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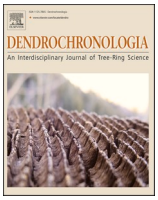

Original article

A multi-scale dendroclimatological analysis of four common species in the southern Canadian boreal forest

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ABSTRACT

A comprehensive assessment of the tree growth/climate relationship was undertaken to better understand the potential impacts of climate change on the growth dynamics of four widespread and common boreal tree species, namely jack pine (*Pinus banksiana)*, black spruce (*Picea mariana)*, eastern larch (*Larix laricina)*, and trembling aspen (*Populus tremuloides*), located at the southern limits of the Canadian boreal forest. Over intra-annual time scales, results show that precipitation is likely the main driver of stem radius change (ΔR), with jack pine radius exhibiting the most consistent positive relationship. Precipitation had a stronger relationship with stem radius variation in black spruce and eastern larch during periods when volumetric water content (VWC) in the root zone was below average, pointing to the likelihood that certain species rely more heavily on available moisture in the uppermost layers of the soil column to replenish stem water, especially during extended dry periods. Warm air temperatures had an immediate negative impact on stem water content due to transpiration. This was most marked during periods of reduced moisture availability in the root zone, when trees are more susceptible to net water volume loss. During periods when moisture was not limiting, a positive relationship between lagged air temperature and ΔR was detected. Warm air temperatures may therefore play an important role in stimulating radial growth when moisture requirements are met. At annual temporal resolution, the growth/climate relationship changed over the lifetime of our study species. Over the last several decades, the relationship between precipitation and annual radial tree growth has weakened, while positive relationships between spring and summer air temperature and annual radial tree growth have emerged, likely signaling a decrease in moisture limitations, and a positive response to spring warming. Our findings reveal that boreal forest tree species may benefit from spring and summer warming over the near term, providing there is sufficient moisture to support growth. Over the long term, rates of evapotranspiration are expected to overshadow gains in moisture related to an increase in precipitation. Under these circumstances, we are likely to see reduced growth rates and an increasingly negative response of boreal tree species growth to warm air temperatures.

1. Introduction

The rate of climate change is faster than anticipated, especially in northern regions (Soja et al., 2007; Bush and Lemmen, 2019), where the most dramatic and rapid land surface warming has occurred and is expected to continue (IPCC, 2013; Huntingford and Mercado, 2016). This warming is having an observable impact on trees in northern forests. For example, there is evidence of treeline advance and shifting ecosystem

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boundaries, of tree growth decline and mortality, and of an intensification of wildfire and insect outbreak across a range of boreal forest ecosystems (Soja et al., 2007; Harsch et al., 2009). These impacts are also quite prevalent across the boreal forest in Canada (Hogg et al., 2002; Kasischke and Turetsky, 2006; Michaelian et al., 2011; Peng et al., 2011; Wang et al., 2015), due to marked warming and changes in the moisture regime (Bush and Lemmen, 2019). Trends in moisture conditions over the last several decades are spatially variable across the Canadian boreal region, with a marked drying trend across much of central and western Canada, while northeastern Canada appears to be trending towards wetter conditions (Wang et al., 2014). Moving forward, mean annual total precipitation is projected to increase across the Canadian boreal region, with the most notable changes to occur over the winter and spring months (Henderson and Sauchyn, 2008; Jeong et al., 2014; Zhang et al., 2019). However, gains in precipitation are likely to be offset by an increase in evapotranspiration over the long term (Wang et al., 2014), leading to a net increase in the frequency and severity of drought, especially in central and western Canada (Tam et al., 2018).

The boreal forest plays a crucial role in governing global-scale land-atmosphere interactions and feedbacks to the climate system (Bonan, 2008). For example, changes in its distribution and extent can have a significant impact on earth's radiative balance through changes in surface and cloud albedo (Betts, 2000; Spracklen et al., 2008). The boreal forest is also a vital component of the global carbon cycle and represents the largest reservoir of global terrestrial carbon (Sellers et al., 1995; Soja et al., 2007; Bradshaw and Warkentin, 2015). Detailed assessments of how climate influences the radial growth of dominant boreal tree species will provide a better understanding of how the region will respond to ongoing climate change (Charney et al., 2016). However, climate-growth relationships change over time and across temporal scales in response to attendant environmental conditions (D'Arrigo et al., 2008). Identifying how and why trees respond to environmental conditions at different temporal scales improves our understanding and ability to adapt to a range of climate change related impacts in the boreal forest.

Traditionally, relationships between climate and radial growth are assessed using dendroclimatological techniques. The standard method of analysis, developed by Fritts et al. (1971), and later revised by Blasing et al. (1984) and Guiot (1991), involves using a bootstrapped response or correlation functions to assess linear relationships between standardized annual tree ring widths and monthly climate variables, most often mean temperature and total precipitation. The main assumption is that the relationship between climate and radial growth remains relatively static over the course of the observation period, a tenet which is increasingly unlikely with ongoing rapid climate change (Biondi, 2000; D'Arrigo et al., 2008; Peltier and Ogle, 2020). Under these conditions, a tree's relationship with climate is likely to evolve over the course of its lifetime (e.g., if limitations suddenly become fulfilled, or if tolerances are exceeded; Jacoby and D'Arrigo, 1995). Alternatively, we can compute correlation and response functions over a moving or evolving window, to address possible non-stationarity in the growth/climate relationship, and to assess how the relationship changes over time (Biondi, 1997).

Over the last few decades, several researchers have turned to automatic stem dendrometers to help examine the tree growth/climate relationship in more detail (Deslauriers, 2003; Bouriaud et al., 2005; Gruber et al., 2009; Duchesne et al., 2011; Cocozza et al., 2016, 2018; Güney et al., 2019; Gao et al., 2019) These studies highlight the potential for dendrometers to provide continuous measurements of stem radius change, capable of providing excellent insight into the mechanisms of tree ring development and its relationship with meteorological conditions within the growing season. However, this method of collecting high-resolution (e.g., 30-minute temporal resolution) stem size data is not without challenges. The main challenge relates to disentangling the growth signal from the water signal (Zweifel and Häsler, 2001, Mäkinen et al., 2003; Deslauriers et al., 2007a; Mencuccini et al., 2017). Dendrometers measure both reversible and irreversible changes in stem size. Reversible changes are related to daily tree water use (Herzog et al., 1995) and irreversible changes are associated with stem radial growth (Deslauriers et al., 2003), which is driven in large part by the expansion of newly formed xylem cells (Cuny et al., 2015). For slow growing trees, it can be difficult to draw conclusions about the relationship between stem radius change and local meteorological variables outside of the main period of stem expansion (Deslauriers et al., 2007a). This is the period during which there is the greatest number of earlywood cells being produced and undergoing radial enlargement (Deslauriers et al., 2003). Further additions to stem size occur beyond this period, as new xylem cells (often latewood cells) continue to be produced and existing cells enter later stages of development, including cell wall thickening and lignification (Samuels et al., 2006). However, these latter processes have a smaller impact on the overall width of actively developing growth rings (Cuny et al., 2015), and can more easily be overshadowed by water related variability in stem size (Deslauriers et al., 2007a).

The goal of this study is to comprehensively assess the radial growth/climate relationship of four widespread boreal tree species, jack pine (*Pinus banksiana),* black spruce (*Picea mariana*), eastern larch (*Larix laricina*), and trembling aspen (*Populus tremuloides*) in the southern boreal forest of Saskatchewan. This includes the application of different dendroclimatological approaches to determine how the tree growth/climate relationship is expressed at different temporal scales (daily, weekly, and monthly), and whether it varies across species and over time. Note that over fine temporal scales, the term radial growth is no longer used, and instead we discuss relationships between stem radius change (ΔR) and weather. These relationships nonetheless provide additional information regarding potential responses of tree secondary growth (or stem size) to local environmental variables in the southern boreal forest. Intra-annual relationships are assessed over four growing seasons between 2015 and 2018, while the observation period for the examination of inter-annual relationships extends back to stand establishment (approx. 100 years).

2. Study sites

This study was conducted at three of the Boreal Ecosystem Research and Monitoring Sites (BERMS), located near the southern edge of the boreal forest in the Boreal Plains Ecozone of central Saskatchewan (Fig. 1). Site characteristics are given in Table 1. The climate of the study area is characterized by short, warm, dry summers and long, cold winters. Mean annual temperature in Prince Albert (PA), Saskatchewan, where the nearest and most complete long-term record of climate is recorded is 1.7 °C (1989 – 2018). This represents a 1.9 °C increase in annual average temperature over the last century, when compared to the 1890 – 1919 reference period (−0.2 °C). Annual average precipitation in PA is 517 mm (1983 – 2012), a 60 mm increase since the 1890 – 1919 reference period (457 mm; ECCC, 2020).

The Old Jack Pine (OJP) site, located northeast of Candle Lake, Saskatchewan, is an even-aged stand of jack pine, naturally established post fire in 1914 (Barr et al., 2012). The understory is composed of clumps of green alder (*Alnus crispa*), and the dominant ground cover includes some bearberry (*Arctostaphylos uva-ursi*), and a nearly continuous cover of reindeer lichen (*Cladina mitis*). The soil is a well-drained Orthic Eutric Brunisol (loamy sand). Water table depth is approximately ~6–7 m below the ground surface, and often decoupled from the root zone.

