Radial-Growth Response of Forest-Tundra Trees to Climate in the Western Hudson Bay Lowlands

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ABSTRACT. The effects of climate on radial growth of *Larix laricina* (Du Roi) K. Koch, *Picea glauca* (Moench) Voss, and *Picea mariana* (Mill) BSP were investigated in the Hudson Bay Lowlands of northern Manitoba. The objective was to characterize spatial and temporal variations in growth of trees across the forest-tundra ecotone. Along a 250 km transect, 299 trees were sampled in three zones: northern forest, central tundra, and southern forest. Ring-width indices were compared with climate through correlation- and response-function analyses. Numerous years of suppressed growth at the three locales resulted from cooling that followed major volcanic eruptions at much lower latitudes. Temperatures during July of the current year and autumn of the previous year were most limiting, particularly for *L. laricina*, which was temperature-sensitive across the region. A weakened growth response to temperature during the 1940–60 period was likely due to atmospheric circulation shifts. Most chronologies were intercorrelated, which suggests common environmental forcing, though environmental influences differed in the southern forest (particularly for *P. mariana*). The source of this disparity has yet to be determined.

Key words: dendroclimatology, forest-tundra, Churchill, ring-width, *Picea glauca*, *Picea mariana*, *Larix laricina*, Wapusk National Park, response-function, Hudson Bay lowlands

RÉSUMÉ. Les effets du climat sur la croissance radiale de *Larix laricina* (Du Roi) K. Koch, de *Picea glauca* (Moench) Voss et de *Picea mariana* (Mill) BSP ont fait l'objet d'une étude dans les basses-terres de la baie d'Hudson, au nord du Manitoba. L'objectif de cette étude consistait à caractériser les variations spatiales et temporelles en matière de croissance des arbres à l'échelle de l'écotone de la toundra forestière. Le long d'un transect de 250 km, 299 arbres ont été échantillonnés dans trois zones : la forêt septentrionale, la toundra centrale et la forêt méridionale. Les indices de la largeur des cernes ont été comparés aux données climatiques au moyen d'analyses de corrélation et de fonction de réponse. De nombreuses années de croissance affaiblie aux trois endroits découlaient du refroidissement ayant suivi d'importantes éruptions volcaniques à des latitudes beaucoup moins élevées. Les températures enregistrées en juillet de l'année courante et à l'automne de l'année précédente étaient plus restrictives, particulièrement dans le cas de *L. laricina*, qui était sensible aux températures dans toute la région. La réponse de croissance affaiblie enregistrée par rapport aux températures au cours de la période allant de 1940 à 1960 était vraisemblablement attribuable aux décalages de circulation atmosphérique. La plupart des chronologies ont fait l'objet d'inter-corrélations, et celles-ci laissent entrevoir un forçage environnemental courant, bien que les influences environnementales différaient dans la forêt méridionale (particulièrement dans le cas de *P. mariana*). La source de cette disparité n'a toujours pas été déterminée.

Mots clés : dendroclimatologie, toundra forestière, Churchill, largeur des cernes, *Picea glauca*, *Picea mariana*, *Larix laricina*, parc national Wapusk, fonction de réponse, basses-terres de la baie d'Hudson

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INTRODUCTION

The Arctic tree line at the limit of the forest-tundra ecotone is an important biogeographical boundary for climate change investigations. The Arctic front oscillates over this ecotone, creating the gradation between the taiga to the south and the tundra to the north, and is reflected in the shift from boreal to tundra taxa (MacDonald et al., 1998). The position of the Arctic tree line has been linked with the historical position of the Arctic front (Scott et al., 1988; Beringer et al., 2001), and vice versa (Foley et al., 1994; Pielke and Vidale, 1995). It has been speculated that Arctic warming could move the Arctic tree line poleward from its present location, as has occurred previously during Holocene warm periods (MacDonald et al., 1998). This displacement could have significant impacts on the ecosystems within this ecotone through changes in habitat (Scott and Stirling, 2002), fire cycles (Arseneault and Payette, 1992), and regional climate (Pielke and Vidale, 1995).

Many researchers have concluded that growing-season temperature is the most important factor limiting tree
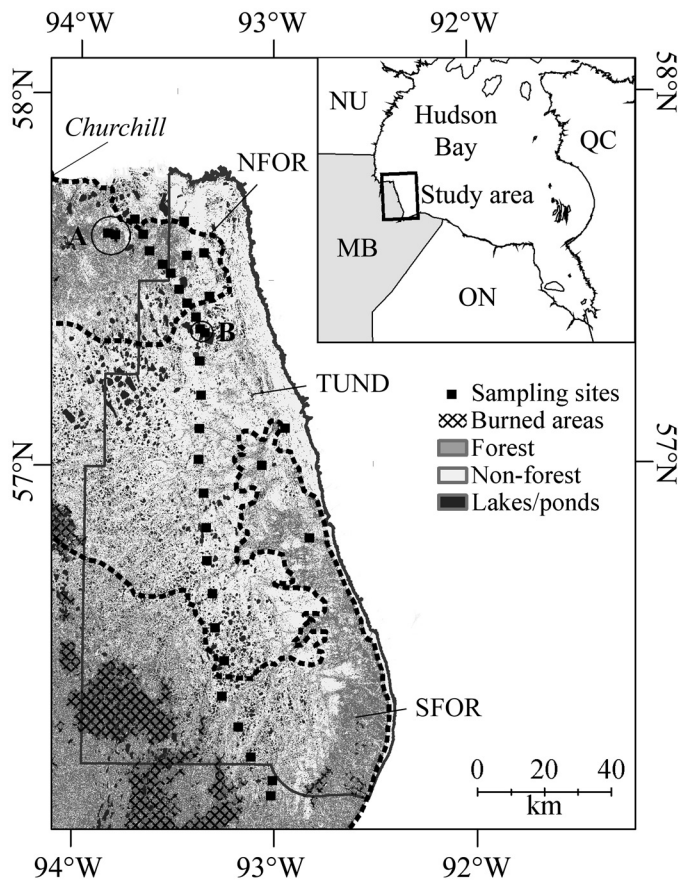
FIG. 1. Locations of the 2004–05 tree core sampling from three areas: the Northern Forest (NFOR), the Central Tundra (TUND), and the Southern Forest (SFOR). The solid grey line outlines Wapusk National Park, and the dashed black lines outline the forested sites. Circles indicate sites sampled in (A) 2002–03 and (B) 2008. The 17 vegetation classes determined by Brook and Kenkel (2002) were grouped into two classes: forest and non-forest.

growth around Churchill in northern Manitoba (Guiot, 1985, 1987; D'Arrigo and Jacoby, 1992; Girardin et al., 2005). Extensive tree-ring research has also been done in northern Quebec, from James Bay up to Hudson Strait and Ungava Bay (e.g., Payette et al., 1985; Jacoby et al., 1988; Arquillière et al., 1990; Hofgaard et al., 1999; Wang et al., 2002). However, little research has examined tree ring–climate relationships in the Hudson Bay Lowlands of northern Manitoba, except close to the town of Churchill. The potential for environmental change in the lowland region is amplified because of climate feedbacks with Hudson Bay (Rouse, 1991), and the region offers an excellent opportunity to evaluate the potential for disparity in growth responses to climate along an environmental gradient that transects the forest-tundra ecotone (Fig. 1). This ecotone extends from the continuous forest limit to the Arctic tree line, and trees at the northern end of this range are at the edge of their ecological amplitude (Danby and Hik, 2007). These individuals are climate-sensitive and thus good candidates for evaluating the impact of climatic change within the ecotone (Payette et al., 2001). If temperatures continue to increase and thus prolong the growing season, then growth conditions could improve for

trees at the northern end of the ecotone (Bunn et al., 2005). However, tree growth could be limited farther south as increased evapotranspiration reduces moisture availability (Dang and Lieffers, 1989).

