

NOTE / NOTE

Tree-ring evidence extends the historic northern range limit of severe defoliation by insects in the aspen stands of western Quebec, Canada

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Abstract: A dendrochronological reconstruction of insect outbreaks was conducted along a latitudinal gradient from 46°N to 54°N in the boreal forest of western Quebec, Canada. Tree-ring chronologies of the host species, trembling aspen (*Populus tremuloides* Michx.), were constructed to identify periods of severe defoliation and comparisons were made with tree-ring chronologies of nonhost species. In addition, the frequency of white and narrow rings was used to further confirm the occurrence of insect outbreaks at these latitudes. Some major outbreaks occurred in relatively close synchrony at the regional scale, but the initiation year, intensity, and extent of the outbreaks varied spatially. For example, the 1950s outbreaks were observed from 1951 to 1952 at 46°N, from 1953 to 1954 at 47°N, and from 1954 to 1956 at 48°N. Other major outbreaks like the 1964 and 1980 outbreaks were fairly well synchronized at northern latitudes. The observed outbreaks in trembling aspen stands at 54°N also provided clear evidence that severe insect defoliation occurs much further north than the currently reported range limit, that is, between 49°N and 51°N, of the most important trembling aspen defoliator, the forest tent caterpillar (*Malacosoma disstria* Hubner). Our study demonstrated that careful identification of white rings in host species can provide valid information allowing the expansion of the forestry insect inventory database both at temporal and spatial scales.

Résumé : Une reconstitution dendrochronologique des épidémies d'insecte a été réalisée le long d'un gradient allant de 46°N à 54°N dans la forêt boréale de l'ouest du Québec, au Canada. Les chronologies de l'espèce hôte, le peuplier faux-tremble, ont été construites de manière à identifier les périodes de défoliation sévère et des comparaisons ont été effectuées avec les chronologies d'espèces non hôtes. De plus, la fréquence des cernes pâles et étroits a été utilisée pour valider l'occurrence des épidémies d'insecte à ces latitudes. Quelques épidémies majeures sont survenues avec une synchronicité relativement étroite à l'échelle régionale mais l'année du début, l'intensité et l'étendue des épidémies variaient dans l'espace. Par exemple, les épidémies des années 1950 ont été observées de 1951 à 1952 à 46°N, de 1953 à 1954 à 47°N et de 1954 à 1956 à 48°N. D'autres épidémies importantes comme celles de 1964 et 1980 étaient assez bien synchronisées aux latitudes nordiques. Les épidémies observées dans les peuplements de peuplier faux-tremble à la latitude 54°N fournissent des preuves manifestes que des défoliations sévères causées par les insectes surviennent beaucoup plus au nord que la limite de l'aire de répartition couramment rapportée, soit entre 49°N et 51°N, dans le cas du plus important défoliateur du peuplier, la livrée des forêts. Notre étude montre que l'identification minutieuse des cernes pâles chez l'espèce hôte peut fournir une information valide qui permet d'élargir la base de données de l'inventaire des insectes forestiers tant à l'échelle temporelle que spatiale.

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Introduction

The forest tent caterpillar (*Malacosoma disstria* Hubner; FTC) constitutes one of the major insects causing disturban-

ces in the boreal forest of North America (Witter 1979). Severe FTC defoliation can significantly reduce tree growth and increase both mortality and crown dieback of the host species (Batzer et al. 1954; Hildahl and Reeks 1960), conse-

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quently decreasing forest productivity (Bergeron and Charon 1994; Hogg and Schwarz 1999). In the boreal zone, trembling aspen (*Populus tremuloides* Michx.; hereinafter referred to as aspen), balsam poplar (*Populus balsamifera* L.), and paper birch (*Betula papyrifera* Marsh.) are the preferred FTC host species (Peterson and Peterson 1992; Hogg et al. 2002a). FTCs feed during early spring (Robison and Raffa 1997), as soon as their eggs hatch during this period and in synchrony with the budding of young, nutritious leaves of the host species (Fitzgerald 1995). Recent studies regarding aspen, balsam poplar, and paper birch have shown that light-coloured rings, that is, "white rings," may develop following severe FTC defoliation early in the growing season (Hogg and Schwarz 1999; Sutton and Tardif 2005). A recent experimental study simulating severe FTC defoliation by manually removing 98%–100% of aspen leaves early in the growing season confirmed that white rings were produced as a consequence of severe defoliation (Hogg et al. 2002b). Jones et al. (2004) also found that both reduced aspen radial growth and earlier growth cessation resulted from artificial defoliation.