The Old Black Spruce (OBS) site is located due north of Candle Lake, and is a black spruce dominated forest with co-dominant eastern larch comprising approximately 10% of the stand composition (Pappas et al., 2018). The stand was established post fire in approximately 1879 (Barr et al., 2012). The understory is mainly comprised of wild rose (*Rosa woodsii)* and Labrador tea (*Ledum groenlandieum*). The groundcover consists of a mixture of feather mosses (*Hylocomium splendens*,

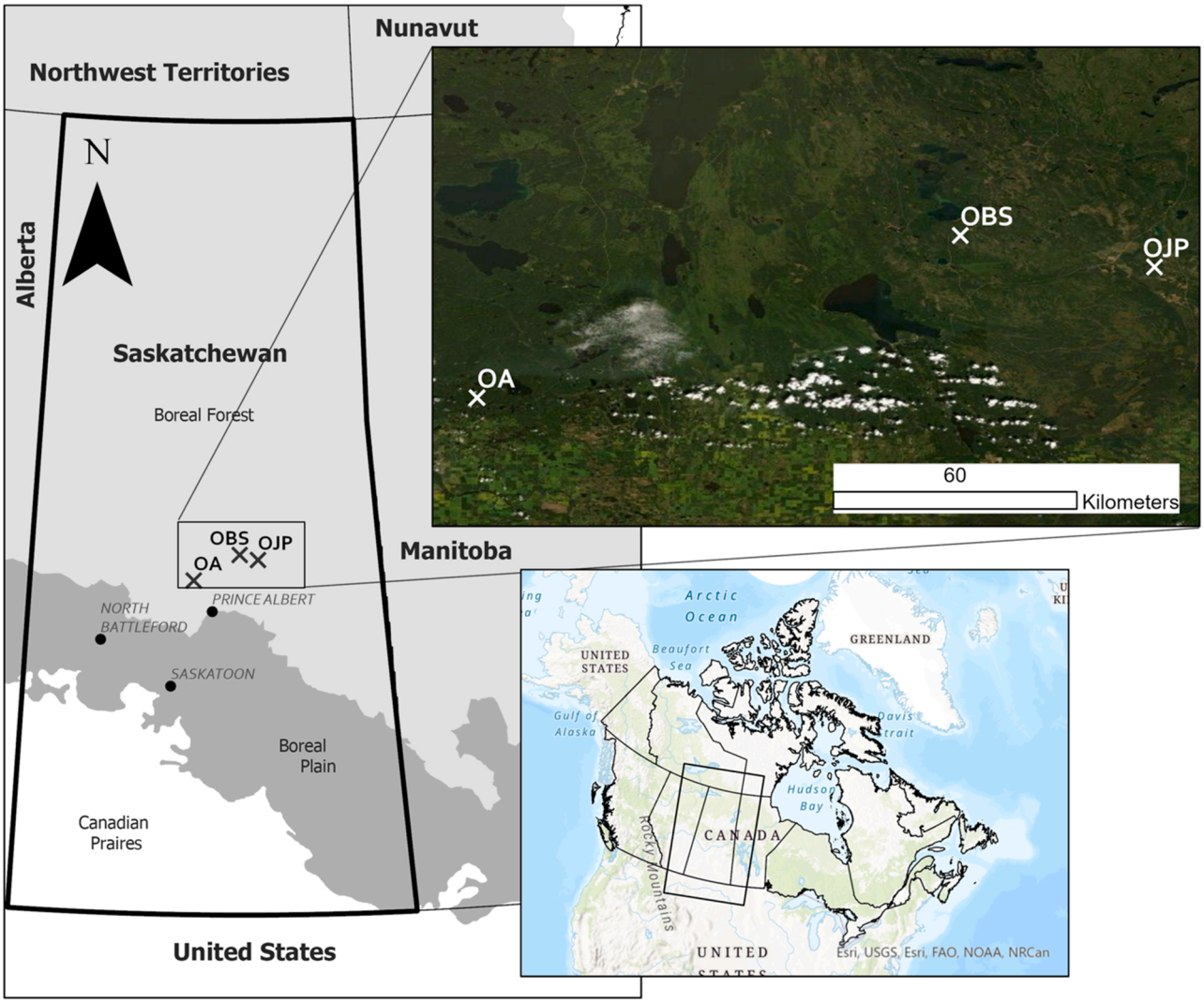


Fig. 1. A map showing the location of the BERMS study sites. The extent of the boreal forest is shown in light gray.

Table 1
Various site characteristics related to this study. Stand age is approximated from site descriptions in Barr et al. (2012) and correspond well with core samples taken in 2016 at OBS and in 2018 at OJP and OA. Stand density is calculated from measurements taken in 2016. The uncertainty value associated with stand density is the standard error between sample plots. The elevated value for standard error associated with stand density at OBS results from a large discrepancy in the number of individuals between the two circular plots within which measurements and core samples were taken.

	OJP	*OBS*	*OA*
Latitude (decimal°N)	53.92	53.99	53.63
Longitude (decimal°W)	104.69	105.12	106.19
Stand age (years, 2018)	~105	~140	~100
Stand density (stem ha^{-1}, 2016)	887 ± 99	5921 ± 2431	473 ± 47

Pleurozium schreberi), sphagnum moss (*Sphagnum* spp.), and lichen (*Cladina* spp.). The soil is poorly drained, with a thick layer of peat (~20 cm) over waterlogged sand. Water table is near or at the ground surface during most of the year, often impinging on the root zone.

The BERMS Old Aspen (OA) site in Prince Albert National Park, is an even aged stand of trembling aspen, naturally established after a forest fire in 1919 (Barr et al., 2012). The understory is mainly hazelnut (*Corylus cornuta*) with a few other shrubs. The soil is an Orthic Gray Luvisol (loam to clay loam). Water table may be as deep as 4 m below the soil surface, at times impinging on the root zone.

3. Methods

3.1. Climate and meteorological data

Several meteorological variables recorded with 30-minute temporal resolution are collected at the BERMS sites. These include precipitation (P), soil volumetric water content (VWC) in the root zone, air temperature (T_A) measured above the canopy, and soil temperature (T_S) measured at several depths. These are all recorded over the 22-year period 1997 – 2018 (21-years, 1997 – 2017, at OA). From these high temporal-resolution data, daily- and weekly-average T_A, T_S, VWC, and P totals were calculated for the short-term observation period (2015 – 2018). Conditions within the short-term observation period (2015 – 2018) are compared to the 22-year average and described at length in the Appendix A (Figures A.1–A.3).

Long-term (100 + years) climate records were acquired for the Environment and Climate Change Canada (ECCC) climate stations in Prince Albert (station #4056240 and #4056241) and Waskesiu Lake (station #4068559; ECCC, 2020). Assessment of the relationship between the ECCC stations and those at the BERMS sites (1997 – 2018) revealed that the Prince Albert dataset represented conditions at the BERMS sites quite well (not shown), and was therefore used in the

analysis. This dataset provides an almost continuous record of homogenized mean-, minimum-, and maximum-monthly T_A from 1890 to 2018 and adjusted monthly P totals from 1890 to 2012.

3.2. Dendrometer data

DC2 type circumference band dendrometers (Ecomatik, 2019) that measure stem radius changes were affixed to four individuals of each study species in 2015, trembling aspen at OA, jack pine at OJP, and black spruce and eastern larch at OBS. The four dendrometers assigned to each species were split into pairs and fed to two HOBO UX120–006M data loggers, for a total of 16 bands, and eight data loggers. In 2016, to increase the sample size and cover a wider spatial area within each site, an additional 12 individuals of each species were instrumented with DC3 type dendrometers (Ecomatik, 2019). Over the short-term observation period (2015 – 2018), the sites were visited regularly during the growing season (May to October), to ensure the smooth running of the instruments, and when necessary, to replace or repair dendrometers. Following the expansion of data collection efforts in 2016, between 12 and 16 individual trees of each species were instrumented at any given time.

Raw data were collected with 30-minute resolution, at time steps corresponding to the meteorological data collected at BERMS. These were converted to data of radius change from a starting point of 0 μm, following procedures suggested by the manufacturer (Ecomatik, 2019). The resulting data were checked for errors relating to sensor failure, or wildlife activity, and low-quality data were omitted accordingly with no attempt at gap filling. At our study sites, the dendrometers recorded synchronous variations in stem size between individuals. Species' averages were therefore calculated and used as site- and species-specific records of radius change. The only exception was for eastern larch in 2016. This species produced two distinct records of stem radius change, which were dependent on where the banded individuals were located in the site. Half of the individuals were located in a wetter section of OBS, and the other half in an area with less standing water. Two species averages were therefore produced for eastern larch in 2016, larch-wet and larch-dry.

For the extraction of the growth signal from the high-resolution dendrometer data, it has been shown that the "daily mean approach" produces similar results and is equally effective as the "stem cycle approach" (Deslauriers et al., 2007a). Daily and weekly-resolved records of mean stem radius were therefore constructed before calculating the difference between each value of mean stem radius and the preceding one, resulting in records of stem radius change (ΔR) over the short-term observation period (2015 – 2018).

3.3. Core samples

Core samples were extracted from trees at OJP and OA using a 5.1 mm increment borer following the 2018 growing season. A plot-based sampling scheme was employed based on the findings from Babst et al. (2014). Existing permanent sampling plots at OJP and OA (Gower, 2001; referred hereafter as the "Gower plots') were examined, and the one which most accurately represented overall stand density at each of the sites was chosen for sampling. Every living individual within these two chosen plots were sampled and plot size was extended on a randomly chosen side to accommodate additional individuals and reach the required sample size based on stand density (Table 1). OJP Gower plot 4 was extended by 2.5 m (27.5 m x 25 m), and OA Gower plot 2 by 15 m (40 m x 25 m). In total, a single core was extracted from 54 and 46 individuals at OJP and OA respectively.

