Tree-ring evidence of larch sawfly outbreaks in western Labrador, Canada

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Abstract: As many insect outbreak reconstructions are typically based on targeted single-site sampling, researchers have often been limited in their ability to draw conclusions about regional trends as opposed to local trends in the data. The results of this paper demonstrate the value of a systematic sampling design when studying spatio-temporal processes that can vary greatly within large continuous areas of forest. Many single-site research programs have been conducted to reconstruct the history of larch sawfly (*Pristiphora erichsonii* Htg.) outbreaks in the eastern boreal region of North America. However, no such research has yet been conducted in the region of Labrador. In an attempt to illustrate the strength of a systematic gridded sampling protocol over a single-site study, we sampled a 12-site grid in western Labrador. Dominant and codominant species were sampled at each grid point, resulting in 24 master chronologies. Six eastern larch (*Larix laricina* (Du Roi) K. Koch) chronologies (host) and a regional black spruce (*Picea mariana* (Mill.) Britton, Sterns, Poggenb.) chronology (nonhost) were used to establish a host–nonhost analysis of past sawfly outbreaks on a regional scale. Both regional and localized larch sawfly outbreaks were identified, but in general, larch sawfly outbreaks in western Labrador appeared to be spatially synchronous and regional in scale.

Résumé : Étant donné que beaucoup de reconstitutions d'épidémies d'insecte sont typiquement basées sur l'échantillonnage ciblé d'un seul site, les chercheurs ont souvent été limités dans leur capacité à tirer des conclusions concernant les tendances régionales par opposition aux tendances locales dans les données. Les résultats de cette étude démontrent la valeur d'un plan d'échantillonnage systématique pour l'étude des processus spatio-temporels qui peuvent varier énormément à l'intérieur de vastes zones continues de forêt. Plusieurs programmes de recherche basés sur un seul site ont été réalisés pour reconstituer l'historique des épidémies de tenthrède du mélèze (*Pristiphora erichsonii* Htg.) dans la région boréale de l'est de l'Amérique du Nord. Cependant, aucune de ces recherches n'a encore été menée dans la région du Labrador. Pour tenter d'illustrer la puissance d'un protocole d'échantillonnage systématique en grille par rapport à l'étude d'un seul site, nous avons échantillonné 12 sites déterminés par une grille dans l'ouest du Labrador. Les espèces dominantes et codominantes ont été échantillonnées à chaque intersection de la grille produisant 24 chronologies de référence. Six chronologies de mélèze laricin (*Larix laricina* (Du Roi) K.Koch) (espèce hôte) et une chronologie régionale d'épinette noire (*Picea mariana* (Mill.) Britton, Sterns, Poggenb.) (espèce non hôte) ont été utilisées pour faire une analyse des épidémies passées de tenthrède à l'échelle régionale en se basant sur une comparaison entre les espèces hôte et non hôte. Tant les épidémies régionales que locales de tenthrède du mélèze ont été identifiées mais, en général, les épidémies de tenthrède du mélèze dans l'ouest du Labrador semblent spatialement synchrones et d'envergure régionale.

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Introduction

Larch sawfly (*Pristiphora erichsonii* Htg.) is an important defoliator in North America's eastern boreal forest (Coppel and Leius 1955; Ives 1976). In the eastern boreal forest, larch sawfly targets eastern larch (*Larix laricina* (Du Roi) K. Koch) (Lejeune 1955; Tailleux and Cloutier 1993; Jardon et al. 1994*a*). Larch sawfly emerge from May to July, depositing their eggs on newly developed larch shoots on which they feed for several weeks (Lejeune 1955; Ives 1976). Larvae drop to the ground in July and August, spin cocoons, and overwinter before reaching adulthood the following May or June (Lejeune 1955). Host eastern larch respond to defoliation by reducing needle production for the following year, which can in turn inhibit larch sawfly population density (Lejeune 1955). It is their ability to produce new foliage each spring that renders the eastern larch remarkably resilient (Graham 1956; Ives and Nairn 1966). While repeated defoliation can result in mortality (Graham 1956), nonmortal infestations result in dramatic decreases in radial growth (Ives and Nairn 1966) and are thus observable in the tree-ring record.

