Radial Growth of Tamarack (Larix laricina) in the Churchill Area, Manitoba, Canada, in Relation to Climate and Larch Sawfly (Pristiphora erichsonii) Herbivory

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Radial Growth of Tamarack (*Larix laricina*) in the Churchill Area, Manitoba, Canada, in Relation to Climate and Larch Sawfly (*Pristiphora erichsonii*) Herbivory

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Abstract

Tree-ring chronologies for tamarack (*Larix laricina* (Du Roi) K. Koch) growing in four stand types covering a dry-to-wet gradient were developed to investigate the association between radial growth and climate as well as evidence of larch sawfly (*Pristiphora erichsonii* Hartig) herbivory near Churchill, subarctic Manitoba. The chronologies, produced using both living and subfossil material, were well replicated for the period 1800 to 2000. Our results indicated that climate explained more than 60% of the growth variation in tamarack with temperature from May to July of the growing season being most important. This was unusual considering that other studies showed a weak radial growth-climate association in tamarack because of signal contamination due to severe larch sawfly defoliation. Potential outbreak episodes were investigated by looking at pointer years and by contrasting the variance within the tamarack tree-ring series with that observed in climate and in nonhost species. A weak correspondence was observed among pale latewood rings, growth suppression period, and incomplete rings. Comparison of host and nonhost chronologies revealed synchronized growth suppression periods in tamarack during 1818–1824, 1857–1864, 1891–1892, 1903–1912, and 1959–1964, with seldom more than 25% of the trees being affected. The 20th-century suppressions corresponded to known outbreaks identified in Manitoba. However, they also corresponded to periods of little residues in the climate model suggesting that they may be due to short-term changes in site hydrology. This study stresses the difficulties to use dendrochronology to identify what may be low severity or "subepidemic" defoliation events. It also stresses the potential differences in the larch sawfly dynamics between the boreal forest and the forest-tundra. Further studies using an extended network of chronologies will be needed to decipher the short-term impacts of climate from those of low severity defoliation episodes.

Introduction

Larix laricina (Du Roi) K. Koch. (tamarack, eastern larch) is a shade-intolerant conifer with a wide distribution across the boreal zone of North America (Johnston, 1990; Sims et al., 1990). It is a deciduous conifer that produces a fresh supply of foliage each year. It occupies the northernmost part of the boreal forest bordering the tundra in association with black spruce (*Picea mariana* [Mill] BSP) and white spruce (*Picea glauca* [Moench] Voss). Pure tamarack forests occur in poorly drained inland fen sites in subarctic Manitoba, but tamarack also occurs on drier uplands sites associated with white spruce and on inland peat plateaus with black spruce (Brook, 2001; Monson, 2003). Tamarack is also mainly found with white spruce along the maritime coast of the Hudson Bay of Manitoba, whereas inland it is most frequently encountered in poorly drained sites with black spruce (Monson, 2003).

The larch sawfly (*Pristiphora erichsonii* Hartig) has a Holarctic distribution (Turnock, 1972; Ives, 1976) that approaches the northern distribution limit of tamarack in western and central North America (Turnock and McLoad, 1966). The insect is also active in the forest-tundra of northern Quebec and reached the northern treeline during an outbreak in the mid-1980s (Cloutier and Filion, 1991). The larch sawfly is among the most important defoliators in North America and its origin (whether indigenous or introduced) has long been debated (Coppel and Leius, 1955; Graham, 1956; Löve, 1959; Nairn et al.,

1962; Ives, 1976; Jardon et al., 1994; Case and MacDonald, 2003). The first Canadian record of larch sawfly outbreak came from the Quebec City region and dates from the early 1880s (Fyles, 1884; Provancher, 1885; Coppel and Leius, 1955; Turnock, 1972; Rose and Lindquist, 1992). In northern Saskatchewan, tree-ring evidence provided by Case and MacDonald (2003) showed no indication of outbreaks prior to the late 1800s and this agrees with our preliminary observations in western Manitoba (not published). However, tree-ring evidence from one larch tree in the Lake States (Michigan) suggested that catastrophic defoliation events occurred as early as the 1700s (Graham, 1956). Tree-ring studies conducted on the east side of Hudson Bay in subarctic Quebec also presented evidence of 10 distinct larch sawfly outbreaks, the earliest outbreak occurring from 1744 to 1749 (Jardon et al., 1994). The authors argued that the observed intensification of the larch sawfly activity around 1880, as depicted by more severe outbreaks, could have resulted from a change in climate. Improved tamarack growth and long shoot formation could have increased the food source thus allowing population growth of larch sawfly (Jardon et al., 1994).

In Manitoba, records of defoliation indicate three major outbreaks in the first half of the 20th century (Nairn et al., 1962). These outbreaks occurred from 1911 or earlier to 1920, 1924 to 1927, and 1938 to 1944 (Nairn et al., 1962; Ives and Nairn, 1966a). In northern Manitoba, the first observations of defoliation by the larch sawfly were made in the Flin Flon (approximately 700 km southwest of Churchill) and
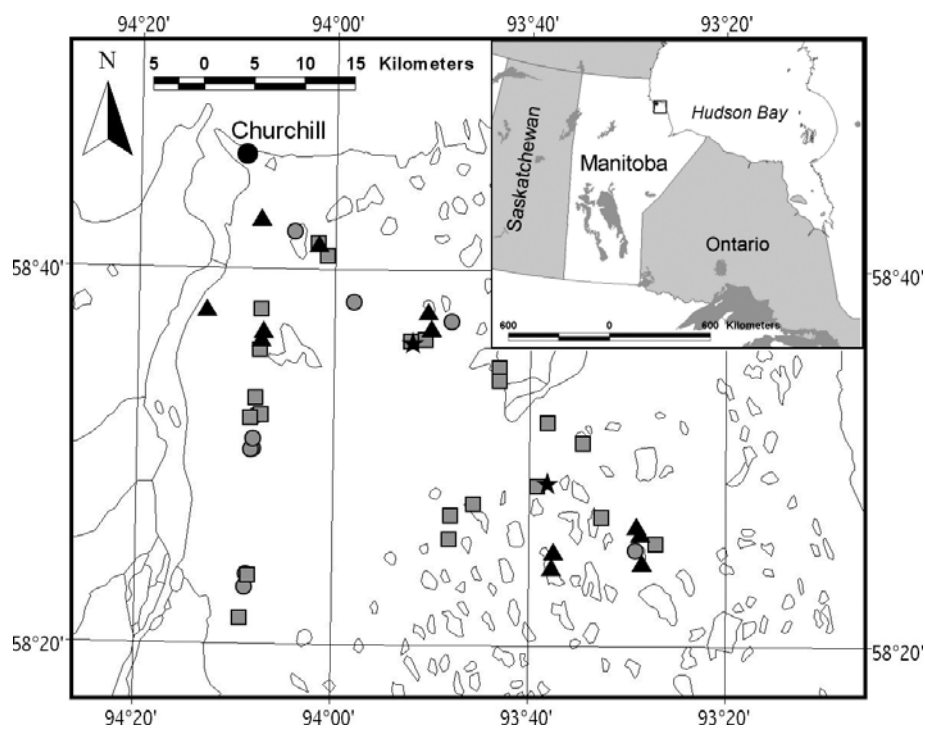
FIGURE 1. Map of the study area and the location of the sites respective with the vegetation types. Circles refer to LLA1 sites (n = 10), squares to LLA2 sites (n = 21), triangles to LLA3-4 sites (n = 12) and stars to LLA5 sites (n = 2). LLA3-4, LLA2, LLA1, and LLA5 represent the driest to wettest sites.