OBS was sampled in 2015 (Pappas et al., 2020). Here, a single core was extracted from 93 black spruce and eastern larch trees located in two 5 m-radius circular plots in random locations within the site. Because of the limited sample size, eastern larch cores were excluded from study, along with black spruce cores, which contained missing or heavily fragmented segments. The final master chronology included 73 black spruce trees (ITRDB site code CANA610; https://www.ncdc.noaa.gov/paleo-search/study/29612).

All samples were processed using standard dendrochronological techniques (Speer, 2010) in the Mistik Askiwin Dendrochronology (MAD) Lab. After being mounted to slotted boards and sanded with progressively finer grits of sandpaper, each ring was measured with 0.001 mm precision on a Velmex stage system, under a Nikon 63X stereomicroscope using ProjectJ2X software (VoorTech, 2017). The resulting ring-width series were crossdated using COFECHA software (Holmes, 1983; Speer, 2010), and re-measured to account for human error and minimize the amount of flagged problematic segments (Table 2). The resulting cross-dated series were standardized using the detrend function in the "dplR" R package (Bunn, 2008). A negative exponential curve was fit to each series, before species specific master chronologies were built.

3.4. Statistical Analysis

All data analysis and preliminary visualization was done in R (R Core Team, 2020). Moving-window correlations at both the daily and annual scale were done using the "treeclim" R package (Zang and Biondi, 2015). Static correlation analyses at weekly and annual scales were also undertaken using the treeclim package. Bootstrapped Pearson's correlations were computed over a 30-day/year moving window offset by 1-day/year. The resulting relationships were "flagged" if statistically significant at the 99% confidence level. The treeclim package was also utilized to undertake a lag analysis, computing bootstrapped Pearson's correlations between variations in stem radius and lagged meteorological variables, offset from the records of ΔR by 0–11 days. In the case of precipitation, which returned errors in two instances when Pearson's correlations were bootstrapped, a non-bootstrapped version was computed. In this instance, significance was flagged at the 99% confidence level but based on a critical p-value rather than the bootstrapped confidence intervals.

Since this type of analysis is not often undertaken at such fine temporal resolution, the daily data were tested for normality across each of the 30-day intervals using the Shapiro-Wilk test. This test was inconclusive, with data normality varying from year to year and between species. However, it has been shown that the Pearson's correlation coefficient is relatively insensitive to data non-normality, and that the rate of type 1 and type 2 errors only increases when data are exceptionally non-normal, with a "highly kurtotic" shape (Bishara and Hittner, 2012). A second test was therefore undertaken to ensure Pearson's correlations are appropriate for use with these datasets. Results from the moving-window Pearson's correlation were compared to equivalent analyses using non-parametric tests, Kendall's tau and Spearman's rank correlations. The results from these three equivalent analyses were nearly indistinguishable.

Table 2
Characteristics of annual radial growth chronologies built from core samples taken at OJP and OA in the fall of 2018, and at OBS in the spring of 2016.

	OJP	*OBS*	*OA*
Number of Individuals in Chronology	54	73	46
Series Intercorrelation	0.632 critical value 0.366	0.548 critical value 0.328	0.692 critical value 0.366
Chronology Length	1923–2018 96 years	1894–2015 122 years	1925–2018 94 years
Number of Flagged Segments	6 of 215	13 of 279	5 of 179
Segment Length	40-year segments 20-year overlap	50-year segments 25-year overlap	40-year segments 20-year overlap

4. Results

4.1. Intra-annual drivers of stem radius change

Figs. 2 to 6 show the relationships between ΔR and meteorological variables at weekly and daily scale resolution during four individual growing seasons within the short-term observation period (2015 – 2018). Of the nine meteorological variables examined, P was the only one that had a significant correlation with ΔR at weekly-scale resolution (Fig. 2). Relationships between weekly P totals and ΔR were generally positive for all species assessed in 2017 (jack pine, black spruce, eastern larch, and aspen), and in 2018 (jack pine, black spruce, and eastern larch), with statistically significant results for jack pine, eastern larch, and black spruce in both years. The relationship between weekly jack pine ΔR and P was also moderately positive in 2016. Beyond P, VWC was the only other meteorological variable that had noteworthy relationships with the ΔR of the study species at weekly resolution. Aspen ΔR had a relatively strong positive correlation with weekly VWC in 2017, and jack pine ΔR had a relatively strong negative correlation with weekly VWC in 2015. A lag analysis at weekly resolution showed no significant results.

At daily resolution, P and T_A had the most important relationships with ΔR. This assessment is based on the strength (r-values) and persistence (consecutive instances of statistical significance) of correlations at the 99% confidence level. Shallow T_S (measured at 2, 5, and 10 cm) also had a significant relationship with the ΔR of the study species, but only for brief periods of time during the 2016, 2017, and 2018 growing seasons (Fig. 3).

The relationship between ΔR and P at daily resolution was generally weakest for aspen, most persistent for jack pine, and strongest for black spruce and eastern larch (Figs. 3 and 4). In Fig. 4, relationships between daily P and ΔR at lag = 0 provide information regarding the correlation between total rainfall and the change in mean stem radius since the last 24 h cycle. This correlation was always positive and was generally stronger towards the beginning and end of the growing seasons. Correlations between ΔR and P at lag = −1 day were also positive and generally strongest near the beginning and end of each growing season. Beginning at lag = −2 days, this relationship transitions from positive to negative. Therefore, rainfall frequently corresponded with an increase in stem radius compared to the previous day, or by the next day and a decrease during subsequent days, most frequently during the subsequent two days. These three modes can exist simultaneously during the same 30-day interval, or over distinct periods throughout different parts of the growing season. Regardless of our attempts to troubleshoot and rectify the situation, the bootstrapping technique continuously failed and returned errors when assessing the relationship between daily P totals and daily variations in jack pine and aspen stem radius in 2017. This particular correlation analysis, shown in Fig. 4, was therefore done without bootstrapping. Results at lag = 0 in Fig. 4 can be compared to bootstrapped versions of these same correlations in Fig. 3 and the results were unaffected.

T_A had a negative relationship with variations in mean daily stem

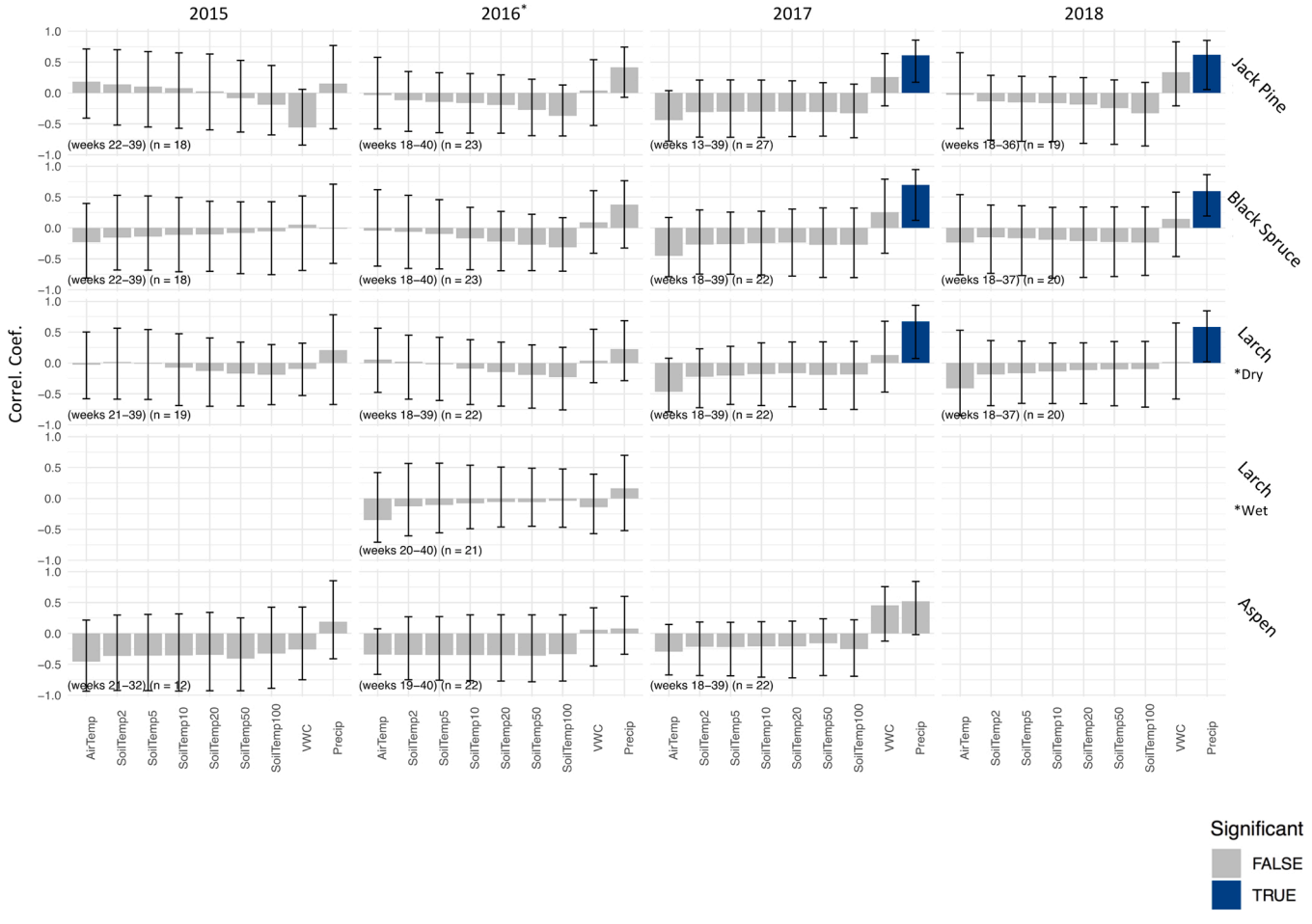


Fig. 2. Correlation analysis between weekly variations in stem radius and local meteorological variables (x-axis). Relationships were assessed within each growing season from 2015 to 2018. The height of each column represents Pearson's correlation r-value from − 1 to 1. Bootstrapped confidence intervals (99%) are depicted by each error bar and statistical significance is denoted in blue. Graphs are arranged in a two-dimensional matrix with growing season year listed above each column and site/species names labeled to the right of each row.