Defoliation caused by larch sawfly can have significant influence on radial growth response (Bergeron et al. 2002) and thus offers a unique opportunity for study. Dendrochronology is a useful tool in the area of insect outbreak hindcasting, as tree rings can serve as reliable proxies for historical outbreak occurrence (Fritts 1971). In the case of larch sawfly, evidence of outbreaks can be found in the tree-ring record in the form of radial-growth depressions, light latewood rings, and missing or incomplete rings

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(Harper 1913; Arquilliere et al. 1990; Girardin et al. 2001). Insect outbreaks affecting multiple tree species have also been identified by the computer program OUTBREAK (Holmes and Swetnam 1996), wherein an outbreak signature is mathematically deduced through a comparison of host and nonhost tree-ring series (Swetnam et al. 1995; Speer et al. 2001), even when the outbreak signal was not easily seen in the raw samples but was found only through the mathematical correction (Ryerson et al. 2003).

In the eastern boreal forest, dendrochronological studies attempting to reconstruct the outbreak history of larch sawfly and to study its impacts have been conducted at sites in southern Quebec (Girardin et al. 2001, 2002; Bergeron et al. 2002) and northern Quebec (Arquilliere et al. 1990; Tailleux and Cloutier 1993; Jardon et al. 1994*a*). Each of these localized studies is extremely valuable in the collective attempt to hindcast the occurrence of larch sawfly outbreak in the eastern boreal forest, and when examined comparatively, they can provide a reliable basis for inferring outbreak magnitude at a regional scale.

To date no such study has been conducted in Labrador, Canada. Recent accounts of larch sawfly activity focus primarily on neighbouring Newfoundland (Clarke and Carew 1987), while early documentation of infestation in Labrador is scarce (Fletcher 1906; Coppel and Leius 1955). Bordering the province of Quebec, Labrador has been assumed, perhaps, to have a similar ecological constitution and history to its neighbour to the west. Nevertheless, it remains one of the more under-researched boreal areas (Roberts et al. 2006) and no outbreak reconstructions for this region exist. The primary objective of this study was to reconstruct the outbreak history of larch sawfly in the region of western Labrador. Such a reconstruction could prove extremely useful in helping to determine the scale and degree of synchrony of outbreaks, both locally and when studied in conjunction with other studies in the eastern boreal forest. A secondary objective of this study, then, was to conduct dendrochronological sampling in such a way that inferences regarding the magnitude of larch sawfly outbreak could be made at a regional scale, as opposed to a local scale. Sampling was conducted within a gridded network of sites, thus allowing for a broad spatio-temporal analysis of the data within a single study.

Methodology

Sampling design and study sites

Dendrochronological sampling for the purposes of insect outbreak analysis in the eastern boreal region has often been limited to a small number of sites within relatively short distances of each other (Girardin et al. 2001, 2002; Bergeron et al. 2002). Jardon et al. (1994*b*) sampled across different moisture regimes, while Tailleux and Cloutier (1993) compared coastal sites with a continental site, allowing them to find a spatial gradient within their data. In general, however, any attempt to draw broader regional conclusions regarding outbreak history in the eastern boreal region can only be done while considering multiple individual studies in relation to one another. We seek here to conduct a regional analysis within the context of our own sampling grid before continuing on to a broader comparative examination. The ultimate goal of our sampling design was to maximize our ability to capture differences in the occurrence of outbreak across a spatial gradient. Specifically, we have aimed to use a systematic sampling grid as a tool to evaluate the scale or spatial extent of the reconstructed outbreaks.

