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Climate and atmospheric circulation related to frost-ring formation in *Picea mariana* trees from the Boreal Plains, interior North America

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ABSTRACT

Earlier spring and earlier onset of growth, as a consequence of climate change, may expose trees and crops to increased risk of exposure to frost damage. In this study, we compare the frequency of frost rings in three regions [Porcupine Provincial Forest (PPF; north-latitude); Duck Mountain Provincial Forest (DMPF; mid-latitude) and Riding Mountain National Park (RMNP, south-latitude)] located in the Boreal Plains of interior North America. In each of PPF and DMPF, twenty upland black spruce [*Picea mariana* (Mill.) BSP] trees were sampled using stem analysis and others were sampled at breast height or below. In RMNP, multiple coniferous tree species were sampled at breast height or below to allow comparison among species. Results from stem analysis indicated that frost rings were more frequent in DMPF than PPF (north of DMPF). Frost rings identified up to a height of 16 m and were formed predominantly in the early cambial age zone. As a general pattern, frost rings recorded in PPF occurred more abundantly in years with warm April temperatures and this association was less prevalent in DMPF. Frost rings were formed following extreme frost events in late May - early June and frost-ring years corresponded to years with cooler June temperatures. A significant positive association was found between frost-ring frequency and the El Niño Southern Oscillation. In the absence of an early spring, black spruce trees were less affected by frost damages. Stem analysis provided a better record of spring frosts than solely sampling at breast height or below. The multi-species approach used in RMNP revealed many years with synchronous frost rings among species. The development of a large network of frost-ring chronologies from tree species of various age classes and/or from stem analysis will help with assessing the impact of late spring frosts on forest dynamics and to document large-scale climate anomalies in areas with low climate data coverage and/or prior to instrumental records.

1. Introduction

1.1. *Climate changes and late spring frosts*

Global surface temperature has significantly risen during the last century with both associated environmental and socioeconomic impacts (Dell et al., 2012; Wheeler and von Braun, 2013; IPCC, 2018). Climate change also impacts the frequency and intensity of extreme climatic events, including unusual cold spells in spring. These events can affect society, agriculture and both reproduction and survival of plants and animals (Augspurger, 2009; Rusticucci et al., 2016; Unterberger et al., 2018; Vitasse and Rebetez, 2018). Extreme weather events have recently received increasing attention as a result of increased societal costs (Gu et al., 2008; Augspurger, 2013; Ault et al., 2013).

As a consequence of a warming climate, there is increased variability in the frequency and timing of freeze and thaw events. These fluctuations may delay plant hardening and hasten de-hardening (Gu et al., 2008) altering plant phenology, possibly leading to greater risk of spring frost damage (Augspurger, 2013). Increasing mean spring temperatures and the occurrence of anomalous warm springs (false springs) have been linked to early phenological development in plants and to a greater risk of frost damage when followed by periods of unusually cold (sub-zero) temperatures (Gu et al., 2008; Augspurger, 2009; Marino et al., 2011). Analyzing 120 years of climate data, Augspurger (2013) found that in

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recent decades earlier and warmer spring events followed by cold temperatures (greater temperature variability) have become more common in the temperate deciduous forest, thus rendering plants more susceptible to frost damage. In the United States, earlier onset of plant growth has also been documented following climatic warming (Allstadt et al., 2015). In addition to the potential increase in phenological mismatches between plant and dependent animals, an increase in false spring prevalence may lead to increased plant damages due to subsequent freezing temperatures (Allstadt et al., 2015; Ma et al., 2018).

1.2. *Impacts of late spring frost*

Hiratsuka and Zalasky (1993) provided an extensive review of frost damage that trees may be experiencing in the Canadian Prairies. In the province of Manitoba, a severe frost that occurred on two successive nights in the first week of June 1951 (Tucker et al., 1968) caused damage to new growth in 67–79 percent of white spruce (*Picea glauca* (Moench) Voss) seedlings in plantations. Extreme frost events and the damage they cause also have evolutionary and ecological consequences (Augspurger, 2009; Hufkens et al., 2012; Fisichelli et al., 2014). An early spring bringing vegetation out of dormancy "prematurely" and associated with climate variability and change may increase damages to forests and crops (Ault et al., 2013; McKenney et al., 2014).

In addition to directional selection and impacts on population demography and regeneration, late spring frost events also play an important role in regulating duration and frequency of insect outbreaks (Volney, 1996; Sutton and Tardif, 2007; Robson et al., 2015). Spring frost has also been hypothesized to favour infestation by decay fungi like *Armillaria* spp. root rot in trembling aspen (*Populus tremuloides*; Zalasky, 1976; Wolken et al., 2009) and black spruce (*Picea mariana* (Mill.) B.S.P.); Waito et al. (2013) stands. Ecological ramifications of late spring frost are also important. By affecting food stocks, late spring frosts were reported to impact squirrel (Nixon and McClain, 1969) and black bear populations (Poulin et al., 2003). Leidolf and Ryel (2013) reported that frost damage in trembling aspen also had a negative impact on avian communities.

1.3. *Frost-ring formation and distribution*

Frost rings may be the most extreme form of wood anatomical imprints of temperature extremes (Bräuning et al., 2016). They are formed when trees are physiologically sensitive after winter de-hardening (Bräuning et al., 2016). Prior studies indicated that black spruce can record episodes of extreme cold in their tree rings (Dy and Payette, 2007; Payette et al., 2010; Waito et al., 2013). Although Glerum and Farrar (1966) experimentally induced the formation of frost rings in coniferous seedlings at temperatures below −8 °C; in natural environments, studies have shown that temperatures below 0 °C may lead to frost-ring formation (Stöckli and Schweingruber, 1996; Gurskaya, 2014). In black spruce, frost rings were reported to form when nocturnal temperatures fell below 0 °C for 6 h and reached −6 °C (Dy and Payette, 2007). Sub-freezing temperatures at a time when the cambium is active interfere with the normal reproductive activity of vascular cambium triggering the formation of an annual growth ring characterized by traumatic tissues referred to as a frost ring (Kaennel and Schweingruber, 1995). In general, these traumatic tissues, which can be observed in both broadleaf and coniferous species, are composed by unusual axial parenchyma cells and tracheids with irregular structure and appear in the annual ring as a layer of crushed and bent xylem cells (Glerum and Farrar, 1966; Kaennel and Schweingruber, 1995; Schweingruber, 2007).

Most frost-ring studies have observed this anomaly in tree rings produced by a young cambium (Gurskaya and Shiyatov, 2006; Kidd and Copenheaver, 2014; Arco Molina et al., 2016; Hadad et al., 2019). Gurskaya and Shiyatov (2006) found frost rings to be mainly distributed along the first 0.2 m of the stem, whereas they were reported to form up to 14 m in red pine (*Pinus resinosa* Ait.) trees (Fayle, 1981) and up to 16 m in black spruce trees (Waito et al., 2013). Other studies have revealed that variations in frost-ring frequency among sites may reflect landscape variability (Hadad et al., 2012, 2019; Arco Molina et al., 2016; Gurskaya et al., 2016).

1.4. *Objectives*

The main objectives of this study were 1) to compare frost-ring chronologies derived from stem analysis to those derived from sampling at breast height or below, 2) to determine the climatic conditions leading to the formation of frost rings in black spruce trees along a latitudinal gradient, and 3) to assess the potential for long reconstruction of late spring frost events using tree rings. In order to complete these objectives, frost-ring chronologies were developed from three regions located along the Manitoba Escarpment. It was hypothesized that no differences in frost-ring frequency would be observed among regions and that early onset of spring followed by sub-freezing temperatures would be the dominant climate signal leading to the formation of frost rings. This study provides background historical data about the frequency of frost-ring events in interior North America in a context when late spring frost events may increase with future climate changes.

2. Materials and methods

2.1. *Study area*

The study area is located within the Manitoba Escarpment, part of the mid-Boreal Uplands Ecoregion which is a southern extension of the Boreal Plains Ecozone (Fig. 1). Porcupine Provincial Forest (PPF, 52°40′ N, 101°22′ W; north-latitude region), Duck Mountain Provincial Forest (DMPF, 51°41′ N, 101°01′ W; mid-latitude region) and Riding Mountain National Park (RMNP, 50° 51′ N; 100° 07′ W; south-latitude region) are part of the Boreal Plains Ecozone, a transition area between northern boreal forest and southern aspen parkland (Smith et al., 1998). Topography of the study area varies between 400 and 830 m asl (Smith et al., 1998). The dominant tree species are trembling aspen, white spruce, balsam poplar (*Populus balsamifera* L.), black spruce, paper birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* (L.) Mill.) and tamarack (*Larix laricina* (DuRoi) K. Koch) (Smith et al., 1998; Tardif, 2004; Westwood et al., 2012; Tardif et al., 2016).

