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Climatic controls on peatland black spruce growth in relation to water table variation and precipitation

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Abstract

Prior research has demonstrated the importance of water limitations and increasing temperatures on upland black spruce (*Picea mariana* [Mill.] B.S.P.) tree growth, which is a dominant component of the North American boreal forest. However, little work has been done to investigate the connectivity between growth and hydro-climate in peatland black spruce systems. The boreal forest is the largest global terrestrial biome and is highly threatened due to current and projected increases in temperatures for the northern latitudes. Here we explore the dynamics among annual black spruce growth, climate, and water table elevations using 45 years of in situ precipitation, temperature, and water table elevation coupled with dendrochronological analysis from six research peatlands at the Marcell Experimental Forest, MN, USA. From 1963 to 2010, we found weak relationships between water table elevation and black spruce growth at the six study sites. Instead, annual black spruce growth was most favourable during three climatic periods: (a) cool, moist conditions in mid-summer; (b) warm mid-spring temperatures; and (c) cool temperatures in the fall prior to the current growing season. The disconnect between black spruce growth and water table dynamics was surprising and suggests that either annual black spruce growth is minimally responsive to hydrological fluctuations at the timescale we analysed or there is great elasticity of black spruce growth to peatland water table and evapotranspiration dynamics under the range of hydrological fluctuations contained in our record.

KEYWORDS

boreal forest, dendroclimatology, peatland, *Picea mariana*, plant-water-use, water table fluctuation

1 | INTRODUCTION

Boreal forests are the largest terrestrial biome by area, globally, and store over 50% of the earth's carbon in biomass and soil (Pan, Birdsey, Phillips, & Jackson, 2013; Sellers et al., 1997). Within the boreal forest, much of the below-ground carbon is stored in the organic soils of peatlands. Both long-term monitoring and model projections suggest that these ecosystems are highly vulnerable, as climate in high-latitude regions is warming faster than the global average (Richter-Menge, Overland, Mathis, & Osborne, 2017). Evidence from boreal experiments indicate that carbon is translocating among storage pools within the soil without massive losses to the atmosphere (Sistla et al., 2013), but warming temperatures generally increases decomposition (and potentially atmospheric carbon), and future temperature changes may lead to unknown consequences in these regions (Weltzin et al., 2003). Additionally, rising temperatures in the boreal forest may increase ecosystem evapotranspiration (ET), leading to a negative feedback loop between increasing ET and declining soil moisture and water tables. Surficial and deep saturation is essential for stabilizing peatland carbon pools, with the possibility of enhanced degradation

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if typically saturated peat is exposed to prolonged drying in response to climatic change (Wilson et al., 2016). In order to comprehensively predict the impact of warming on boreal forest water budgets and ecosystem processes, a historical understanding of relationship between tree growth, temperature, and water availability is needed.

The relationship between climate and tree physiology can be captured at an annual time scale using tree ring records, as fluctuations in monthly temperature and precipitation can explain over 50% of the variation in annual tree growth (e.g., Cook & Briffa, 1990; Fritz, 1976). Tree-ring records from across the globe have been used to reconstruct temperature and precipitation back to CE 1400 and prior (e.g., Briffa et al., 2002; Briffa, Osborn, & Schweingruber, 2004), historic streamflow and drought (Meko et al., 2007; Stockton & Jacoby, 1976), and snowpack conditions (Woodhouse, 2003). In the boreal forest, there is an extensive body of literature exploring the climatic controls on upland black spruce growth (e.g., Gewehr, Drobsyhev, Berninger, & Bergeron, 2014; Girard, Payette, & Gagnon, 2011; Girardin et al., 2016; Walker & Johnstone, 2014; Walker, Mack, & Johnstone, 2015), but the dendroclimatology of peatland black spruce is reported less.

The southern extent of the boreal forest extends into northern Minnesota, where the landscape includes over 1.1 million hectares of forested peatlands (MN DNR, 2013). Black spruce and tamarack dominate the forest overstory. Unlike upland forests where the annual growth of black spruce may be limited by water availability (Dang & Lieffers, 1989), overstory tree species in these lowland habitats occur where water tables are perennially at or near the land surface. These trees grow in peat (e.g., Typic borosaprists and borohemists) and often have shallow rooting systems to avoid the complete submersion of roots in water (Iverson et al., 2018; Lieffers & Rothwell, 1987). Boreal peatland swamps can be classified in two categories: bogs that receive hydrologic inputs from precipitation, and snowmelt runoff, and fens, which, in addition to the above inputs, can also receive groundwater from a surrounding aquifer. As such, fens tend to have more nutrient rich and less acidic soils than bogs (Verry, Brooks, Nichols, Ferris, & Sebestyen, 2011). Hydrologic loss pathways in boreal peatlands include streamflow, groundwater recharge, and ET. Streamflow is usually at its maximum during spring snowmelt. Vegetation growth in these black spruce-dominated peatlands is thought to be a function of water table elevation, as wetland root growth is often restricted by the presence of the phreatic zone (Boggie, 1972; Boggie & Miller, 1976; Lieffers & Rothwell, 1987). In addition to water table elevation, physical and chemical properties of the peatland (i.e., distance to mineral soil, pH, depth, and nitrate concentration) can also influence species assemblages in these systems (Girardin, Tardif, & Bergeron, 2001). Previous dendroclimatological studies in forested wetlands have documented similar dynamics, with high water tables inhibiting growth of northern white cedar, black ash, and baldcypress (Keim & Amos, 2012; Tardif & Bergeron, 1997). However, these wetland systems are not directly comparable to peatlands, which have a characteristic hummock-hollow microtopography that may separate black spruce roots from water table fluctuations (Pepin, Plamodon, & Britel, 2002; Verry, 1984). Thus, black spruce peatlands may be responding in a unique fashion to water table dynamics.