Thompson (approximately 450 km southwest of Churchill) areas in 1916 and 1917, respectively (Nairn et al., 1962). Records also indicate that outbreaks varying from light to moderate and severe defoliation swept westward across Manitoba to Saskatchewan from 1938 to 1958. These outbreaks mainly occurred in the boreal forest but extended as far north as in the transition zone between the boreal forest and the tundra (Chipewyan Lake area, approximately 260 km southwest of Churchill) during its peak intensity, that is from 1951 to 1954 (Nairn et al., 1962). In the early 1960s, patches of light defoliation were also reported near Chipewyan Lake. Larch sawfly defoliation was also reported in the Hudson Bay lowlands along the Nelson River, approximately 250 km south of Churchill (Turnock and McLoad, 1966). North of Churchill, moderate defoliation was reported in the Nueltin Lake area (Nunavut, about 60°N; 100°W, approximately 400 km northwest of Churchill) in 1963 and 1964 (Turnock and McLoad, 1966). Despite historical records of the presence of one strain of the larch sawfly in the Churchill region (Shelford and Twomey, 1941; Wong, 1974), no defoliation surveys were done in the area. Little is still known about the northern distribution and abundance of the larch sawfly in the transitional area between the commercial boreal forest and the tundra in central Canada even though almost 40 yr have passed since Turnock and McLoad (1966) made their observations.

In this study we investigate the radial growth of tamarack in relation to climate and potential evidence of larch sawfly herbivory in the Churchill region of subarctic Manitoba using a dendrochronological approach. Few records of tamarack defoliation exist in subarctic regions of North America and there is a need to extend our network of tree-ring chronologies to understand better the distribution of larch sawfly outbreaks and their impacts (Cloutier and Filion, 1991; Tailleux and Cloutier, 1993; Jardon et al., 1994). To meet this objective, four multicentury-long tree-ring chronologies for tamarack were developed, each from trees growing along a gradient from poorly to moderately well drained sites. Previous studies have indicated that outbreaks of the larch sawfly in hydric sites have lower intensity and duration due to the severe restriction on sawfly development and survival that the habitat imposes (Lejeune, 1955; Graham, 1956; Ives and Nairn, 1966b; Ives, 1976). It was hypothesized that outbreaks would be more severe and detected more frequently on better drained sites. It was also observed

that the association between climate and radial growth was greatly weakened in tamarack due to episodes of defoliation (Girardin et al., 2001; Case and MacDonald, 2003; Girardin and Tardif, 2005). Therefore, it was hypothesized that the association between radial growth and climatic variables would be disrupted by the presence of defoliation events.

Study Area and Methods

The study area is located in the Hudson Bay Lowlands ecoregion and south of the town of Churchill, Manitoba (58°44′N; 94°04′W) (Fig. 1). It lies within the Hudson Plain ecozone on the western coast of the Hudson Bay, referred to as the forest-tundra (Zoladeski et al., 1995). The forest-tundra forms a transitional boundary between the true boreal forest to the south and the tundra to the north (Ritchie, 1962). The study area is considered to be within the ecoclimatic region of the high subarctic (Scott, 1995).

Ordovician and Silurian limestone and dolomites characterize the geology of the area and overlie the Precambrian Shield (Johnson, 1987; Dredge and Nixon, 1992). However, glacial tills of the Pleistocene or marine deposits of the Holocene cover the most of the region. As a result of the permafrost and a lack of slope, the landscape is a poorly drained peatland interspersed with thermokarst lakes and ponds. There are also well-drained glacial and beach formations such as moraines, beach ridges, and eskers (Johnson, 1987; Scott, 1995). The entire study area is uniformly low (<50 m elevation) and flat, forming a vast wetland adjacent to Hudson Bay (Dredge and Nixon, 1992).

Regional climate is highly influenced by the effects of nearby Hudson Bay (Rouse, 1991), with long cold winters and short cool summers. Data from the nearest meteorological station in Churchill show a mean annual temperature of −6.9°C for the reference period 1971–2000 (Environment Canada, 2003). The mean daily temperature during the coldest month (January) is −26.7°C and is 12°C during the warmest month (July). The total annual precipitation is 431.6 mm with 264.4 mm falling as rain and 191 mm falling as snow. In the area, snowmelt usually occurs in May/June and the first snowfall occurs in

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mid-September (Scott et al., 1993). There are on average 594.7 degree-days above 5°C annually (Environment Canada, 2003).

The vegetation of the area is dominated by three tree species: black spruce, white spruce and tamarack. White spruce communities are found almost exclusively on well-drained sand or gravel ridge in the forest-tundra or, at the junction of sand and rock at the northern treeline of the study area (Ritchie, 1962; Brook, 2001). The black spruce communities, referred as the "black spruce muskeg" (Ritchie, 1962), are mainly associated with sphagnum moss over peat deposits. Tamarack grows freely throughout the study area in association with both black spruce and white spruce (Brook, 2001; Monson, 2003). Pure tamarack stands are confined to fen areas with water levels at or near the surface. The trees are usually found on hummocks that form in this type of landscape (Ritchie, 1962).

SAMPLING

A total of 45 sites were sampled within the study area (Fig. 1) as part of a larger study on fire history and secondary succession (Monson, 2003). At each site, one to four tamarack trees were sampled and either disks or two cores were extracted from the basal most portions of each tree. Cross sections from snags and downed woody material were also collected to increase the length of the chronologies being constructed. To differentiate variations in ring width and growth suppression caused by climatic factors from those caused by defoliation events, a nonhost species was sampled on each site. Two cores (or one disk) were collected from five to eight black spruce or white spruce trees according to the dominant species (Monson, 2003). The choice of the nonhost species was justified by the fact that the larch sawfly is specific to tamarack (Lejeune, 1955). Black spruce has particularly been used with success in previous larch sawfly studies (Arquillière et al., 1990; Tailleux and Cloutier, 1993; Jardon et al., 1994; Girardin et al., 2001; Case and MacDonald, 2003). It should be noted, however, that this analysis is valid only if no synchrony is observed in defoliation events affecting both the host and nonhost species. Synchronous cycles of defoliation by multiple defoliators have been reported (Myers, 1998) and presumably occurred in the 1880s in tamarack and white spruce growing in the Lake States (Graham, 1956).

The 45 sampled sites have been classified according to vegetation composition by Monson (2003) and four chronologies were developed from trees growing across a gradient from poorly to moderately well drained sites. The LLA1 ($n = 10$) and LLA2 ($n = 21$) sites were black spruce–dominated bog types found inland of the Hudson Bay coast on deep peat deposits with thin active layers (permafrost close to surface). The main vegetation difference between the two black spruce–dominated sites was the greater importance of fruticose lichen in LLA1 sites and of *Sphagnum* spp. in LLA2 sites. The LL3-4 sites ($n = 12$) were white spruce–dominated upland sites on inland relic beach ridges or coastal rock outcrops. The LLA5 sites ($n = 2$) were tamarack-dominated fens typified by deep active layers, silt and clay substrates, very poor drainage and the presence of surface water (Monson, 2003). Therefore, the sequence from the driest to the wettest sites was LLA3-4, LLA2, LLA1, and LLA5.

DEVELOPMENT OF CHRONOLOGIES

All of the sample cores and cross sections were dried, and then sanded with progressively smoother sandpaper to reveal the individual cells of each ring. This allowed for accurate identification of each ring. Once sanded, the samples were visually cross-dated using a technique similar to that described by Yamaguchi (1991). This technique allowed the careful identification of marker rings (i.e., narrow, large, light rings) to be used in the cross-dating of the wood sample. Cross-dating ensured that the actual date of the formation of any one ring was exact

in all of the trees sampled (Swetnam, et al., 1985). A VELMEX Uni Slide stage micrometer interfaced with a computer was used to measure the ring widths of each series to a precision of 0.01mm. Visual cross-dating of the wood samples and accuracy of the measurement was validated using COFECHA (Holmes, 1983). The program calculated cross-correlations up to a 10-yr lag between each individual measurement series and a reference chronology derived from the remaining series. All measurement series were standardized using a short cubic spline to remove low-frequency variance (Holmes, 1983) before the calculation of cross-correlations.