In the boreal forest, the large aspen tortrix (*Choristoneura conflictana* Walker; LAT) is another major defoliator of aspen as well as of the secondary host species, which include balsam poplar, paper birch, and willow (*Salix* spp.) (Cerezke 1992). During early spring (May), bud and leaf tissue may be destroyed prior to aspen bud expansion as young LAT larvae mine into aspen buds. Later stages of larvae continue to feed within rolled leaves or within two or more leaves pulled together and secured with silken webbing, until mid-June when feeding is completed (Cerezke 1992). The feeding may cause partial or complete defoliation of trees, thus resulting in reduced tree vigor and stem growth (Cerezke 1992). Previous studies have documented aspen growth reduction caused by LAT outbreaks across the Canadian boreal forest, including the province of Quebec (Martineau 1985; Hogg and Wein 2005). The severe LAT outbreaks could also occasionally lead to the formation of white rings. Hogg and Wein (2005) observed the occurrence of a distinct white ring in aspen stands in 1968 near Whitehorse, Yukon, which they attributed to LAT outbreaks. The documented severe LAT outbreaks in 2000–2001 also led to fairly frequent white ring formation in aspen trees in northwestern Alberta and adjacent northeastern British Columbia (E.H. Hogg, unpublished data, 2005).

LAT outbreaks generally occur earlier and cause less defoliation compared with FTC outbreaks (Frey et al. 2004). However, since white rings occasionally form after severe LAT defoliation and frequently form after severe FTC defoliation in aspen, they could be used as indicators of past severe insect defoliation in boreal aspen stands. Studies regarding aspen wood anatomy also showed that white rings were characterized by smaller diameter fibres with reduced cell wall thickening and a higher proportion of lumen area and an overall decreased wood density compared with normal rings (Sutton and Tardif 2005). In addition to white ring formation, growth suppression was also observed in host trees during severe outbreak years (Hogg and Schwarz 1999; Sutton and Tardif 2007). Owing to association of these distinctive characteristics with aspen defoliation, both white rings and growth suppression were used in past studies as reliable indi-

cators to reconstruct severe insect outbreaks, particularly of FTC outbreaks (Cooke 2001; Sutton and Tardif 2007).

The northern limit of FTC distribution in Quebec was previously determined from forest inventory data as illustrated in Fig. 1. Fitzgerald (1995) reported that the northern limit of FTC distribution in Quebec corresponded to 47°N, whereas Cooke and Lorenzetti (2006) set this limit between 49°N and 51°N. Given the wide distribution of both aspen and paper birch in Quebec and their occurrence as far north as the Hudson Bay region near 54°N–55°N (Little 1971), the present study aimed to address whether insect outbreaks could be observed as far north as the distribution limit of both host species. We hypothesized that insect outbreaks would occur as far north as the distribution of their host species and thus at more northern latitudes than currently reported.

The present study was conducted along the latitudinal gradient from 46°N to 54°N in western Quebec, Canada. Our objectives were (i) to reconstruct past major insect outbreaks along this latitudinal gradient using both the presence of white rings and growth suppression and a dendrochronological comparison of host and nonhost species, (ii) to explore possible systematic changes in the spatial distribution of insect outbreaks in the study area, and (iii) to assess the northern limit of insect activity in western Quebec, Canada.