The nearest meteorological station to both DMPF and PPF is located in Swan River (52°03′ N, 101°13′ W, elevation of 347 m asl; Fig. 1). The nearest meteorological station to DMPF and RMNP is located in Dauphin (51°06′ N, 100°03′ W, elevation of 305 m asl; Fig. 1). In general, the southern region experiences a warmer and drier climate. For the reference period 1981–2010 at the Swan River station (Dauphin station data in parentheses), the January daily average temperature was −17.2 (−15.4) °C and the July daily temperature averaged 18.1 (18.7) °C. Overall yearly average temperature was 1.8 (2.5) °C, and average yearly total precipitation was 546.6 (481.9) mm, of which 417.8 (383.7) mm fell as rain (Environment Canada, 2016). During the reference period, the average length of the frost-free period was 105 days with the average date of late spring frost being May 28. The number of days with minimum temperature being equal or below 0 °C in the month of May and June summed to 9.0 (8.8) and 0.62 (0.20) days respectively. Past June 11th in Swan River (12th in Dauphin), the probability of encountering a frost is less than 10% (Environment Canada, 2016). Since the inception of these two stations, the extreme maximum temperature for April was recorded in 1949 (32.2 °C) at Swan River and in 1980 (35.2 °C) at Dauphin. The coldest June minimum temperature was recorded in 1915 (−5.0 °C) at Swan River and in 1958 (−3.9 °C) at Dauphin (Environment Canada, 2016).

2.2. *Tree-ring sample origins*

Samples analyzed for frost rings were drawn from several studies.

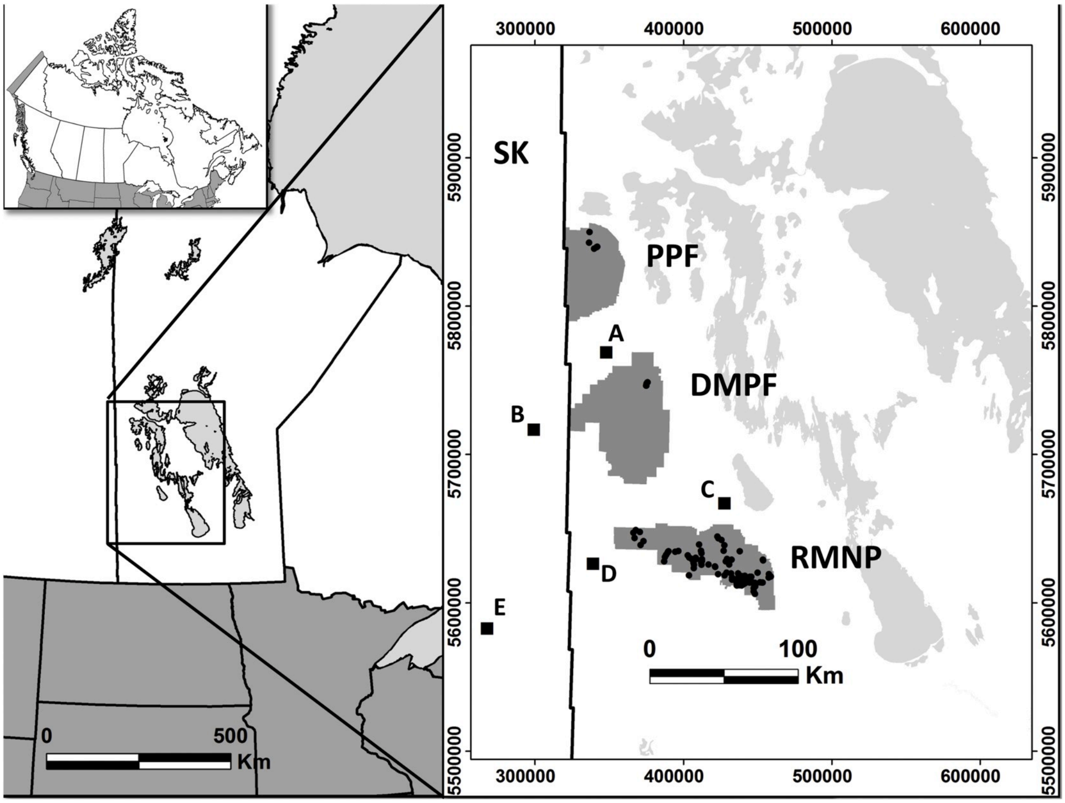

Fig. 1. Study area and location of the black spruce stands sampled (PPF: Porcupine Provincial Forest; DMPF: Duck Mountain Provincial Forest and RMNP: Riding Mountain National Park). The black squares indicate the location of meteorological stations (A: Swan River, B: Kamsack, C: Dauphin, D: Russell and E: Whitewood). The dots in each region indicate sampled locations. In RMNP numerous coniferous species and sites were sampled at breast height or below.

First, in 2007, linear transects were established in six upland black spruce stands from the Clearwater Creek Operating area located in DMPF (Fig. 1). Along each transect, every tenth living black spruce tree was selected for two increment cores at diameter at breast height (DBH) for a total of 144 cores, and two disks were removed from each dead black spruce encountered along the transect (one at DBH, one at base) for a total of 392 cross-sections. This protocol was repeated in six upland black spruce stands from the Rice Creek operating area located in PPF in 2008 (Fig. 1) producing a total of 138 cores and 331 cross sections (Knowles, 2004, 2007; Westwood et al., 2012).

Second, in 2009 two of the previously sampled six black spruce stands in each of PPF and DMPF were revisited and black spruce trees sampled using stem analysis (Fig. 1). In each stand, ten black spruce trees (five living and five dead) were sampled along a 100 m transect for stem analysis (Westwood et al., 2012; Waito et al., 2013). Two black spruce stands were sampled in the DMPF and two in the PPF for a total of 40 trees (20 live and 20 dead). Trees were felled and cross-sections were taken from each tree at 0 m, 0.5 m, 1.3 m, 2 m and each subsequent 0.5 m until stem diameter was less than 2 cm. These stands originated following forest fires in the late 19th century and had a mean origin date at breast height of 1894 (±3.18 StD) and a mean height of 14.6 m (±2.3 StD).

Third in 2009, tree-ring samples were also derived from a large-scale sampling effort in RMNP (Fig. 1) aimed at locating old-trees and reconstructing large-scale disturbances (unpublished data) and from other studies (Tardif et al., 2011, 2016). While only black spruce was sampled in PPF and DMPF; in RMNP black spruce as well as jack pine, white spruce, and tamarack were sampled. Multiple coniferous tree species (dead and alive and of various ages) were sampled at breast height or below (cores and cross-sections). The objective with these data was to compare frost rings among major boreal coniferous species.

2.3. *Laboratory procedures*

All samples collected (cores and cross-sections) were prepared using the same dendrochronological procedures. All samples were air-dried, mounted (if necessary) and sanded using a progression of sandpaper from 80 to 600 grits. All samples were dated, visually crossdated and tree-ring width measured. Visual crossdating and width measurements were also validated using the COFECHA computer program (Holmes, 1983).

For each sample (cores and cross-sections), frost rings were systematically identified using macroscopic features (Glerum and Farrar, 1966) enhanced by a binocular dissecting microscope. For the stem analysis, which only included black spruce trees, each year at each sample height was assessed and the frequency of frost rings was compiled along four radii. In addition, frost rings were also recorded in relation to their cambial age at the time of formation (rings from the pith) and for each cross-section used in stem analysis. Additionally, bark thickness was measured along four radii for the black spruce trees used in the stem analysis.

2.4. *Frost-ring chronologies and climate analyses*

Frost-rings chronologies were compiled for each species and each region (PPF, DMPF and RMNP). Frost rings as a proportion of total rings (pFR) was also determined for black spruce samples originating from stem analysis. For each of PPF and DMPF, the sample proportion ρ, representing the fraction of tree-ring samples k (an integer ≥ 0) of a given population N (an integer >0) identified positively as a frost ring was computed for each year (Tardif et al., 2011). This yielded two black spruce frost-ring pFR chronologies.