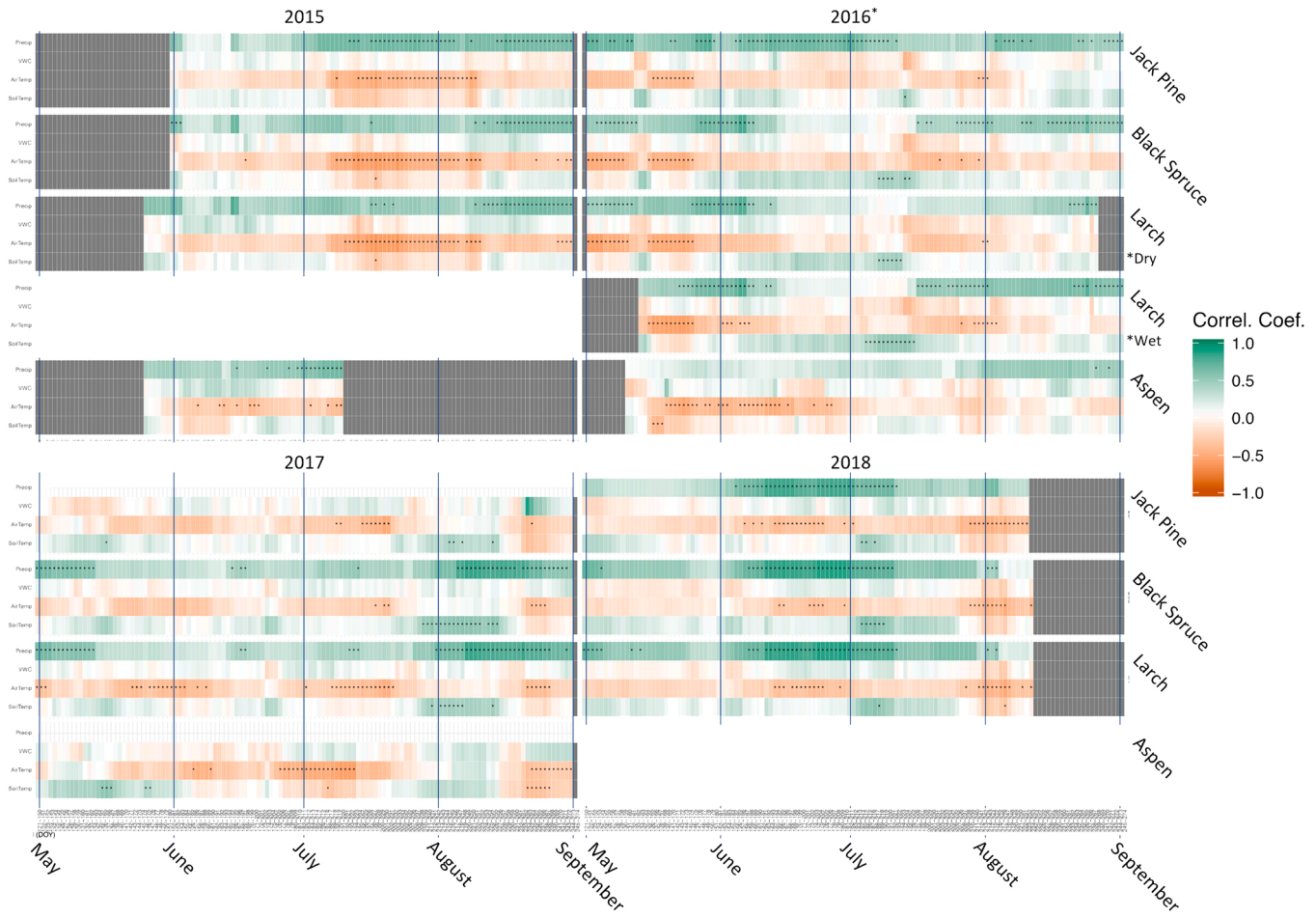


Fig. 3. Moving window correlation functions of the relationship between daily resolved variations in stem radius and local meteorological variables (precipitation, VWC, air temperature, soil temperature) within each of the four growing seasons during the observation period (2015 – 2018). Relationships were assessed over a 30-day moving window, jogged by 1-day, using bootstrapped Pearson's correlations (1000 iterations). The labels on the x-axis correspond with the start date of each 30-day interval. For example, intervals with start dates in May are found between the May and June x-axis labels. Significance at the 99% confidence level is flagged with * .

radius of the study species at lag = 0 (Fig. 5). This shows that warm air temperatures often corresponded with a decrease in stem radius since the previous day. This relationship transitioned to positive at lag = −1, − 2, and − 3 days, with the strongest and most persistent positive correlations at lag = −2 days. Therefore, warm air temperatures at times corresponded with a decrease in the stem radius of the study species compared to the previous day and a subsequent increase in stem radius within the next three consecutive days, most frequently during the following two consecutive days. Again, these modes can exist simultaneously (e.g., during intervals with start dates in May and June 2016 and 2017), but more frequently occurred over distinct periods during the growing season (Fig. 5).

The relationship between daily T_S and ΔR was weak and inconsistent when compared with P and T_A (Fig. 3). They were most often positive, and only statistically significant for brief periods of time, primarily during the 2016, 2017, and 2018 growing seasons. T_S was measured at multiple depths, with the shallowest (2, 5, and 10 cm) having the most important relationship with the ΔR of the study species. For this reason, only shallow soil temperature (measured at 2 cm) is represented in Figs. 3 and 6. Patterns remained the same for T_S taken deeper in the soil column. The only difference was that relationships were weaker.

Overall, the coniferous species (i.e., jack pine, black spruce, and eastern larch) had similar relationships with meteorological conditions within each of the growing seasons (Figs. 3–6). Trembling aspen too, at times, exhibited a somewhat similar relationship with meteorological conditions. However, there were several potential issues regarding the dataset of aspen stem radius that must be considered when interpreting these data. Firstly, due to issues with site access, the record of aspen stem radius was quite limited in 2015, both in terms of length and sample depth. Secondly, during the following growing season (2016), there was a severe forest tent caterpillar outbreak, which resulted in a near complete defoliation and two separate leaf out events (Stephens et al., 2018). This undoubtedly had a severe impact on radial tree growth, and likely altered how these trees reacted to meteorological conditions over the course of this growing season. The 2017 growing season was a recovery year, and it too was likely impacted by the 2016 outbreak. The 2016 and 2017 growth years are therefore not representative of normal growing seasons. The aspen time series ends in 2017 due to the decommissioning of the Old Aspen site in 2018. Despite these challenges, we believe it is important that these data be presented, to show how aspen might react to meteorological conditions compared to its coniferous counterparts, even under these exceptional circumstances. However, a great deal caution is exercised when interpreting results from OA at daily and weekly resolution.

4.2. *Inter-annual growth/climate relationships*

An assessment of the static relationships between standardized annual ring-widths and monthly climate variables (maximum, mean, and minimum T_A and total P) over the long term (94–122 years) yielded