Materials and methods

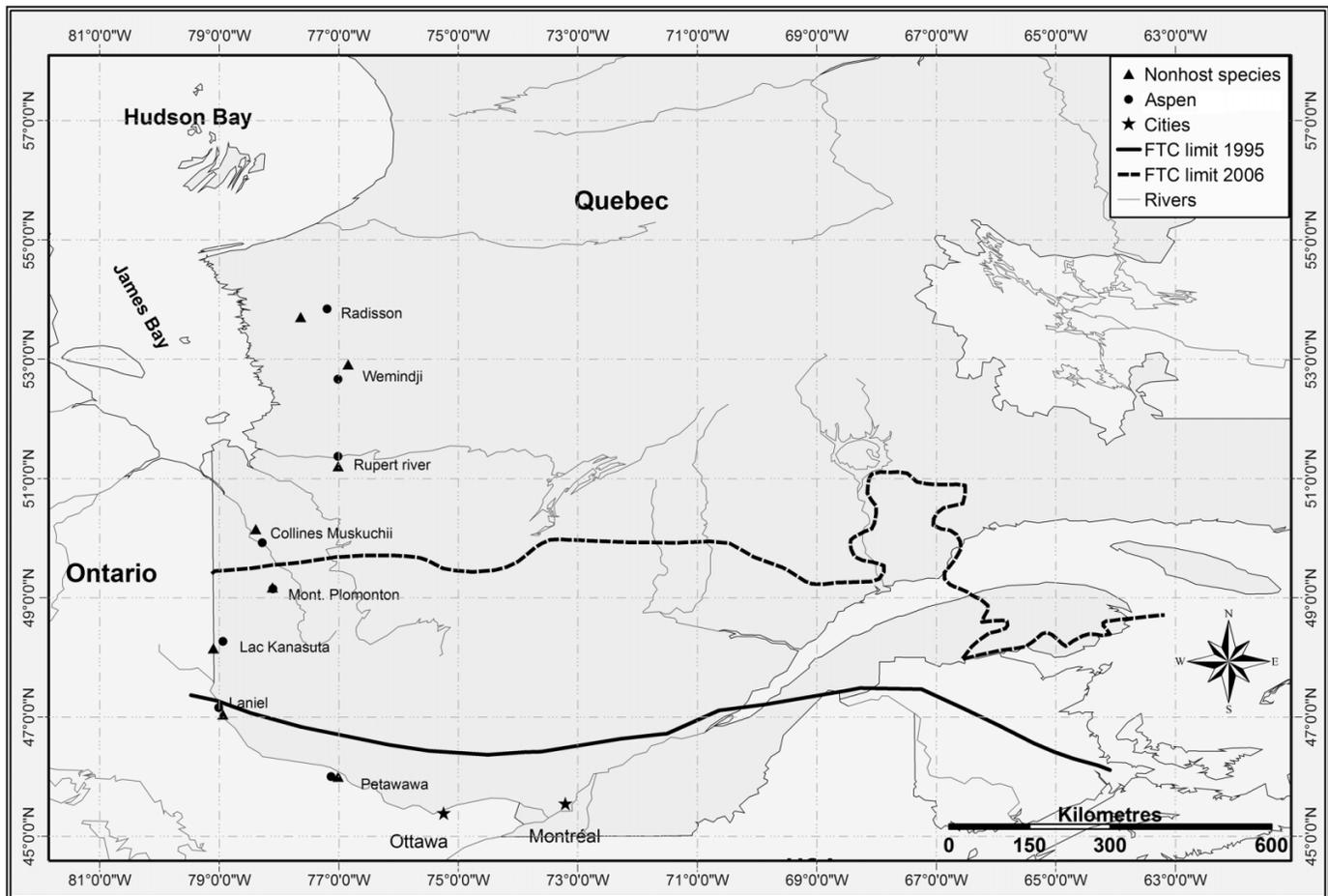
Study area

The study area is located in western Quebec along a latitudinal gradient ranging south from Petawawa (located in Ontario but very close to Quebec, approximately 46°N) to Radisson (approximately 54°N) in the north (Fig. 1). The topography along the gradient is generally flat and uniform with low-elevation hills and rock outcrops (300–400 m a.s.l.). The area is affected by cold, dry arctic air from the north during the winter and by warm, moist air originating from the south during the summer. A climate gradient is also enclosed within the latitudinal gradient. The climate normals for 1971–2000 showed a decrease in mean annual temperature (from 4.73 to –3.14 °C), annual total precipitation (from 868 to 684 mm), and growing degree-days (>5 °C) (from 1 868 to 862 °C) from the southernmost meteorological station (Sheenboro, 45°58'N, 77°15'W) to the northernmost station (La Grande Rivière, 53°38'N, 77°42'W) (Environment Canada 2002). The common boreal tree species, including aspen, paper birch, black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), and balsam fir (*Abies balsamea* (L.) Mill), occur in the study area, but their abundances change from south to north (ESWG 1996). The vegetation transition zone between the mixedwood forests (both broadleaf and conifer) and the conifer-dominated boreal forests occurs at approximately 49°N (Hofgaard et al. 1999).

Sampling and chronology development

We collected tree-ring samples from aspen (host species) stands as well as from black spruce and jack pine (nonhost species) stands along the latitudinal gradient from 46°N to 54°N at approximately 1° intervals in western Quebec (Fig. 1). At 48°N, the existing black spruce chronology de-

Fig. 1. Map showing sampling sites and the northern limit of forest tent caterpillar (FTC) distribution along the latitudinal gradient from 46°N to 54°N in western Quebec, Canada. The thick black line represents the northern limit of FTC distribution in Quebec reported by Fitzgerald (1995). The broken line represents the northern limit of FTC distribution in Quebec identified by Cooke and Lorenzetti (2006).



veloped by Hofgaard et al. (1999) was included in our analysis as a nonhost species. Towards the northern end of the gradient, available old aspen stands were fairly rare and only two stands were sampled between 52°N and 54°N. In total, eight aspen sites with corresponding nonhost sites were established at intervals along the latitudinal gradient (Fig. 1). In each stand, at least 20 old and healthy trees of each species were cored or cut transversely.

In the laboratory, all samples were dried, polished, and then visually crossdated under a binocular microscope. Most dated samples were carefully measured using a Velmex Measuring system interfaced with time series analysis program (TSAP) (Frank Rinntech, Heidelberg, Germany) to a precision of 1/1000 mm. Some black spruce and jack pine discs were scanned using WinDENDRO 2005 to obtain ring-width values. The visual crossdating was further validated using COFECHA (Holmes 1983). To identify possible insect outbreaks, occurrences of white and (or) narrow rings were recorded for all aspen samples. An independent validation regarding the occurrence of white and (or) narrow rings was also conducted at the Centre for Forest Interdisciplinary Research of the University of Winnipeg by an experienced technician, to assure accuracy.