To investigate the spatial coherence in the correlation structure between climate and pFR, we used KNMI Climate Explorer (http://www.

knmi.nl; Trouet and Van Oldenborgh, 2013) and the CRU TS4.01 gridded monthly mean of maximum temperature (Tmax) data (Harris et al., 2014). The climate analyses were conducted for the period 1910–2008 and used the black spruce pFR chronologies derived from stem analysis for DMPF, PPF and a regional pooled chronology for both regions (DMPF and PPF). In addition, we compared these pFR chronologies with monthly Tmax from four meteorological stations located closest to the study area (Swan River, MB; Kamsack SK, Whitewood, SK and Russell; MB; Fig. 1). Furthermore, we compared the pFR chronologies with different atmospheric circulation indices including the North Atlantic Oscillation (NAO), the Artic Oscillation (AO); the North Pacific index (NPI); the Pacific Decadal Oscillation (PDO) and the El Niño Southern Oscillation (ENSO 3.4). All climate analyses were conducted using the months of March to June. Furthermore, we compared the regional pooled pFR chronology (DMPF and PPF) with sea surface temperature from March to June. Meteorological data and atmospheric circulation indices were obtained from KNMI Climate Explorer (http://www.knmi.nl) with the exception of data from one meteorological station (Whitewood) which were obtained from Environment Canada (2016, http://climate.weather.gc.ca/historical_data/search_historic_data_e.html). In all climate analyses, years with a pFR below 2% were considered as non-frost years.

3. Results

3.1. Frost-ring frequency

The frost-ring chronologies developed from stem analysis of black spruce trees from DMPF and PPF covered the period 1894–2008 (Fig. 2). Frost rings were found to be more abundant in DMPF compared to PPF (north of DMPF), with a respective total of 182 and 65 frost rings observed for the common period 1894–2008 (Fig. 2). The number of frost-ring years was also higher in DMPF compared to PPF with respectively 51 and 30 frost-ring years over the common period 1910–2008. Comparing both regions, ten frost-ring years were common for the period 1910–2008 with synchrony observed in 1915, 1921, 1926, 1932, 1942, 1946, 1949, 1952, 1969 and 1980. The last frost-ring year was observed in 1998 in DMPF and in 2005 in PPF (Fig. 2). As black spruce trees became older and taller, frost rings also became restricted to the higher portion of the stem and they were observed up to a stem height of 16 m. However, frost rings were most frequently observed in the stem portion below 4 m in height (Fig. 2A and C).

The analysis of cambial age at the time of frost-ring formation indicated that they were more abundant in the early period of the trees life with frost rings essentially recorded at any height in the first 15 years in DMPF and in the first 20 years in PPF (Fig. 3). The stem analysis of black spruce trees also revealed that bark thickness was not a variable associated with frost-ring occurrence. In black spruce, bark thickness varied little along the stem (Fig. 4).

In addition to results derived from stem analysis of black spruce trees, frost rings identified in black spruce trees sampled at the base and at DBH in DMPF and PPF revealed that they were mainly observed in tree rings corresponding to a young cambial age (Fig. 5). Compared to stem analysis (Fig. 2), samples produced at a fixed height did not allow

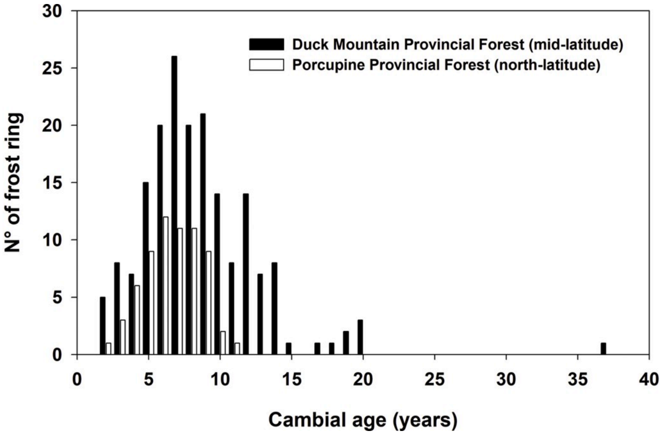

Fig. 3. Number of frost rings according to cambial age in *Picea mariana* trees from Duck Mountain Provincial Forest (mid-latitude; black bars) and Porcupine Provincial Forest (north-latitude; white bars) and derived from stem analysis data.

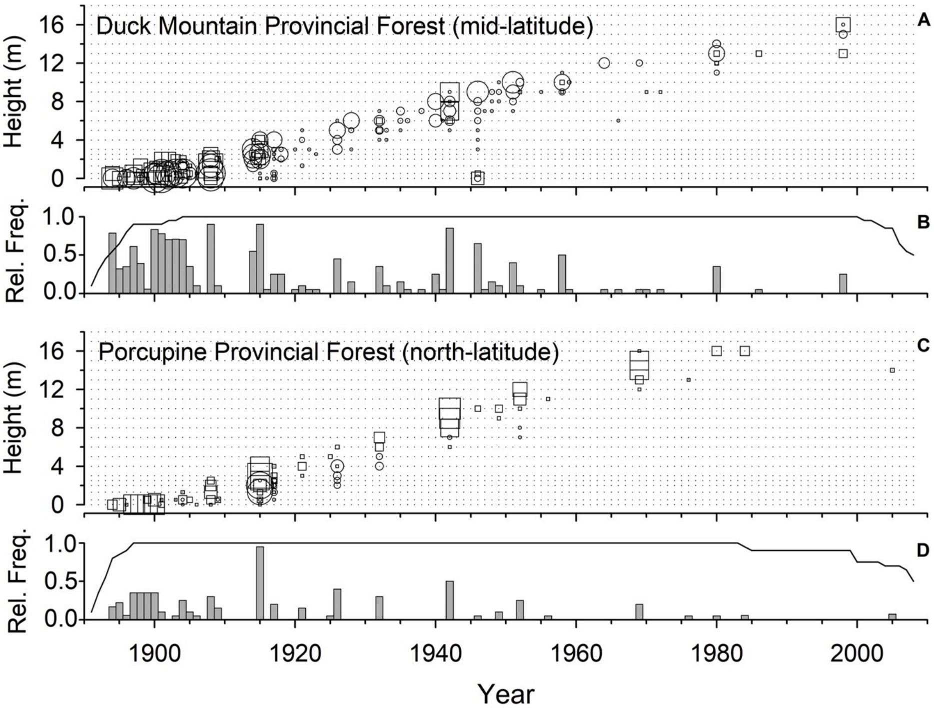

Fig. 2. Distribution of frost rings in *Picea mariana* trees from Duck Mountain Provincial Forest (mid-latitude, A and B) and Porcupine Provincial Forest (north-latitude, C and D). The height at which frost rings were identified is indicated (A and C) and the size of the symbol is relative to frost-ring frequency (A and C). The circle and square symbols refer to the two black spruce stands selected in each region for stem analysis. The relative frequency of frost rings is also indicated for each region in B and D. The number of tree-ring series for each year has been divided by twenty (1 = 20 series; black line) in B and D.

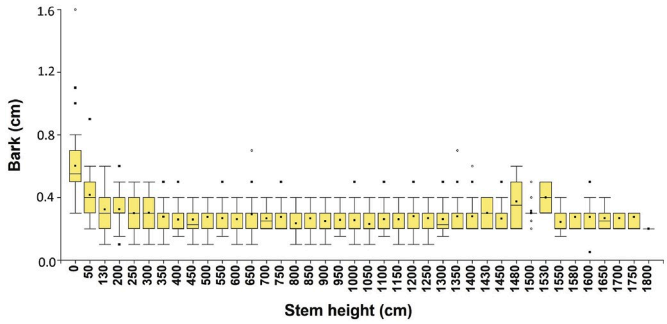

Fig. 4. Mean values (±standard error) of the bark thickness of *Picea mariana* trees from the base to the top and derived for stem analysis data from Duck Mountain Provincial Forest and Porcupine Provincial Forest.

reconstruction of the full spectrum of frost-ring events. In RMNP, sampling of multiple coniferous species and trees of various ages (dead and alive) allowed a frost-ring reconstruction from the early 1800's to the late 1900's (Fig. 6). In RMNP, frost-ring years were observed abundantly and numerous and were synchronous among coniferous species. When comparing frost-ring chronologies from RMNP with those observed in black spruce from PPF and DMPF, frost rings were common to both sites in the years 1900, 1901, 1904, 1905, 1917, 1918, 1926, 1935, 1940 and 1946. When strictly comparing black spruce from RMNP with those of PPF and DMPF, common frost-ring years included 1895, 1900, 1901, 1904, 1905, 1908, 1915, 1917, 1926, 1932 and 1946.