Environmental conditions within Wapusk National Park (NP) and the Churchill Wildlife Management Area (CWMA) are modified by a number of factors operating at various spatial and temporal scales, including frontal activity, Hudson Bay ice and circulation dynamics, regional advection, and inherent variations in temperature and precipitation from north to south (Scott et al., 1988; Rouse, 1991). Thus, the objective of this study was to evaluate spatial and temporal variations in tree growth in terms of ring width variation in Wapusk NP and the adjacent CWMA. It was hypothesized that tree growth is less sensitive to temperature in the southern region of the study area. Within this context, two research questions were formulated: (1) What are the main climatological controls on the growth of trees within the study area? and (2) How does this growth response vary at the landscape scale? Tree ring analyses (Cook and Kairiukstis, 1990; Fritts, 2001) were used to address these questions. Dendrochronology (the scientific dating of tree rings) and dendroclimatology (the use of dated tree rings to study past and present climate) provide an effective means to gain insight into climatic and environmental change (Fritts, 2001). Ring-width chronologies provide annually resolved time series of tree growth, which can then be used to make inferences about the environmental factors that control development of tree rings (Hughes, 2002; Luckman, 2007).

MATERIALS AND METHODS

Study Area

The study area extended from just north of the Nelson River in southwest Wapusk NP to the edge of the northern forest (NFOR), east of Churchill (Fig. 1). The southern forest (SFOR) of the CWMA and Wapusk NP is primarily open forest dominated by *Picea glauca* (Moench) Voss (white spruce) and *Picea mariana* (Mill) BSP (black spruce). *Larix laricina* (Du Roi) K. Koch (tamarack) becomes more common as conditions change from upland forest and wetland bog/forest to fen. The central region of the park (TUND) is primarily open tundra peatlands, with forest ranging from isolated krummholz individuals to patches of open forest. Riparian forests are common in this central region, where better drainage makes riverbanks more favourable to recruitment (Lloyd et al., 2003). The northern forest portion of the region is similar to the southern forested area in terms of open forest, peatlands, and fens. However, an important ecological barrier separates the two forests in the form of the central TUND region, where trees are limited primarily to isolated krummholz stands. The NFOR region also presents considerably different growing conditions because of frequent, cool northwesterly onshore

TABLE 1. General characteristics of the three regions sampled in Wapusk National Park and the Churchill Wildlife Management Area.

Region[1]	Latitude (°N)[2]	Longitude (°W)	Jan/July/Annual: Temperature (°C)[3]	Precipitation (mm)	Elevation (m)[4]
NFOR	58°45′00″	94°00′00″	-27.0/12.3/-6.8	16.0/56.3/421.6	16.0 ± 9.0
TUND	58°00′00″	93°30′00″	-26.5/13.1/-6.0	16.3/65.9/450.2	34.4 ± 16.0
SFOR	57°22′48″	93°07′48″	-25.9/13.9/-5.3	16.0/73.2/470.0	45.6 ± 8.0

[1] NFOR = northern forest, TUND = central tundra, SFOR = southern forest.
[2] Latitude and longitude listed are for the centroids of all sampling sites per zone.
[3] 1971−2000 normals (New et al., 2000).
[4] Mean elevation of all sites sampled per zone, plus or minus one standard deviation.

winds from Hudson Bay (Rouse, 1991). Although Hudson Bay is typically completely ice-covered from January to May and ice-free from mid August to late October (Wang et al., 1994), the ice-free period has lengthened in recent years (Gagnon and Gough, 2005; Scott and Marshall, 2010).

Churchill Climate

All climate data refer to the 1971−2000 normal (Environment Canada, 2010). Mean annual air temperature at Churchill (58°45′ N, 94°04′ W) is -6.9°C. Temperatures typically range from -26.7°C in January to 12.0°C in July, and mean June−August temperature is 10.1°C. From 1980 to 2009, summer temperatures increased by 0.4°C relative to the normal. A mean total of 558.9 mm of precipitation falls each year, with 52% occurring as snow.

To account for differences in climate across the 250 km sampling transect, we obtained gridded climate data at 0.5° × 0.5° intervals covering the 1901−2006 period from the Climate Research Unit (New et al., 2000) in order to determine the climate of each of the three sampling areas. Mean annual temperature, precipitation sums, and elevation all increase from north to south at rates per km of ~0.01°C, 0.31 mm, and 0.19 m, respectively (Table 1). Thus, the NFOR region is on average 1.5°C cooler, receives 48.4 mm less precipitation annually, and is 29.6 m lower than the SFOR; while the TUND region is 0.7°C cooler, receives 19.8 mm less precipitation, and is 11.2 m lower than the SFOR.

In the Churchill area, summers (July–August) with mean temperatures lower than 11.5°C occur over 33% of the record (Environment Canada, 2010) and indicate the influence of an Arctic air mass over Churchill (Scott, 1996). Conversely, mean summer temperatures between 11.5°C and 13.3°C (45% of the time) indicate a dominant Pacific air mass. During relatively hot summers (> 13.3°C), either Maritime Tropical air masses from the Gulf of Mexico or Pacific air masses that have traveled northward from California across deserts and prairies dominate over Churchill (Scott, 1996). These hot summers are usually characterized by either wet (Maritime air: 13%) or dry (Pacific air from California: 9%) conditions (wet or dry represents > ± 0.5σ of the mean precipitation for the 1971−2000 period). These climatic conditions are comparable to those found by Bryson (1966)

for the entire Hudson Bay lowlands and illustrate a marked variability in summer conditions, which could contribute to the high floristic diversity at Churchill (Scott, 1996).

Fieldwork

During the 2004 and 2005 field seasons, sampling was completed along a transect from the CWMA across the interior peatlands to the southeast and into the continuous forest zone of southern Wapusk NP. Samples collected in those years from the northern portion of the CWMA were supplemented with cores collected in 2002 and 2003 near the Churchill Northern Studies Centre (indicated by "A" in Fig. 1). In 2008, several *L. laricina* at sites within the TUND region ("B" in Fig. 1) were cored opportunistically during maintenance of meteorological stations erected in the area in 2004.

Sample sites (at intervals of 5 km in 2004 and 10 km in 2005) were visited by helicopter, and at least two (2004) or three (2005) trees were bored to extract two breast-height cores from each. Since the intent of this work was to cover the CWMA and Wapusk NP, the sample size was kept small in order to ensure complete coverage within time and budget constraints. For analysis, study sites were grouped into the three distinct zones—NFOR, TUND, and SFOR—on the basis of vegetation composition and location.

