Radial growth analysis of *Larix laricina* from the Lake Duparquet area, Québec, in relation to climate and larch sawfly outbreaks

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Abstract: A dendrochronological study was performed at six sites dominated by eastern larch, *Larix laricina* in Québec’s southwestern boreal forest. The objectives were to reconstruct periods of larch sawfly (*Pristiphora erichsonii*) outbreak in the region and to determine which physical factors (precipitation, temperature, water level or drought) explained the greatest variation in radial growth. From the presence of light latewood rings followed by periods of growth suppression, we identified larch sawfly outbreaks for the years 1895-1912, 1937-1942, and 1955-1962. We suspect that additional outbreaks occurred in the early 1920s, late 1970s and early 1980s as well, but at the same time as spruce budworm outbreaks (*Choristoneura fumiferana*). Response function analysis demonstrated negative relationships between larch radial growth and May and August precipitation and May and September current year water level, and demonstrated positive relationships with May current year drought index and September previous year drought index. These results suggest that flooding in the early growing season and excessive water levels at the end of the growing season may negatively affect larch radial growth. Our results also indicate an increase in the year-to-year variation in radial growth in larch sites subjected to flooding. This may reflect the increase in the Lake Duparquet water level at spring break up.

Keywords: larch, dendrochronology, insects, climate, light latewood, *Pristiphora erichsonii*, response function, water level.

Introduction

Populations of eastern larch or tamarack, *Larix laricina* (Du Roi) K. Koch, are mainly confined to hydric sites in subarctic, boreal and temperate North American forests (Nairn et al., 1962; Schooley & Pardy, 1981; Bergeron et al., 1982; Martineau, 1985; Johnston in Burns & Honkala, 1990). The growth of this species is limited by water saturated conditions (Bergeron et al., 1982), low nutrient availability, absence of oxygen in soils, and low soil temperature (Kozlowski, 1982). In these environments, particularly in wetlands next to water bodies, larch distribution is influenced by its tolerance to the frequency, duration and timing of spring flooding (Robertson et al.; Weaver & Cavanaugh, 1978; Kenkel, 1986; Tardif & Bergeron, 1992; Denneler, Bergeron & Bégin, 1999).

A climatic analysis conducted in the northern Québec temperate forest by Jean and Bouchard (1996) revealed negative relationships between larch growth and high spring and autumn water levels. These authors also reported that both monthly precipitation and temperature play a major role in controlling larch radial growth (Jean & Bouchard, 1996). Similar results were found in Québec’s northern boreal forest by Kaminski (1997), who reported a negative effect of May precipitation on larch radial growth. A positive effect of June precipitation, which was attributed to a possible depletion of the meltwater reserve in the soil, was also observed.

In addition to climate, the radial growth of larch may be seriously affected by defoliation by the larch sawfly (*Pristiphora erichsonii* [Hartig]) (Coppel & Leius, 1955; Rose & Lindquist, 1980; Turnock, 1972; Jardon, Filion & Cloutier, 1994a,b). In northern Québec, Jardon, Filion and Cloutier (1994a) found six periods of suppressed radial...
growth between 1847 and 1993 corresponding to sawfly outbreaks: 1847-1861, 1883-1890, 1894-1906, 1907-1911, 1938-1952 and 1984-1989. Arquillère et al. (1990) also mentioned sawfly epidemics in the same region for the periods 1905-1908 and 1940-1946. In the southwestern Québec boreal forest, field records indicate severe infestations for the years 1939, 1940, 1955 and from 1959-1965 (Ministère de l'Énergie et des Ressources, Québec, rapports annuels 1937-1982). Smaller outbreaks were also reported during the 1970-1982 period. It has also been suggested that larch may be defoliated to a lesser extent during severe spruce budworm (Choristoneura fumiferana [Clem.]) outbreaks (Johnston in Burns & Honkala, 1990). In the Lake Duparquet region, budworm outbreaks have been reported during the periods 1919-1929, 1930-1950 and 1970-1985 (Morin, Laprise & Bergeron, 1992).