Each measured series was standardized using a 60 year spline function, which preserved approximately 99% of the

variation within individual series at a wavelength of 19 years (Cook and Peters 1981). Standardization involved transforming ring-width measurements into dimensionless indices by dividing the observed ring-width measurements by those estimated using the spline function (Fritts 1976). These growth indices contain relatively stable means and variances over time (Cook 1990). This procedure retained high-frequency variations (interannual to decadal) and filtered out medium- to low-frequency trends, such as trends in growth due to age and (or) size, biological persistence, and long-term stand dynamics (Fritts 1976; Cook 1990). Autoregressive modeling was also performed on each standardized series to remove temporal autocorrelation and enhance the common signal. To further eliminate the effect of endogenous stand disturbances and enhance the common signal, all residual series were averaged by site using a biweight robust mean, which reduced the effect of outlier values. Chronology construction was carried out using ARSTAN (ARSTAN Windows 4.0a; Cook 1985).

Insect outbreaks and spatial pattern

Aspen (host) residual chronologies were compared with nonhost species residual chronologies to determine periods of insect outbreaks using OUTBREAK (Swetnam et al. 1985; Holmes and Swetnam 1996). To eliminate the climate

Fig. 2. Insect outbreaks identified along the latitudinal gradient from 46°N to 54°N in western Quebec, Canada. The thick black line represents the aspen residual chronology (host species) and the light broken line represents the nonhost species residual chronology. Periods identified by OUTBREAK as possible insect outbreaks are indicated by a solid bar above the chronologies. Stacked bar chart shows the percentage of samples with white rings (solid bar) and narrow rings (shaded bar). The broken lines in the lower panel indicate 50% and 75% criteria for severe insect defoliation.

Table 1. Characteristics of the host and nonhost residual chronologies along a latitudinal gradient from 46°N to 54°N in western Quebec, Canada.

Sites (°N)	Latitude	Longitude	Elevation (m a.s.l.)	Tree species	Chronology dates
46	45°59.687'	77°31.707'	184	Aspen (host)	1911–2004
46	46°00.419'	77°25.092'	160	Jack pine (nonhost)	1925–2004
47	47°09.539'	79°25.341'	210	Aspen (host)	1894–2004
47	47°02.517'	79°20.746'	258	Jack pine (nonhost)	1883–2004
48	48°14.189'	79°21.822'	285	Aspen (host)	1908–2004
48	48°09.203'	79°30.065'	330	Black spruce (nonhost)	1690–1993*
49	49°09.592'	78°32.885'	341	Aspen (host)	1864–2004
49	49°08.905'	78°32.038'	440	Black spruce (nonhost)	1917–2004
50	49°56.754'	78°42.881'	292	Aspen (host)	1870–2004
50	50°08.674'	78°48.804'	245	Jack pine (nonhost)	1915–2004
51	51°20.957'	77°25.343'	172	Aspen (host)	1925–2004
51	51°11.775'	77°27.184'	215	Black spruce (nonhost)	1761–2004
53	52°39.180'	77°24.019'	237	Aspen (host)	1862–2004
53	52°53.953'	77°15.704'	226	Black spruce (nonhost)	1757–2004
54	53°48.402'	77°35.785'	36	Aspen (host)	1927–2004
54	53°42.028'	78°04.350'	125	Black spruce (nonhost)	1869–2004

Note: The site names are 46°N, Petawawa; 47°N, Laniel; 48°N, Lac Kanasuta; 49°N, Mont. Plomonton; 50°N, Collines Muskuchii; 51°N, Rupert River; 53°N, Wemindji; and 54°N, Radisson.

*Black spruce chronology at 48°N from Hofgaard et al. (1999).

signal at each latitude in the residual host chronology, the nonhost species chronology best correlated with the host species chronology (Swetnam et al. 1985) was used for subsequent comparison. Dendroclimatic analyses also demonstrated that these host and nonhost species responded to climate similarly (J.G. Huang, unpublished data, 2008). The OUTBREAK program eliminates the common signal (presumably climatic) by subtracting the nonhost chronology from the host chronology (Holmes and Swetnam 1996). After exploratory analyses, we selected the same criteria as those used by Sutton and Tardif (2007) to identify possible insect outbreaks at aspen sites along the latitudinal gradient. A potential insect outbreak was identified when three or more consecutive years of negative growth departure (in standard deviation, SD) occurred in the host series, including ≥ 1 years with a maximum growth departure of at least -1.28 SD. A fractional power of 0.1 was used to raise the index value of the nonhost chronology to the selected power, thus avoiding false identification of outbreaks when high growth values were observed in the nonhost species (Holmes and Swetnam 1996). The frequency of white and (or) narrow rings was also used as a key indicator for identifying outbreaks. The potential insect outbreak periods identified were then compared with those reported by Cooke and Lorenzetti (2006) and other related studies. Based on the identified insect outbreak years and growth reduction years of aspen residual chronologies, comparisons among the latitudes were made to explore possible systematic changes in

the spatial distribution of insect outbreaks across the study area.

Results

Insect outbreaks reconstructed along the latitudinal gradient in western Quebec

A total of eight host residual chronologies and eight nonhost residual chronologies (Table 1) corresponding to each degree of latitude were developed, including the black spruce chronology at 48°N from Hofgaard et al. (1999) (Fig. 2). The aspen chronologies varied from 78 to 143 years in duration, with the longest aspen chronology dating back to 1862 at 53°N. The nonhost chronologies ranged from 80 to 248 years. Growth pattern comparisons of host chronologies revealed high similarity at interannual scales, particularly for some growth reduction years (Fig. 2).