3.2. Frost rings and climate

The frost ring-climate associations were found to be similar using either monthly average of minimum or maximum temperatures and thus only results using Tmax are presented (Figs. 7–9). Differences were observed in the frost ring-climate associations between DMPF and PPF (north of DMPF). The frost rings in DMPF showed a weak positive correlation with April Tmax (Fig. 7B) whereas in the PPF this positive correlation was significant ($p < 0.05$) and spatially coherent over a large area (Fig. 8B). The same field correlation was observed after both frost-ring chronologies (DMPF and PPF) were pooled (Fig. 9). All three frost-ring chronologies also showed a negative and significant association ($p < 0.05$) with June Tmax (Figs. 7–9); this correlation being more spatially coherent with the DMPF frost-ring chronology (Fig. 7D). Using Tmin revealed similar correlations with DMPF being more strongly associated with June temperature whereas PPF (north of DMPF) displayed a positive association with May Tmin and weaker negative association with June Tmin (not presented). Comparing the two frost-ring chronologies (DMPF and PPF) with meteorological data from nearby stations indicated similar spatial coherencies (Table 1). Generally, the two frost-ring chronologies were positively correlated with April Tmax and negatively correlated with June Tmax (Table 1).

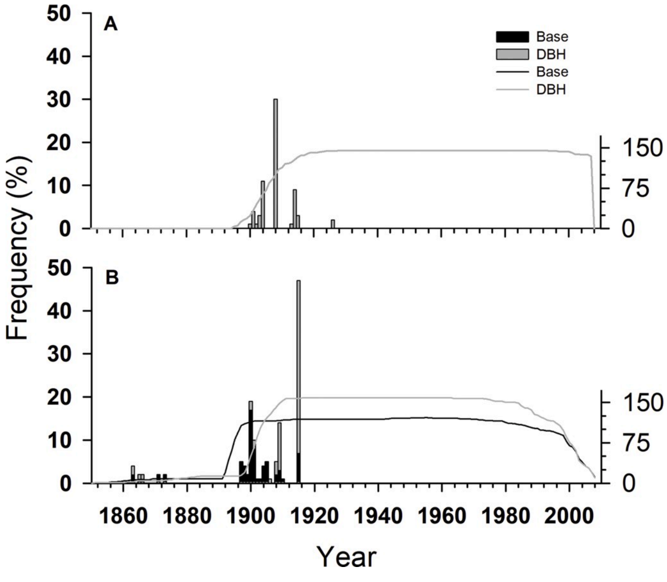

Fig. 5. Distribution of frost rings in *Picea mariana* trees sampled at diameter at breast height (DBH) in Duck Mountain Provincial Forest (A) and sampled at the base and DBH in Porcupine Provincial Forest (B). Solid lines indicate number of tree-ring series.

Quantifying the potential relationship between frost rings and atmospheric circulation indices, a majority of frost-ring chronologies showed to be positively and significantly correlated with the April and May ENSO 3.4 index and negatively and significantly correlated with the May and June AO index (Table 2). The three (PPF, DMPF and regional) frost-ring chronologies were also negatively and significantly correlated with April NPI (Table 2). The NAO and PDO indices showed no significant correlation with the frost-ring chronologies. The correlation field between frost-ring regional chronology and temperature at the 850 mb for the months of March to June showed that there was a strong positive relationship between frost rings and March–April temperature at the 850 mb in the El Niño 3.4 area (Fig. 10AB). Similarly, it corresponded to the formation of a high-pressure system over central Canada in April and to a lesser extent in May (Fig. 10BC).

4. Discussion

4.1. Frost-ring distribution

In this study we presented frost-ring chronologies derived from trees growing in three regions located more than 100 km apart in the mid-Boreal Uplands Ecoregion of interior North America. These frost-ring chronologies resulted from different sampling approaches. The RMNP multi-species frost-ring chronologies developed from dead and living trees revealed greater than expected synchrony among species despite black spruce being known as a late spring frost avoider, given its late initiation of growth compared to other boreal conifers (O'Reilly and Parker, 1982). Referring to the specific weather conditions leading to the damages caused by the 1958 spring frost events in southeastern Manitoba, Cayford et al. (1959) stated that black spruce trees growing in dry upland sites recorded frost injuries that were comparable to those found in white spruce trees. Identifying past frost-ring years may be of interest in stand dynamics studies as late spring frosts have been associated with reduced establishment and survival of coniferous species in both plantations (Tucker et al., 1968) and natural ecosystems (Dy and Payette, 2007). Late spring frosts have also been linked to early insect outbreak termination (Volney, 1996; Sutton and Tardif, 2007; Robson et al., 2015). For example, Sutton and Tardif (2007) reported a termination in forest tent caterpillar outbreaks associated with severe late spring frosts in 1984. Robson et al. (2015) reported that severe spring frosts in 1958 may have limited the northern expansion of jack pine spruce budworm by increasing mortality of overwintering larvae and of terminal tree buds on which the larvae feed on.

Stem analysis revealed that in both DMPF and PPF, most frost rings were observed in the first 20 years of cambial age. Payette et al. (2010) reported similar findings with frost rings in black spruce trees observed before an average maximum cambial age of 37 years. In Siberian larch and Siberian spruce, 80% of frost rings were recorded in the first 20 and 30 cambial years respectively (Gurskaya and Shiyatov, 2006). In another study using Siberian spruce, Gurskaya et al. (2016) reported that 90% of frost rings were observed in trees with a cambial age younger than 40 years. Moreover Kidd and Copenheaver (2014) reported that in jack pine 90% of frost rings occurred within the first 10 cm of diameter. These findings are consistent with the hypothesis that the frequency of frost rings gradually decreases with cambial age (Fayle,

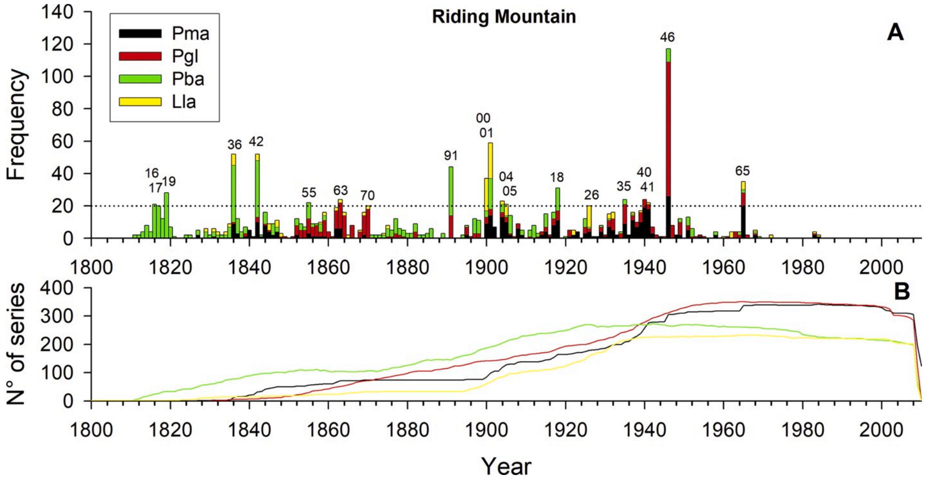

Fig. 6. Frequency of frost rings observed from 1800 to 2010 in four coniferous species (Pma: *Picea mariana*; Pba: *Pinus banksiana*; Pgl: *Picea glauca* and Lla: *Larix laricina*) sampled from Riding Mountain National Park at breast height or below (A). Major frost-ring years are indicated. Solid lines indicate the number of series (B).