Although it is reasonable to assume that black spruce decrease growth rates with rising water table elevations, as has been observed with other species (e.g. Tardif & Bergeron, 1997), this hypothesis has not been demonstrated using in situ water table data. With this study, we use over 50 years of water table elevation data to test the hypothesis that peatland black spruce exhibit negative trends in growth response with increasing water table elevation.

2 | MATERIALS AND METHODS

2.1 | Study site

We studied four peatlands within the U.S. Department of Agriculture Forest Service's Marcell Experimental Forest (MEF, 47°52′N, −93°46′ W; Figure 1). Overstory species in the peatlands consist of primarily black spruce (*Picea mariana* [Mill.] B.S.P.) and tamarack (*Larix laricina* [*Du Roi*] K. Koch) with understory layers largely dominated by bog birch (*Betula pumila*), leatherleaf (*Chamaedaphne calyculata*), Labrador tea (*Ledum groenlandicum*), cotton grass (*Eriophorum angustifolium*), and bog rosemary (*Andromeda glaucophylla*; Sebestyen et al., 2011; Verry, 2018). The climate at the MEF is continental, with warm, moist summers and cold, dry winters. Mean annual air temperature from 1963 to 2010 ranged from −15.0°C in January to 18.9°C in July. Annual precipitation is dominated by summer rainfall events and averaged 779 mm from 1963 to 2010 (Sebestyen et al., 2011). Topographic relief in the research catchments is low, with elevations ranging from 412 to 438 m (Sebestyen et al., 2011). Soils developed after glaciers retreated over 10,000 years ago and upland soils and tills are generally well mixed and deep (>3 m) loamy sands and sandy clay loams (Verry & Jansenns, 2011). The peatlands formed as shallow postglacial lakes and ice-block depressions, which are filled with organic soils that can range from 3 to 10 m in depth (Sebestyen et al., 2011). The research peatlands presented in this study have not undergone any experimental treatment since 1962.

2.2 | Field and laboratory methods

Six study sites were randomly placed within four of the research peatlands at the MEF and sampled in spring 2010 and 2014 (Table 1). Circular plots, 1/20th ha in size, were flagged around randomly placed plot centres. For every tree greater than 10-cm diameter at breast height (1.3-m height) located within the plot, height, diameter at breast height, crown class, distance from plot centre, and azimuth were measured. Additionally, two perpendicular increment cores were collected at breast height from each tree.

Cores were mounted and sanded, and annual ring-widths (RWs) were measured using a VELMEX measuring system (0.001-mm resolution; Velmex, Inc., Bloomfield, New Jersey, USA) outfitted with MeasureJ2X measuring software (VoorTech Consulting, Holderness, New Hampshire, USA). We visually cross-dated each individual tree-ring series against the master chronology developed for each site, and the quality of cross-dating techniques was statistically verified