Accordingly, sampling was conducted at 12 remote sites across west-central Labrador and adjacent Quebec along a latitudinal and longitudinal network (Fig. 1). Three north-to-south transects at 62°W, 64°W, and 66°W longitude consisted of four sites each at 52°N, 53°N, 54°N, and 55°N latitude. Sampling was carried out as close as possible to the 12 intersecting points of the grid. Where the logistical challenges of accessing these remote locations prevented sampling at the exact node, a suitable site within 5 min of the targeted latitude and longitude was used. The sampling grid was located primarily within the boreal forest zone, though its northern and western sites were found along the border between boreal forest and southern forest tundra zones (Payette 1983). Its forest stands are dominated by black spruce (*Picea mariana* (Mill.) Britton, Sterns, Poggenb.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and eastern larch or tamarack (Bearnes 1967). Sampling was conducted at the 12 sites in July 2007 and July 2008 as part of a larger study designed to sample a range of boreal forest species and ecological relationships.

Development of master chronologies

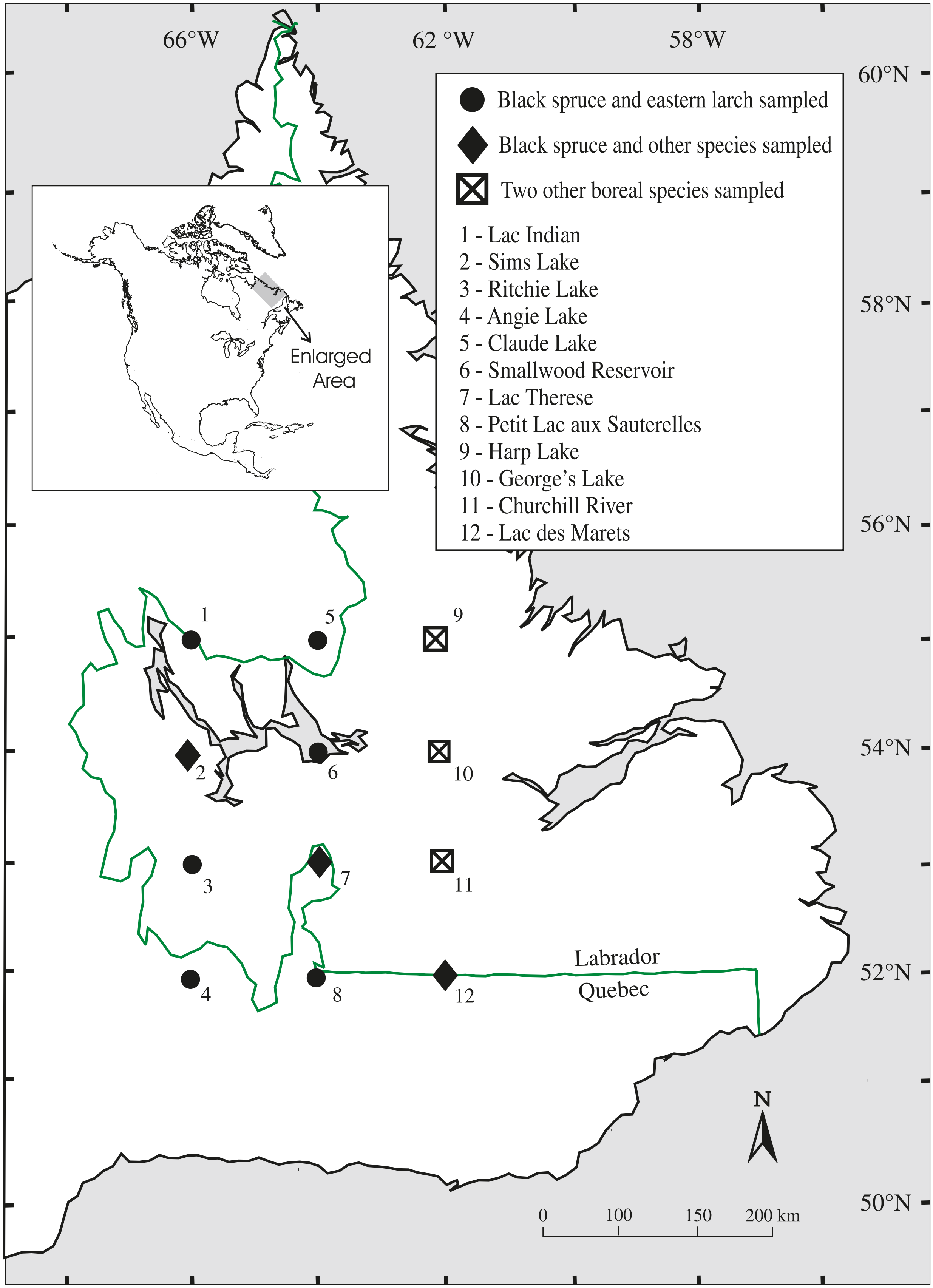
At each site, mature trees of dominant or codominant size were selected for sampling. As much as possible, sampling was conducted away from adjacent water bodies to minimize their influence upon the tree-ring pattern. Upon visual survey, the two most dominant conifer species at each site were selected for sampling. To form a chronology, 40 increment cores from 20 trees (two cores from each tree) were obtained at breast height for each species, at each site. A total of 480 trees were sampled, and radial growth measurements from each core were checked for homogeneity of signal by cross-dating with the program COFECHA (Holmes 1983).