Four tamarack chronologies and two nonhost chronologies were developed following standardization of the measurement series. The standardized chronologies were constructed using the program ARSTAN (Cook, 1985). In ARSTAN, a spline function giving a 50% frequency response of 50 yr (Cook and Peters, 1981) was applied to each measurement series to remove the age/size related trend and other low frequency trends not related to defoliation or climatic events. Standardized tree-ring indices retained 99% of the variance at wavelengths inferior to 15 yr using this method. This indicated that growth suppression related to larch sawfly defoliation could be adequately detected. Standardization of the ring-width measurement series assured that the mean and the variance of all the series were made comparable. Six residual standardized chronologies were created in the same manner as the standard ones except that the series were averaged using residuals from autoregressive modeling of the standardized measurement series (Cook and Holmes, 1986). This resulted in chronologies with a strong common signal and without persistence. The presence of autocorrelation reduces the effective number of independent observations and thus reduces the degrees of freedom used to determine the confidence in estimates of correlation coefficients (Legendre and Legendre, 1998). Along with general statistics describing our chronologies, their mean sensitivity was calculated. This index ranges from 0 (no differences between successive ring widths) to 2 (every second ring missing) and larger values indicate the presence of considerable high-frequency variance (Fritts, 1976). The agreement with the population chronology statistic is an indicator of chronology reliability. It 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 0.0 to 1.0, i.e. from no agreement to 1.0 for perfect agreement with the population chronology.

SAWFLY OUTBREAK IDENTIFICATION

Identification of larch sawfly outbreaks was performed using both pointer years and the host nonhost analysis approach using criteria comparable to other studies (Harper, 1913; Jardon et al., 1994; Girardin et al., 2001; Case and MacDonald, 2003). The key attributes described in the annual tree-rings during an outbreak are (1) the presence of a pale-latewood ring during the first year of defoliation with no subsequent decrease in ring width, (2) a decrease in radial growth, and (3) an increase in the number of missing or incomplete rings. A pale latewood ring followed by a sharp decrease in annual growth leading to numerous years of depressed growth has constituted the typical signature used to identify past larch sawfly outbreaks.

Light rings (pale latewood rings) were qualitatively identified. They were recognized by their characteristic thin-walled latewood cells that appeared "lighter" when viewed through a microscope (Liang et al., 1997). Although tamarack withstands repeated defoliation, radial increment is markedly reduced during severe infestations (Ives and Nairn, 1966a). The larch sawfly larvae feed on current year foliage and defoliate stands over large areas for successive years when populations periodically reach epidemic levels (Graham, 1956). The common response of tamarack to defoliation is a reduction in the amount of

foliage produced in the next year (Turnock, 1972), a reaction that accentuates growth reduction and missing/incomplete ring formation. Light and moderate defoliation in young tamarack are known to produce reduction in growth (Harper, 1913; Graham, 1931). Graham (1956) reported that incomplete rings are formed during minimum foliage year in severely defoliated trees. Arquillière et al. (1990) observed growth suppression lasting 4 to 7 yr with presence of incomplete rings during severe outbreaks. Fillion and Cournoyer (1995) observed a pale latewood ring in 1939 followed by suppression from 1940 to 1947 including recovery. Drooz (1960) reported that a marked decline in radial increment occurred during outbreaks that lasted 4 to 6 yr and tamarack died after 6 to 9 yr of moderate to heavy defoliation (Turnock, 1954; Beckwith and Drooz, 1956; Nairn et al., 1962; Drooz, 1960).

To further identify potential outbreaks, a host/nonhost analysis was conducted with the program OUTBREAK (Ver. 6.00, Swetnam et al., 1985; Holmes and Swetnam, 1996; Girardin et al., 2001; Speer et al., 2001; Case and MacDonald, 2003). Separate analyses were done for each tamarack chronology using one nonhost species at a time. The rational of this analysis has been well described by Swetnam et al. (1985). Essentially, past potential outbreaks are detected when a decrease in the growth of the host species occurs with no corresponding decrease in the nonhost species. In this analysis, the values of the nonhost residual chronologies (black spruce and white spruce) were subtracted from their respective host residual tree-ring series to highlight specific growth suppression in the tamarack series. Before proceeding with subtraction, the variance in both series being compared was adjusted for mean and standard deviation differences and each index value in the nonhost chronologies exceeding 0.1 was raised to a fractional power of 0.1. This adjustment is intended to suppress the effect of increased radial growth in the nonhost chronology which, when subtracted from the host series, would introduce apparent growth reductions that have been incorrectly diagnosed as potential sawfly outbreaks (Holmes and Swetnam, 1996). Potential larch sawfly outbreaks were identified when the corrected tamarack series had negative values lasting from 4 to 8 yr and that the maximum growth reduction in that period reached a fixed threshold value of −1.28 in standard deviation. For each year, the percentage of tamarack series meeting these criteria was calculated. Although nonhost comparison processes can be done without this information and without a routine such as OUTBREAK, they may lack systematic and consistent rules when analyzing large number of tree-ring measurement series (Speer et al., 2001).

CLIMATE

The effects of climatic fluctuation on the radial growth of tamarack and the nonhost species were analyzed using both correlation analyses (Fritts, 1976; Briffa and Cook, 1990) and bootstrap response function analyses (Fritts et al., 1991). The bootstrap analysis provided a test of significance of the regression coefficient stability within a specific time period by repeated, random sampling of the data. The bootstrap response function coefficients were obtained from the regression with principal components of climate variables and 999 iterations. Mean monthly temperature and total monthly precipitation data sets from Vincent and Gullett (1999) and Mekis and Hogg (1999), respectively, were used in these analyses (station 5060600, Churchill). Program Precon (Ver 5.16) was used for all of the climatic analysis (Fritts et al., 1991). The residual chronologies were used for these analyses and mean temperature and total precipitation during a 16 month period, prior to and concurrent with the period of growth were used. The last component of our climatic analysis was to compare the residual chronologies for each species with the predicted radial growth from the response function for the reference period 1933–1999. By

comparing the predicted and the actual radial growth, it was possible to verify whether each of the species reacted in a similar way to climatic influences and the ability of the climate model to estimate periods of lower radial growth.

Results

CHRONOLOGY STATISTICS OF HOST/NONHOST SPECIES

Figure 2 presents the six chronologies with their respective statistics gathered in Table 1. The tamarack chronologies were well replicated for a period covering approximately 200 yr (Fig. 2). Prior to 1800, only one tamarack chronology, LLA2, was replicated at a satisfactory sample depth (12 series in 1750, for an agreement with the population chronology of 0.79 [recalculated on the interval 1750–1799]). The LLA5 tamarack chronology was less replicated, with a sample depth above 10 in the interval 1895–2000 and below 7 prior 1818 (Fig. 2). Nevertheless, the LLA5 agreement with the population chronology statistic was above the 0.80 threshold (Table 1) and thus we believe that the chronology contains meaningful information. As opposed to the tamarack chronologies, the spruce chronologies were well replicated over the entire time span 1750–2000.

Chronologies statistics (Table 1) were similar among tamarack residual chronologies. Correlation coefficients among series were in the order of 0.30 to 0.40 for all chronologies with an exception in the LLA5. Not only did the mean correlation among series exceeded 0.50 in LLA5, but the frequency of missing rings was also higher than in any other chronology (one missing ring for every 164 rings). Missing rings were also encountered more frequently in tamarack chronologies than in spruce (Table 1). The percentage of variance expressed by the first eigenvector and the mean sensitivity statistics were also higher in tamarack than in spruce. These statistics were suggestive of a much stronger environmental forcing on tamarack (the strongest response being in the LLA5) as opposed to spruce. No pattern was observed in the mean ring-width and autocorrelation statistics.