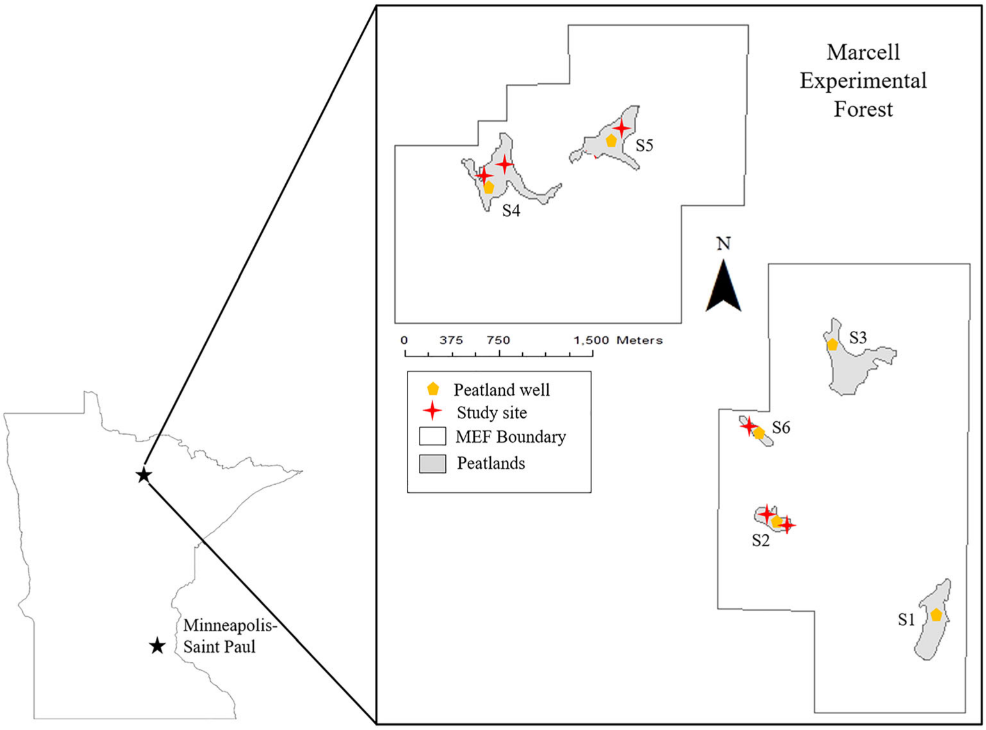

FIGURE 1 The six research plots are located within four well-instrumented research peatlands on the Marcell Experimental Forest in northern Minnesota

TABLE 1 Six study plots were sampled from 2010 to 2014

Site	Research WS	No. of trees	No. of cores	Record start year	Mean tree age	Mean tree ring width (*SD*; mm)	R_{BAR}	Mean sensitivity
BS03	S6	16	14	1828	100	0.55 (0.14)	0.37	0.241
BS04	S2	77	24	1848	133	0.41 (0.24)	0.53	0.214
BS05	S2	54	20	1858	114	0.67 (0.36)	0.47	0.213
BS07	S4	45	24	1839	120	0.44 (0.26)	0.49	0.190
BS08	S4	46	20	1877	120	0.45 (0.27)	0.45	0.203
BS09	S5	45	24	1818	121	0.55 (0.35)	0.43	0.211

Note. Number of trees was the total number of *P. mariana* trees in the 1/20th ha plot, and number of cores is the number of individual trees cored in each plot and used in the analysis. Two increment cores were taken from each sampled tree. *SD* is the standard deviation, mean sensitivity is a metric of year-to-year variability within the chronology, and R_{BAR} is the mean series autocorrelation.

using COFECHA software (Grissino-Mayer, 2001; Holmes, 1983). Many of the individual tree-ring series contained deteriorated centres, and these cores were removed from the analysis. Additionally, we focused our attention on dominant and codominant black spruce cores and omitted the tamarack cores from the analysis due to low sample size and confidence in cross-dating.

2.3 | Climate and water data

Precipitation and temperature data were collected at two climate stations located within the S2 and S5 watersheds at the MEF (Figure 1). Daily maximum and minimum air temperature have been recorded since 1961 using Belfort model 594-1 Hygrothermographs (Belfort Instruments, Baltimore, Maryland, USA); data are then averaged to determine daily mean air temperature. Total daily precipitation has been recorded at these sites using Belfort Universal Recording Precipitation Gauges, which were replaced with ETI NOAH IV digital rain gauges (ETI Instrument Systems, Fort Collins, Colorado, USA) in 2009 (S2 watershed) or 2014 (S5 watershed). In addition to climate data, water table elevation has been recorded at six peatland wells in the MEF since 1961 (Figure 1; Verry, Elling, Sebestyen, Kolka, & Kyllander, 2018a). Water level data were recorded daily using Belfort model FW-1 strip chart recorders with float and pulley systems. Total annual precipitation has not changed over the course of the 50-year study period, although mean annual temperature has increased approximately 2.3°C from 1966 to 2012 (Figure 2; Dymond et al., 2010). Monthly potential ET, or PET, was calculated at the MEF using