Insect outbreak identification

Initial identification of larch sawfly outbreaks were conducted using a methodology similar to that of other studies (Harper 1913; Case and MacDonald 2003; Girardin et al. 2005). Visual identification of outbreak-associated tree-ring anomalies was performed on each eastern larch series, with specific attention to the criteria established by Harper (1913) and validated by others: (1) the presence of pale latewood in the annual ring of an imminent infestation, (2) a subsequent decrease in radial growth, and (3) an increased incidence of missing or incomplete rings.

In an attempt to better identify occurrences of larch sawfly outbreak, chronologies were further subjected to a host–nonhost analysis by the program OUTBREAK version 1.50P (Swetnam et al. 1995; Holmes and Swetnam 1996; Speer et al. 2001). In such an analysis, the host species is compared with a nonhost species that, preferably, demonstrates a similar climate–growth response (Swetnam et al. 1985). Outbreaks are then identified by the occurrence of growth depressions in the host species that are absent in the nonhost

Fig. 1. A map of the study area in western Labrador. The sampling grid consists of 12 study sites. The network covers a spatial grid of 1° of latitude × 2° of longitude.



species. For our analysis of larch sawfly outbreak, eastern larch chronologies were compared with a regional chronology of black spruce — a reliable nonhost species for larch sawfly outbreak detection (Girardin et al. 2001, 2005; Case and MacDonald 2003). While year-to-year correlations between eastern larch and black spruce were poor, the use of black spruce as a nonhost can be justified on the basis that the two species' radial growth trend well over the long-term (e.g., Fig. 2F). The regional chronology was constructed from the nine adjacent black spruce chronologies obtained from the sampling grid. The use of a regional chronology, rather than a same-site chronology, as nonhost was chosen for the reason that finer-scale variations present in a same-site nonhost could lead to false identifications of outbreaks. Larch sawfly outbreaks were detected when depressions in the host residual chronology lasted a minimum of 4 years and where at least 1 year occurred below a threshold value of 1.30 standard deviations below the mean ring-width value (calculated to represent the smallest 10th percentile values in the chronology) (c.f., Swetnam et al. 1995; Speer et al. 2001). These threshold parameters developed in this study are comparable to those of similar studies (Girardin et al. 2001, 2005; Case and MacDonald 2003).

Results and discussion

Development of master chronologies

A total of 24 master chronologies were developed from samples obtained at the 12 sampling sites. Nine black spruce, six balsam fir, six eastern larch, and three white spruce chronologies were constructed, each demonstrating highly significant interseries correlations (Nishimura 2009).