Laboratory Processing

Cores were dried prior to being glued into core boxes. They were progressively sanded to ensure all scratches were removed (Stokes and Smiley, 1996). A Velmex tree-ring measuring system (Velmex, Inc., Bloomfield, NY) was used to measure the width of all rings in each core (0.001 mm resolution). Cross-dating between cores was conducted (Yamaguchi, 1991) and statistically validated using the program COFECHA to account for missing and false rings (Holmes, 1992).

Chronology Standardization

A two-stage detrending process was employed to standardize the ring-width chronologies using the program ARSTAN (Holmes, 1992). First, a negative exponential

TABLE 2. Statistical characteristics of residual chronologies produced for Wapusk National Park and the Churchill Wildlife Management Area.

Species:	*Picea glauca*			*Picea mariana*			*Larix laricina*	
Sites:	NFOR[1]	TUND	SFOR	NFOR	TUND	SFOR	NFOR	TUND
Chronology length	1743–2003	1771–2004	1729–2004	1716–2004	1833–2004	1743–2004	1752–2002	1805–2007
Number of years	261	234	276	289	172	262	251	203
Number of trees	65	25	32	39	37	35	40	26
Number of radii	112	34	32	60	41	40	79	34
Mean ring width (mm)	0.78	0.65	0.62	0.33	0.41	0.35	0.34	0.49
Mean sensitivity	0.19	0.22	0.20	0.20	0.22	0.19	0.27	0.27
Mean standard deviation[2]	0.46	0.45	0.41	0.43	0.45	0.42	0.46	0.45
Whitened chronology[3]	0.78	0.76	0.80	0.82	0.75	0.77	0.68	0.77
Mean series correlation[4]	0.58	0.54	0.54	0.54	0.50	0.49	0.57	0.57
Common interval analysis (CIA)	1931–2000	1931–2000	1931–2000	1931–2000	1931–2000	1931–2000	1931–2000	1931–2000
Number of trees used in CIA	36	18	19	25	15	21	21	16
Number of radii used in CIA	56	22	19	30	17	21	34	17
Variance in first eigenvector (%)	41.36	34.71	45.24	36.41	32.59	31.37	36.73	39.75
Agreement with population chronology	0.96	0.89	0.93	0.93	0.84	0.88	0.91	0.89
Mean correlation among all radii	0.39	0.31	0.41	0.34	0.27	0.26	0.33	0.34

[1] NFOR = northern forest, TUND = central tundra, SFOR = southern forest.

[2] Calculated from standard chronology (Grissino-Mayer, 2001).

[3] First-order autocorrelation removed.

[4] Correlation to master series (50-year segments).

function was fit to the earlier portion of the series in order to best characterize the decrease in mean and variance in ring width during early tree development (Cook and Peters, 1981). Next, a 128-year cubic smoothing spline with a 50% frequency cutoff was fit to each series. A 128-year spline preserves 99% of the variation in each ring-width series at a wavelength of 40 years, which results in the preservation of common trends (1–40 years) among trees. For standardization, we then converted each ring-width series into a dimensionless index by dividing the observed values by the predicted values. Using ARSTAN (Holmes, 1992), we created residual standardized chronologies by means of averaging, using residuals from autoregressive modeling of the standardized measurement series (Fritts, 2001), thus making the observations independent to meet the requirements of most statistical analyses (Legendre and Legendre, 1998). The residual indices possessed a strong common signal without persistence, and during preliminary analyses, in comparison to the standard (STNDRD) and ARSTAN chronologies (cf. Holmes, 1992), they exhibited the highest correlation with climate. For each series, we calculated the mean sensitivity, which can range from zero (no differences between successive ring widths) to two (every second ring missing), with larger values indicative of considerable high-frequency variance (Fritts, 2001).

Signal Strength and Chronology Reliability

Mean inter-series correlation (Rbar) was calculated over a 50-year sliding window following Briffa and Jones (1990) as a measure of the common growth signal within the chronology. To accomplish this, a single mean time series was produced for each tree. Expressed Population Signal (EPS) was also calculated to measure chronology reliability (Wigley et al., 1984). According to Briffa and Jones (1990), EPS is a function of Rbar and series replication:

$$EPS(t) = \frac{t\text{Rbar}}{t\text{Rbar} + (1 - \text{Rbar})}$$

where t is the number of trees and Rbar is the mean between-tree correlation. EPS measures how well the chronology compares to the theoretical population chronology based on an infinite number of trees (Wigley et al., 1984). The statistic ranges from zero to one—i.e., from no agreement to perfect agreement with the population chronology.

Statistical Analyses

Response-function analysis is a multiple regression technique that uses the principal components (PCs) of monthly climatic data to estimate indexed values of ring-width growth. The regression components are then multiplied by the PCs of climate to obtain a new set of regression coefficients related to the original monthly climate data (Fritts, 2001). Bootstrapped correlation- and response-functions, in which correlation coefficients of two data sets were repeatedly computed (1000 iterations) from randomly selected subsets of the complete data set, were calculated between climate variables (temperature and precipitation) and the residual ring-width chronologies using the software DendroCLIM 2002 (Biondi and Waikul,
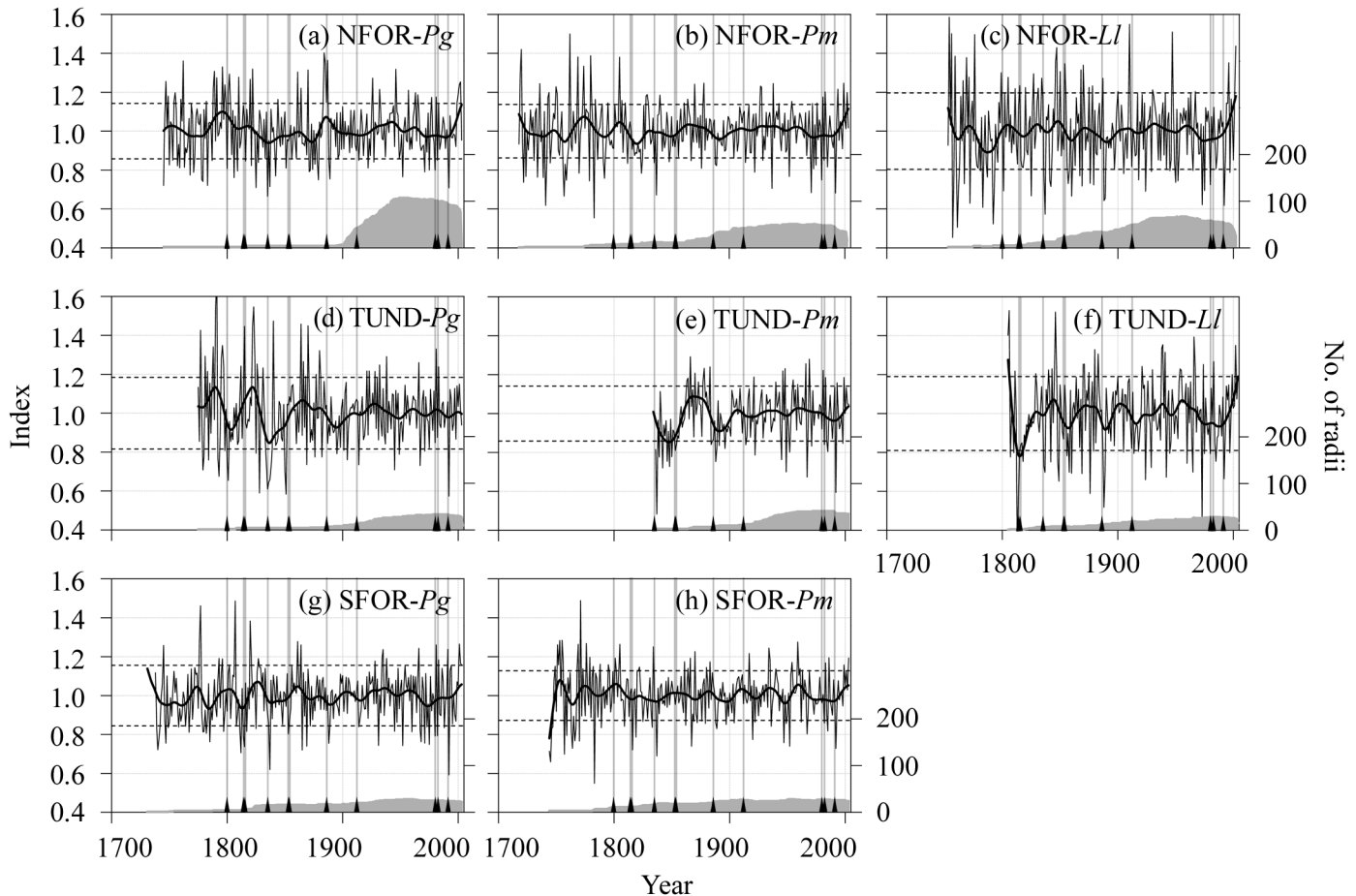
FIG. 2. (a−h) Standardized chronologies for species *P. glauca* (*Pg*), *P. mariana* (*Pm*) in all regions, and *L. laricina* (*Ll*) in the northern forest and central tundra. The shaded region along the x-axis indicates the number of radii for each chronology. The thick black line is a spline that preserves 50% of the variance at wavelengths of 10% the chronology length, and horizontal dashed lines indicate one standard deviation above and below the mean. Black triangles and the associated grey vertical lines indicate timing of notable volcanic eruptions with a volcanic explosivity index (VEI) of 5 or greater (Briffa et al., 1998a).