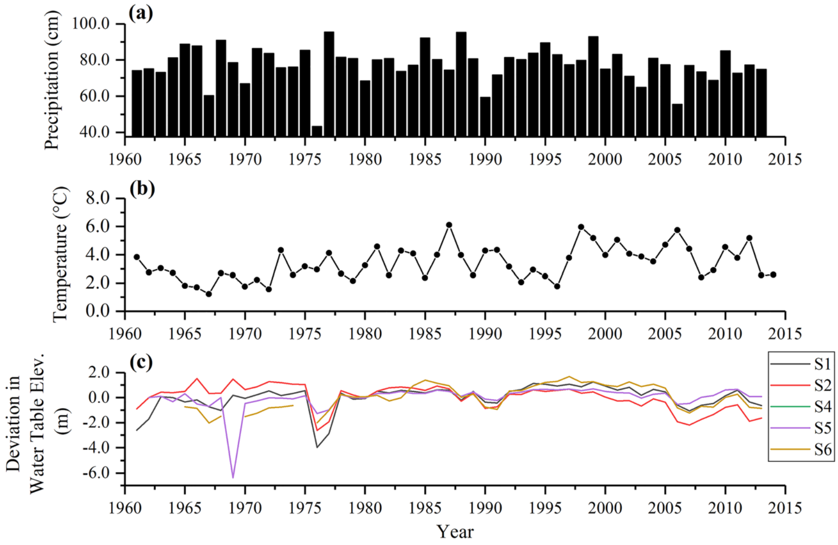

FIGURE 2 (a) Total annual precipitation (cm) as averaged between the S2 and S5 climate stations, (b) mean monthly air temperature (°C) averaged between the S2 and S5 climate stations, and (c) deviation in mean annual water table elevation (m) for the four research watersheds

the Thornthwaite method (Thornthwaite & Mather, 1955), and monthly changes in moisture were quantified using a cumulative moisture index (CMI), where CMI is equal to precipitation less PET (Hogg, 1997). Daily streamflow at each watershed was calculated from stage-discharge relationships for either H-type flumes or v-notch weirs (Verry, Elling, Sebestyen, Kolka, & Kyllander, 2018b).

2.4 | Statistical analysis

Nonclimatic trends were removed from successfully cross-dated individual tree series using a two-third smoothing spline with a 50% frequency response (Cook & Briffa, 1990; Cook, Briffa, Meko, Graybill, & Funkhouser, 1995). Additionally, each series was prewhitened to remove temporal autocorrelation using autoregression (Cook, 1985; Cook & Briffa, 1990). Each dimensionless residual RW chronology was aggregated into one master chronology per site. All standardization techniques were applied using the package "dplR" (Bunn, 2008) in R version 3.4.0 (R Development Core Team, Vienna, Austria).

To determine the growth-climate relationship between individual sites, we used the seascorr function in the R package "treeclim" (Zhang & Biondi, 2014) to calculate the partial correlations between primary (mean monthly temperature) and secondary climate variables (Meko, Touchan, & Anchukaitis, 2011). Secondary environmental variables included total monthly precipitation; minimum, maximum, mean, and deviation from mean water table elevation; total monthly PET; and maximum monthly streamflow. A linear relationship between the environmental variables and annual RW was assumed (see the Supporting Information). Confidence intervals ($\alpha = 0.05$ and $\alpha = 0.10$) were calculated using exact bootstrapping of the tree-ring data (Percival, Constantine, & L. B., 2006). We used the common data period from 1963 to 2010 to ensure consistency across sites. Preliminary analysis of climate metrics suggested no relationship between climate and tree growth in June and July prior to the current growing season, so analyses were run using a shortened 14-month climatic window beginning in August of the previous growing season to September of the current year.

3 | RESULTS

3.1 | Series descriptions

Of the 124 cores used in the analysis, 79 dated prior to 1900, including 7 cores that dated prior to 1850. The oldest core dated to 1818 (Table 1). Across all series, mean tree ring width was 0.52 ± 0.31 mm (mean ± *SD*). Years 1948 and 1949 were common periods of low growth across all chronologies, with other common low periods occurring in the early 1900s (Figure 3). Rbar, or the mean series intercorrelation, ranged from 0.37 to 0.53, which is consistent with other *P. mariana* chronologies (ITRDB, 2018).

3.2 | Site differences in tree growth

The overstory of the sites within this study consisted of either black spruce or a mix of black spruce and tamarack (Table 2). There were noticeable differences in the stand-level basal area and density between some of the study sites (Figure 4). BS05 had one of the highest basal areas of the six study sites (BA = 21.8 m^2/ha; Figure 4) and had a moderate density of trees (1,083 trees/ha; Table 2). Site BS03 had the lowest basal area (8.1 m^2/ha); approximately half of the stand basal area was contained in tamarack trees. With the exception of the low basal area in BS03, sites BS07 and BS08, both of which were located in research watershed S4, had fewer trees and lower basal area than the other study sites (Table 2).

In terms of annual tree growth, the mean series RW varied across sites (Figure 5), with site BS05 having the highest average growth (RW = 0.67 mm) and site BS04 exhibiting the lowest average growth (RW = 0.41 mm). Mean RW for BS05 was significantly higher than the other five sites ($p < .05$).