Observation of the standard chronologies indicated that a low frequency oscillation (in the order of 17 to 32 yr based on a multitaper spectra analysis, not shown) dominated ring-width variation in both tamarack and spruces chronologies (Fig. 2). Small deviations were, however, observed in the timing and amplitude of the maximas and minimas between tamarack and spruces chronologies. The most pronounced discontinuities are the growth releases in spruces in the 1860s, 1910s, and the 1960s that by far exceeded those in tamarack. The growth suppressions observed in spruces in the 1870s, 1890s, and the 1970s were also more pronounced than in tamarack.

On an interannual time scale, tamarack's growth exceeded the highest 1.5 ring-width standard deviation threshold more frequently during 1750 to 1850 than in the period post-1850 (Fig. 2). Years of high ring-width index were notably encountered in all tamarack chronologies in 1777, 1782, 1805, 1830, 1834, 1846, 1847, 1868, 1910, 1991, and 1996. Growth of spruces in these years was generally above average. In addition, years of low tamarack ring-width index were observed in 1759, 1763, 1764, 1786, 1821, 1837, 1842, 1860, 1889, 1924, 1973, and 1992. Within these years, only 1837, 1889, 1924, 1973, and 1992 were observed as years of low ring width in spruces.

CLIMATE ANALYSES OF HOST/NONHOST SPECIES

The climatic analysis for the period 1933–1999 for tamarack, white spruce, and black spruce showed that all species responded in a similar way to precipitation and temperature. With respect to the correlation function (Fig. 3), most residual chronologies were significantly and positively associated with mean temperature in October prior to ring formation $(t - 1)$ and June-July temperature
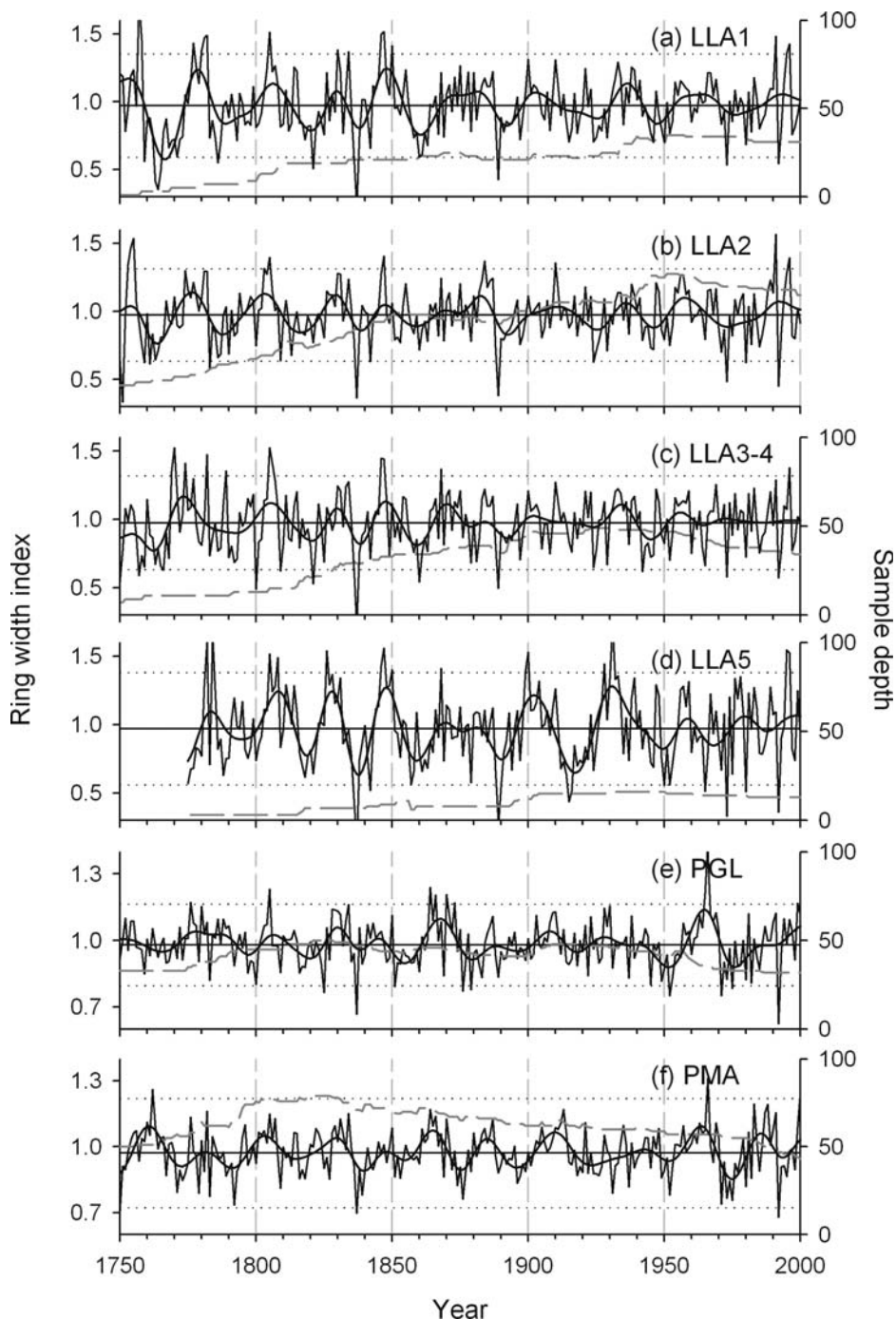
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FIGURE 2. Standardized chronologies for the host species tamarack from vegetation types (a) LLA1, (b) LLA2, (c) LLA3-4, (d) LLA5, and the nonhost species (e) white spruce (PGL) and (f) black spruce (PMA). A dashed-gray line shows the sample depth for each of the standardized chronology. Horizontal dotted lines indicate the upper and lower 1.5 standard deviation levels. The thick-black line is a Savitzky-Golay smoothed curve based on a polynomial fitting across a 10-yr moving window.

during the year of ring formation (t). May temperature (t) was significantly and negatively correlated with radial growth in five of the six chronologies. A contrasting signal was observed between tamarack and spruce with the later showing an association with summer temperature the year prior to ring formation ($t − 1$). Precipitation was not strongly associated with ring width, except for July precipitation prior to ring formation that was negatively correlated to three tamarack chronologies and the white spruce chronology (Fig. 3).

This strong association between ring width and climate was further illustrated by the high goodness of fit between the actual versus predicted radial growth estimation for each residual chronology following the response function analyses (over the period 1933–1999; Fig. 4). The combination of monthly temperature and precipitation variables explained nearly 70% of ring-width variations. Most variations in radial growth (highs and lows) were adequately predicted, with the exception of the 1940s and 1950s for which the prediction models underestimated the growth reductions in both tamarack and spruces.

LARCH SAWFLY OUTBREAKS

A running correlation coefficient between tamarack and spruce residual chronologies was used to verify that both the host and the nonhost chronologies were sharing common environmental signals (as suggested by results of the response function analyses). As shown in Figure 5, over the period 1776 to 1900 tamarack correlated very well with both white spruce and black spruce, with correlation coefficients exceeding 0.50 and as high as 0.60 in the analyses of LLA1 and LLA2 (Fig. 5a). An abrupt decline of the correlation was, however, observed starting with the 1876–1925 interval. In some instances, the correlation

TABLE 1

Statistical characteristics of host and nonhost residual chronologies produced for subarctic Manitoba.