2004). Precipitation data were available only back to 1929, and therefore the correlation- and response-function analyses cover the period 1929–2002. Sliding correlations of 50 years were used to evaluate the temporal relationship of each ring-width chronology to all the others, as well as the relationship between tree growth and temperature.

RESULTS

Statistical Characteristics of Residual Chronologies

In total, 299 trees were included in the analyses (Table 2). Preliminary ageing of *L. laricina* individuals indicated that most were too young to yield sufficiently long chronologies, so in light of logistical constraints, no *L. laricina* trees were sampled from the SFOR region. However, the NFOR and TUND *L. laricina* chronologies were extended back to 1752 and 1805, respectively (Fig. 2).

All eight chronologies were well replicated for the duration of the 20th century (i.e., the period of overlap with climate data). The number of series representing the chronologies in 1900 ranged from seven for the NFOR

P. glauca to 39 for the NFOR *L. laricina* (Fig. 2). All chronologies except for SFOR *P. mariana* had mean correlations among series greater than or near to the generally acceptable value of 0.5 when comparing 50-year portions of series (Grissino-Mayer, 2001) (Table 2). Mean sensitivity of *Picea* ranged from 0.19 to 0.22 across the study area, though *Larix* appeared more sensitive, with values of 0.27 for each chronology. These statistics indicate that all chronologies were well replicated, well cross-dated, and thus adequate for climatic analyses. Previous studies (Girardin et al., 2005) found similar statistics for *Picea* and *Larix* chronologies in the Churchill area.

Numerous occurrences of decreased growth have followed notable volcanic eruptions during the last 200 years (Fig. 2). Particularly notable eruptions produced either a dramatic decrease in growth during one season within two to three years after the eruption, or suppressed growth for several years post-eruption. These included the eruptions of the Tambora volcano in Indonesia (1815); Cosigüina in Nicaragua (1835); Mount St. Helens in Washington, USA (1980); El Chichón in Mexico (1982); and Mount Pinatubo in the Philippines (1991) (Briffa et al., 1998a).
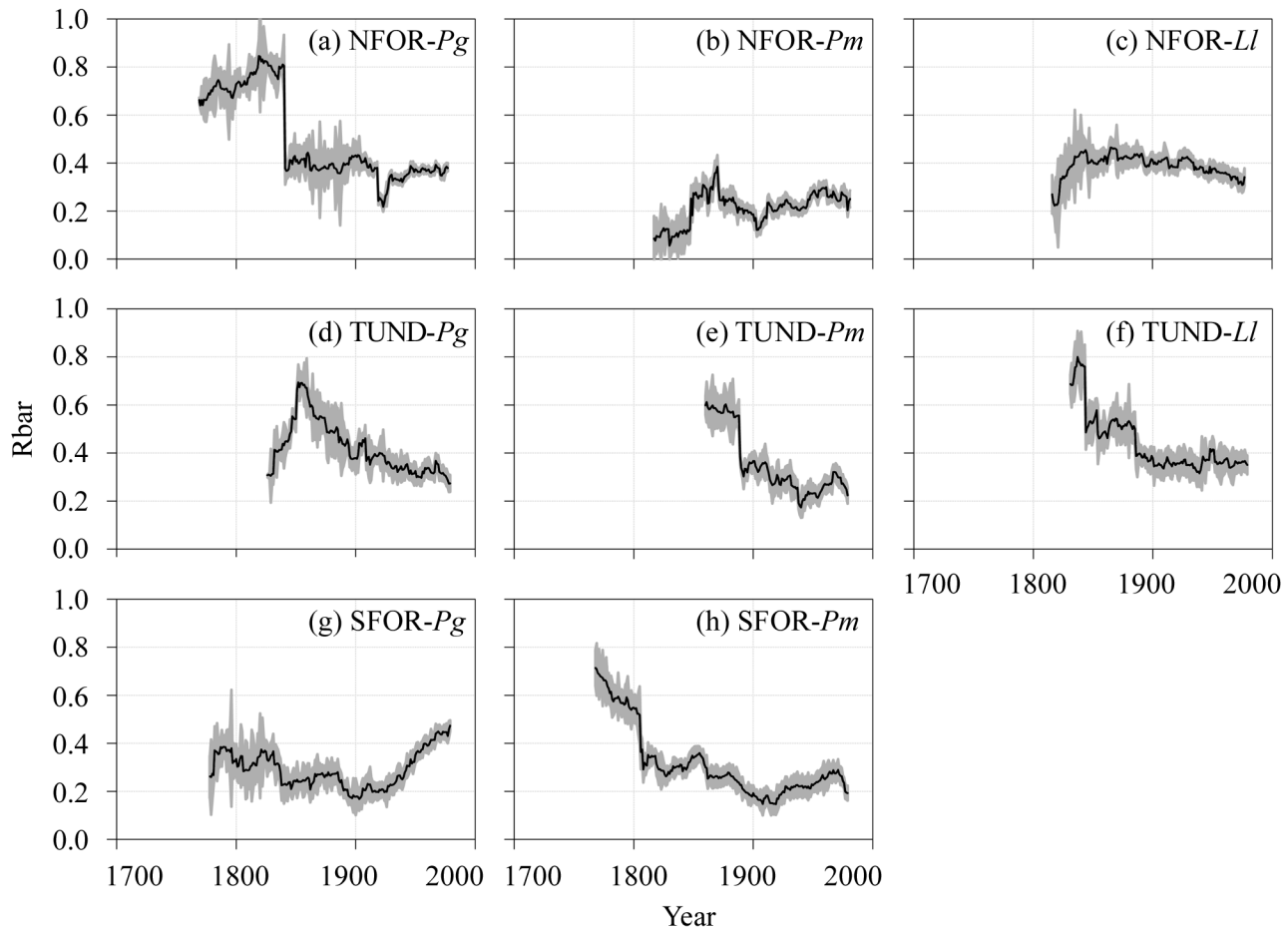
FIG. 3. (a–h) Running mean correlation between all ring-width series (Rbar) of each species. Rbar statistics were computed using a 50-year moving window with one-year time steps. The shaded region is one standard error. Species included were *P. glauca* (*Pg*), *P. mariana* (*Pm*), and *L. laricina* (*Ll*).