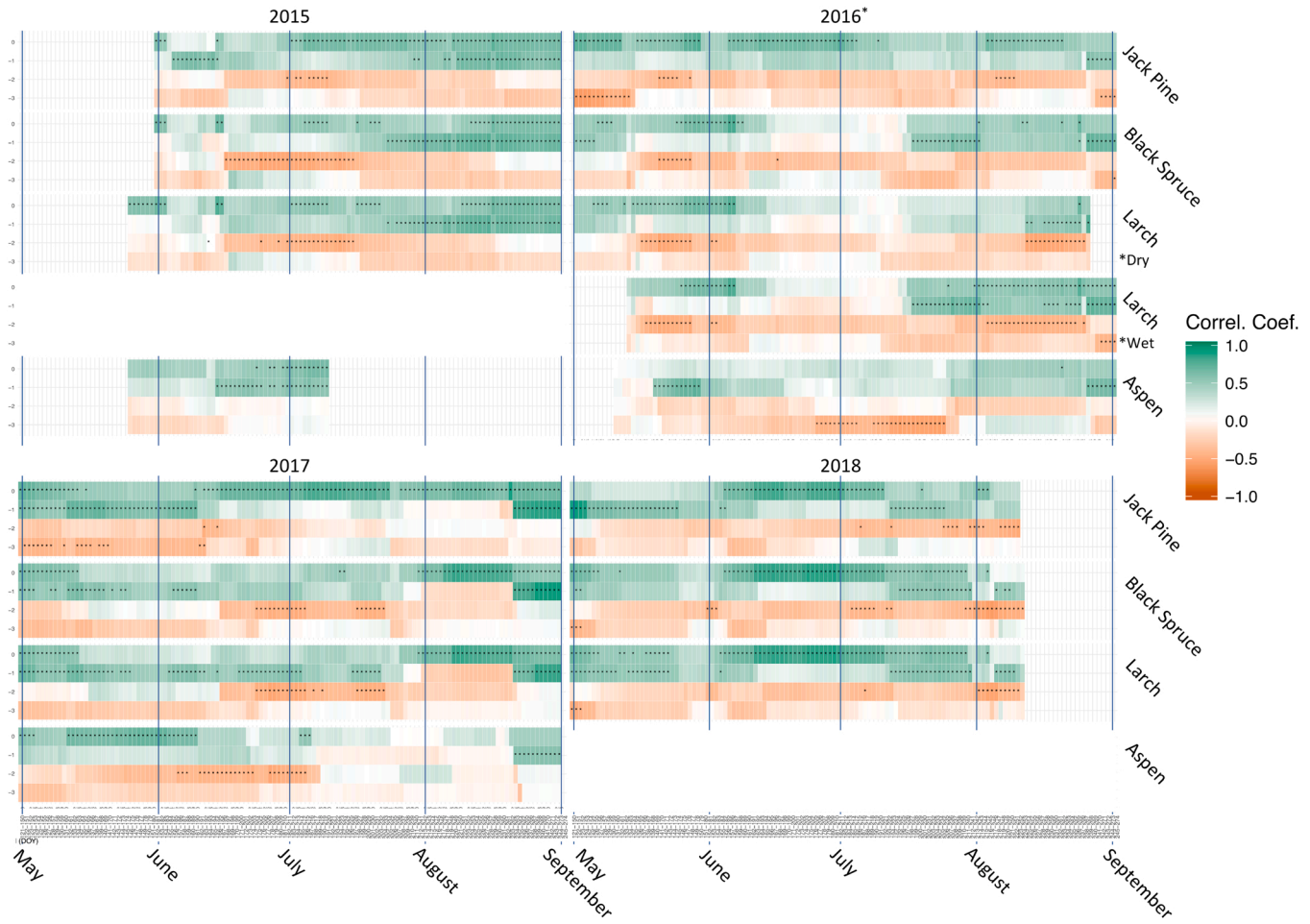


Fig. 4. Moving window correlation functions assessing lag in the relationship between daily variations in stem radius and precipitation, which is lagged from the stem radius data by 0–3-days (y-axis). Relationships were assessed over a 30-day moving window, jogged by 1-day, using bootstrapped Pearson's correlations. The labels on the x-axis correspond with the start date of each 30-day interval. Significance at the 99% confidence level is flagged with * .

generally weak correlations, with few instances of statistical significance at the 99% confidence level. Black spruce radial growth had a negative association with current spring maximum monthly T_A, including a statistically significant negative relationship with maximum-June T_A (Fig. 7-A-i.). The relationship between aspen radial growth and T_A during the late-spring and summer months, both from the current and previous growing season was generally positive, including a significant positive relationship with mean-July T_A from the current growing season (Fig. 7-B-i.). There were no statistically significant relationships between the radial growth of the study species and minimum monthly T_A, however relationship between aspen radial growth and minimum monthly T_A during the late-spring and summer months were generally positive (Fig. 7-C-i.). Black spruce was the only species whose annual radial growth was significantly related to monthly P totals (Fig. 7-D-i.). Current spring P (April – June), as well as previous-May and previous-August P (year n-1), were positively correlated with black spruce radial growth. Relationships between jack pine radial growth and the monthly climate variables (T_A and P) were generally weak, with no instances of statistical significance. However, perhaps the only climate variable of note was May P from the current growing season, which had a relatively strong positive correlation with jack pine radial growth (Fig. 7).

4.3. Non-stationary growth/climate relationships

Considering the possibility of non-stationarity in the long-term growth/climate relationship, a 30-year moving-window correlation analysis revealed a changing relationship between annual-radial growth and climate (Fig. 7-ii.). Black spruce radial growth was negatively correlated with monthly T_A during the spring and summer (March-August) from the mid-1910s to the mid-1960s (Fig. 7-ii.). Previous July T_A also had a negative relationship with black spruce radial growth over this same period. Beginning in the mid- to late-1940s, there was a long period where previous September T_A had a negative relationship with black spruce radial growth (Fig. 7-ii.). Overall, there were very few intervals during which there were significant positive correlations between black spruce growth and monthly T_A. Mean and maximum July and September T_A had a positive relationship with black spruce radial growth for a few decades during the early-1900s, and more recently, a positive relationship with current summer T_A, notably minimum September T_A, appears to be emerging (Fig. 7-C-ii.).

Compared with black spruce, jack pine and aspen radial growth had weaker relationships with monthly T_A, and most were positive (Fig. 7-ii.). Only recently, since about 1980, has there been significant positive correlations between monthly T_A variables and jack pine radial growth. These emergent positive relationships occur during the early-spring (April) and winter (November, December) from the previous growing season, as well as January, early-spring (April), and late-summer (July, August, September) from the current growing season (Fig. 7-ii.).

The strongest and most persistent relationships between aspen radial growth and monthly T_A occurred during the beginning and end of the growth record (Fig. 7-ii.). Early in the growth record, from about 1925 to the late 1950s, mean- and minimum-monthly T_A had a positive association with aspen radial growth during July of the previous year, and

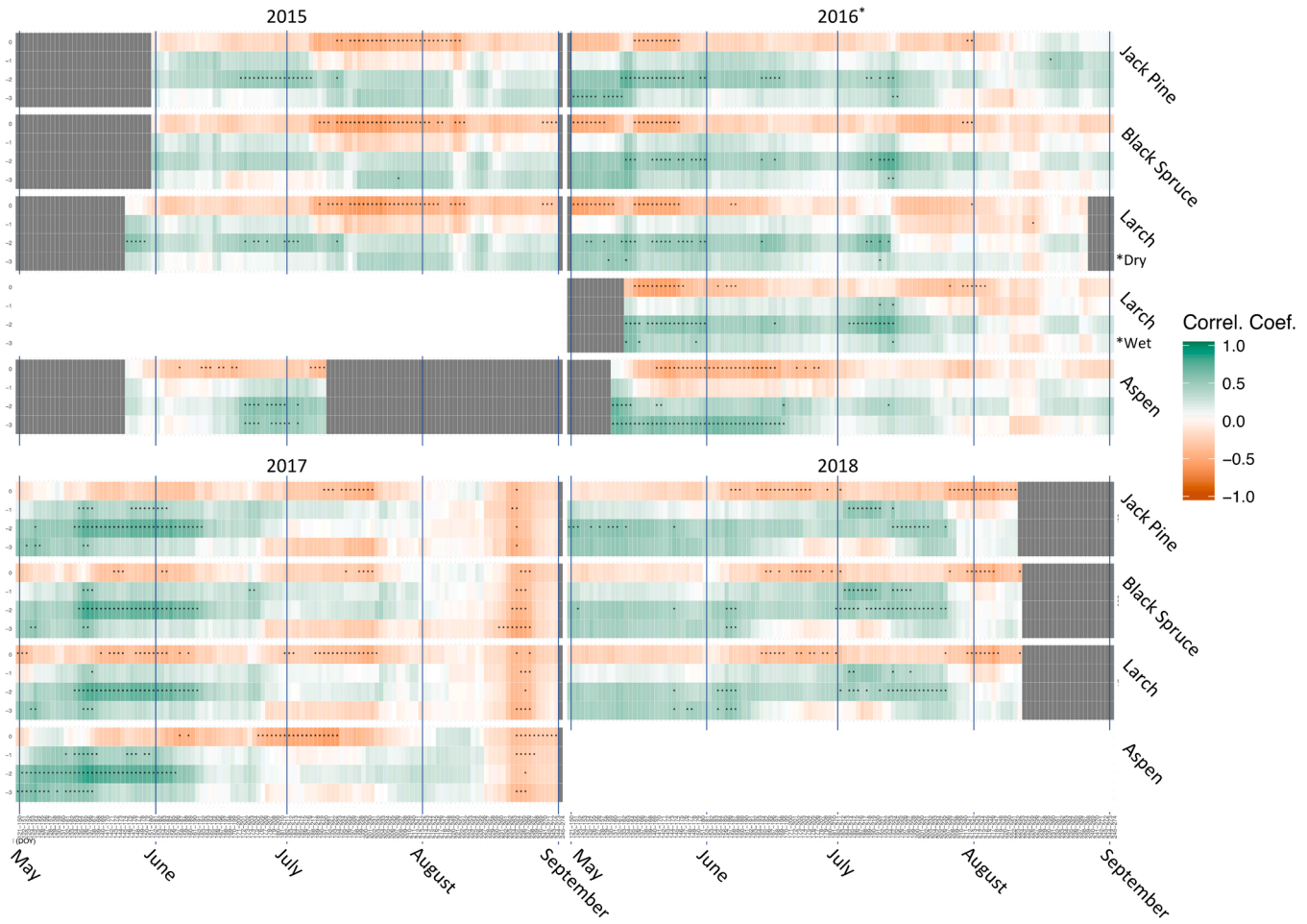


Fig. 5. Moving window correlation functions assessing lag in the relationship between daily variations in stem radius and mean air temperature, which is lagged from the stem radius data by 0–3-days (y-axis). Relationships were assessed over a 30-day moving window, jogged by 1-day, using bootstrapped Pearson's correlations. The labels on the x-axis correspond with the start date of each 30-day interval. Significance at the 99% confidence level is flagged with * .

during May, June, July, and September of the current year (Fig. 7-B and C-ii.). In recent decades, since about the 1970s and 80 s, positive relationships between aspen radial growth and previous growing season T_A have again emerged, including a significant positive correlation with minimum May and June T_A (year n-1) (Fig. 7-C-ii.), and with mean and maximum September T_A (year n-1) (Fig. 7-A and B-ii.).