Species:	Tamarack				Spruce	
Sites:	LLA1	LLA2	LLA34	LLA5	White	Black
Chronology length	1730–2000	1644–2001	1655–2000	1775–2000	1600–2001	1556–2000
Number of years	271	358	346	226	402	445
Number of trees	23	49	27	8	35	55
Number of radii	50	98	60	21	66	114
Mean ring width (mm)	0.47	0.43	0.42	0.41	0.50	0.32
Missing rings (%)	0.19	0.13	0.16	0.61	0.01	0.02
Mean sensitivity	0.26	0.24	0.24	0.29	0.13	0.14
Standard deviation	0.22	0.21	0.20	0.24	0.12	0.14
First order autocorrelation[a]	0.46	0.39	0.30	0.39	0.49	0.40
Common interval analysis	1903–2000	1903–2000	1903–2000	1903–2000	1903–2000	1903–2000
Number of trees	6	19	17	6	13	19
Number of radii	11	37	32	11	24	33
Variance in first eigenvector (%)	44.29	45.53	37.85	57.15	35.75	30.87
Agreement with population chronology	0.77	0.93	0.90	0.86	0.85	0.88
Mean correlation among all radii	0.38	0.44	0.35	0.53	0.32	0.28
Mean correlation within trees	0.53	0.67	0.64	0.63	0.59	0.51

[a] Calculated from standard chronology.

attained 0.10 (LLA5 vs. black spruce, Fig. 5b), suggesting that the chronologies had lower common environmental influences. This trend was reversed starting with the interval 1931–1980 with correlation coefficients increasing to previous levels. The analysis conducted between the tamarack chronologies indicated that they shared common environmental influences over the entire period (Fig. 5c). The lowest correlation coefficients were observed with LLA5 chronologies. Strong correlations were also observed between the two spruce chronologies (Fig. 5d).

Program OUTBREAK identified several periods of growth suppression in tamarack lasting four or more years (Fig. 6). Synchronies

in growth suppression periods were observed in most tamarack residual chronologies during the early 1820s, early 1860s, mid-1880s to early 1890s, early 1900 to 1910s, early 1940s, early 1960s, and late 1980s. Rarely, however, were these suppression periods observed in more than 25% of the series suggesting the absence of major regional disturbances. More specifically, we identified five periods having growth suppressions recorded in more than 10% of tamarack series and in all four tamarack chronologies (when considering black spruce as the nonhost species). These periods are 1818–1824, 1857–1864, 1891–1892, 1903–1912, and 1959–1964. These episodes of growth suppressions in tamarack were clearly highlighted when looking at the host and nonhost
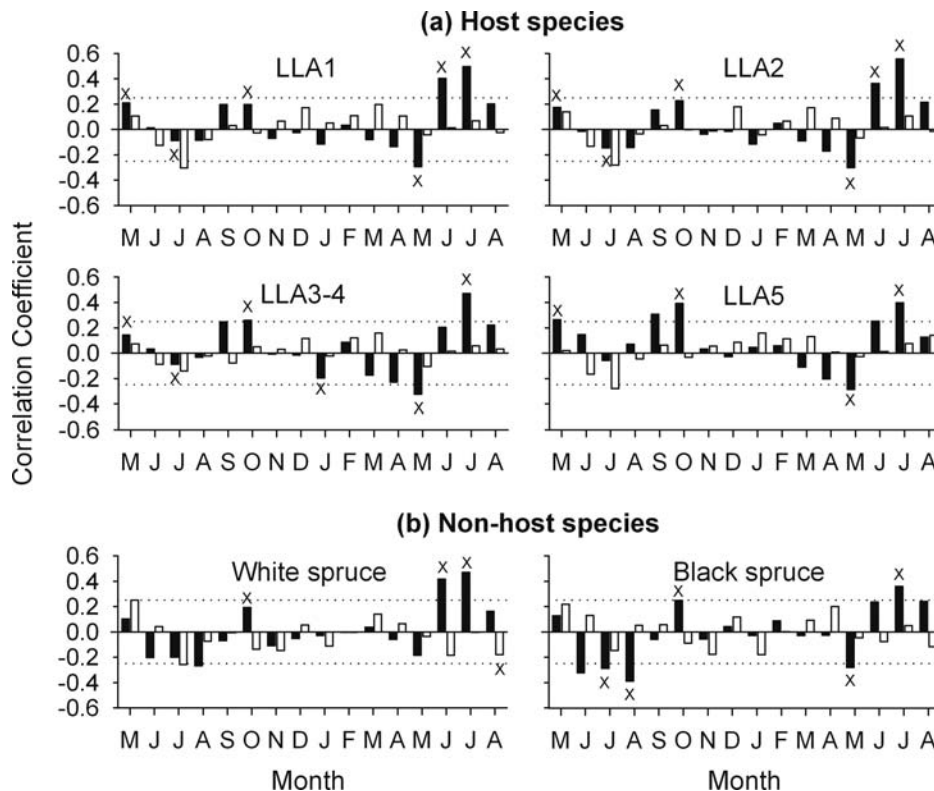

FIGURE 3. *Correlation function between the (a) residual host for LLA1, LLA2, LLA3-4, LLA5 and (b) nonhost PGL and PMA chronologies and temperature (solid bars) and precipitation (empty bars). Correlation coefficients above 0.25 and below −0.25 (horizontal dotted lines) are significant at* P < 0.05. *The X indicates significant variables after the response function analysis.*

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(a) Host species
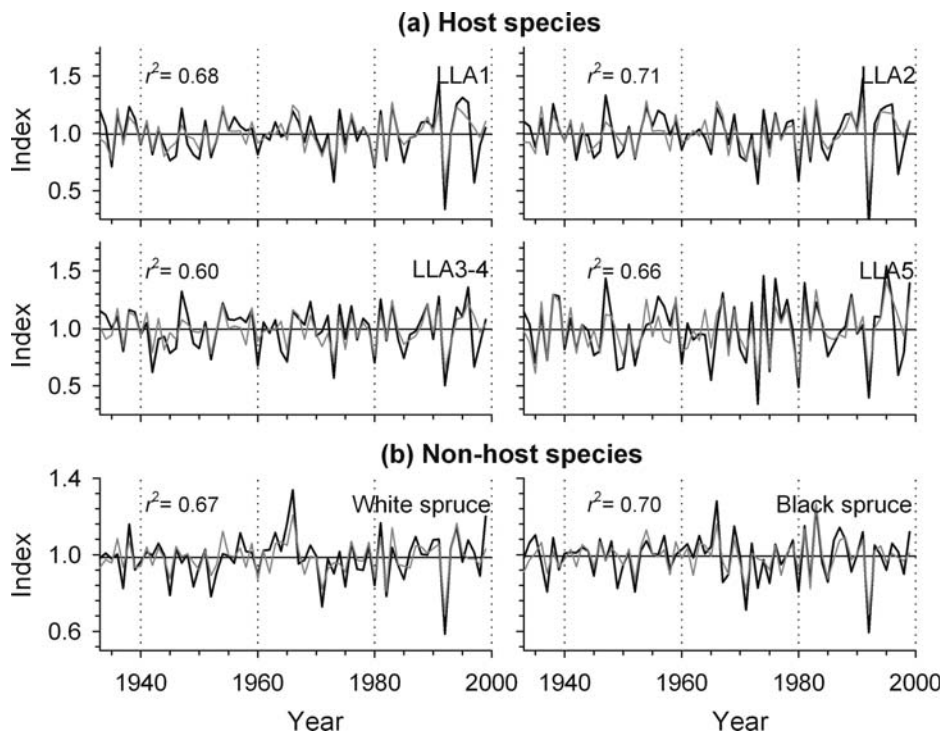
(b) Non-host species

FIGURE 4. Host and nonhost residual chronologies from 1933–1999 (black line) and the estimated growth based on climatic data from the same time period from Churchill, Manitoba (thin gray line). Estimated growth was determined using the program PRECON.

residual chronologies (Fig. 6). Comparison of the standard chronologies however indicated that through the 19th century, radial growth of the nonhost species was in most cases lower than average and followed the same direction as that of the host species. No contrasting growth suppressions were observed between tamarack stand types, though the frequency of affected trees in the 1903–1912 episode was higher in LLA5 (Fig. 6d). In general, the use of either white spruce or black spruce as the nonhost species led to the same general conclusion.