Quality of the Chronologies

Within NFOR, the mean common signal measured by Rbar during 1901–2002 ranged from 0.23 for *P. mariana* to 0.38 for *L. laricina* (Fig. 3). Within the TUND region, values ranged from 0.27 for *P. mariana* to 0.36 for *L. laricina*. Rbar was lowest in the SFOR with values of 0.22 for *P. mariana* and 0.30 for *P. glauca*. All chronologies were reliable back to at least 1901 using an EPS value of 0.85 as acceptable (Wigley et al., 1984), with the exception of the TUND *P. mariana* and SFOR chronologies (Fig. 4). The two *L. laricina* chronologies had the highest inter-tree correlation (Rbar) and the longest period of reliability relative to total series length using EPS values as a gauge.

Influence of Climate on Radial Growth

Most species across the region responded to spring, summer, and autumn temperatures during the whole or part of the season in the current year (*t*) and previous year (*t*-1) (*p* < 0.05) (Fig. 5a–c). With the exception of SFOR *P. mariana,* all species across the region responded positively to July temperatures.

Precipitation was infrequently associated with ring width (Fig. 5d–f). Correlations were observed during March or April or both (*t*) for NFOR *P. mariana* and *L. laricina*; May (*t*-1) for TUND *P. glauca*, January (*t*) for TUND *P. mariana*, and March and April (*t*) for TUND *L. laricina*; and January (*t*) for SFOR *P. glauca*.

Radial Growth Response to Climate through Time

The relationship between July temperature and growth was maintained for most or all of the duration of the comparison for both *Larix* chronologies and for TUND *P. mariana* (Fig. 6). The NFOR *Picea*, TUND *P. glauca*, and SFOR *P. glauca* chronologies were correlated with July temperature for 28–38%, 72%, and 64% of the comparison, respectively. With the exception of the SFOR *P. mariana* index, which was not associated with July temperature, all chronologies had responded significantly to July temperature since the early 1940s. Nonetheless, reductions in the actual correlation between growth and temperature occurred during the 1940s to 1960s almost without exception throughout the region.
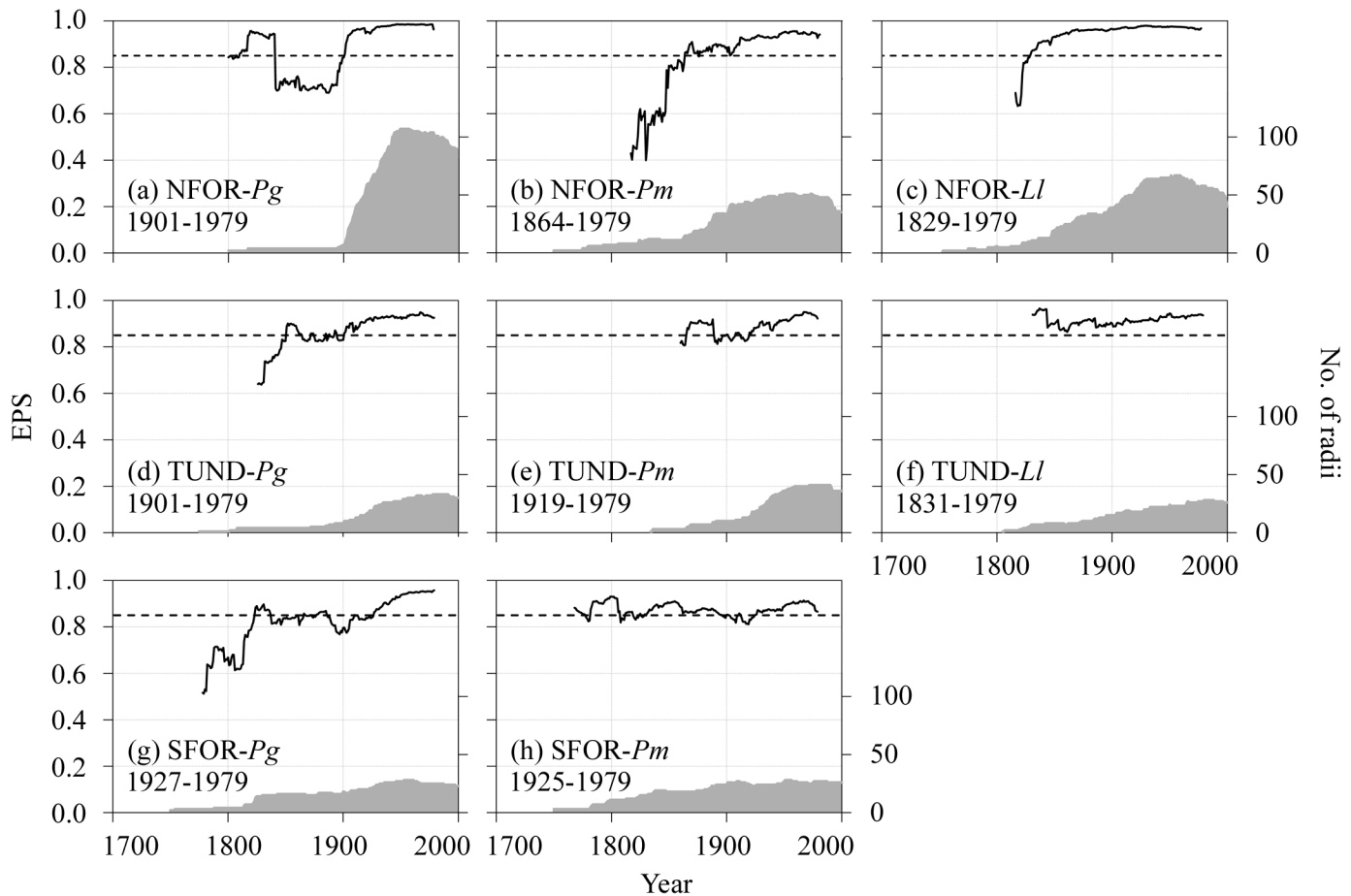
FIG. 4. (a–h) Expressed population signal (EPS) statistics for each species. EPS statistics were computed using a 50-year moving window with one-year time steps. The shaded region is the sample depth (number of radii). Species included were *P. glauca* (*Pg*), *P. mariana* (*Pm*), and *L. laricina* (*Ll*). The most recent time period during which EPS values are greater than 0.85 is shown for each species.