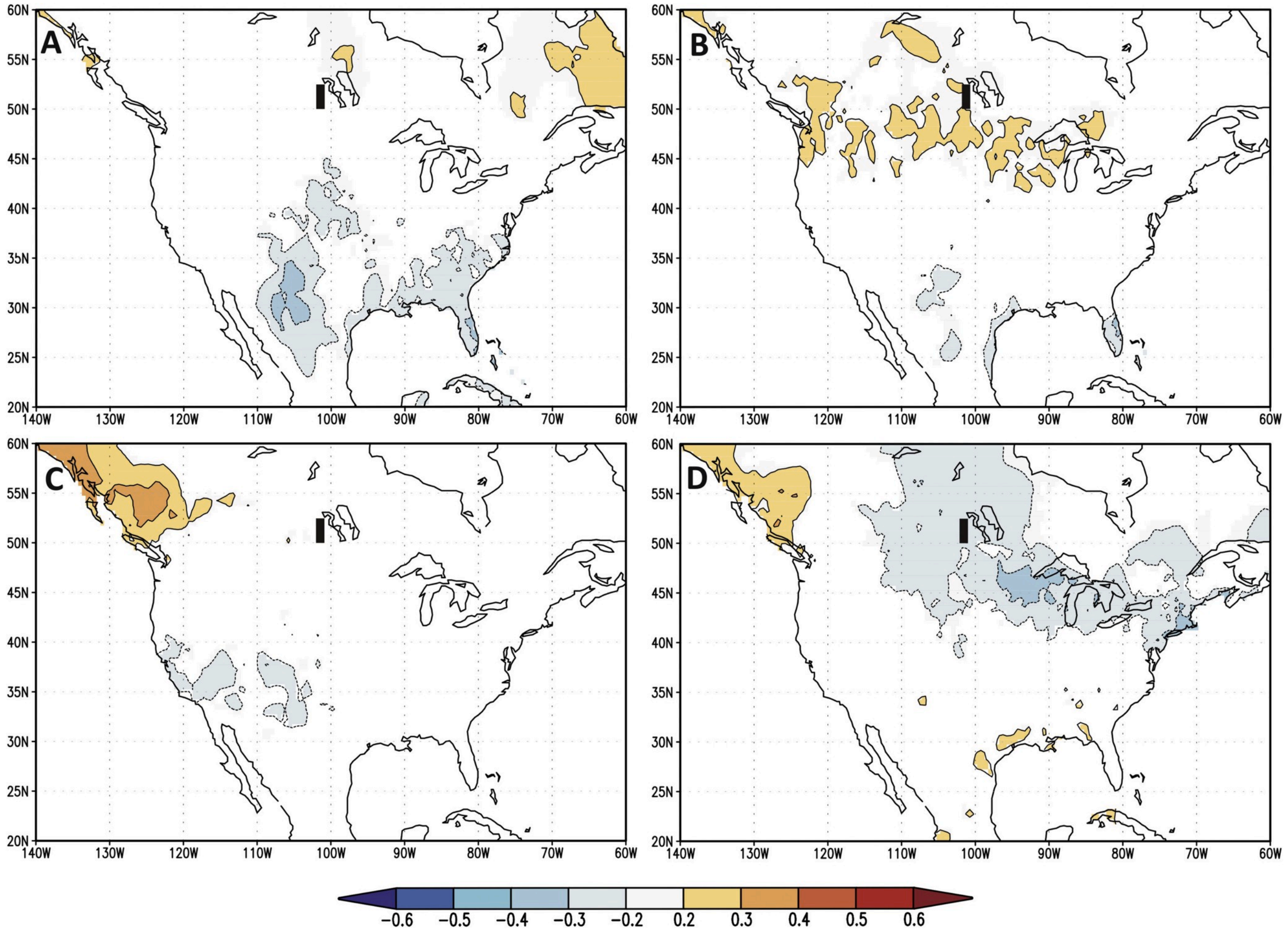

Fig. 7. Spatial Pearson correlation calculated between Duck Mountain Provincial Forest (mid-latitude) frost-ring proportion (pFR>2%) derived from stem analysis and Tmax of the months of March to June (A–D) for the period 1910–2008. The black box shows the location of the study area. The field significance of the maps are below 0.05. Maps were obtained using the KNMI Climate Explorer webpage (http://climexp.knmi.nl/).

1981; Stöckli and Schweingruber, 1996; Schweingruber, 2007; Payette et al., 2010; Arco Molina et al., 2016; Hadad et al., 2019) and this decrease has generally been associated with increased thermal protection to the cambium provided by increasing bark thickness as a tree ages (Bégin et al., 2010; Payette et al., 2010; Kidd and Copenheaver, 2014; Arco Molina et al., 2016). Our stem analysis results however do not fully support this interpretation as in black spruce bark thickness varied little along tree stems (above 30 cm).

Our results suggest that the lack of recorded frost rings at the base of black spruce trees with time may reflect height growth and the basipetal

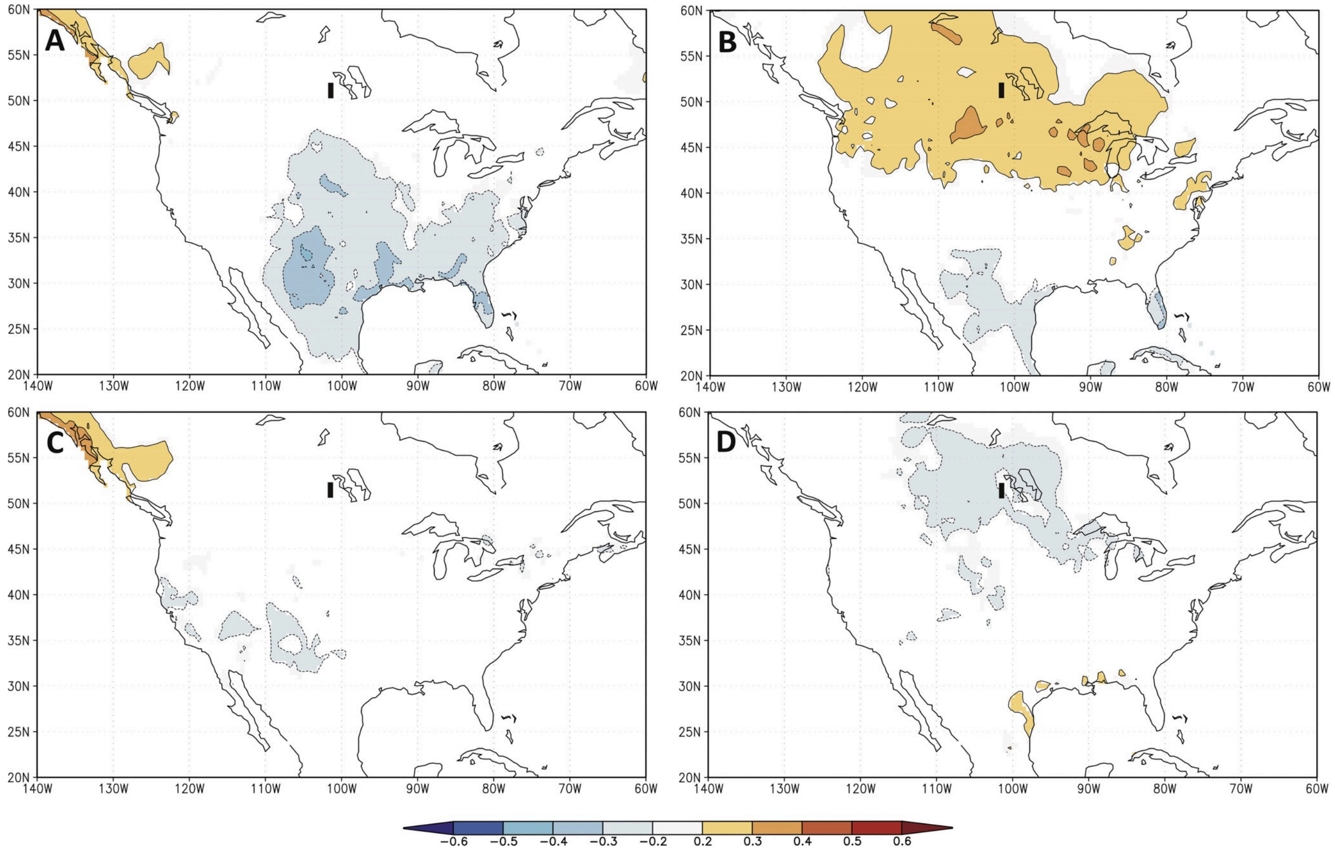

Fig. 8. Spatial Pearson correlation calculated between the Porcupine Provincial Forest (north-latitude) frost-ring proportion (pFR>2%) derived from stem analysis and Tmax of the months of March to June (A–D) for the period 1910–2008. The black box shows the location of the study area. The field significance of the maps are below 0.05. Maps were obtained using the KNMI Climate Explorer webpage (http://climexp.knmi.nl/).