An important component in the identification of larch sawfly outbreak is the presence of pale latewood and missing rings in the host species. Pale latewood was identified in the years 1782, 1817 (4 times), 1832, 1837, 1850, 1857, 1878, 1882, 1930, 1931, 1937, 1945, 1958, 1961, 1964 (3 times), 1965, 1968, 1974, 1978 (7 times), 1980, 1991, and 1992 (Fig. 6). However, there was a lack of synchrony between the identified pale latewood and the identified growth suppressions in the host species. Also, missing rings in tamarack series did not correspond to the identified growth suppression periods, nor they followed a year of pale latewood formation (Fig. 6).

Discussion

LARCH SAWFLY HISTORY

Our results indicated that over the last two centuries large-scale outbreaks by the larch sawfly were not detectable in the forest tundra south of Churchill, Manitoba. This was stressed by the absence of a tree-ring signature similar to that observed in the boreal forest and indicative of large-scale repeated defoliation (Harper, 1913; Jardon et al., 1994; Girardin et al., 2001; Case and MacDonald, 2003). Our results further contrast with those from the forest tundra of the east side of the Hudson Bay where both direct (Cloutier and Filion, 1991; Tailleux and Cloutier, 1993) and tree-ring evidence (Arquillière et al., 1990; Jardon et al., 1994; Filion and Cournoyer, 1995) of severe larch sawfly outbreak were reported. Cloutier and Filion (1991) observed important larch sawfly oviposition activity, up to the treeline, in isolated groves, and in both coastal and continental areas. As in the boreal forest, tree-ring evidence of larch sawfly outbreaks in subarctic

Quebec were based on the synchrony among pale latewood rings, growth suppression periods, increase percentage of missing/incomplete rings, and the lack of correspondence between the host and nonhost tree-ring chronologies.

MISSING/INCOMPLETE RINGS AND PALE LATEWOOD

The presence of pale latewood and missing/incomplete rings in only a small percentage of tamarack trees support the argument that large-scale larch sawfly outbreaks have been absent in the region. In tamarack, missing/incomplete rings were observed in years of reduced growth but not during prolonged periods of growth suppression. Our results contrast with those of Jardon et al. (1994) who observed as many as 11 successive missing/incomplete rings during an outbreak, with the maximum number of missing/incomplete rings occurring in the second or third year. Jardon et al. (1994) also mentioned that the large majority of sawfly outbreaks in subarctic Quebec since 1744 could be identified by the presence of a pale latewood during the first year of defoliation. In northern Saskatchewan, Case and MacDonald (2003) only observed three pale latewood years in their 314-yr-old chronology from northern Saskatchewan. These occurred in the 20th century and also coincided with onsets of growth suppression (Case and MacDonald, 2003). Only in Arquillière et al. (1990) was a systematic absence of pale latewood ring noted during larch sawfly outbreaks. Among all the larch sawfly reconstruction done in subarctic Quebec, Arquillière et al. (1990) had the most northern site with their second site located south along the Hudson Bay coast.

Pale latewood rings have also often been associated with the occurrence of colder summers, potentially associated with the impact of volcanic eruptions (Filion et al., 1986; Yamaguchi et al., 1993; Szeicz, 1996; Gindl, 1999; Tardif et al., 2004). Likely, many of the pale latewood rings observed in the Churchill area are from climate origin. Despite the absence of a systematic quantification of pale latewood years in black spruce and white spruce, the pale latewood rings of 1815 and 1817 were observed in both host/nonhost species. The Tambora eruption of 1815 was associated with a cooling of summer temperatures leading to the formation of pale latewood ring in
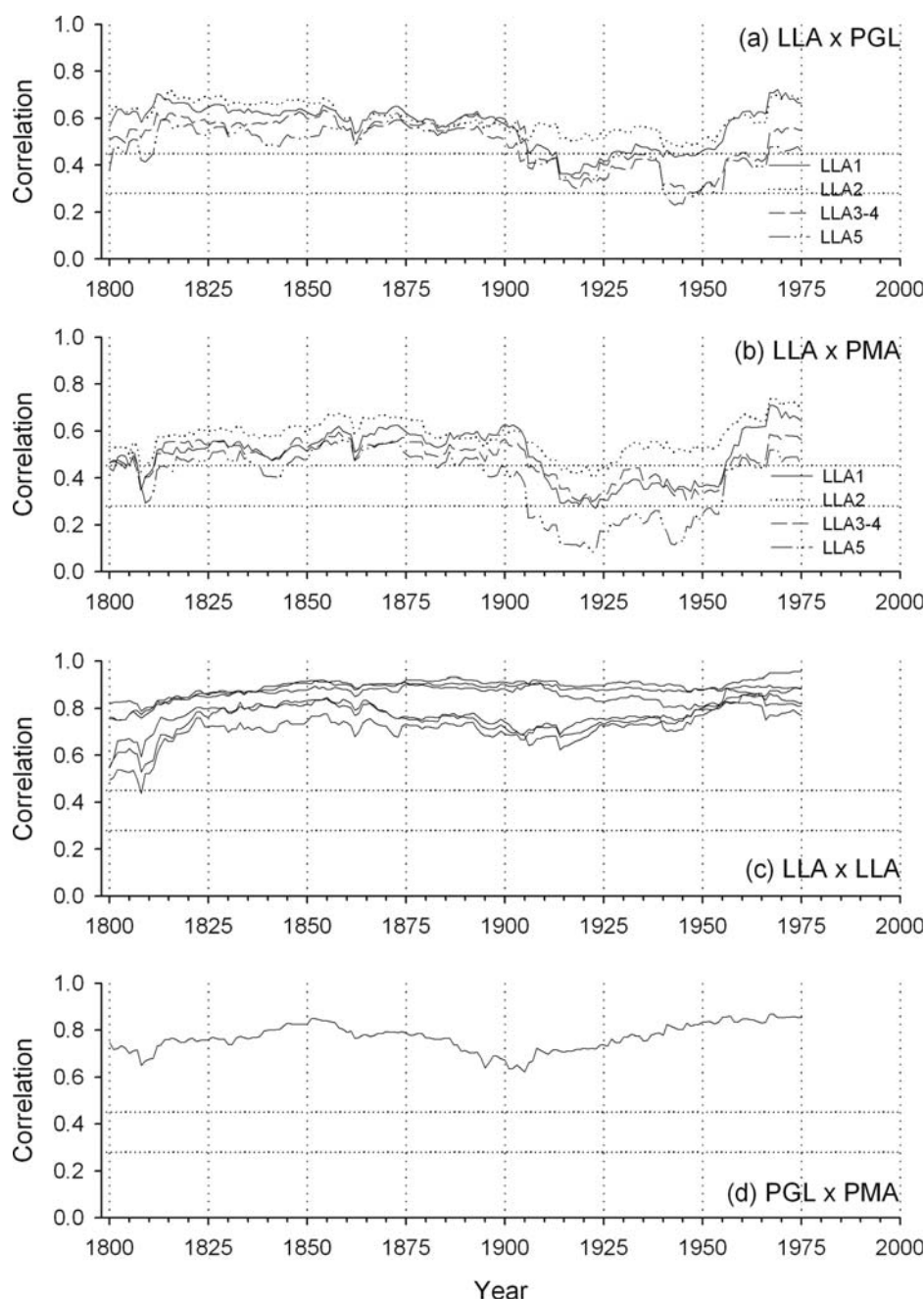
FIGURE 5. 50-yr window running Pearson correlation lagged by 1 yr between each of the four tamarack residual chronologies and (a) the white spruce and (b) the black spruce residual chronologies; (c) shows the same analysis conducted between the tamarack residual chronologies themselves; (d) shows the analysis conducted between the black spruce and the white spruce residual chronologies. The analysis runs from 1776 to 2000; the window median was used for plotting on the time scale. Horizontal dotted lines indicate the 0.1% (upper line) and 5% (lower line) significance levels.