Inter-Species / Inter-Site Correlations

The NFOR chronologies were correlated with each other for most of the comparison, as were the SFOR chronologies, though both regions declined in correlations during the early 20th century (Fig. 7a, c) ($p < 0.05$ significance). The TUND *Picea* chronologies were correlated during the entire comparison, and *P. glauca* was correlated with *L. laricina* except during the mid-1800s, but there was little correlation between *P. mariana* and *L. laricina* (Fig. 7b). To some extent, correlation increased for all comparisons from the early years to the present.

An evaluation of inter-site associations showed that all NFOR and TUND chronologies were correlated for the entire comparison, except the *P. glauca* indices, which were uncorrelated for brief periods during the early 1900s and prior to the mid-1800s (Fig. 7d). The NFOR and SFOR chronologies were correlated for most of the comparison, but correlation between the *P. glauca* chronologies degraded during the same period as for the NFOR and TUND comparison (Fig. 7e). Growth of *Picea* within the TUND and SFOR was correlated, except for *P. glauca* during the early 1800s (Fig. 7f).

DISCUSSION

Volcanic and Frontal Influences

Numerous occurrences of enhanced growth (above one standard deviation) and suppressed growth (below one standard deviation) were found in the chronologies (Fig. 2). Suppressed growth was recorded for all species in 1992, the year following the eruption of Mount Pinatubo, when a decrease of 0.5°C occurred in global temperatures (Parker et al., 1996) and July temperatures at Churchill were reduced by 4.5°C relative to the 1971–2000 normal (Fig. 2). Numerous cold years, such as 1784, 1816, and 1888, correspond to years following other major volcanic eruptions (at Laki, Iceland, in 1783; Tambora, Indonesia, in 1815; and Mt. Tarawera, Okataina, New Zealand, in 1886) that caused global cooling (Briffa et al., 1998a) and suppressed growth. A cold period that occurred around 1837 has been attributed to a southward migration of the Arctic front (Hofgaard et al., 1999) that might have been related to volcanic forcing (D'Arrigo and Jacoby, 1999).
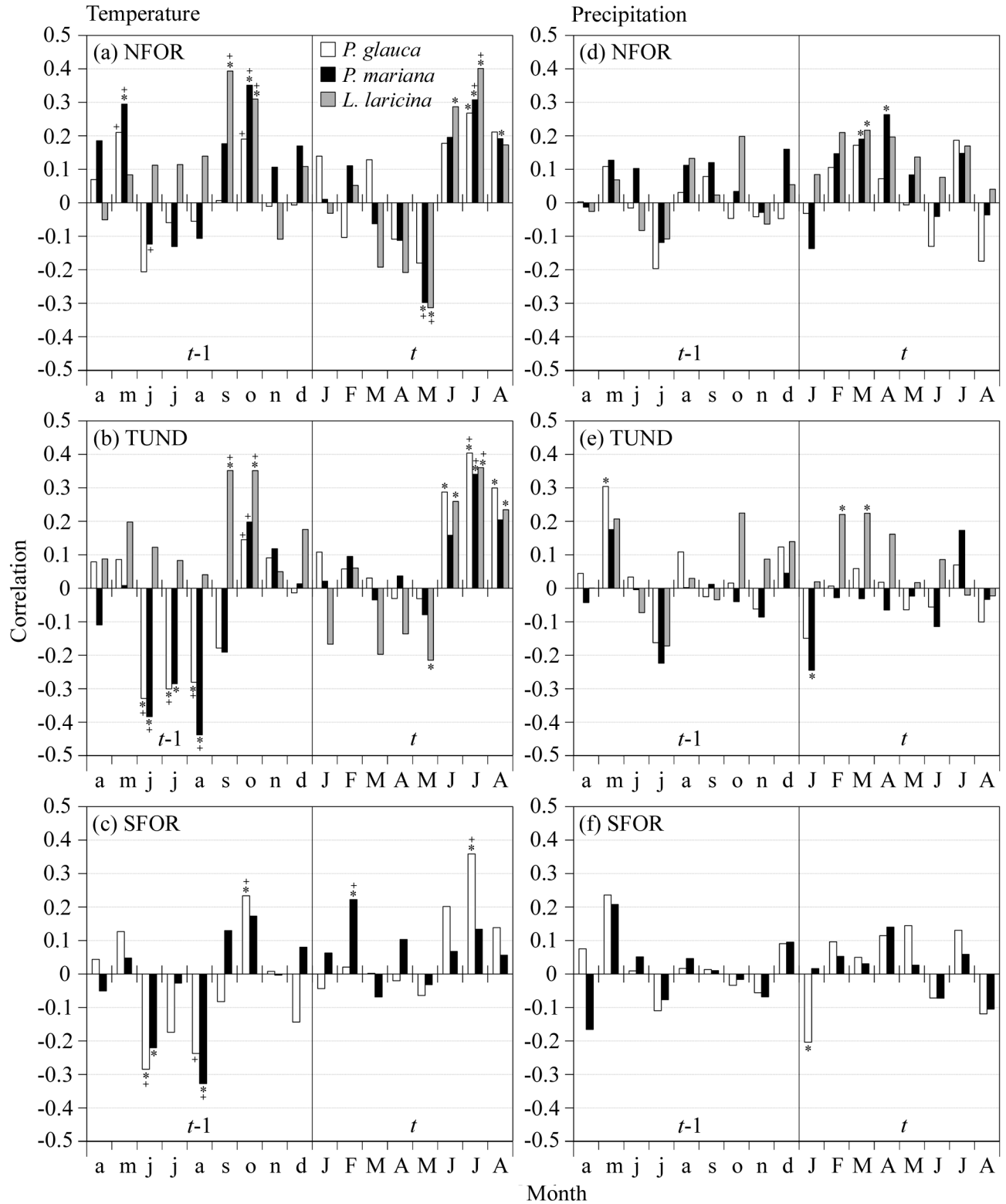
FIG. 5. Correlation between mean monthly temperature (1901–2002; a–c) and precipitation (1929–2002; d–f) within each zone and the residual chronologies from each site. An asterisk (*) indicates significance at $p < 0.05$. A plus sign (+) indicates significant variables after response-function analyses.