Periods of growth suppression were identified by OUTBREAK, as listed in Table 2. Among those periods, growth suppression in the 1950s appears to be common at almost all latitudes, despite differences in the initial year, duration, and ending year (Table 2). The consistent recent periods of suppressed growth were identified at southern latitudes, that is, 2001–2004 at 47°N, 2000–2004 at 48°N, and 2001–2004 at 49°N. At northern latitudes, recent periods with depressed growth were also very similar, that is, 1997–1999 at 50°N, 1998–2004 at 51°N, 1998–2000 at 53°N, and 1994–2002 at 54°N. Other periods of suppressed growth were identified at

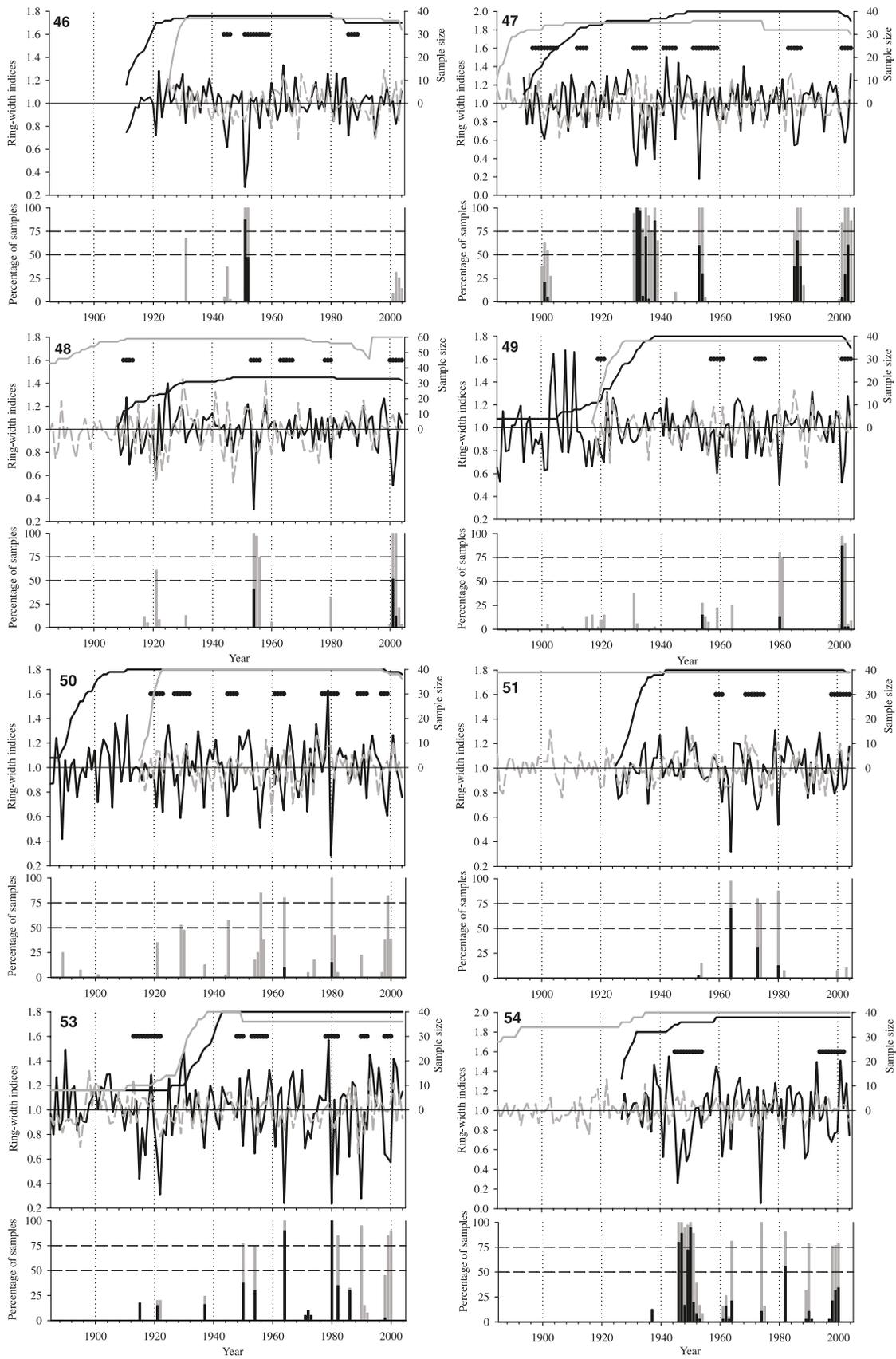


Table 2. Periods of growth suppression identified by OUTBREAK, years in which white rings were observed in the samples, and years in which severe insect defoliation occurred, as determined along a latitudinal gradient from 46°N to 54°N in western Quebec, Canada.