1816–1817 (Filion et al., 1986) in eastern Canada and in 1815–1817 in central and western Canada (Szeicz, 1996). Further work will be needed to assess the origin of the pale latewood rings (abiotic or biotic) observed in the Churchill area but these were observed to be infrequent in all three species (Monson, 2003).

GROWTH SUPPRESSION

In our study, many radial growth reductions were synchronized in both host/nonhost chronologies. This was observed in the 19th century and also toward the end of the 20th century. Program OUTBREAK did, however, identify periods in which tamarack registered growth suppressions not observed in the nonhost species. These periods, potentially associated with insect defoliation, were seldom observed in more than 25% of the tamarack series. In boreal studies, past growth suppressions presumably caused by severe larch sawfly outbreaks occurred in more than 50% and up to 100% of the host trees (Girardin

et al., 2001; Case and MacDonald, 2003). Despite these differences, some of these periods were synchronized among stands and could reflect light defoliation associated with "subepidemic" levels of larch sawfly. This could support the absence of strong pale latewood development. According to Graham (1956), tamarack is characterized by a series of defoliation periods of a short duration or intensity and only at long intervals are disastrous outbreaks observed. Arquillière et al. (1990) noted that two years of severe defoliation followed by years of light defoliation had no serious impact on tree growth.

In the absence of strong evidence supporting larch sawfly outbreak, it could also be speculated that the growth suppressions observed in tamarack originated from poor growing conditions associated with years of higher water table. This hypothesis is supported by the fact that the stand least susceptible to sawfly outbreak (LLA5) showed the weakest correlation with the nonhost chronologies and the highest percentage of affected trees in the outbreak analysis (Fig. 6) during the interval 1903–1912. Denyer and Riley (1964)

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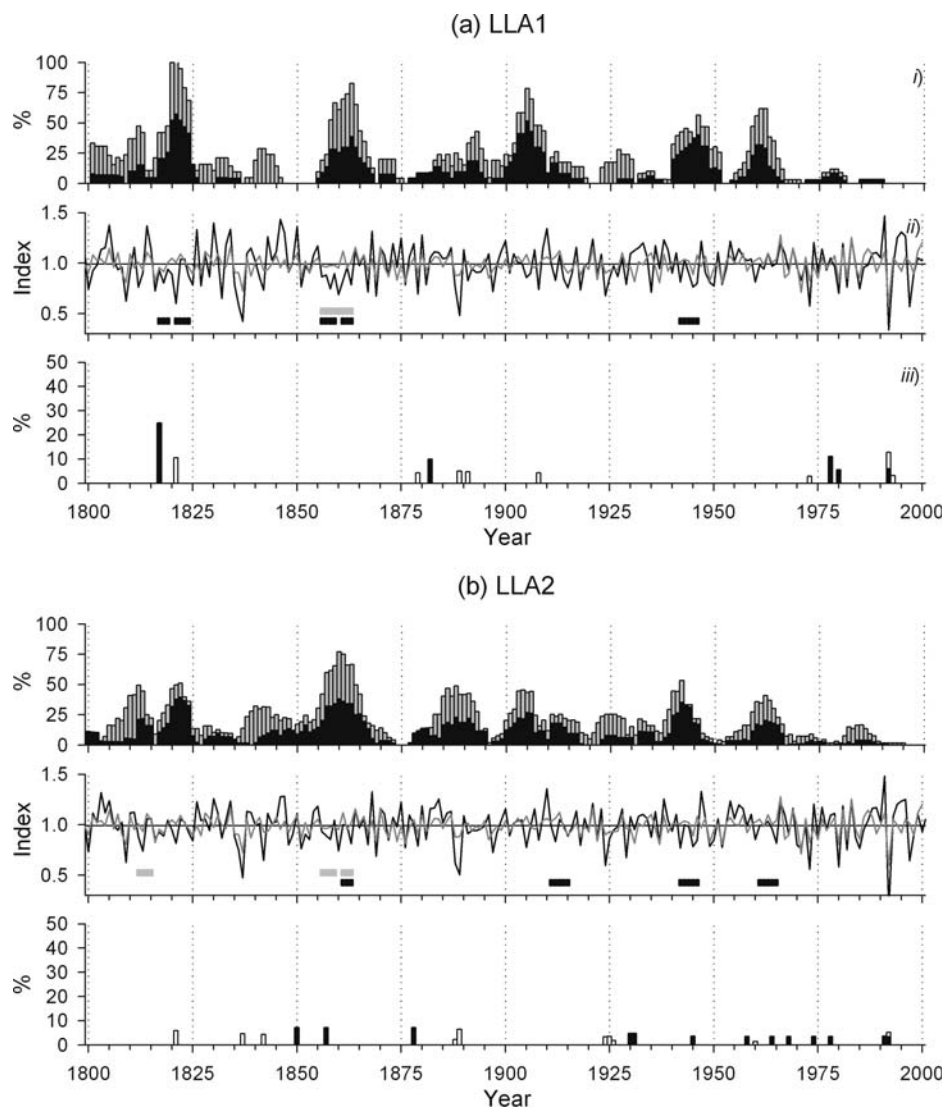
(a) LLA1

(b) LLA2

FIGURE 6. Results of the host and nonhost analyses for identification of sawfly outbreak episodes in (a) LLA1, (b) LLA2, (c) LLA3-4, and (d) LLA5. For each stand type, the upper stacked vertical bar chart shows the percentage of tamarack series that were recorded as having growth reductions in a given year as identified by the program OUTBREAK (see methods). Black bars refer to the analysis in which black spruce was the nonhost species; gray bars refer to the analysis in which white spruce was used (the percentage indicated is the sum of both analyses). The middle chart shows the residual chronologies for tamarack (thick line) and black spruce (gray line). Vertical thick marks (black for black spruce and gray for white spruce) indicate years of growth suppressions in the tamarack corrected residual chronology as recorded by the program OUTBREAK. The lower stacked vertical bar chart shows the relative frequency of light latewood rings recorded in trees (solid bars) and missing rings recorded in measurement series (empty bars).

reported important dieback and root mortality in tamarack growing in "treed muskeg" due to rising water levels. Black spruce was less impacted because of its habit of growing on hummocks formed from the accumulation of moss or the buildup of sphagnum. Our data indicated that during many growth suppression periods in tamarack, radial growth of the nonhost species was also lower than average and followed the same direction. Periodic flooding of bogs was reported to produce growth reduction which, were "indistinguishable" from those caused by larch sawfly defoliation (Nairn et al., 1962; Ives and Nairn, 1966a).

THE ROLE OF CLIMATE AND OTHER FACTORS

The correlation function, response function, and estimated growth as predicted for the period of 1933–1999 stressed that all three species, regardless of sites, responded to climate in a very similar way. This is an important condition in the host/nonhost comparison process and furthers the validity of black spruce and white spruce as nonhost species (Swetnam et al., 1985; Girardin et al., 2001; Case and MacDonald, 2003). Temperature dominated the radial growth-climate profile with temperature in May-June-July of the current growing season being most important. Previous September-October temperatures were also positively correlated to current year growth in most species. Guiot (1985) mentioned that the warm autumn anomaly is

important in the Hudson Bay Lowland region of Manitoba. Jacoby and Ulan (1982) observed that white spruce from the Churchill area responded positively to both warm October-November of the year previous to ring formation and warm July temperature of the year of ring formation. In the Hudson Bay lowland as in most high-latitude chronologies, warm early summer temperatures are beneficial to tree growth (Jacoby and Ulan, 1982). The generalized negative association between May temperature and radial growth may relate to the impact of an early snowmelt at a time the soil is still frozen. These conditions may increase evaporation or runoff and reduce water percolation in the peat thus limiting the ground water recharge and subsequent availability (Scott et al., 1993). An earlier onset of the growing season at a time the soil is still frozen and covered with snow may also have negative impact.