Larch sawfly outbreak identification

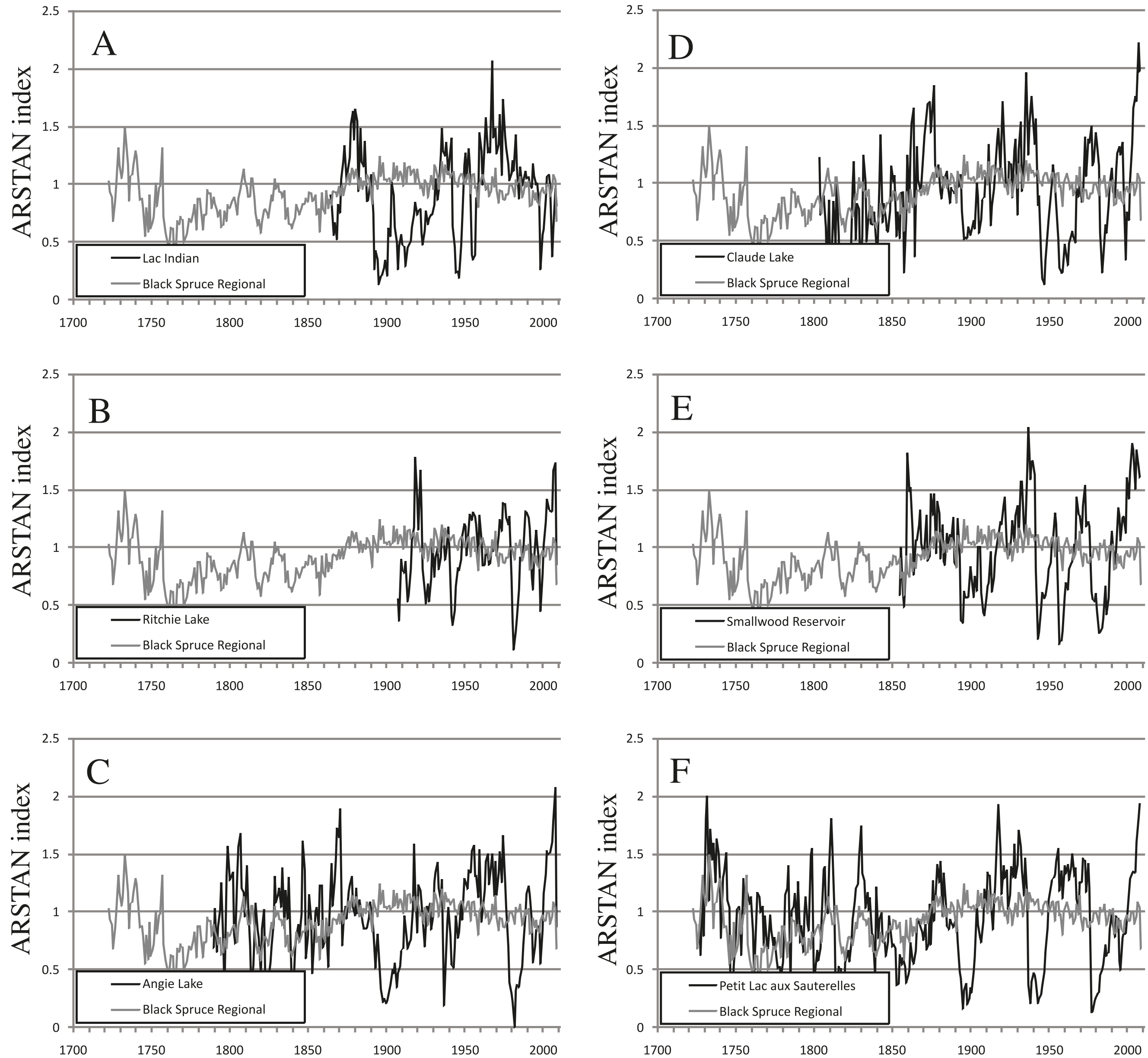
Visual identification of outbreak-associated anomalies was attempted both through field examinations at the sampling site and through pale latewood analysis in the laboratory. Field examinations revealed no visible evidence of insect damage, while visual identification of outbreak-associated tree-ring anomalies yielded unexpected results. Pale latewood was identified in 74 of all 240 larch cores (30.8%), but with limited synchrony between series and with little correspondence to the onset of growth suppressions identified here. These results are somewhat similar to those found by Girardin et al. (2005), who observed the presence of pale latewood in only a small proportion of larch series, and which did not coincide well with the growth suppressions they identified. In central Saskatchewan, Case and MacDonald (2003) observed few but consistent occurrences of pale latewood years, which corresponded well with the onset of their identified larch sawfly outbreaks. Jardon et al. (1994*a*) consistently found pale latewood to precede each of their identified outbreaks. Meanwhile, Arquillière et al. (1990) observed evidence of larch sawfly outbreak in northern Quebec despite observing no defoliation-associated pale latewood at all. We believe that this inconsistency in the relationship between insect outbreak and the occurrence of pale latewood, possibly clouded by the influence of climatic factors in the formation of pale latewood (Liang et al. 1997), renders it unreliable as a sole indicator of past defoliation events.