Our first objective was to reconstruct larch sawfly outbreaks for the twentieth century in the Lake Duparquet region (northwestern Québec), using dendrochronological methods. This provides additional data, in relation to the spatial aspect of the outbreak, which may be compared with other information sources. Our second objective was to determine the main climatic factors (mean monthly water level, average temperature, total precipitation and drought index) controlling larch radial growth. A dendrochronological study conducted by Tardif and Bergeron (1997b) on white cedar (Thuja occidentalis L.) revealed that Lake Duparquet water levels at spring breakup have increased in height (~100 cm) and frequency over the past 150 years. We thus suspected that the spring flooding regime plays an important role in larch growth, notably over the last few decades. In this study, the six sites were chosen in relation to the severity of spring flooding (Denneler, Bergeron & Bégin, 1999).

Material and methods

Study area

The study area is located in the forests surrounding Lake Duparquet in the Abitibi region, Québec (48° 28’ N, 79° 17’ W; Figure 1). The lake covers an area of 50 km² and drains northward via the Duparquet River to James Bay. The region is part of the Northern Clay Belt of Québec and Ontario, associated with the maximum extension of post-glacial lakes Barlow and Ojibway (Vincent & Hardy, 1977). Mean annual temperature is 0.8°C and total annual precipitation varies from 800 to 900 mm (Environment Canada, 1993). The mean frost-free period is 64 days, although frost may occur at any time of the year (Anonymous, 1982).

Six larch stands from the Lake Duparquet area were selected for this study, including all larch stands surrounding Lake Duparquet (Figure 1). The lake water regime has not been modified in the past. The six sites were chosen along a gradient of flooding severity (Denneler, Bergeron & Bégin, 1999). Sites BL1, BL2, BL3 and CC are all subject to flooding and wave action from Lake Duparquet (Denneler, Bergeron & Bégin, 1999). Site LS is subject to flooding from Lake Soisson, a much smaller lake (~700 m wide in contrast to ~10 km for Lake Duparquet; Figure 1). Site CM, being non-riparian, is not subject to any external flooding.

The site BL1 is dominated by larch at its lowest points and by white cedar at its highest part, with some black spruce (Picea mariana [Mill.] BSP.) scattered throughout. Sampling was conducted in the lower section, 200 to 400 m from shore. Three other sites (BL2, BL3 and CC) are pure larch stands while the fifth site, on the shore of Lake Soisson (LS), is a mixed stand of larch, black spruce and white cedar, with an understory composed of white cedar, black spruce and balsam fir (Abies balsamea [L.] Mill.). The sixth site is located just off Matheson Road (CM). This site, also dominated by larch, black spruce and white cedar, was disturbed by the construction of the road early in the twentieth century and more recently by the establishment of claim trails. On the north side of the road, the ground is poorly colonized by vegetation (Carex sp.) and decomposition is far more advanced than on the other sites, suggesting that drainage may have been modified following road construction. For this site, sampling was conducted on the northern side at a minimal distance of 50 m from the road and 20 m from the land claim trails. All study sites are located on organic deposits (> 0.6 m thick) where the depth to groundwater is at least 20 cm.

Sampling

In this study, the largest diameter of larch and black spruce trees were sampled for each site at the end of the 1997, 1998 and 1999 growing seasons (each site 2 to 4 ha in size). A total of 118 larch trees were sampled from which two to three cores per tree were taken at 1.5 m above ground. Some cores were rejected (two in site BL1, two in BL3 and four in CM) because of young age and presence of compression wood. Generally, such cores show low correlation with the reference chronologies (Stokes & Smiley, 1968). A total of 230 cores (115 trees) were retained for the study (Table I). As for black spruce, 50 cores from 26 trees were considered.
Table I. *Larix laricina* and *Picea mariana* residual chronology statistics.