progression of cambium re-activation from the tip to the base in the early growing season rather than variation in bark thickness. This interpretation is supported by the continuous observation of frost rings higher along the tree stem as black spruce trees grew taller from 1894 to 2008. Fraser (1952) had established that in black spruce the cambial activity begins at the tip with no signs of growth at the base, which is delayed by almost two weeks compared to the tip. The lack of frost rings in the lower stem of older trees may thus simply reflect that radial growth had not been initiated compared to the stem portion closest to the tree crown. This hypothesis concurs with Fritts (1976) who mentioned that frost rings were less frequently observed in larger stems than in small branches due to a later initiation of cambial activity. If this finding is generalized among tree species, it indicates that stem analysis of living and/or dead trees, when feasible, could provide a better proxy of extreme frosts than solely sampling at a pre-determined height (i.e., 30 cm or 1.3 m), especially in even-aged forests. Many questions remain, and one concerns the heights across the tree at which the frost events were recorded in the rings. Oke (1970) had reported that under nearly calm, clear sky conditions minimum temperatures occurred 1–50 cm above the soil surface, while the temperature increases towards the tree tip. Assuming a threshold of −6 °C for frost-ring formation in black spruce during the active growing season (Dy and Payette, 2007), is the severity of the climate anomaly leading to a frost ring greater as frost rings are recorded higher along the stem? Comparing young and old trees in uneven-aged black spruce stands using stem analysis may help to answer this question. In all cases, the proximity of frost rings to the pith stresses the higher vulnerability of cambium to frost when the cambium is young (Stöckli and Schweingruber, 1996; Gurskaya and Shiyatov, 2006; Gurskaya, 2007; Payette et al., 2010; Kidd and Copenheaver, 2014; Arco Molina et al., 2016).

4.2. *Frost ring and historical frosts in interior North America*

In this study, frost-ring chronologies developed from stem analysis indicated that late spring frost damage was recorded more frequently in DMPF compared to PPF (north of DMPF). While variations in topography, microclimate, canopy density and soil moisture (Dy and Payette, 2007; Payette et al., 2010; Waito et al., 2013; Gurskaya, 2014; Kidd and Copenheaver, 2014; Arco Molina et al., 2016) may all predispose trees as to whether or not they record extreme frost events, the synchrony/asynchrony observed among the frost-ring chronologies is expected to reflect large-scale climatic phenomenon. Frost rings have been associated with volcanically-forced cooling events (LaMarche and Hirschboeck, 1984; Brunstein, 1996; Salzer and Hughes, 2007), among other causes.

At the regional scale, the PPF frost-ring chronology had a stronger positive association with maximum temperature in April indicating the importance of early (false) spring for cambial reactivation. Hadad et al. (2019) also stressed the importance of early spring and cambial reactivation in the response of *Araucaria araucana* (Molina) K. Koch trees to frosts. Compared to Kidd and Copenheaver (2014), who did not observe any association between frost rings and temperature in jack pine populations from Michigan, our results clearly indicated that years with abundant frost rings in PPF (north-latitude region) tended to occur in years characterized by an early growing season start (warm April). This likely rendered trees more susceptible to frost damage from late spring sub-freezing temperatures. The association between a warm spring and frost damage was more prominent in PPF compared to DMPF, where the growth season usually starts earlier due to warmer conditions. Interestingly, the DMPF recorded more total frost-ring years than the PPF and this may be associated with a generally milder/earlier spring leading to

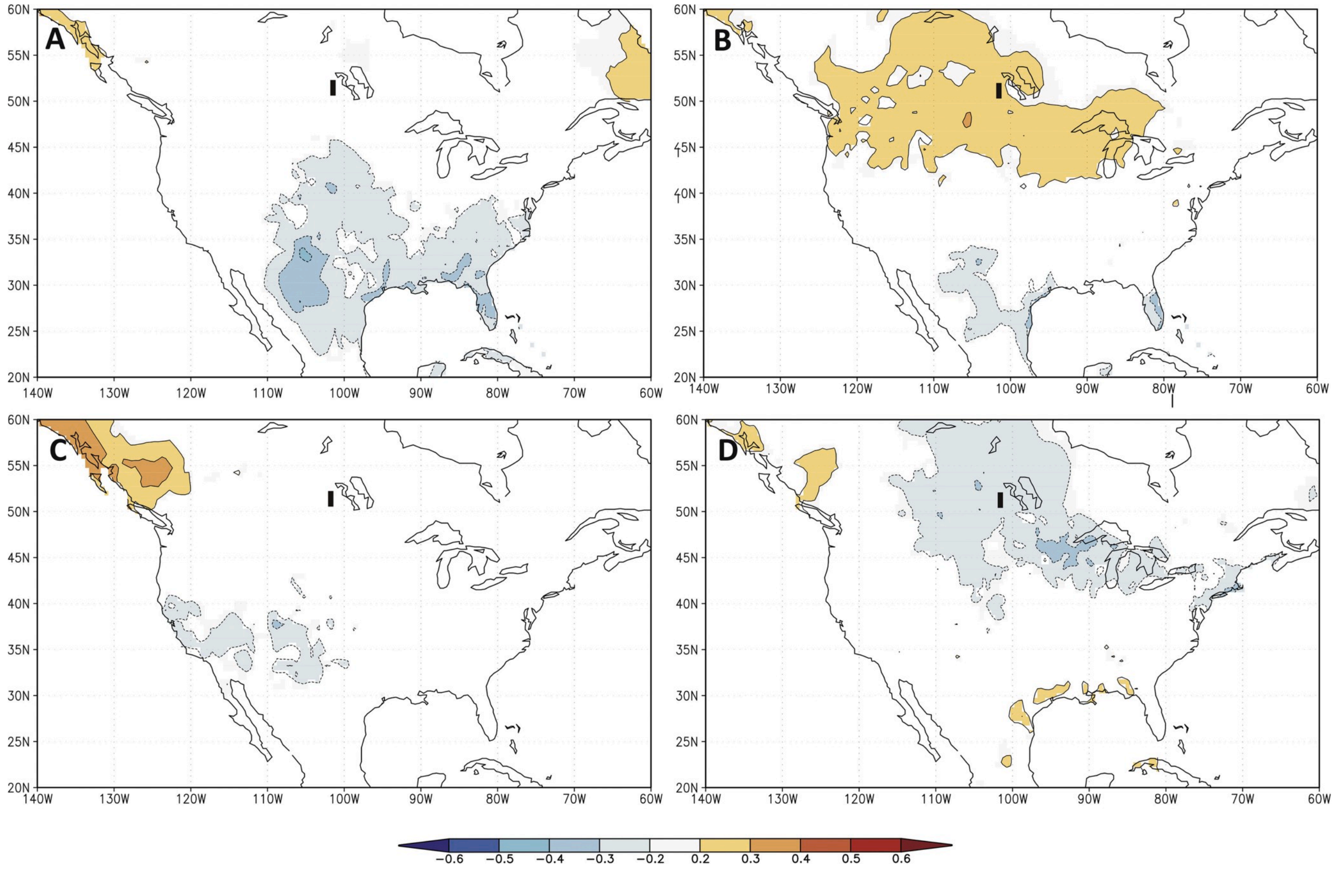

Fig. 9. Spatial Pearson correlation calculated between regional pooled frost-ring proportion (pFR>2%) derived from stem analysis and Tmax of the months of March to June (A–D) for the period 1910–2008. The black box shows the location of the study area. The field significance of the maps are below 0.05. Maps were obtained using the KNMI Climate Explorer webpage (http://climexp.knmi.nl/).