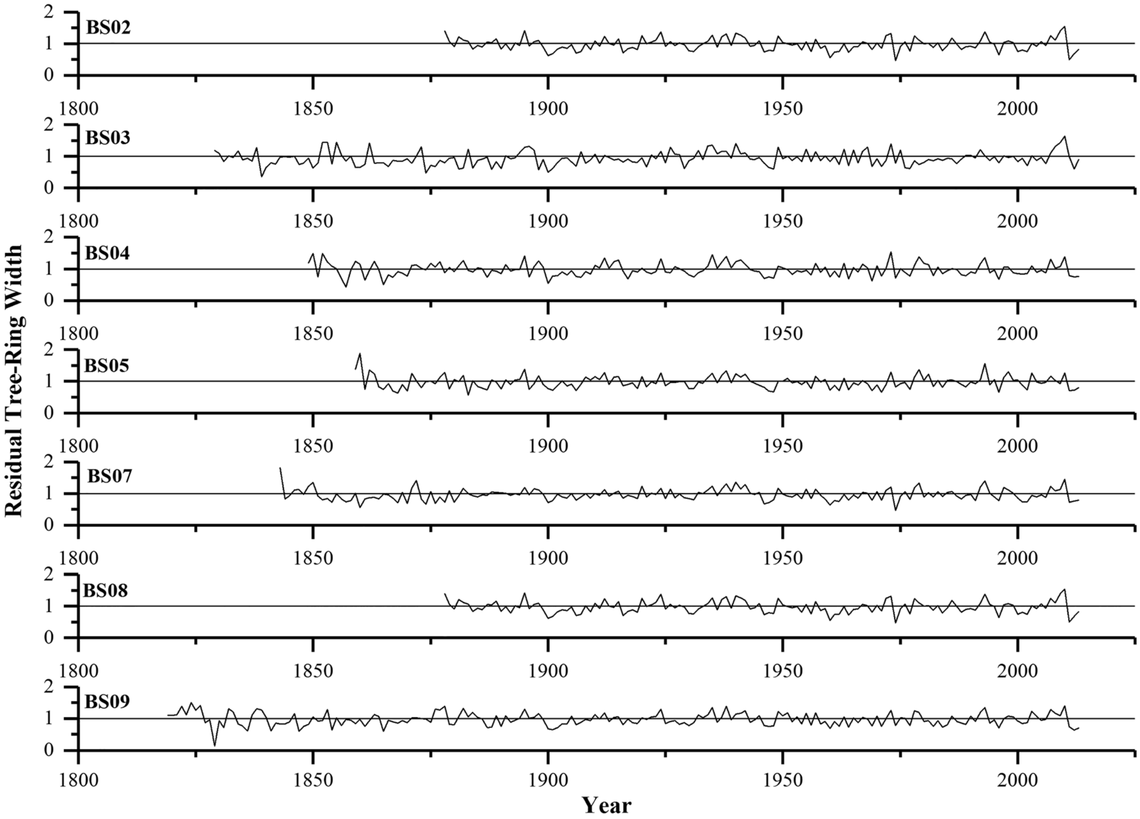

FIGURE 3 Residual tree-ring chronologies for the six study sites at the MEF. Site chronologies are averages of the individual tree chronologies at each site

TABLE 2 Stand productivity measurements for overstory trees in each of the study sites

			Stand basal area (m²/ha)			Stocking density (trees/ha)		
Site	Research WS	WS area (ha)	Black spruce	Tamarack	Total	Black spruce	Tamarack	Total
BS03	S6	2.0	3.8	4.6	8.4	622	301	923
BS04	S2	3.2	21.5	0.4	21.9	1,544	20	1,564
BS05	S2	3.2	21.8	0.0	21.8	1,083	0	1,083
BS07	S4	8.1	10.1	0.0	10.1	842	0	842
BS08	S4	8.1	11.2	0.4	11.6	842	20	862
BS09	S5	6.1	16.6	0.0	16.6	922	0	922

Note. All productivity measurements were based on trees sampled in one 1/20th ha circular plot.

3.3 | Climatological analysis

Overall, *P. mariana* exhibited greater growth rates (i.e., RWI) during cool and wet summers, cool growing conditions in the fall prior to the growing season, and warm early spring growing conditions (Figure 6). Five of the six sites exhibited negative correlations with temperature in the October prior to the current growing season, and two sites (BS04 and BS08) also exhibited negative correlations with August temperature in the prior growing season. Growth was also favoured by warm March conditions and cooler July conditions at the majority of sites. Most of the sites exhibited positive correlations between July precipitation and RWI. Two sites showed negative correlations between February precipitation and RWI.

Despite being located within peatlands, water table elevation was only weakly negatively correlated with RWI across sites in our study (Figure 6). Analyses were run using mean monthly water table elevation, maximum water table elevation, minimum water table elevation, and deviation from mean for all of these metrics. No metric of water table elevation was statistically significant in any of the analyses, although this could be indicative of a type II error due to our low sample size. We also ran analyses of other water metrics, including total monthly PET, maximum monthly streamflow, and total monthly CMI.