<table>
<thead>
<tr>
<th></th>
<th>BL1</th>
<th>BL2</th>
<th>BL3</th>
<th>CC</th>
<th>LS</th>
<th>CM</th>
<th>Picea mariana</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of trees</td>
<td>19</td>
<td>15</td>
<td>24</td>
<td>20</td>
<td>19</td>
<td>18</td>
<td>15</td>
</tr>
<tr>
<td>Number of radii</td>
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<td>48</td>
<td>40</td>
<td>39</td>
<td>36</td>
<td>50</td>
</tr>
<tr>
<td>Percentage of absent rings*</td>
<td>0.21</td>
<td>0.32</td>
<td>0.08</td>
<td>0.36</td>
<td>0.13</td>
<td>0.46</td>
<td>0.05</td>
</tr>
<tr>
<td>Mean ring width (mm)</td>
<td>1.59</td>
<td>1.41</td>
<td>1.39</td>
<td>1.03</td>
<td>1.30</td>
<td>1.20</td>
<td>0.54</td>
</tr>
<tr>
<td>Mean sensitivity</td>
<td>0.31</td>
<td>0.32</td>
<td>0.33</td>
<td>0.27</td>
<td>0.24</td>
<td>0.20</td>
<td>0.15</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>0.25</td>
<td>0.30</td>
<td>0.30</td>
<td>0.25</td>
<td>0.20</td>
<td>0.20</td>
<td>0.13</td>
</tr>
<tr>
<td>First order autorrelation</td>
<td>-0.05</td>
<td>0.11</td>
<td>0.08</td>
<td>0.01</td>
<td>-0.01</td>
<td>0.11</td>
<td>-0.06</td>
</tr>
<tr>
<td>First order autorrelation for standard chronologies</td>
<td>0.63</td>
<td>0.59</td>
<td>0.49</td>
<td>0.53</td>
<td>0.71</td>
<td>0.73</td>
<td>0.28</td>
</tr>
<tr>
<td>Number of trees</td>
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<td>15</td>
<td>18</td>
<td>20</td>
<td>19</td>
<td>16</td>
<td>14</td>
</tr>
<tr>
<td>Number of radii</td>
<td>30</td>
<td>30</td>
<td>36</td>
<td>39</td>
<td>36</td>
<td>31</td>
<td>25</td>
</tr>
<tr>
<td>Signal to noise ratio</td>
<td>20.22</td>
<td>22.03</td>
<td>36.95</td>
<td>27.73</td>
<td>23.98</td>
<td>15.63</td>
<td>4.47</td>
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<tr>
<td>Variance in first PCA vector (%)</td>
<td>61.29</td>
<td>62.16</td>
<td>68.71</td>
<td>59.81</td>
<td>58.67</td>
<td>52.25</td>
<td>29.16</td>
</tr>
<tr>
<td>Intercore correlation</td>
<td>0.59</td>
<td>0.63</td>
<td>0.68</td>
<td>0.58</td>
<td>0.56</td>
<td>0.50</td>
<td>0.25</td>
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<tr>
<td>Intratree correlation</td>
<td>0.57</td>
<td>0.63</td>
<td>0.67</td>
<td>0.58</td>
<td>0.56</td>
<td>0.49</td>
<td>0.24</td>
</tr>
<tr>
<td>Intertree correlation</td>
<td>0.81</td>
<td>0.74</td>
<td>0.78</td>
<td>0.77</td>
<td>0.78</td>
<td>0.66</td>
<td>0.46</td>
</tr>
</tbody>
</table>

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**DEVELOPMENT OF CHRONOLOGIES**


To remove the effect of the age/size-related trend, a spline function giving a 50% frequency response of 45 years was applied to the measured series (Cook & Peters, 1981). This was done to produce the standard chronologies. Residual chronologies were computed in the same manner as the standards, but in this case the series were averaged using residuals from autoregressive modelling of the detrended measurement series (Cook & Holmes, 1986; Holmes, Adams & Fritts, 1986). This resulted in chronologies with a strong common signal and without persistence. Both chronologies were constructed using ARSTAN (Holmes, 1983; Cook, 1985).

A common interval analysis, which contains the maximum possible number of data in a rectangular matrix (length of common interval times number of series), was performed for the 1935-1996 period. Finally, a Pearson correlation was calculated among site residual chronologies.