The relationship between annual-radial growth and P was most often positive (Fig. 7-D). There were however a few periods of negative correlations with previous June and current March P for jack pine, and previous October and December P for black spruce. Persistent positive relationships with P occurred in May for jack pine, both from the previous and current growing season. Current June and August P also had a significant positive relationship with jack pine radial growth, but during only a few 30-year intervals (Fig. 7-D-ii.). There were several instances over the course of the growth record where black spruce radial growth was positively associated with monthly P. There were sporadic instances of statistical significance in this relationship during May, July, and August of the previous year, and over the spring and summer months of the current year (March – August) (Fig. 7-D-ii.). There were only two months during which there were significant relationships between P and aspen radial growth. The strongest and most persistent relationship between these two variables occurred in September of the previous year, which was positive from the early-1930s to the mid-1970s. Previous April P also had a significant positive correlation with aspen growth, but over only two 30-year intervals (Fig. 7-D-ii.). It should also be noted that relationships between P and radial growth appear to be weakening in recent decades. There are no significant correlations between radial growth and P since the mid-1950s for aspen, and since the late 1970s for jack pine and black spruce (Fig. 7-D-ii.).

5. Discussion

This study represents a comprehensive assessment of relationships between radial tree growth metrics and local environmental variables across multiple temporal scales. This cross-scale analysis provides insight into the mechanisms and potential drivers of tree growth, beyond what is achievable using only traditional dendroclimatological methods. Fig. 8 provides an overview of observed relationships, and the potential cause of these relationships are discussed below.

5.1. Assessment of growth/climate relationships over intra-annual scales

The observed relationship between daily and weekly precipitation and the ΔR of the study species (Figs. 2 and 3) was likely related to the influence of stem water content on variations in stem radius rather than the influence of radial growth. At daily resolution, a pulse in moisture often corresponded with an increase in stem radius either since the previous day, or by the next day, most frequently beyond the main period of stem expansion. An increase in stem size following a rain event has been observed by many others (Mäkinen et al., 2003; Deslauriers et al., 2007b; Turcotte et al., 2011; King et al., 2013; Güney et al., 2019) and is likely driven by daily changes in stem water storage. During the day, when transpiration is taking place, water storages in elastic tissues (i.e., bark, phloem, cambium) are depleted, resulting in stem shrinkage

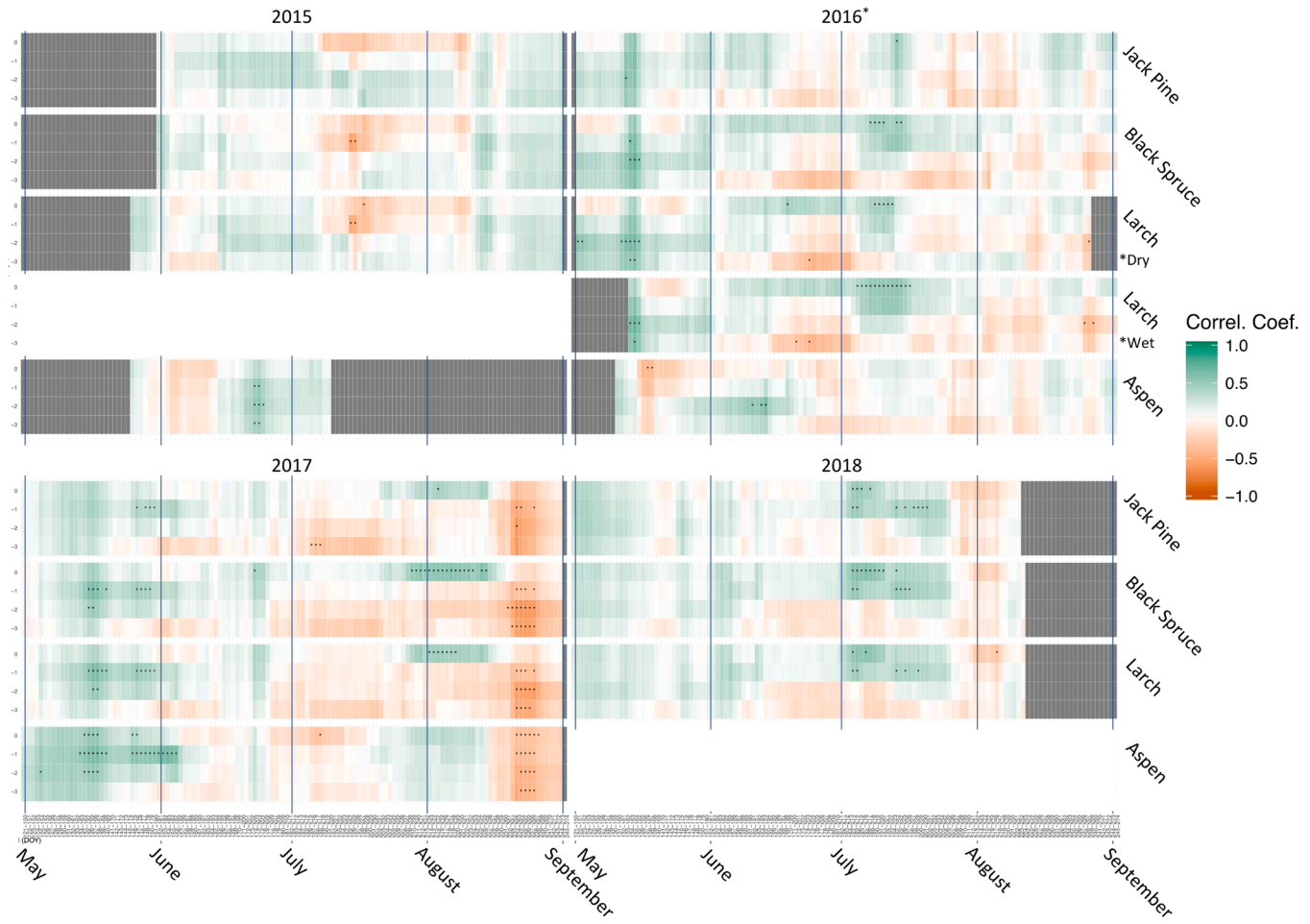


Fig. 6. Moving window correlation functions assessing lag in the relationship between daily variations in stem radius and shallow soil temperature (2 cm depth), which is lagged from the stem radius data by 0–3-days (y-axis). Relationships were assessed over a 30-day moving window, jogged by 1-day, using bootstrapped Pearson's correlations. The labels on the x-axis correspond with the start date of each 30-day interval. Significance at the 99% confidence level is flagged with * .

(Zweifel et al., 2000; Zweifel et al., 2001; Steppe et al., 2006). This is less likely to occur during rain events, under cloudy conditions and low vapour pressure deficit (VPD). Overnight when transpiration is low or ceased, water stores are replenished resulting in stem radius expansion. A net increase in stem size is therefore more likely to occur following days when VPD is low, when stem water recharge overnight can more easily surpass the volume of stem water depleted during the day. Daily changes in stem water storage is therefore dependent on environmental conditions such as precipitation, due to its influence on atmospheric demand and moisture availability (Zweifel et al., 2005; Drew et al., 2011).

The link between stem size and stem water content was present at the BERMS sites regardless of speciation. However, based on the strength and persistence of relationships between ΔR and precipitation, jack pine appeared to be most susceptible to stem radius fluctuations in response to precipitation (Fig. 3). Similarly, black spruce and eastern larch stem radius were more strongly correlated with precipitation during periods of depressed VWC in the root zone, towards the end of the 2017 growing season and during the main period of growth in 2018 (Figures A.2 and 3). It is hypothesized that jack pine is restricted in terms of water availability, whereas black spruce and eastern larch may change the depth at which they are uptaking water according to shifting availability. Jack pine is located over well drained sandy soil and while the roots extend deep into the soil column, most are concentrated near the surface. Conversely, the high water-table at OBS limits the rooting depth of black spruce and eastern larch but allows for increased water availability in the root zone (Figure A.2). Jack pine must therefore take advantage of water in the shallow soils when it is replenished by precipitation, while black spruce and eastern larch may rely on water table resources during wet periods and shift to shallow soil resources when water table depth drops well below the root zone. There are reports of similar shifts in the depth of water uptake in the literature (Nehemy et al., 2020). Ellsworth and Sternberg (2015) investigated intra-seasonal water use in a dry plant community in Florida, USA, and showed that during the dry season the depth of water uptake changed according to water availability. Similarly, Carrière et al. (2020) showed that three Mediterranean species acquired more deep soil water during drier years. Species' ability to quickly acquire transient water sources and shift the depth of water uptake under limited supply is an ecological trait (Ehleringer et al., 1991; Volkmann et al., 2016).

It is likely that, during periods of reduced moisture, instances of stem water replenishment were immediately followed by water loss, as it is more difficult for trees to maintain high levels of water storage in the stem under these conditions. This is evidenced by the observation that negative relationships between precipitation and stem radius variations (strongest at lag = −2 days) were strongest during periods with below average precipitation (e.g., May – June, 2016) (Fig. 4).