Latitude (°N)	Periods of growth suppression identified by OUTBREAK	Years in which white rings were observed	Years in which severe insect defoliation occurred
46	1944–1946, 1951–1959, 1986–1989	1951–1952	1951–1952
47	1897–1905, 1912–1915, 1931–1935, 1941–1945, 1951–1959, 1983–1987, 2001–2004	1901, 1932–1935, 1938, 1953–1954, 1985–1987, 2001–2003	1931–1938, 1953–1954, 1985–1987, 2001–2004
48	1910–1913, 1953–1956, 1963–1967, 1978–1980, 2000–2004	1954, 2001–2002	1954–1956, 2001–2002
49	1919–1921, 1957–1961, 1972–1975, 2001–2004	1878, 1954, 1980, 2001–2002	1980–1981, 2001–2002
50	1919–1923, 1927–1932, 1945–1948, 1961–1964, 1977–1982, 1989–1992, 1997–1999	1879, 1980	1956, 1964, 1980, 1999–2000
51	1959–1961, 1969–1975, 1998–2004	1964, 1973, 1980	1964, 1973–1974, 1980
53	1913–1922, 1948–1950, 1953–1958, 1978–1982, 1990–1992, 1998–2000	1869, 1915, 1921, 1937, 1950, 1954, 1964, 1980, 1982, 1986	1950, 1954, 1964, 1980, 1982, 1986, 1990, 1998–2000
54	1945–1954, 1994–2002	1937, 1946–1951, 1961, 1964, 1974, 1982, 1990, 1998–2000	1946–1952, 1964, 1974, 1982, 1990, 1998–2000

local or regional scales (Table 2). White-ring years were also observed along the latitudinal gradient, as shown in Table 2 and Fig. 2. It is interesting to note that white rings were only observed in 2 years at 46°N, that is, 1951–1952. In contrast, white rings were observed frequently at 47°N, 53°N, and 54°N. In southwestern Quebec, white rings were observed in similar periods in 2001–2003 at 47°N, 2001–2002 at 48°N, and 2001–2002 at 49°N. In northwestern Quebec, white rings were commonly observed at northern latitudes in 1964 and 1980. In spite of low sample replications in 1878 (4 samples), 1879 (2 samples), and 1869 (6 samples) at 49°N, 50°N, and 53°N, respectively, white rings were observed in these years in all samples at these latitudes (Table 2; not shown in Fig. 2). These white-ring years generally corresponded to small annual growth increments. Severe insect defoliation was classified as years in which more than half of the samples showed white rings or more than three-quarters of the samples showed both white and (or) narrow rings. Otherwise, isolated white ring years were considered indicative of insect defoliation. When associating white and (or) narrow ring years with periods of abrupt growth suppression as identified by OUTBREAK (Table 2; Fig. 2), the severe insect outbreaks were determined along the latitudinal gradient in western Quebec (Table 2). Overall, it appears that some major outbreaks reconstructed in western Quebec occurred in relatively close synchrony at the regional scale, but the initiation year, intensity, and extent of the outbreaks varied spatially. For example, the 1950s outbreaks were observed from 1951 to 1952 at 46°N, from 1953 to 1954 at 47°N, and from 1954 to 1956 at 48°N. Other major outbreaks were fairly well synchronized at the northern latitudes. As shown in Table 2 and Fig. 2, the 1964 and 1980 outbreaks were identified in most aspen stands at 48°N–54°N. In addition, several severe insect outbreaks and insect defoliation periods were found prior to 1938. For instance, severe insect outbreaks were observed in 1931–1938 at 47°N. Insect defoliation periods were identified in 1901–1902 at 47°N, in 1915, 1921–1922, and 1937 at 53°N, and in 1937 at 54°N. Among the latitudes, only one severe insect outbreak was identified for aspen stands at

46°N in the past, that is, 1951–1952. However, frequent severe insect outbreaks were observed in aspen stands at 53°N and 54°N (Table 2).

Discussion

Owing to less forest harvesting activity in northern Quebec, long aspen chronologies established at northern latitudes provided a unique opportunity to confirm major insect outbreaks documented in forest insect databases and identify possible insect outbreaks before 1938. Cooke and Lorenzetti (2006) have found that the 1950s (1951–1954, with most extensive outbreak years 1952–1953) outbreaks were exceptionally extensive and covered >95% of the identified outbreak range in Quebec. This observation corresponds to the severe insect outbreaks during the 1950s reconstructed at many of our sites. Bergeron and Charron (1994) and Cooke and Roland (2007) also reported the 1950s outbreaks at Lac Duparquet of northwestern Quebec and Ontario. In the Abitibi-Temiscamingue region (approximately 47°N–49.5°N) of western Quebec, Cooke and Lorenzetti (2006) found the most recent FTC outbreaks peaked in 2001 and this observation supports the severe insect outbreaks reconstructed for 47°N–49°N. The reconstructed recent outbreaks at 47°N–49°N also correspond to a severe FTC outbreak in 1999–2002 in the neighbouring province of Ontario (Cooke and Roland 2007). The outbreaks peaking in 1988 in the Temiscamingue region (Cooke and Lorenzetti 2006) also coincided with the 1985–1987 outbreaks in the same area as our study site at 47°N. Cooke and Roland (2007) showed FTC outbreaks in 1989–1991 in Ontario as well. In addition, Cooke and Lorenzetti (2006) observed a period characterized by less severe and less extensive defoliation cycles in Abitibi region in 1960–1990. These findings are very consistent with the insect outbreaks we reconstructed in this region (48°N–49°N), with the exception of the 1980 outbreak at 49°N. Differences in timing and duration of the outbreaks among different sites could be ascribed to multiple factors, such as topography, forest structures, insect populations, insectivores, and climate factors (Roland and Taylor 1997;