**SAWFLY OUTBREAK IDENTIFICATION**

Outbreak periods of the larch sawfly were first identified using the criteria described by Harper (1913) and Jardon, Filion and Cloutier (1994a). These periods are characterized by i) the presence of a light latewood ring without a decrease in the width of the whole tree-ring (thin-walled latewood cells; Harper, 1913); ii) a decrease in radial growth; and iii) an increase in the presence of missing or incomplete rings. Light latewood rings are characterized by a reduction in the thickness of latewood cells. This is a response to a lack of assimilated products that supply the cells during the current growth year (Harper, 1913; Filion & Cournoyer, 1995; Liang, Filion & Cournoyer, 1997).

To better identify the larch sawfly outbreak periods, a chronology of black spruce growing on sites BL1 and LS (Figure 1) was used for a non-host comparison analysis. The rationale of the host/non-host comparisons are fully described in Swetnam, Thompson and Sutherland (1985). Essentially, the effects of current or past insect outbreaks are detectable when a decrease in the growth of the host species occurs, with no corresponding decrease in the non-host species. Analysis of the host and non-host chronologies was done with the OUTBREAK program following the BUDWORM options (Holmes & Swetnam, 1996). In this analysis, the non-host chronology (black spruce residual chronology) was subtracted from each host series (larch individual residual series) to reduce the common effects of climatic variation. Years in which the normalized series were negative were recorded as possible outbreak periods. However, if the period identified did not reach a threshold for maximum growth reduction (–1.28 in standard deviation) or a minimum length for sawfly outbreaks (in this case it was fixed at four consecutive years), then this period was eliminated as a possible outbreak. The minimum length of outbreaks was fixed at four years to eliminate possible effects of individual tree responses to a yearly, specific environmental condition. It has also been reported that larch cannot survive more than three years of complete defoliation and more than eight years of moderate defoliation (Ives & Nairn, 1966; Nairn et al., 1962). As for the thresholds with a standard deviation of –1.28, our trials revealed that the percentage of trees in possible outbreak periods was stable inside the interval –1.10 to –1.40.
CLIMATE AND HYDROLOGY

The effects of hydrological and climatic fluctuations on radial growth of larch were analyzed using both correlation analyses (Briffa & Cook, 1990; Fritts, 1976) and response function analyses (Fritts et al., 1991). The bootstrap response function analysis provides a test of significance of the regression coefficient stability within a specific time period by repeated, random sampling of the data (Guiot, 1993). A weight was associated with each monthly variable, expressing the separate relative effects of several climatic factors on ring width (Fritts, 1976). This method offers the advantage of avoiding errors caused by collinearity among variables and providing a more realistic estimate of tree response to climate. In addition, observations of the original data with the estimated growth computed from the bootstrap response function showed little effects of the outbreak periods on the calibration. All climatic analyses were performed using PRECON (Fritts et al., 1991) and 999 bootstrap iterations were generated.

As an estimate of the Lake Duparquet water level, hydrological data (mean monthly river discharge) from the Harricana River station (1915-1998), 100 km east of Lake Duparquet (48°36' N, 78°06' W), were used in the absence of data closer to Lake Duparquet. Tardif and Bergeron (1997b) reported that both hydrological systems respond to the same regional climate. Regional mean monthly temperature and total monthly precipitation (1896-1997) from the bootstrap response function showed little effects of the outbreak periods on the calibration. All climatic analyses were performed using PRECON (Fritts et al., 1991) and 999 bootstrap iterations were generated.

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All dendroclimatic analyses were conducted for the period 1915-1996. This period was chosen to preserve a constant degree of freedom in all analyses. A second response function analysis using data for the period 1962-1996 was also calculated to assess the response to climate in the more recent years and as a verification test to confirm there was no major interference from the outbreak periods.