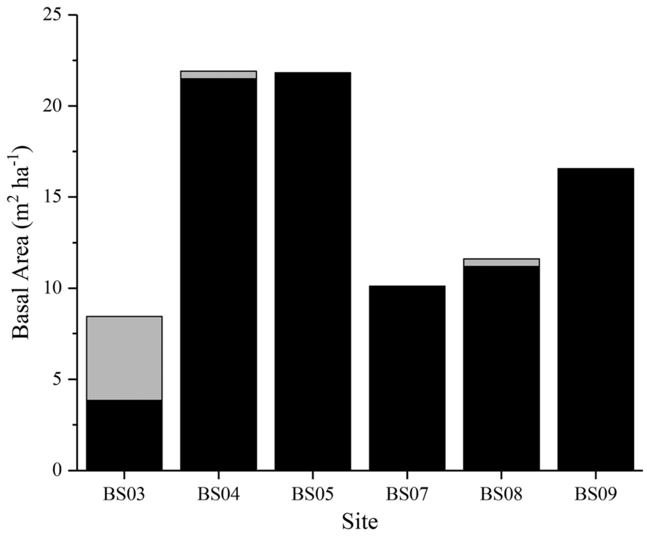

FIGURE 4 Total stand basal area in black spruce (black) and tamarack (grey) for each of the six study sites

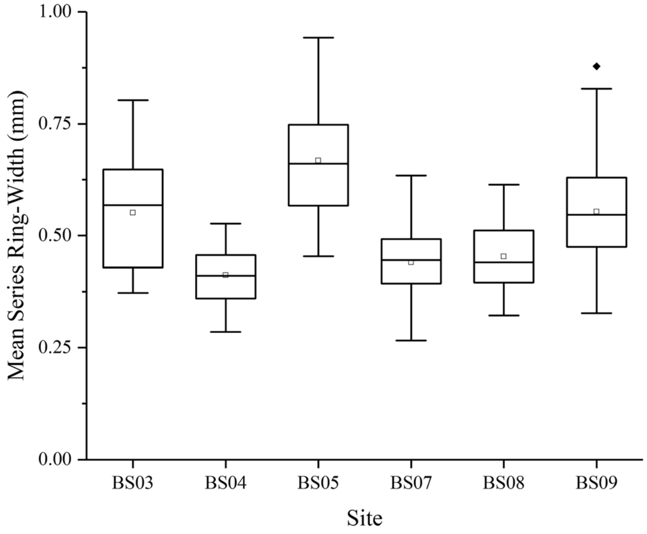

FIGURE 5 Mean ring-width for six research sites at the Marcell Experimental Forest

Although we found significant correlations between some of these variables, they were typically not as strong as precipitation and indicated the importance of water availability during similar seasons.

We did find evidence that the sites respond differently to the various climate metrics. In general, there was a negative relationship between the magnitude of the growth response to temperature and the growth response to precipitation (Figure 7). The site with the lowest basal area, BS03, was the only site where the magnitude of growth response to precipitation and temperature was positively related (Figure 7). The strength of the growth-temperature response was generally not related to the response of tree growth to water table elevation (Figure 8). However, for two sites (BS07 and BS09), there was a strong negative association between the strength of the temperature response and the strength of the response of tree growth to water table elevation (Figure 8). In other words, a strong growth response to warm temperatures was associated with more inhibited growth under higher water tables at these two sites. Interestingly, the two sites with the highest basal area had a more positive (albeit not statistically significant) association with water table elevation than the other sites (Figure 8).

4 | DISCUSSION

Our results suggest that peatland black spruce growth is limited by both temperature and precipitation and that there is a decoupling of phreatic zone dynamics and forest growth in these systems. We found that the following conditions most favoured black spruce growth: (a) cool, moist conditions in mid-summer; (b) warm mid-spring temperatures; and (c) cool temperatures in the fall prior to the current growing season. Prior studies of upland black spruce populations in interior Canada have found similar negative responses to warm conditions during the growing season (Dang & Lieffers, 1989; Huang et al., 2010; Walker et al., 2015; Walker & Johnstone, 2014; Wolken et al., 2016). Black spruce is a boreal species, with average July temperatures of 16–24°C across the species range and daily extremes as high as 27°C (Viereck & Johnston, 1990). No months exceeded a mean temperature of 24°C during our study, although summer temperatures have been increasing across the length of record at the MEF (Dymond, Kolka, Bolstad, & Sebestyen, 2010). A range-wide synthesis of upland black spruce found that this species might be susceptible to increases in temperature, although associated declines in growth may be offset by increases in atmospheric CO_2 (Girardin et al., 2016). Similar to our findings, Huang et al. (2010) also found positive growth relationships with late winter and early spring temperature for upland black spruce living above 47°N. Evergreen species in general can readily take advantage of warm conditions during the early growing season (Graumlich, 1992), and black spruce in particular can have earlier bud bursts and increased respiration following spring warming (Bronson, Gower, Tanner, & van Herk, 2009; Goulden et al., 1997). One dendroclimatological study of peatland black spruce found similar sensitivity to the climate metrics assessed in this study (Dang & Lieffers, 1989), although the growth-water table connections in their study were inferred based upon precipitation metrics.