In our samples, missing rings were identified in each larch series, with the most frequent occurrences taking place from 1893 to 1901, 1936 to 1947, 1955 to 1958 (observed only at Claude Lake and Smallwood Reservoir), and 1977 to 1984. In one tree, as many as nine consecutive missing rings were identified, and virtually all missing rings occurred within identified growth suppressions in our larch chronologies. This finding parallels that of Jardon et al. (1994*a*), whose analysis revealed similar occurrences of consecutive missing rings coinciding with identified outbreaks. While missing rings were identified in each larch series, none were present in the same year for all trees, thus confirming their identification as indeed locally absent.

As noted by Girardin et al. (2005), the limited presence of pale latewood can suggest the absence of large-scale outbreaks. However, despite the sporadic occurrence of pale latewood in our series, the results of our host–nonhost analysis indicate several periods of large-scale or regional larch sawfly outbreaks. The host–nonhost comparison revealed significant and occasionally synchronous growth suppression in each of the larch chronologies (Fig. 2). The computer program OUTBREAK identified several periods of larch sawfly disturbance in the larch chronologies (Fig. 3), suggesting both regional and localized larch sawfly outbreak. Three larger, regional outbreaks were observed: from 1891 to 1919, 1927 to 1950, and 1976 to 1985. The first regional outbreak (1891–1919) is evident at each of the sites, with the sole exception of Ritchie Lake. This could be an artefact in the data due to the young age of the Ritchie Lake site. The second regional outbreak (1927–1950) appears to have lasted longer at the more northern sites (Lac Indian, Claude Lake, Smallwood Reservoir). The three southernmost (and continentally influenced) sites at Ritchie Lake, Angie Lake, and Petit Lac aux Sauterelles appear to have recovered by around 1945. The third regional outbreak (1976–1985) was again observed at five of the six sites, with Lac Indian the exception this time. Two smaller, perhaps more localized outbreaks (1954–1970 and 1877–1886), were also identified. A regional outbreak from 1954 to 1970 was expressed at the four northernmost sites (Lac Indian, Claude Lake, Ritchie Lake, Smallwood Reservoir), and a small central outbreak (Angie Lake, Claude Lake, Smallwood Reservoir, Petit Lac aux Sauterelles) was observed during 1877 to 1886. Evidence of very early outbreaks at Claude Lake (1806–1811) and Petit Lac aux Sauterelles (1812–1818, 1752–1756, 1732–1741) was also observed (Figs. 2 and 3).