Regional Climate

Similar temperature-correlation relations were found by Girardin et al. (2005) and D'Arrigo and Jacoby (1993) within

the Churchill area and by Briffa et al. (2002) for east-central Canada. The correlation with autumn temperatures has been found to be important in affecting tree growth in northern Manitoba (Girardin et al., 2005), as increased late-season
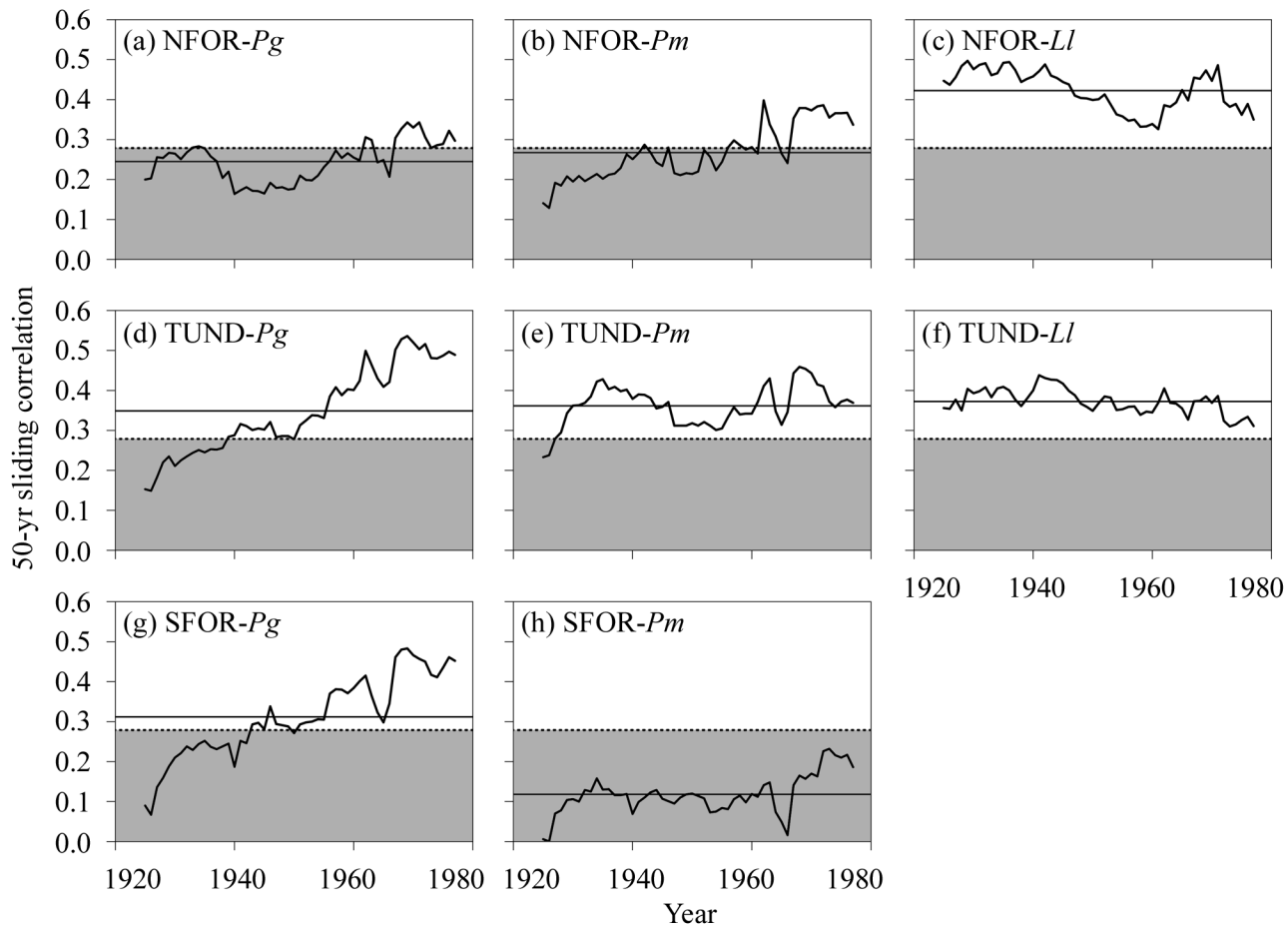
FIG. 6. (a−h) Correlations between the residual chronologies for each species and mean July temperatures within each zone (1901−2002), calculated within a 50-year sliding window with one-year time steps. The solid horizontal line represents the mean of each correlation, and all values outside the shaded area under the dotted line are significant at $p < 0.05$. Species included were *P. glauca* (*Pg*), *P. mariana* (*Pm*), and *L. laricina* (*Ll*).

photosynthesis results in greater reserves of carbohydrates for the following year (Garfinkel and Brubaker, 1980). However, carbon balance (Körner, 1998) is probably not a primary factor limiting radial growth in the region (Hoch and Körner, 2009; Susiluoto et al., 2010). The negative association with January precipitation of the current year has been linked to a delay in snowmelt, caused by enhanced winter snowfall, which postponed spring dormancy release and initiation of growth (Vaganov et al., 1999) through the insulating effects of the snowpack (Kershaw and McCulloch, 2007). The negative association of radial growth with May temperature is likely a consequence of a combination of early snowmelt (leading to reduced percolation and increased runoff) and onset of the growing season while the roots of trees are still encased in frozen soil though air temperatures are above zero (Girardin et al., 2005). Thus, timing of snowfall and duration of snowpack clearly are important factors regulating conifer radial growth during the subsequent growing season.

A positive response to current summer temperatures was expected; however, the negative correlation with summer of the previous year is somewhat complicated. The reasoning behind producing ring-width indices using residuals from auto-regressive modeling is to remove the effects of growth