Warm air temperatures corresponded with either a decrease in stem radius since the previous day (negative correlations at lag = 0), or an increase in stem radius during subsequent days (positive correlations at lag = −1, −2, and −3 days) (Fig. 4). Negative relationships between air temperature and stem radius variations over daily to sub-daily scales are well documented and are attributed to an increase in transpiration rates and a decrease in stem water volume in response to warm air

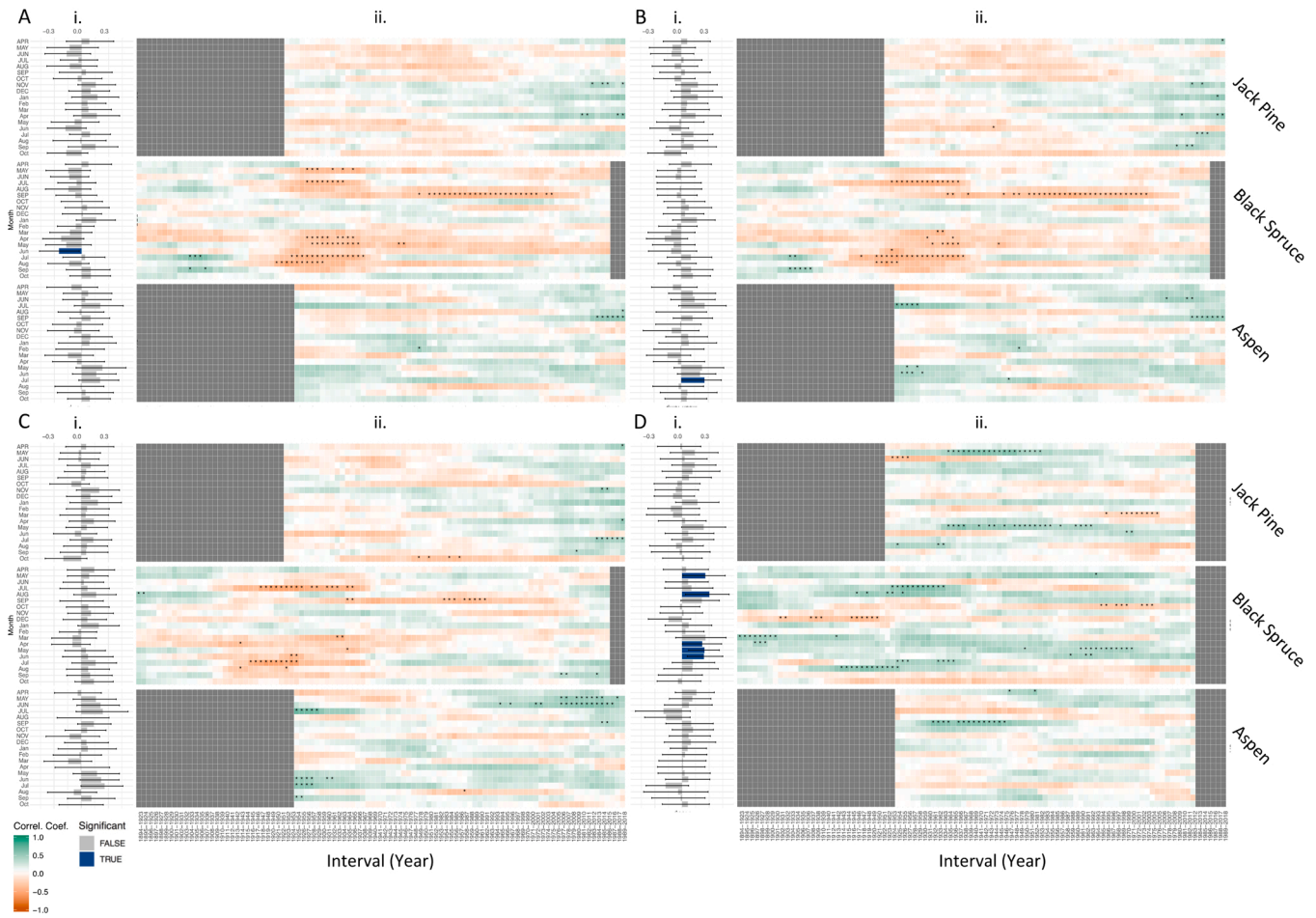


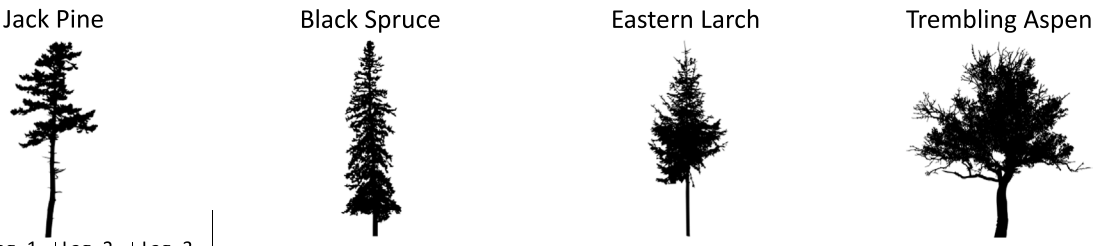
Fig. 7. Static (i.) and moving window (ii.) correlation analyses between annual radial growth and monthly maximum (A), mean (B), and minimum (C) monthly temperature, and total monthly precipitation (D). Pearson's correlations were computed 1000 times with random resampling. Significance at the 99% confidence level is based on the bootstrapped confidence intervals and is highlighted in blue (i.), or flagged with * (ii.).

temperatures (Peng et al., 2017; Cocozza et al., 2018; Güney et al., 2019; Gao et al., 2019). Moisture availability also plays a role in governing this relationship, since net volume loss is more likely to occur during periods with limited moisture, when daily water loss is not easily offset by stem water replenishment overnight (Mäkinen et al., 2003; Turcotte et al., 2011). This ultimately results in a persistent reduction in amplitude of the diurnal stem size cycle as dryness persists (King et al., 2013). Furthermore, it has been found that xylem cell production may cease in response to water limitations (Deslauriers et al., 2016), making it more likely for stem radius to be dominated by the stem-water signal during periods of water deficit (Zweifel et al., 2016). This explains why negative relationships between the ΔR of our study species and air temperature at lag = 0 are most prevalent during periods with little precipitation (Figures A.1 – A.3, and 5).

Conversely, air temperature, within an optimal range, may play an important role in stimulating radial growth (Gruber et al., 2009; Oberhuber et al., 2014; Cocozza et al., 2016), perhaps most importantly towards the beginning of the growing season, when air temperature exerts significant control over the onset of xylem cell production (Rossi et al., 2007, 2008). There is evidence of this at the BERMS sites, but only during periods of increased moisture availability. Under these conditions, observations suggested that elevated air temperature may result in a stimulation of the processes contributing to radial growth in the study species over the next 1–3 days, resulting in a positive correlation with lagged air temperature (lag = −1, −2, and −3 days) (Fig. 5). Positive relationships between lagged-air temperature and variations in stem radius occurred during the main period of stem expansion in 2016, specifically during intervals with start dates in early to mid-July, corresponding with a period of increased moisture availability (Figures A.1 – A.3, and 5). Spring 2017 was also extremely wet, with about twice the average amount of precipitation during May (Figures A.1 – A.3). Following this input of moisture, around the time one would expect the onset of radial growth for the season, there were strong positive relationships between the ΔR of the four study-species and air temperature (lag = −2 days) (Fig. 5), pointing to the importance of temperature in stimulating radial growth when moisture requirements have been met.

A good illustration of the dual nature of the relationship between temperature and daily stem radius variations occurred in 2018. There was below-average precipitation during much of the 2018 growing season, with pulses of moisture in late-May to early-June, and in July (Figures A.1 – A.3). It is during these periods of increased moisture that the strongest positive correlations between lagged air temperature and variations in stem radius were observed (Fig. 5). Negative relationships with air temperature at lag = 0 occurred intermittently in 2018, during the driest periods, in late-June and August (Fig. 5).

Observed correlations between stem radius variations and soil temperature, which were weak compared to correlations with precipitation and air temperature, were likely spurious, due to a co-occurring positive relationship with air temperature. Periods during which the positive relationship between ΔR and soil temperature were strongest included early in the growing season in 2016 and 2017, during intervals with start dates in mid-May towards the end of the main period of stem expansion, during intervals with start dates in July 2016 and 2018, and beyond the main period of stem expansion during intervals with start dates in



	Jack Pine				Black Spruce	Eastern Larch	Trembling Aspen
	Lag 0	Lag -1	Lag -2	Lag -3			
Daily	↑ P* ↓ T_A* ↑ T_s	↓ P* ↑ T_A ↑ T_s	↑ T_A*	↑ T_A	Beyond some slight variability, relationships between ΔR and local meteorological variables were common across our study species at daily-scale temporal resolution. See Jack Pine for our list of observed relationships.		
Weekly	↓ VWC (2015) ↑ P* (2016, 2017, 2018)				↑ P* (2016, 2017)	↑ P* (2016, 2017)	↑ P, VWC (2017)
Static Annual	↑ May P				↓ Spr, Jun* T_A ↑ MAY*, AUG*, Spr* P	NA	↑ SPR, SUM, Spr, Sum, Jul* T_A
Dynamic Annual *Past/ Lapsed*	↓ JUN, Mar P ↑ MAY*, May*, Jun, Aug P				↓ JUL*, SEP*, Spr*, Sum* T_A ↓ OCT, DEC P ↑ MAY, JUL, AUG, Spr, Sum P	NA	↑ JUL*, May, Jun, Jul, Sep T_A ↑ APR, SEP* P
Dynamic Annual *Recent/ Emergent*	< ↑ APR, WIN, Apr*, Sum T_A > ↑ P since late-1970s				< ↑ Sum T_A, Sep* T_A > ↑ P since late-1970s	NA	< ↑ MAY*, JUN*, SEP* T_A > ↑ P since mid-1950s

* signifies strong, persistent, and/or statistically significant relationships.