Cooke and Lorenzetti 2006). For example, topography was suggested to be an important factor limiting the frequency and duration of outbreaks in Quebec (Cooke and Lorenzetti 2006).

Cooke and Lorenzetti (2006) partitioned the Quebec province into nine areas with substantial regional-scale coherence in the spatiotemporal pattern of FTC occurrence. After detailed comparisons among those clusters, they revealed that 1963 was a year of decline in insect populations across most of Quebec, except for the Outaouais region. This decline in FTC activity was attributed to the following factors: (i) the FTC eggs at high altitudes in western Canada failed to hatch in the spring of 1963 (Gautreau 1964) and (ii) the hatchling died in May 1963, owing to a late spring frost. In our study region, we did not observe severe outbreaks in 1963 in terms of white rings, which is consistent with their conclusion. However, the 1964 and 1980 outbreaks were extensively observed in the north of the Abitibi-Temiscamingue region of western Quebec, as shown in Table 2 and Fig. 2, and were found well above the northern limit of distribution of FTC as identified by Cooke and Lorenzetti (2006). This suggests that during past aerial surveys these two severe outbreaks were not reported in the north, either because aspen distribution in the north is sporadic or because the region was not traditionally surveyed, since these areas were beyond the previously reported limit of FTC distribution. Sutton and Tardif (2007) have also observed FTC activities unreported by aerial survey.

Owing to limited availability of forest inventory data (1938–2002), Cooke and Lorenzetti (2006) did not reveal other possible outbreaks prior to 1938. However, based on white and (or) narrow rings, we reconstructed severe and persistent outbreaks in 1931–1938 for 47°N. In addition, the observed white rings in 1878, 1879, and 1869 at 49°N, 50°N, and 53°N, respectively, might indicate severe insect defoliation in study region in the past. This is very consistent with the suspected broad-scale outbreaks during the 1870s in western Manitoba (Sutton and Tardif 2007). Other outbreaks that are not recorded in forest insect inventory databases, such as 1901–1902 at 47°N, 1915, 1921–1922, and 1937 at 53°N, and 1937 at 54°N, provided additional insect outbreak evidence for better understanding of insect disturbances and dynamics in the past in western Quebec. It also illustrates that white and (or) narrow rings are valid parameters for exploring insect outbreak history prior to available insect inventory data.

Systematic changes in the spatial distribution of insect outbreaks across the landscape

As illustrated in Table 2 and Fig. 2, along the south–north latitudinal gradient the relatively close-synchronized 1950s outbreaks at southern latitudes could indicate that the insect outbreaks were spread from south to north and occurred at a large spatial scale in this region. The fairly well synchronized outbreaks of 1964 and 1980 at 48°N–54°N might suggest that the severe but short insect outbreaks in these 2 years occurred at a broad spatial scale in the north. These two major outbreaks were also widely observed across large areas of Saskatchewan and Alberta (Simpson and Coy 1999; Hogg et al. 2005). The close synchronized and well synchronized outbreaks at the regional scale might be related to re-

gional environmental factors (e.g., regional climate), forest structures, population dispersal rate, and insect population density regulation (Fleming and Volney 1995; Cooke and Roland 2007). However, these factors require further investigation to be validated. Other important outbreak years, such as 1974 and 1990 at northern latitudes and 2001–2002 at southern latitudes (47°N–49°N), indicate that outbreaks in those years also generally occurred at the regional scale in western Quebec (Table 2; Fig. 2). Cooke and Roland (2007) reported severe FTC outbreaks in 1951–1953, 1963–1966, 1976–1978, 1989–1991, and 1999–2002 in both northeastern and northwestern Ontario, indicating that those large spatial and (or) regional scale insect outbreaks observed in northwestern and southwestern Quebec in our study best relate to Ontario. In spite of no white rings having been observed in 1921 and 1945, the consistently significant growth suppression during this period may indicate insect defoliation at the regional or local scale (Fig. 2). The potential factors causing growth reduction in those years, such as drought or moisture stress, were excluded because drought-induced growth reductions in aspen ring widths were often observed in climatically dry areas such as the aspen parklands of western Canada, where annual total precipitation is approximately 350–450 mm (Hogg et al. 2005). However, in our study region annual total precipitation in growth reduction years was ample, ranging from 650 to 1000 mm. Cooke and Roland (2007) suggested that ring widths of aspen growing in northeastern and northwestern Ontario, where annual precipitation is approximately 535.6 mm and 656.5 mm, respectively, appear to be far less sensitive to drought or moisture stress than annual defoliation by aspen defoliators, mostly FTC.