The timing of these outbreaks coincides to varying degrees with previous Labrador accounts and studies from adjacent regions. As recorded observations of outbreaks in Labrador are few, a comparison with documented and reconstructed infestations in neighbouring Quebec proved useful. The 1976 and 1927 outbreaks coincide roughly with adjacent records from Quebec. In their analysis of shoot scars in larch, Cloutier and Filion (1991) reconstructed a larch sawfly outbreak in northern Quebec beginning in the late 1970s and ending in the mid- to late-1980s. Jardon et al. (1994*a*) also reported growth depressions from 1984 to 1989. Arquillière et al. (1990) documented a growth depression from 1940 to 1946, Jardon et al. (1994*a*) from 1938 to 1952, and Girardin et al. (2001) from 1937 to 1942 and from 1955 to 1962. Filion and Cournoyer (1995) also docu-

Fig. 2. Eastern larch master chronologies (by site) (host) versus black spruce regional master chronology (nonhost). Host series show dramatic and synchronous growth reductions.

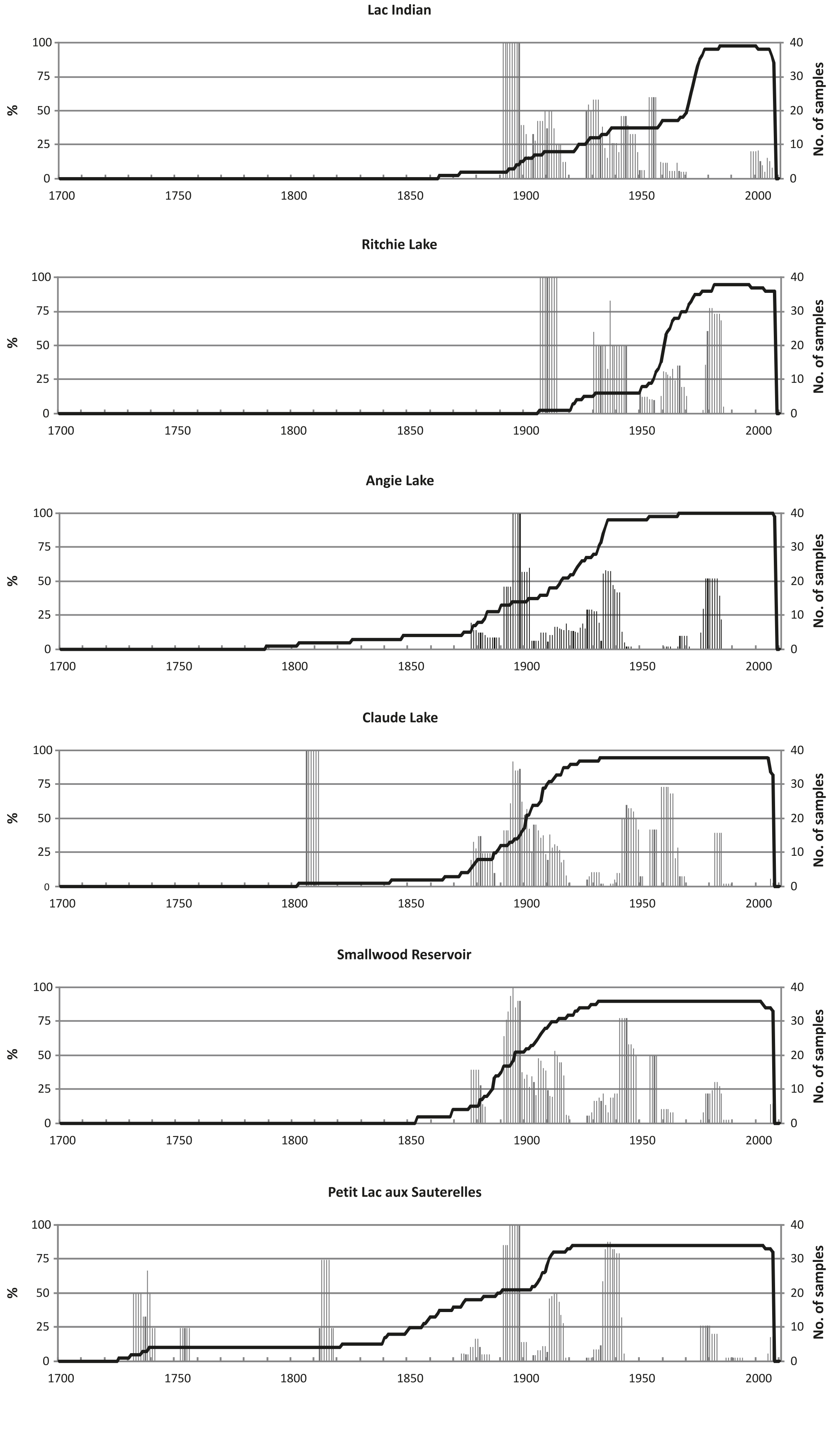


mented a larch sawfly infestation in subarctic Quebec beginning in 1939. The 1891 outbreak also appears to coincide with previously documented growth suppressions, including overlap with the 1910 outbreak referenced by Coppel and Leius (1955). Jardon et al. (1994*a*) reported growth suppressions in northern Quebec from 1894 to 1906 and 1907 to 1911, the latter of which also coincided with the 1905–1908 suppression identified by Arquillière et al. (1990) in the same region. Girardin et al. (2001) have documented radial growth reduction from 1895 to 1912 in southern Quebec. This supports the hypothesis of an east-to-west movement by the larch sawfly at the end of the 19th century (Coppel and Leius 1955; Ives 1976). The 1877 outbreak coincided with a similar growth suppression observed by Jardon et al. (1994*a*) and is likely the outbreak to which Fletcher (1906) and Coppel and Leius (1955) have referred. Because of low sample depth, it remains unclear whether the growth suppressions beginning in 1812, 1806, 1752, and 1732 are associated with larch sawfly activity. However, the suppressions identified in 1806 and 1752 do coincide with those documented by Jardon et al. (1994*a*). In any case, these results both favour the argument that the larch sawfly was active in North America well before 1880 and attest to the relatively synchronous widespread occurrence of larch sawfly outbreak in the eastern boreal region.