RESULTS

TREE-RING STATISTICS OF LARCH

A large amount of the total variance was accounted for by the first eigenvector, and trees collected in pure larch stands (BL1, BL2, BL3 and CC) generally had higher mean sensitivity and standard deviation (Table I). In contrast, high autocorrelation was observed in the standard chronologies of sites LS and CM. First-order autocorrelation values from residual chronologies were very low. The common pattern among trees is reflected by the strong intercore, inter-tree and intra-tree correlations and by the large amount of variance explained by the first principal component vector (52% to over 68%). Inter-tree correlations from pure stands are generally higher than those from mixed stands (LS and CM). Finally, Pearson correlations indicate a relatively high correlation among all site residual chronologies (p < 0.01, Table II). The majority of larch trees sampled were established after 1875, as shown by the larch residual and standard chronologies (Figure 2).

Three larch sawfly outbreak periods were determined using Harper (1913) and Jardon, Filion and Cloutier (1994a) criteria. The most recent outbreak appeared to have started in 1955 and the period of growth suppression generally ended in 1962 (Figure 2). Light latwood cells were observed to be most abundant in 1955 (3.1% of all series), 1957 (5.3%) and 1958 (14.6%) (Figure 4). Missing or incomplete rings were sometimes found for years 1959 (7.7% of all series), 1960 (4.8%), 1961 (0.5%), 1962 (0.4%) and 1964 (1.2%) (see Figure 4 for site frequencies). The CM site was the site most affected by this last outbreak, as indicated by the high number of incomplete and missing rings and growth suppression (Figure 2 and Figure 4).

A second outbreak period was observed from 1937-1942, and light latwood rings were observed in 1937 for 4% of the individuals. No missing rings resulted from this outbreak (Figure 4). The longest suppression period caused by the larch sawfly started in 1895 as indicated by the first light latwood ring (8.2% of all series), and ended around 1912. A light latwood ring also characterized the years 1896 (10.4%), 1897-1907, 1909 and 1910. Few missing rings occurred from 1897-1901, 1904-1906, 1909 and 1910 (Figure 4).

TABLE II. Pearson correlation among sites residual chronologies for Larix laricina (BL1, BL2, BL3, CC, LS and CM) and Picea mariana (PMA) for the interval 1919 to 1996. Critical values: r = 0.27; p < 0.01, r = 0.21; p < 0.05.

<table>
<thead>
<tr>
<th></th>
<th>BL1</th>
<th>BL2</th>
<th>BL3</th>
<th>CC</th>
<th>LS</th>
<th>CM</th>
<th>PMA</th>
</tr>
</thead>
<tbody>
<tr>
<td>BL1</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BL2</td>
<td>0.88</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BL3</td>
<td>0.83</td>
<td>0.91</td>
<td>1.00</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>CC</td>
<td>0.85</td>
<td>0.87</td>
<td>0.79</td>
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<td></td>
</tr>
<tr>
<td>LS</td>
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<td>0.79</td>
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<tr>
<td>CM</td>
<td>0.52</td>
<td>0.49</td>
<td>0.43</td>
<td>0.50</td>
<td>0.70</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>PMA</td>
<td>0.34</td>
<td>0.40</td>
<td>0.41</td>
<td>0.36</td>
<td>0.21</td>
<td>0.15</td>
<td>1.00</td>
</tr>
</tbody>
</table>
FIGURE 2. Standard (solid lines) and residual (dotted lines) chronologies for *Larix laricina* in sites BL1, BL2, BL3, CC, LS and CM. Dates of the first appearance of a light latewood ring indicating sawfly outbreak periods are shown. The dashed lines represent sample depths.

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The black spruce residual chronology, used as the non-host species, is presented in Figure 5. Two periods of minor growth suppression were observed in this chronology: 1910-1915 and 1930-1935. However, these periods of radial growth suppressions did not coincide with any of the growth suppressions observed in larch chronologies.

Correlations between the host and non-host residual chronologies (Table II) indicated that most of the series correlations were statistically significant. The two species would thus respond to similar environmental factors, a necessary condition for using OUTBREAK (Holmes & Swetnam, 1996).