Table 1
Pearson correlation between the frequency logarithmic of frost-ring chronologies (DMPF = Mid-latitude, PPF=North-latitude, and Regional) and maximum temperature data from nearby meteorological stations for the month of April to June. The location of the meteorological stations in relation to the sampling sites is indicated on Fig. 1. Correlation coefficient, pvalue and number of observations are presented. Bold numbers are significant.

Station	Period	Elev.	FR	March	April	May	June
Swan River	*1904–2006*	*347*	***DMPF***	*−0.16; 0.36; 33*	***0.36;0.003; 62***	*0.08; 0.512; 60*	***−0.28; 0.02; 64***
			PPF	*−0.16; 0.34; 33*	***0.37; 0.002; 62***	*0.00; 1.00; 60*	***−0.31; 0.01; 64***
			Regional	*−0.21; 0.23; 33*	***0.39; 0.001; 62***	*0.05; 0.69; 60*	***−0.31; 0.01; 64***
Kamsack	*1907–1969*	*440*	***DMPF***	*0.12; 0.39; 49*	***0.29; 0.02; 57***	*0.22; 0.09; 56*	*−0.19; 0.16; 56*
			PPF	*−0.08; 0.54; 49*	***0.37; 0.004; 57***	*0.21; 0.10; 56*	*−0.19; 0.14; 56*
			Regional	*0.05; 0.72; 49*	***0.35; 0.007; 57***	***0.24; 0.07; 56***	*−0.20; 0.12; 56*
Whitewood	*1902–2007*	*598*	***DMPF***	*0.05; 0.65; 92*	***0.23; 0.03; 92***	*0.16; 0.14; 92*	***−0.22; 0.04; 92***
			PPF	*0.02; 0.83; 92*	***0.26; 0.01; 92***	*0.16; 0.54; 92*	***−0.22; 0.04; 92***
			Regional	*0.04; 0.71; 92*	***0.26; 0.02; 92***	*0.13; 0.23; 92*	***−0.24; 0.03; 92***
Russell	*1883–1989*	*567*	***DMPF***	*0.13; 0.27; 69*	*0.20; 0.07; 74*	*0.17; 0.13; 75*	***−0.24; 0.03; 76***
			PPF	*0.07; 0.52; 70*	***0.27; 0.01; 75***	*0.10; 0.39; 76*	***−0.26; 0.02; 76***
			Regional	*0.11; 0.35; 69*	***0.24; 0.03; 74***	*0.15; 0.18; 75*	***−0.27; 0.01; 76***

earlier resumption of cambial activity, thus increasing the risk of frost injuries.

Many historical observations originating from central Canada support the fact that frost-ring years were associated with either early (false) springs and/or normal springs followed by anomalous subfreezing temperatures. For instance, in the year 1836 a frost ring was observed in four coniferous species growing in RMNP. Historical observations indicate that on June 8th 1836, a late spring frost occurred in Manitoba severely damaging grains, root crops and tree foliage (Hill, 1890). Rannie (1992) also reported frost to occur in August 1836 and in July–August 1836. The lack of data regarding the position of the frost ring within tree rings in RMNP precludes discussing the impact of these late summer frosts on tree growth in interior North America. The year 1836 appeared to have been characterized by severe frost in the early and late growing season and interestingly many frost-ring years also corresponded to years in which light rings (pale latewood) were produced in jack pine trees (Girardin et al., 2009; Tardif et al., 2011). Light rings in jack pine are indicative of cool late spring and cool late summer (particularly daytime maximum temperatures) and these temperature anomalies were associated with increased cyclonic activity over much of central Canada (Tardif et al., 2011). In the samples from RMNP, the year 1965 was associated with an earlywood frost ring in numerous coniferous species, a pale latewood (light ring) in jack pine (Tardif et al., 2011) and a latewood frost ring was recorded in Great Basin bristlecone

Table 2

Person correlation between the logarithmic of frost-ring chronologies (DMPF = Mid-latitude, PPF = North-latitude, and Regional) and both monthly atmospheric circulation indices for the months of March to June. Correlation coefficient, pvalue and number of observation are presented. Bold numbers are significant.

Indices	FR	March	April	May	June
NAO	***DMPF***	*−0.16; 0.10; 96*	*0.14; 0.14; 96*	*−0.17; 0.09; 96*	*−0.10; 0.31; 96*
	PPF	*−0.19; 0.06; 96*	*0.18; 0.07; 96*	*−0.15; 0.12; 96*	***−0.20; 0.04; 96***
	Regional	*−0.19; 0.06; 96*	*0.17; 0.08; 96*	*−0.17; 0.08; 96*	*−0.15; 0.12; 96*
AO	***DMPF***	***−0.21; 0.03; 93***	*0.05; 0.6, 93*	*−0.17; 0.09; 93*	***−0.23; 0.02; 93***
	PPF	*−0.19: 0.06; 93*	*0.06; 0.51; 93*	***−0.24; 0.01; 93***	***−0.24; 0.01; 93***
	Regional	***−0.22; 0.03; 93***	*0.06; 0.56; 93*	***−0.21; 0.03; 93***	***−0.25; 0.01; 93***
NPI	***DMPF***	*−0.01; 0.96; 99*	***−0.29; 0.003; 99***	*−0.08; 0.41; 99*	*0.16; 0.11; 99*
	PPF	*−0.16; 0.12; 99*	***−0.27; 0.01; 99***	*−0.18; 0.07; 99*	*0.18; 0.07; 99*
	Regional	*−0.07; 0.47; 99*	***−0.31; 0.001; 99***	*−0.13; 0.19; 99*	*0.18; 0.07; 99*
PDO	***DMPF***	*−0.08; 0.47; 95*	*0.21; 0.07; 95*	*0.11; 037; 95*	*0.10; 0.30; 95*
	PPF	*−0.15; 0.19; 95*	*0.14; 0.23; 95*	*0.03; 0.94; 95*	*0.104; 0.31; 95*
	Regional	*−0.12; 0.30; 95*	*0.19; 0.09; 95*	*0.08; 0.50; 95*	*0.11; 0.27; 95*
ENSO 3.4	***DMPF***	*0.18; 0.07; 96*	***0.24; 0.02;96***	***0.29; 0.003; 96***	*0.08; 0.39; 96*
	PPF	*0.06; 0.52; 96*	*0.15; 0.12; 96*	***0.21; 0.03; 96***	*0.04; 0.64; 96*
	Regional	*0.14; 0.16; 96*	***0.21; 0.03; 96***	***0.28; 0.005; 96***	*0.07; 0.46; 96*

NAO: North Atlantic Oscillation.
AO: Artic Oscillation derived from Sea Level Pressure.
NPI: North Pacific Index.
PDO: Pacific Decadal Oscillation.
ENSO: El Niño Southern Oscillation.

pine (LaMarche and Hirschboeck, 1984). These findings indicate that a large-scale network of tree-ring anomalies for interior North America and prior to instrumental records may help to reveal intricate climate relationships.

In general, many of the frost rings we noted and that occurred since the commencement of instrumental weather measurement in the area corresponded to the historical weather records. For example, the 1915 frost ring, well-represented in the trees of DMPF and PPF, corresponded to the coldest June minimum temperature recorded at Swan River (−5.0 °C on June 8th; Environment Canada, 2016). In 1951, a frost ring observed in three coniferous species in RMNP corresponded to the coldest June minimum temperature recorded at Whitewood station (−4.4 °C on June 1st; Environment Canada, 2016). In RMNP, Tucker et al. (1968) indicated that in 1951 frost damage was observed on more than 65% of young white spruce transplants resulting from a warm May followed by severe frost occurring in June. In RMNP, Tucker et al. (1968) also reported that frost damage was generally more severe on moist to very moist sites in low-lying areas. In DMPF, a frost ring was observed in 1958 and corresponded to the coldest June minimum temperature at Dauphin (−3.9 °C on June 5th; Environment Canada, 2016). The spring of 1958 corresponded to massive frost damages to trees following an early onset of growth associated with a warm April (Cayford et al., 1959). Some of the most recent late spring frosts were also recorded in the samples included a late June frost in 1998, which forced many farmers in the eastern Prairies and Ontario to re-seed their crops (Environment Canada, Canada's Top Ten Weather Stories of 1998, http://www.ec.gc.ca/meteo-weather/default.asp?lang=En&n=3DED7A35-1#t5).