Historical studies have suggested that overstory growth in boreal peatlands may be limited by high water table elevations (Boggie, 1972; Boggie & Miller, 1976; Dang & Lieffers, 1989; Jasieniukm & Johnsone, 1982; Lieffers & Rothwell, 1987). However, we found that black spruce trees exhibited minimal annual growth response to in situ water table elevation. We analysed monthly minimum, maximum, mean, and deviation from mean water table elevation at all of our study sites and found no relationship with black spruce growth for any month or site. Our findings could be due to the lack of overall variation in water table elevations during the 45-year study period—fluctuations in mean monthly water table elevation ranged from −6.0 to 2.0 m across the different sites (Figure 2). The number of large deviations from mean water table elevation may not have been frequent enough to be statistically significant in the partial correlation analysis (Cook & Briffa, 1990).

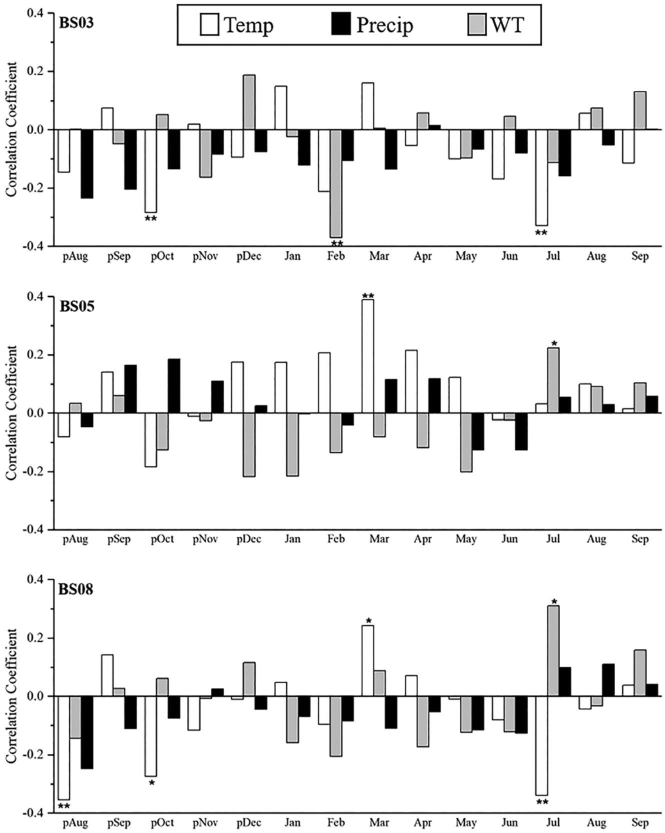

FIGURE 6 Seascorr output for six sites at the Marcell Experimental Forest. *p* denotes a month prior to the current growing season. Bars indicate correlation coefficients for average monthly temperature (Temp), total monthly precipitation (Precip), and mean groundwater table elevation (WT). Bars with an asterisk or double asterisk indicate significant correlations between ring-width index and the climate variable for the particular month ($p < .10$ and $p < .05$, respectively)

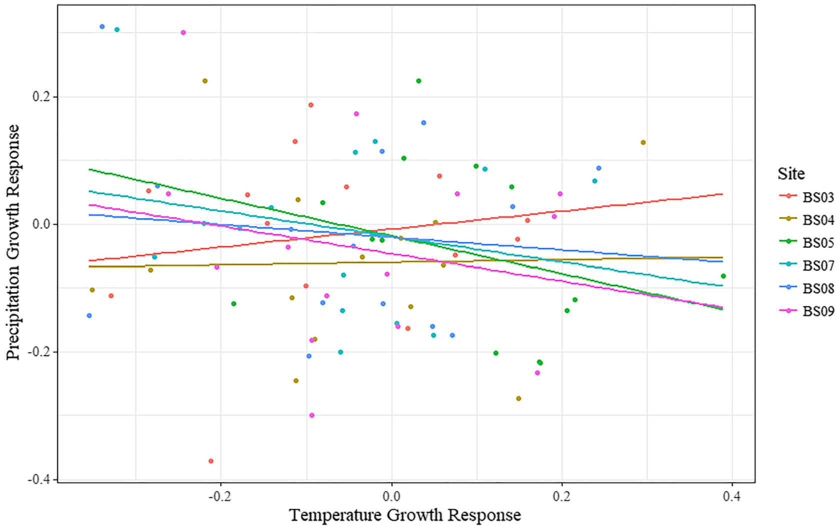

FIGURE 7 Magnitude of correlation between ring-width index and temperature (temperature growth response) and the magnitude of correlation between ring-width index and precipitation (precipitation growth response) produced by partial correlation analysis for six study sites at the Marcell Experimental Forest