Host and non-host analysis using the black spruce residual chronology (Figure 5) and the larch residual chronologies revealed five periods of growth anomalies that could be identified as possible outbreak periods (Figure 6). These periods were also observed using a white cedar chronology (from sites BL1, LS and CM) and a Fraxinus nigra chronology from Tardif and Bergeron (1997a) as non-host species (not presented). The most recent possible outbreak period started in 1975. Maximum peaks in trees characterized by a reduction in radial growth were observed from 1978-1980 and 1983-1986 (Figure 6). A possible outbreak period was also observed from 1950-1961 with its maximum intensity occurring between 1957 and 1958. More than 95% of the trees were affected during this period, also coinciding with the period detected using the light latewood criteria. A third possible outbreak period occurred around 1935 and ended in 1946. Another one was found from 1916-1930 for which the maximum intensity was from 1923-1925. The BL1 and LS sites were the sites most affected during this period. The longest and most important period occurred from 1895 to about 1912. Over 80% of all series would have been affected for a period length of ten years. This period was also detected using the light latewood criteria. Note that the periods reported here as possible outbreak periods do not correlate with any decrease in black spruce radial growth residual chronology (Figure 5).

CLIMATE ANALYSIS

The climate analysis performed for the period 1915-1996 indicated that larch stands located on the shores of Lake Duparquet (BL1, BL2, BL3 and CC) and Lake Soisson (LS) responded more to temperature and precipitation than to drought and river discharge (first response function models adjusted $r^2$; Figure 7b). However, growth at the Matheson site (CM) was more related to precipitation and river discharge, as shown by the higher adjusted $r^2$ of the response function models when compared to temperature alone (Figure 7).

In the current year of growth (year $t$), climatic conditions in May were found to be significantly related to the drought index (Figure 7; all six sites). This same relationship was observed for August precipitation. Also, BL3, LS and CM sites showed a negative relationship with September river discharge. Observation of climatic conditions in the previous year of growth suggested that for LS and CM sites, October precipitation in year $t-1$ had a negative effect on growth of year $t$ (Figure 7).

Analysis conducted using the 1962-1996 interval indicated that during the last 34 years, larch growth was most...
strongly related to precipitation and river discharge, although drought and temperature were also important factors related to the variation in radial growth (Figure 7; second response function models adjusted $R^2$). In the current year of growth (year $t$), a positive relationship with the May drought index (BL2, BL3, CC, LS and CM sites) and a negative relationship with May river discharge (BL1, BL3 and LS) indicated a negative effect of flooding early in the growing season. This was shown at the CM site by a negative relationship with the March river discharge and a change in the correlation sign. A positive relationship between the September drought index in year $t-1$ and the larch radial growth in year $t$ was also observed (BL1, BL2 and CM sites).

**Discussion**

Larch growth in the wetland forests surrounding Lake Duparquet was influenced by a common factor. This was highlighted by a high mean sensitivity (similar to that obtained by Arquillère et al. (1990) and Jardon, Filion & Cloutier 1994b), a high variance in the first eigenvector and a high correlation among trees and sites. In contrast, the lower correlation and signal-to-noise ratio obtained in the CM site could be attributed to a slight effect of competition, notably for light (see Fritts, 1976, for competition effects).

In similar mixed larch and cedar stands of the Lake Duparquet area, the tree cover is dense, with little light reaching the ground (Girardin, Tardif & Bergeron, in press).

**Sawfly Outbreaks**

Based on appearance of the light latewood rings, growth suppression periods and observations made by the Ministère de l’Énergie et des Ressources, Québec, (rapports annuels 1937-1982), we conclude that larch sawfly outbreaks occurred in the Lake Duparquet region for the periods 1895-1912, 1937-1942, and 1955-1962. We also suspect possible outbreaks in the early 1920s, at the end of the 1970s, and in the early 1980s. Although no light latewood rings were observed, we found a low frequency of missing rings in years 1979 and 1980. Field observations by the Ministère de l’Énergie et des Ressources, Québec, (rapports annuels 1937-1982) reported high densities of the sawflies in 1979 and 1980. However, since spruce budworm outbreaks were occurring at the same time (1919-1929, 1930-1950 and 1970-1985; Morin, Laprise & Bergeron, 1992), it may be possible that factors other than the larch sawfly contributed to the growth suppression observed in these periods. Furthermore, although less literature exists on the subject, it has been reported that the larch casebearer (Coleophora laricella) could also be a serious defoliator in eastern North America (Rose & Lindquist, 1980; Johnston in Burns & Honkala, 1990). Several severe outbreaks have caused extensive mortality in some areas of the United States (Wilson, 1977).