Conclusion

The historical record of larch sawfly activity in the eastern boreal forest has been well documented. The results presented here offer concrete evidence supporting the long-held assumption that there exists a lengthy and similar history in

Fig. 3. Percentage of eastern larch series affected by larch sawfly, by year, with sample depth. Bars indicate the relative frequency; solid black line is sample depth.



Labrador, too, and they suggest an ecological constitution in western Labrador that is comparable to neighbouring Quebec. To the extent of our tree-ring record, we have identified both the temporal and spatial distribution of larch sawfly outbreaks in western Labrador. Larch sawfly outbreaks beginning in 1976, 1927, and 1891 appear to have been regional in nature, while outbreaks beginning in 1954 and 1877 appear to have been more localized. Growth depressions in the early 1800s, the 1750s, and the 1730s lend credence to the theory that the larch sawfly was present in North America prior to 1880. In general, the impact of larch sawfly activity in Labrador appears to be more regional than localized in scale.

These results demonstrate the usefulness of a systematic sampling grid in the study of historical insect outbreak or any other feature with a distinct spatial dimension. Specifically, such grids improve our ability to make spatial inferences about the degree of synchronicity of outbreaks across a region, while simultaneously highlighting localized events that stand out more easily within a gridded system than within a mere point source study. A further advantage of this sampling methodology is the fact that this established grid can also be easily expanded in all directions. We suggest that further research could benefit from similar grids, which could provide useful frameworks for studying boreal forest processes that vary over time and space (e.g., insect outbreaks, fire history, dendroclimatologies). A more complete overall picture of past disturbance regimes can thus be obtained, which will contribute greatly to future projections and risk assessments.

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