In contrast to boreal studies, the radial growth-climate association in tamarack did not appear to be contaminated by the presence of larch sawfly outbreaks. This was highlighted by the strong goodness-of-fit between the radial growth and the predicted growth curves and contrast with previous conclusions made about the little potential of tamarack for climatic reconstruction (Case and MacDonald, 2003). Case and MacDonald (2003) reported a strong similarity of their host-nonhost chronologies up to the late 1800s, after which, a decoupling was observed and associated to repeated defoliation event by the sawfly during the 20th century. Our results indicated that tamarack and spruce
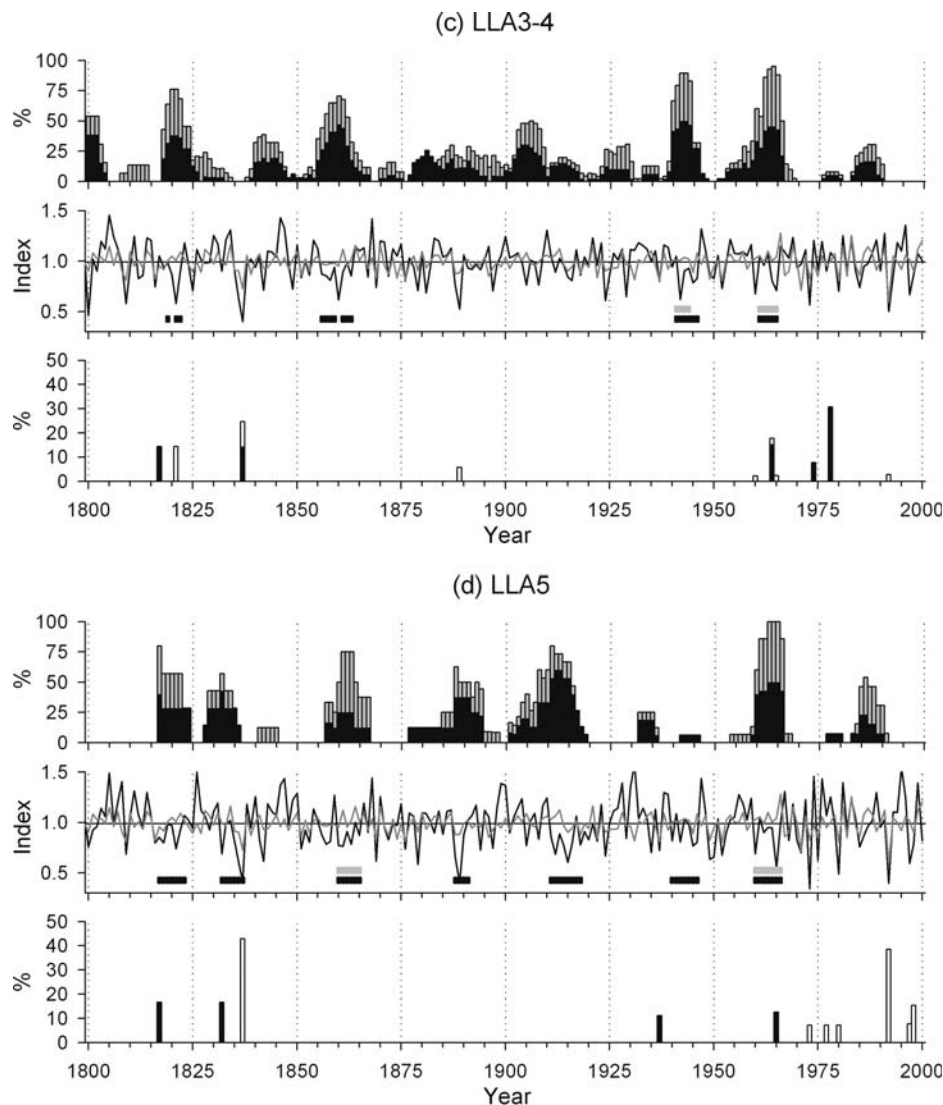
(c) LLA3-4

(d) LLA5

FIGURE 6.   (Cont.)

chronologies had a highly significant intraspecies correlation but that the cross-correlation between them systematically drop from interval 1876–1925 to interval 1930–1980. This period of lower correlation between tamarack and spruce in the Churchill area could reflect small-scale or localized outbreak from the larch sawfly. During this period, growth suppression periods were not synchronized between the host/nonhost species and these periods also corresponded to the defoliation history observed at more southern latitude in Manitoba (1911–1920, 1924–1927, 1938–1958, early 1960s (Nairn et al., 1962; Ives and Nairn, 1966a; Turnock and McLoad, 1966).

At Churchill, both spring and early summer temperature over the period 1933–1999 have significantly increased (Vincent and Gullett, 1999; Zhang et al., 2000). A tree-ring study by Scott et al. (1988) revealed that the period 1921–1970 could have been characterized by a shift in atmospheric circulation leading to frequent incursion of temperate air masses during the summer and particularly in July. The authors refer to a resurgence of arctic conditions after the 1970, which also coincided with better correlation among species chronologies. These observations are consistent with trends observed in the recent synoptic classification scheme of North America (Sheridan, 2002; data covering the period 1953–1993). The period 1953–1993 at Churchill was characterized by a significant increase in the number of days dominated by Dry Polar air (DP; cold and dry air) and a decrease in the domination of Moist Polar air (MP; cool, cloudy, and humid air, with

light precipitation). These shifts were highly significant in spring (March-April-May, $P < 0.001$) and less important in summer (June-July-August, $P < 0.100$).

These fluctuations in atmospheric circulation reported at Churchill may have affected the connections between tamarack growth and sawfly defoliation. A greater penetration of temperate air masses in the Churchill area over the period 1921–1970 and the subsequent shift to drier polar air would reflect a decrease in inland advection and an increase in the frequency of days dominated by northerly winds. These two periods were indicated by the outbreak analyses as a transition between a period with potential defoliation from the larch sawfly to one of lower activity. Intriguingly, mass flights of sawfly adults invading northern sites (e.g., Nueltin lake, approximately 400 km northwest of Churchill) were observed in June 1965 and associated with periods of favorable southerly winds and warmer temperature (Turnock and McLoad, 1966).

Conclusion

This study provides evidence that the larch sawfly did not reach widespread epidemic level in the Churchill region, subarctic Manitoba. Synchronized growth suppressions of low amplitude were, however, observed in tamarack with no correspondence in the nonhost species. These events could be associated with "subepidemic" defoliation by

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the larch sawfly. The lower correlations observed between the host/nonhost chronologies from about 1876 to 1970 and the correspondence between periods of growth suppression and periods of known outbreaks in the boreal forest of Manitoba support this view. These events could also be attributed to climate fluctuations. The period of low correlation between the host/nonhost chronologies coincides to a period of greater penetration of warmer temperate air masses in the Churchill area lasting from 1921 to 1970. Host/nonhost species may have responded differently to warmer climate because of local changes in site hydrology. This is supported by the more pronounced growth suppressions (lower correlation) observed in tamarack growing in hydric sites, which are also the less proper for larch sawfly survival. To add complexity, greater penetration of temperate air masses could also favor larch sawfly migration from southern location. To better understand the impact of climate and larch sawfly defoliation on tamarack growth, a network of tree-ring chronologies extending farther into the boreal zone and inland will be needed. This study stresses the need for more studies (1) on the host-insect dynamics to determine the parameters controlling larch sawfly dynamics within the distribution range of tamarack and (2) on the climatic controls of larch sawfly populations in relation to future climatic change in subarctic Manitoba.

Acknowledgments

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