Fig. 8. An overview of dendroclimatological relationships observed across temporal scales. Green arrows indicate positive relationships and red arrows indicate negative ones. Asterisks (*) indicate important or statistically significant relationships. The growing season(s) during which relationships were observed at weekly scale resolution are indicated in parentheses. At annual scale resolution, month and season names are presented as three-letter abbreviations. Spring (Spr) represents the three months from March – May. Summer (Sum) represents the three months from Jun – Aug. Fall (Fal), not present above, would represent the three months from Sep – Nov. Winter (Win) represents the three months from Dec – Feb. When month and season abbreviations are fully capitalized, this represents observed relationships with conditions from the previous year (year n-1). Recent / emergent relationships with annual radial-growth (the final row of this table) are described as either increasing (<) or decreasing (>) in importance.

August 2017 (Fig. 6). These examples co-occurred with the most marked positive relationships with air temperature (Fig. 5), except with a reduction in lag time; likely the time required for warmth to penetrate the uppermost layers of the soil.

Negative relationships with daily air and soil temperature observed late during the 2017 growing season initiated almost synchronously across the four study-species immediately following a rain event (Figs. 5 and 6). This is likely indicative of a response to the input of moisture late in the growing season, during a time when air and soil temperature are falling naturally.

5.2. *Dendroclimatological analysis at annual resolution*

Important relationships that were identified following static dendroclimatological analyses are not necessarily those that had the strongest impact on radial stem growth. When the long-term radial-growth record was broken down into 30-year segments, and relationships were reassessed over a moving window, the monthly climate variables that had the strongest associations with radial growth over the long term (~ 100 years) often showed weak associations over the medium term (30 years). For example, the relationship between maximum-June temperature and black spruce radial growth, which was strong negative over the full length of the growth record, was rather weak when the growth record was broken down into 30-year intervals (Fig. 7-A-i. and A-ii.). Similarly, the relationship between mean-July temperature and aspen radial growth, which was strong positive over the long term, was again weak over the medium term, with a single 30-year interval showing a statistically significant result (Fig. 7-B-i. and B-ii). The static correlations that were strongest over the long term are those that were most consistent in terms of their quality, with the direction of their relationship remaining the same over time. Therefore, the static correlation analysis was only successful in highlighting the relationships that were most consistent over time, not necessarily those that were most meaningful in terms of their overall influence on radial growth.

For the entire growth record, relationships between black spruce radial growth and monthly temperature during the current and previous growing season (April – September) have in large part been negative, most significantly between the mid-1910s and 1960s Huang et al. (2010) attributed negative correlations between black spruce radial growth and growing season temperatures to enhanced water-stress due to increased rates of respiration and evapotranspiration under warm conditions. Earlier studies by Dang and Lieffers (1989) and Hofgaard et al. (1999) reported similar relationships, and the timeframe of these studies may overlap more closely with the period of enhanced negative correlations between black spruce radial growth and growing season temperatures observed in this study. The sensitivity of black spruce to water-stress also explains its significant positive relationship with growing season precipitation, an association which is more important in this species than it is in jack pine and aspen. In this study, jack pine was generally insensitive to the monthly climate variables assessed. Over the course of the growth record, May precipitation, both from the current and previous growing season had the most persistent relationship with jack pine radial growth, a relationship which is significantly positive from about the mid-1930s to the mid-1980s. May precipitation was also found to enhance the radial growth of jack pine in Huang et al. (2010) due to the potential importance of spring precipitation for replenishing water supply at latitudes north of 52°. Aspen radial growth had generally positive relationships with spring temperature in this study, primarily

during the current growing season. A positive correlation between aspen radial growth and May temperature was also identified in Chen et al. (2017) and is attributed to the enhancement of aspen growth in response to early leaf emergence and photosynthesis. Therefore, the findings from our dendroclimatological analysis are consistent with those from recent studies.

The moving-window correlations revealed some emergent trends in the growth/climate relationship. Those between radial growth and temperature included: positive correlations between radial growth and current summer temperatures for jack pine and black spruce (Fig. 2-ii.); positive correlations between jack pine radial growth and April temperatures (both current and previous), as well as previous-winter temperatures (November, December, and current January) (Fig. 7-ii.); and positive correlations between aspen radial growth and previous-growing-season temperatures (April to September). Relationships between radial growth and precipitation have also decreased in significance in recent decades, since the mid-1950s for aspen, and since the late 1970s for jack pine and black spruce (Fig. 7-D-ii.). Non-stationarity in the growth/climate relationship has been observed by many and is widely discussed in D'Arrigo et al. (2008). However, in contrast to their reporting of weakening relationships with temperature, this study showed an enhanced positive relationship with temperature and weakening relationships with precipitation. The main difference is that the BERMS sites are located at lower latitudes than those reporting a reduction in sensitivity to temperature. In Prince Albert, Saskatchewan, there is an overall trend towards warmer and wetter conditions since at least the mid-1940s, especially during the spring and summer (see Appendix B; Figures B.1 and B.2). Non-stationarity in the radial growth/-climate relationship is often attributed to shifting limitations (D'Arrigo et al., 2008), and in this case, it is likely signaling a decrease in moisture limitations, and a positive response to warming.

6. Conclusion

The ΔR of the study species at daily and weekly scales often had a strong correlation with precipitation, likely signalling the importance of stem water dynamics in driving intra-annual variations in stem radius. Bearing in mind the limitations associated with the record of aspen stem radius, we identified a response to moisture input that was common among the four study-species. Furthermore, the relationship between precipitation and ΔR in black spruce and eastern larch was enhanced during periods of below average VWC in the root zone. This points to the likelihood that certain species in the southern boreal forest rely more heavily on available moisture in the uppermost layers of the soil column during periods when moisture in the root zone is limiting. This information would be of interest to those conducting research regarding tree-water relations in the southern boreal forest.

We also observed that warm air temperatures have an immediate negative impact on stem water content. This occurred most frequently at the BERMS sites during periods of reduced moisture availability, when the stem radius data are more likely to be dominated by the water signal, and when trees are more susceptible to net volume loss due to high evaporative demand. When moisture requirements are met however, warm air temperatures may have the opposite effect, playing a role in stimulating radial growth and resulting in an increase in stem radius during subsequent days. Note that this interpretation of results is based on detailed observation over a limited timeframe. Continued observation and alternative methods of analysis are required to test this hypothesis, and to determine whether these results persist over a longer period.

The tree growth/climate relationship is often not static through time. This relationship has been shown to evolve over the short- and long-term in response to changes in weather, stand dynamics, and climate. In this study, the most common dendroclimatological analysis, a static bootstrapped correlation function analysis between annual-ring width and monthly climate variables, only identified the growth/climate relationships which were most consistent over time, not necessarily those that had the most meaningful impact on the growth of the study species, especially in recent years. This type of analysis may therefore become increasingly inappropriate in this era of climatic change. To account for the dynamic nature of the growth/climate relationship, we computed bootstrapped correlation functions over a moving window. In doing so, we identified a general increase in the strength of positive relationships between spring and summer air temperature and radial growth, and a weakening of the relationship between precipitation and radial growth over time, likely signaling a positive response to spring warming, and a decrease in moisture limitations in this region. These findings provide evidence that non-stationarity in the growth/climate relationship may be more widespread than originally anticipated, or perhaps that these issues are becoming far reaching as climate change progresses. The identification of dynamic growth/climate relationships in the southern boreal forest has implications for researchers using tree rings for paleoclimate reconstruction and for projections of future climate.

It has been suggested that some boreal forest trees may end up benefitting from spring warming over the near term, providing there is sufficient moisture to support growth (Boisvenue and Running, 2006; Zhang et al., 2008; D'Orangeville et al., 2018). In response to the recent wetting trend, trees in the southern boreal forest may be particularly well positioned to take advantage of this short-term benefit, considering that moisture is the dominant limiting factor controlling the distribution and growth of trees in this region (Sellers et al., 1995; Ireson et al., 2015) and that the dominant species in this region may benefit from moderate climate warming (D'Orangeville et al., 2018). The results from this study support this hypothesis and build on our understanding of a potential response of common boreal forest trees to changing environmental conditions in the southern boreal region. It is likely that the recent warming and wetting trend has contributed to a decrease in moisture limitations and an enhanced positive response to spring and summer air temperature over the last several decades at the BERMS sites. There is evidence of this at annual temporal resolution, in the shifting growth/climate relationships, and in the more nuanced response of daily variations in stem radius to environmental conditions within the growing season. It is recommended that high-resolution stem-size data should continue to be collected at these sites to establish a proper baseline for active ring development and its response to meteorological conditions within the growing season. Moving forward, rates of evapotranspiration are expected to overshadow any gains in moisture related to an increase in precipitation (Wang et al., 2014), a trend which is likely already occurring further north, in Alaska and the Yukon Territory (Walker and Johnstone, 2014). Under these circumstances and based on our results, species in the southern boreal forest will need to rely more heavily on effective precipitation to support their growth, until a point when water becomes extremely limiting, in which case we are likely to see reduced growth rates, and a negative response to warm air temperature (Barber et al., 2000; Walker and Johnstone, 2014).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2022.125936.

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