4.3. Frost ring and atmospheric circulation

Global patterns of change have been attributed to changes in large-scale climatic processes such as the North Atlantic Oscillation, the Arctic Oscillation and the El Niño Southern Oscillation (MacGillivray et al., 2010). Many extreme temperature events were caused by extremes in atmospheric circulation, the predisposition of these circulation patterns can be influenced by the underlying sea surface temperature patterns (Arblaster and Alexander, 2012). During El Niño years the chances of warm temperature anomalies are increased over southern Canada from early winter to early spring (Shabbar and Bonsal, 2004). Arblaster and Alexander (2012) showed that the hottest days were found to be significantly influenced by the phase of the El Niño. In Alberta, there have been registered significant correlations between stronger El Niño events, warmer ocean temperatures and warmer winter-spring temperatures and early growing season (Beaubien and Freeland, 2000).

In our study, a weak but significant positive association was found between frost-ring frequency and ENSO suggesting that during an El Niño event an increased probability of false springs is observed. In these years in particular, northern trees may begin their growing earlier than average making them more sensitive to subsequent frost events. In Canada, warmer springs were associated with El Niño. The maximum value of daily maximum temperatures in each month in Canada were observed during El Niño events (Arblaster and Alexander, 2012). Four frost years that were synchronous in both PPF and DMPF regions (1926, 1952, 1969 and 1980) exhibited El Niño weather conditions. Inversely, in Argentina, large-scale synchrony in earlywood frost rings in *A. araucana* trees was associated with weather conditions associated with ENSO and frost rings were more abundant in La Niña events, which corresponded to earlier spring in South America (Hadad et al., 2019). Barbosa et al. (2019) also showed a relationship between frost rings in bristlecone pine and atmospheric circulation in the west-central United States. Therefore, the building of a large-scale frost-ring network may provide a better understanding of how the atmospheric circulation affects the forests around the world. Interestingly, the Arctic Oscillation (AO) was also significantly and negative associated with frost-ring formation in spring. Thus, our results suggest that during the positive phase of the AO fewer cold air events may be observed over the study area. In contrast, Wettstein and Mearns (2002) analyzed the AO index in eastern Canada and showed more extreme cold events in AO positive years in spring.

5. Conclusion

Results revealed a strong spatial coherency regarding the climate conditions at the origin of frost rings in black spruce growing in the Boreal Plains Ecozone. A warm spring (or early onset of radial growth) was implicated in frost-ring formation and this was most strongly observed in the more-northern PPF than in DMPF. After the onset of radial growth, sub-freezing temperatures are of prime importance for frost-ring formation. As black spruce exits dormancy earlier under a changing climate, southern populations will be more affected by late frost. In our study area, these cold events usually occur from mid-May to mid-June. Atmoshperic circulation indices suggest that warm springs may be related to El Niño events and frost events may be affected by phases of the Arctic Oscillation. The results of this study also revealed that "continuous" frost-ring chronologies may be successfully developed following stem analysis of even-aged stands from the boreal forest. Compared to sampling at a fixed height, stem analysis as a technique was more successful to identify the sub-freezing temperature signal as frost rings were progressively recorded in smaller and younger sections forming along the stem as trees grow. Holding sampling height constant, trees from various age classes would need to be sampled over a larger area to obtain similar results. In contrast to the commonly accepted view that bark thickness is an important factor in frost-ring formation, our results suggest that bark thickness may not play an important role for

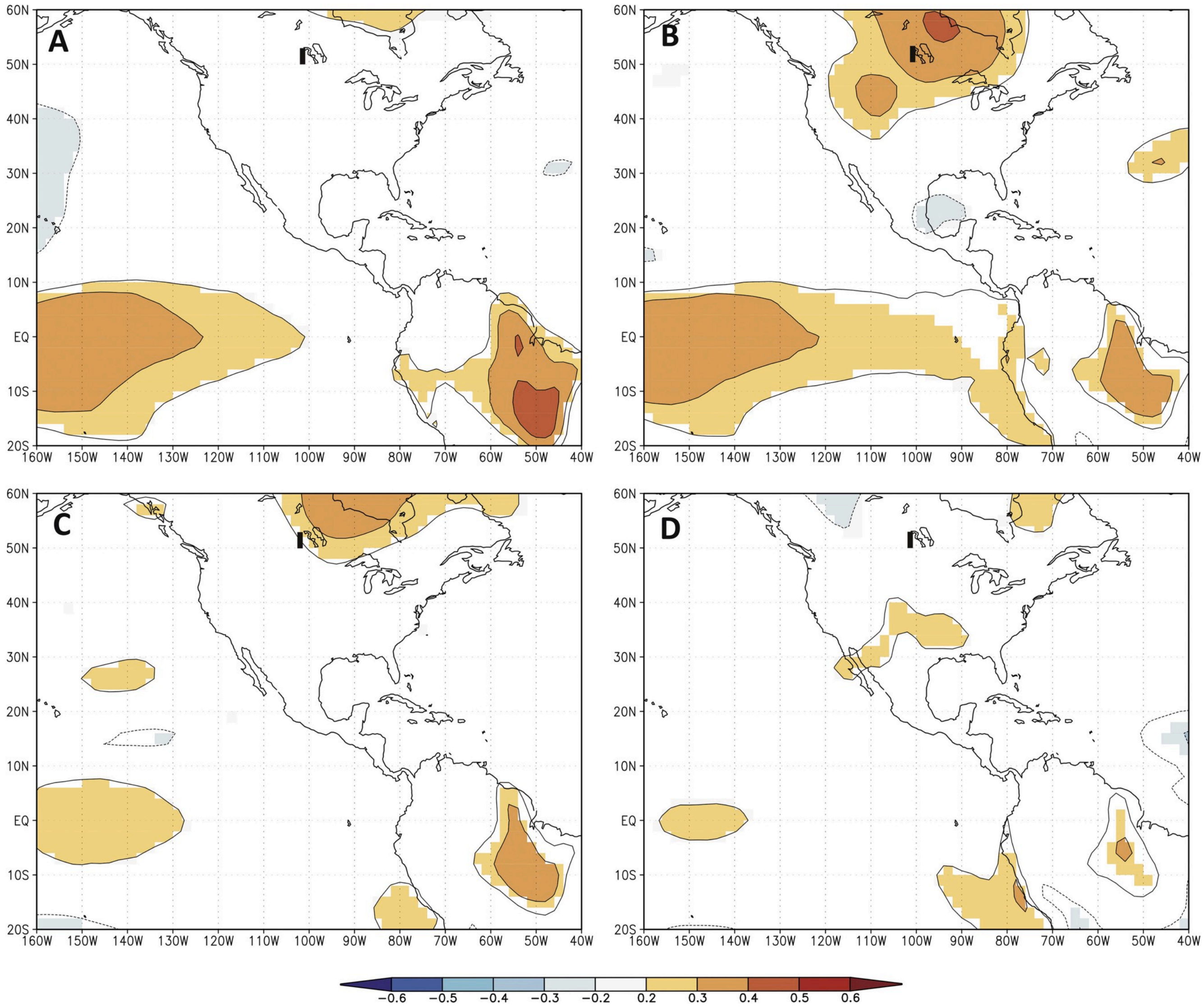

Fig. 10. Spatial Pearson correlation calculated between regional pooled frost-ring proportion (pFR>2%) derived from stem analysis and temperature at the 850 mb of the months of March to June (A–D) for the period 1910–2008). The black box shows the location of the study area. The field significance of the maps are lower than 0.05. Maps were obtained using the KNMI Climate Explorer webpage (http://climexp.knmi.nl/).

black spruce. The lack of frost rings recorded along the lower stem as cambial age increases probably reflects the basipetal progression of the onset of radial growth rather than insulating properties of the bark. Further analysis using micro-core sampling at various heights could help confirm this hypothesis. Finally, our study indicated that developing an extended network of frost-ring chronologies prior to the period of instrumental climate data would be helpful to document large spatial climate anomalies in areas with low climate data coverage and to assess the impact of future climate changes by providing long-term background records.

Declaration of competing interest

The authors declare no conflict of interest.

CRediT authorship contribution statement

Martin Hadad: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Jacques C. Tardif:** Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Formal analysis, Writing - review & editing. **France Conciatori:** Validation, Writing - review & editing. **Justin Waito:** Data curation, Writing - review & editing. **Alana Westwood:** Data curation, Writing - review & editing.

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