during the previous year on growth during the current year (Holmes, 1992). In addition, DendroCLIM 2002 uses bootstrapping (Biondi and Waikul, 2004) to reduce the chances of a Type I error when interpreting correlation coefficients. Therefore, if robust statistical techniques were employed in correlation- and response-function analyses, presumably relevant ecological relationships would reveal themselves. Nonetheless, there is evidence that numerous climatic factors precondition trees in various ways and influence growth the following year without necessarily affecting the autocorrelation (Fritts and Xiangding, 1986). It is no easy task to distinguish ecological significance and statistical artifact when interpreting relationships between growth and climate in previous years, and this difficulty likely explains the lack in interpretation of the association between tree growth and temperature of the preceding year in previous studies (cf. Girardin et al., 2005; Tardif et al., 2008). Some researchers have suggested that the negative association with previous summer temperatures was related to moisture stress and found a positive correlation with previous June precipitation to support this hypothesis (Hofgaard et al., 1999; Huang et al., 2009). However, no clear relationship between radial growth and the previous year's precipitation was found in this study. Other factors,
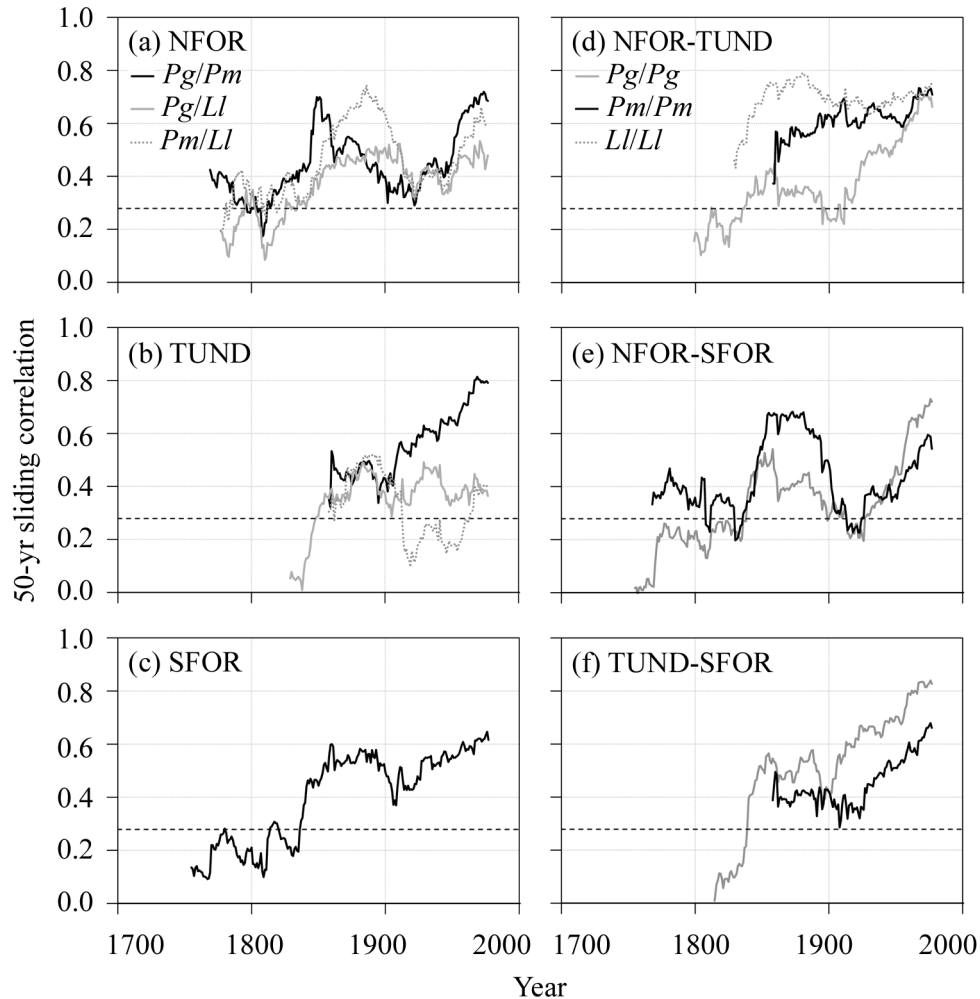
FIG. 7. Correlations between the residual chronologies, calculated within a 50-year sliding window with one-year time-steps. Panels (a) to (c) show correlations within each site, while panels (d) to (f) show inter-site correlations. Species included were *P. glauca* (*Pg*), *P. mariana* (*Pm*), and *L. laricina* (*Ll*). The dashed lines indicate significance at $p < 0.05$.

such as snowpack drifting and duration (Hiemstra et al., 2002) resulting in soil moisture conditions not related to precipitation (Liptzin and Seastedt, 2009) and edaphic characteristics such as the presence of permafrost (Körner and Hoch, 2006), as well as potential feedbacks of these and other factors with climate change, likely contribute to the radial growth patterns observed in the Hudson Bay lowlands, though measurement of such factors was beyond the scope of this study. Clearly further research is warranted into this dendroclimatological conundrum.

Both NFOR and TUND *L. laricina* chronologies exhibit the most coherent association with growing-season climate. Correlation analyses and the length of the records that surpass the 0.85 EPS threshold indicate that *L. laricina* trees in the region offer the most potential for further climate investigations. It is possible that exogenous defoliation events, such as larch sawfly (*Pristiphora erichsonii* Hartig) outbreaks in the area, could reduce the potential for dendroclimatic analyses. However, there is no evidence of such events occurring in the Churchill area over the last two centuries (Girardin et al., 2005),

indicating a strong radial growth–climate signal present in *L. laricina*.

Mid-Century Decrease in Correlation between Tree Growth and Climate

The change in the relationship between radial growth and temperature from the 1940s through the 1960s was evident in all chronologies in the study area. However, this change was less obvious in the SFOR chronologies. It has been suggested that the attenuation of correlation can be attributed to a shift in atmospheric circulation, which drove shifts in temperate air mass distributions during the summer months (Scott et al., 1988). As well, Briffa et al. (2002) alluded to potential factors reducing the sensitivity of tree growth to temperature, such as reduced soil moisture from warmer springs and earlier snowmelt or unknown anthropogenic influences. However, the sliding correlation analyses suggest that, despite the lower correlation with climate, the relationship of growth to temperature has remained statistically significant since the 1940s for all species across the region.

Inter-Chronology Correlations

The correlations among chronologies decrease as years from present increase. This pattern is likely due to a smaller sample depth (and hence, a decreased signal-to-noise ratio) earlier in the chronologies. The NFOR chronologies are highly replicated ($n > 60$), so their correlations do not decrease as much as at the other sites. Furthermore, as the ages of most trees sampled in the TUND region fall within the 20th century and sample depth decreases abruptly before that time, correlations among the chronologies also decrease as a result of lower replication (Cook and Kairiukstis, 1990). Nonetheless, there is a significant correlation between most chronologies during the last century, suggesting some common environmental influences.

Unusual Climate Response from SFOR Picea mariana

There are several plausible reasons why the response of SFOR *P. mariana* correlations to current-year climate was weak. These include (1) subtle changes in the seasonality of temperature and precipitation (Groisman et al., 1994), resulting in pronounced disparity in climate (such as a move to warmer springs and earlier snowmelt) (Kirschbaum, 2000); (2) increased insect herbivory and competition with other plants (Fleming and Volney, 1995); or (3) higher UVB levels, resulting in decreased growth (Briffa et al., 1998b). However, a similar response was not expressed by *P. glauca* within the same stands. Thus, further research is needed to determine the primary growth-limiting factor(s) for *P. mariana* in the southern forest of Wapusk NP.

CONCLUSION

This study supports some results from previous tree ring studies around Churchill, while providing new evidence for disparity in the growth response of trees along an environmental gradient south of Churchill to the Nelson River, a disparity that may be related to synoptic climate. Specifically, while July temperatures were the primary factor limiting growth within the northern forest of the study area, this relationship appeared to deteriorate within the southern forest, particularly for *P. mariana*. This disparity in July temperature response suggests that the primary factor limiting tree growth is not homogeneous throughout the western Hudson Bay lowlands, and whatever factor is most growth-limiting in the southern portion of the study area might not be explicitly climate-driven. Autumn and spring temperatures were also important, particularly for *L. laricina*. Overall, the number and magnitude of significant correlation coefficients suggest that the species most sensitive to climate is *L. laricina*. This study illustrates the disparity and complexity in growth response of the subarctic trees of the Hudson Bay Lowlands in northern Manitoba, while filling a conspicuous gap in tree ring research surrounding the Bay. As the Hudson Bay region is predicted to warm during the next century (Gagnon and Gough, 2005), research into vegetation responses to climatic change is important in the forest-tundra of the region because of the potential for synergistic effects (Foley et al., 1994) and impacts on other biota (Scott and Stirling, 2002).

Future work should include additional sampling, particularly of *L. laricina* and *P. mariana*, within the southern regions of Wapusk NP. This sampling would bring the chronologies up to date and resolve signal-to-noise issues related to low sample size within the older portions of the chronologies.

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