It is also interesting to note that more insect outbreaks occurred at northern latitudes 53°N and 54°N than at southern latitudes (Fig. 2). This might be because of increased forest fragmentation (small aspen stands in continuous forest dominated by nonhost tree species) in the northern boreal area. Roland (1993) pointed out that higher forest fragmentation significantly increased the duration of insect outbreaks like FTC. Other modelling or empirical studies (Hastings 1990; Hassell et al. 1991) also support this conclusion. Fragmented boreal forest may limit dispersal of natural enemies like parasitoids and (or) transmission of pathogens of FTC, thus leading to slower suppression of local severe outbreaks (Kareiva 1987; Reeve 1988). As a consequence, these local outbreaks in high host density would act as local sources of dispersing moths, either allowing fast increase during the early phase of an outbreak or keeping mean density high when populations in continuous forests are declining (Roland 1993). In continuous boreal forest dominated by nonhost tree species in the north, small aspen stands could also increase the duration of the outbreaks by isolating caterpillar populations and limiting movement of natural enemies (Roland 1993). In the long run, this may translate into more rapid population cycling (Cobbold et al. 2005).

Northern range limit of severe defoliation by insects in western Quebec

In contrast with the currently reported range limit of the most important aspen defoliator, the FTC (Fitzgerald 1995; Cooke and Lorenzetti 2006), our study showed that insect

outbreaks could occur much farther north. For example, we reconstructed severe insect outbreaks occurring at 54°N in western Quebec. This roughly corresponds to the distributional limit of the host species. Observations in Manitoba (56°N–57°N) also suggest that white rings and corresponding growth suppression that might be related to insect outbreaks occurred close to the actual northern limit of aspen distribution in Manitoba (F. Conciatori, unpublished data, 2007). Furthermore, the differences in northern range limit of severe defoliation by insects may result from the different data sources. Both Fitzgerald (1995) and Cooke and Lorenzetti (2006) used the forestry insect inventory data, whereas we reconstructed insect outbreaks using dendrochronological techniques. Our results clearly demonstrate the limitations of the forestry insect inventory databases. In general, forest ecosystem characteristics (e.g., forest type, forest structure and condition, stand age, soil drainage class, and site index) in forestry insect inventory data varies greatly from location to location, hence leading to incomplete assessment of insect disturbances and dynamics (Cooke and Roland 2007). In addition, standards of data collection and processing during aerial surveys by subjective and imprecise aerial sketch mapping techniques differ across survey areas (NFD 2005). Studies have shown that defoliated estimates are frequently exaggerated during sketch mapping (Harris and Dawson 1979). In addition, in areas with moderate to severe defoliation, the extent and severity of insect outbreaks were usually overestimated as a consequence of including small nonforested regions, roads, cultivated areas, small lakes, or burned areas as well as homogenizing defoliation severity. The overestimation of insect outbreaks may also be caused by including areas or species that were defoliated by multiple agents. For example, the mortality of some aspen stands could be caused by both the LAT outbreaks before aspen bud expansion and subsequently by the FTC defoliation during the early growing season (Hogg et al. 2005). Finally, some areas of defoliation may have been missed in surveys, owing to limited road access or the omission of local observers (for more information, see Generic Forest Health Surveys Guidebook 2002). In remote and less-populated areas of northern Quebec, our results indicated that severe outbreaks failed to be identified for various reasons and hence demonstrated that dendrochronological techniques constitute a valid method of reconstructing the history of severe outbreaks occurring in remote areas missed during the insect surveys. The dendroecological approach was also successfully used to reconstruct several severe FTC outbreaks that were not detected by aerial surveys in Ontario (Cooke and Roland 2007). Sutton and Tardif (2007) also formulated similar conclusions.

Conclusions

Precise prediction of boreal insect dynamics is critical for Canada's sustainable forest development, yet this requires a large database to better understand insect dynamics. Forest insect surveys provide valuable data for investigating insect dynamics; however, they also demonstrate some inherent shortcomings, such as limited available data and some outbreaks and areas have been missed during past air surveys. In this study, we used dendrochronological comparison of host and nonhost species as well as white and (or) narrow

rings as main indicators to reconstruct the history of severe insect outbreaks along a latitudinal gradient from 46°N to 54°N in western Quebec. We found additional severe insect outbreaks that were not reported in previous studies and that occurred prior to available forest insect inventory data. Our findings indicated that analysis of white and (or) narrow rings may extend forestry insect inventory data to a larger spatial scale (e.g., remote areas or areas missed by previous surveys) and to a longer temporal scale (e.g., insect outbreaks prior to forest insect inventory surveys). The identification of severe insect outbreaks at 54°N clearly indicated that the northern limit of defoliating insects is substantially further north than reported in the documentary records. Improved understanding of the historical distributional limits of defoliating insects provides critical baseline information needed to monitor the impacts of environmental change.

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