Our results could also suggest a decoupling between ET and the highest water table levels in these systems. Within a boreal peatland, trees tend to be located on elevated mounds of soil called hummocks, with the water table never rising more than 10 cm into hummocks that may be up to 50 cm high (Ontl & Iversen, 2017). Black spruce may have roots in the higher-elevation hummocks, above the hollow depressions that saturate when water table elevations rise. This has been corroborated at our field site with evidence that *Picea mariana* exhibit most fine root growth in a shallow zone of aerated soil and not into the phreatic zone (Iverson et al., 2018). Similar rooting patterns have been found in baldcypress swamps in Louisiana (Hsueh, Chambers, Krauss, Allen, & Keim, 2016). Additionally, we found no

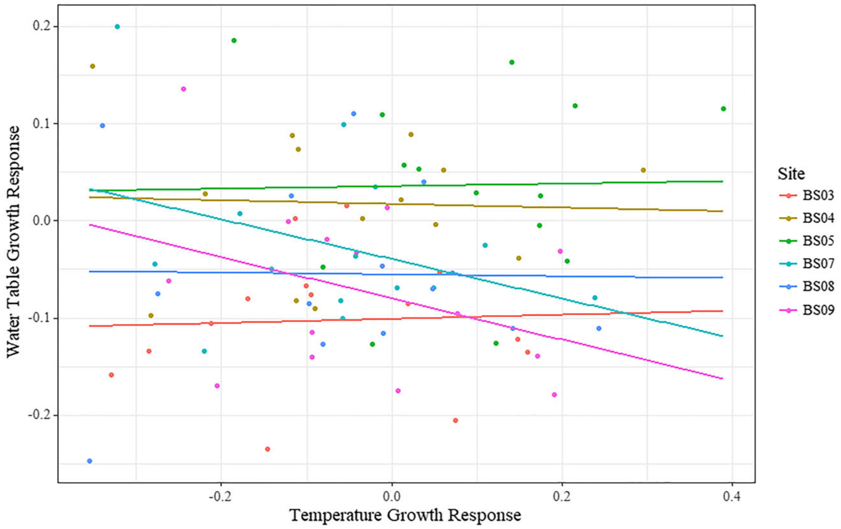

FIGURE 8 Magnitude of correlation between ring-width index and temperature (temperature growth response) and the magnitude of correlation between ring-width index and bog water table elevation (water table growth response) produced by partial correlation analysis for six study sites at the Marcell Experimental Forest

correlation between total daily or monthly precipitation and mean or maximum monthly water table elevation in our four study peatlands. It may take prolonged periods of saturation during the short growing season to impede annual tree growth in black spruce, which are rare summer months at the study site. This is a departure from other wetland systems, where inundation from precipitation and floodwaters can often occur during the growing season, thus impeding tree growth (Keim & Amos, 2012; Tardif & Bergeron, 1997). This finding also contrasts with adjacent uplands, where soil moisture is often below the wilting point of aspen (*Populus tremuloides* and *P. grandidentata*) and red pine (*Pinus resinosa*) in these watersheds (Dymond et al., 2017).

5 | CONCLUSIONS

The boreal forest is vulnerable to increased temperatures, which may negatively impact forest growth and water availability (e.g., Reich et al., 2018; Richardson et al., 2018). Despite being located at the southern extent of the boreal forest where change is expected to be among the most extreme, we found that black spruce in peatlands at the MEF responds to similar climate metrics as black spruce-dominated systems located in more northern latitudes (e.g., Dang & Lieffers, 1989; Huang et al., 2010; Walker & Johnstone, 2014; Walker et al., 2015; Wilmking & Myers-Smith, 2008;). Our results suggests that although local site conditions and competition are important in determining boreal forest growth dynamics (Dymond et al., 2015; Foster, Finley, D'Amato, Bradford, & Banerjee, 2016; Nicklen, Roland, Ruess, Schmidt, & Lloyd, 2016), underlying tree ecology and silvics are still important. Given that black spruce responds negatively to warm summer and fall temperatures, there is the possibility that climate-induced stress may cause growth reductions across its range. If extreme enough, such climate stress could profoundly change the dominant species of the boreal forest. For boreal peatland systems, there may be few overstory species that can fill the unique ecological niche of black spruce and, likely, tamarack. As these keystone species are expected to become more stressed with increased temperatures, we could see an influx of smaller understory species that tolerate highly acidic bog conditions and may utilize less moisture on an individual basis but more water across a peatland due to a higher number of individuals. Depending on the replacement species, this may lead to decreased moisture levels in the hummocks due to increased and prolonged ET or increased surface runoff due to higher water table elevations. Further research is needed to fully investigate the physiological response of black spruce in peatlands to climate at a subannual time step to more thoroughly understand the feedback between forest productivity and climate in these systems.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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