability to predict how *P. mariana* growth will respond to future environmental changes will depend on the ability to simulate and project trends in precipitation, as well as temperature.

4.5.2 A Role for Phenology

SPRUCE warming treatments stimulated an earlier spring growth period in all vegetation types (Richardson et al. 2018; Schädel et al. 2023). This was particularly evident for *P. mariana*, which had overwintered foliage (e.g., Richardson et al. 2018). Tree growth in both species was completed by mid-July in all treatments (J. Warren, unpublished dendrometer data), and the early initiation of leaf and terminal stem development induced by warming did not produce an increase in tree ANPP to take advantage of delayed fall senescence. There was also not an apparent CO₂ effect on seasonal dynamics.

5 Conclusions

The plot-scale manipulations of the SPRUCE peat bog have enabled us to glimpse plausible responses to a wide range of warming conditions with and without the potential effects of a nonlimiting CO₂ atmosphere. The net results for trees and ericaceous shrubs appear to be a positive growth response to warming with a slow-to-develop positive response to eCO₂ in the shrub layer. Here, we attribute the positive warming response to the availability of nutrients from the loss and turnover of some sensitive plant species from the ecosystem (*Sphagnum* and *Maianthemum*) and peat decomposition. The decade of operation for SPRUCE through the end of 2025 is unfortunately insufficient time to document if nutrient enhancements in shrub and tree growth associated with warming would continue into the future or be a transient response that

might diminish with time. We hypothesize that there would be limits to warming-induced decomposition which provide nutrients driving growth enhancements. Forthcoming, analyses of the element budgets (C, N, P, etc.) for the SPRUCE study will enable quantitative testing of such a hypothesis. Fully integrated modeling of the SPRUCE results will be needed to best interpret the decade of warming and eCO₂ responses and to differentiate how phenology, water stress, and biogeochemical cycles contribute to long-term response to climate change realities.

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Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Open Research

Data Availability Statement – Data sets pertaining to this study are in the online project archive at <http://mnspruce.ornl.gov> **and** the U.S. DOE's long-term storage archive (Environmental Systems Science Data Infrastructure for Virtual Ecosystems – ESS-DIVE; <http://ess-dive.lbl.gov>) with established DOIs. The SPRUCE source data are archived as follows: environmental data (doi:10.3334/CDIAC/spruce.032, Hanson et al. 2016); water table data

(<https://doi.org/10.25581/spruce.079/1608615>, Hanson et al. 2020b); pretreatment vegetation and allometry data (<http://dx.doi.org/10.3334/CDIAC/spruce.004>, Hanson et al. 2012); shrub community growth data (<https://doi.org/10.25581/spruce.052/1433837>, Hanson et al. 2018a); tree growth data (<https://doi.org/10.25581/spruce.051/1433836>, Hanson et al. 2018b); terrestrial laser scanning data (<https://doi.org/10.25581/spruce.067/1515552>, Graham et al. 2019); and pre- and post-treatment tissue element data (<http://dx.doi.org/10.3334/CDIAC/spruce.038>, Phillips et al. 2017 and <https://doi.org/10.25581/spruce.090/1780604>, Phillips et al. 2021).

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