In our study, light latewood rings were not observed in all trees nor in all outbreak periods. Similar results were obtained by Filion and Cournoyer (1995). As mentioned by these authors, the variation among trees and sites may reflect variation in the intensity of the defoliation. Furthermore, according to Liang, Filion and Cournoyer (1997), tree age and outbreak frequency could explain some variation found in the expression of this character in tree rings.

Climate is an important factor in the dynamics of the larch sawfly, notably in relation to water level fluctuations. Lejeune (1955) reported that one or two weeks of high water levels in late summer induces heavy mortality of sawfly larvae population. High water levels in spring (for several weeks) would also induce high mortality of the pupae population. An observation that suggests a relationship between the sawfly and water levels relates to the 1937 outbreak in the LS and CM sites, where radial growth was more affected than at the other, more flood-prone sites. The CM site was not subject to spring flooding because of its non-riparian position. Furthermore, these two sites were characterized by a lower water table than those at Lake Duparquet, and thus it is believed that they are subjected less to prolonged flooding. This situation is similar to the 1984-1989 outbreak studied by Tailleux and Cloutier (1993). These authors observed a strong decrease in growth of inland larch, in contrast to coastal site trees where no significant effect of the sawfly outbreak could be detected. Jardon, Filion and Cournoyer (1994b) also found similar results comparing mesic and hydric sites. In the present study, the same explanation can be extended to the observed delay of the 1955 outbreak, where the outbreaks recorded for the CM site occurred, on average, three years before sites located around Lake Duparquet (1958).
Figure 6. Vertical bar chart showing the percentage of larch series at sites BL1, BL2, BL3, CC, LS and CM affected by a sawfly outbreak in a given year as identified by program OUTBREAK in the host and non-host analysis (*Picea mariana* as the non-host species).
Further comparison between the outbreaks around Lake Duparquet with those of other studies mentioned previously (Arquillère et al., 1990; Jardon, Filion & Cournoyer, 1994a) revealed a similarity in the timing of the outbreaks from south to north. Although one of the outbreaks on Lake Duparquet characterized by light latewood rings (1955-1962) was not observed in northern Québec, the two others (1895-1912 and 1937-1942) showed similar timing with those observed by Jardon, Filion and Cournoyer (1994a) for 1894-1906, 1907-1911 and 1938-1952 and Arquillère et al. (1990) for 1940-1942. In addition, the possible outbreak that may have occurred at the end of the 1970s and in the early 1980s coincides with the 1984-1989 outbreak reported by Jardon, Filion and Cournoyer (1994a).

CLIMATE EFFECTS

At most of our sites, larch radial growth was highly influenced by hydric conditions in May, August and September (first interval period). In all these cases, a negative relationship with growth was observed. It has previously been demonstrated that below average water table or reduced flooding may improve growth of wetland trees (Crawford, 1983; Lieffers & Rothwell, 1986; Macdonald & Lieffers, 1990). Hydric stress caused by prolonged flooding leads to a reduced recycling of organic matter, since in submerged soils temperature is low, oxygen is absent, and thus bacterial decomposition is retarded (Kozlowski, 1982; Tallis, 1983; Macdonald & Lieffers, 1990). More specifically, Macdonald and Lieffers (1990) reported that in submerged...
conditions, there is a significant lack of nitrogen mineralization and depletion of mineral nutrition, which results in decreased carbon assimilation by larch. Moreover, oxygen deficiency in roots would decrease nutrient uptake in coniferous species, leading to lower plant productivity (Zinkal, Jeglum & Harvey, 1974). To overcome such anoxic problems, wetland trees have developed adventitious roots at the soil surface to maintain roots in the better-aerated surface peat layers (Rigg & Harrar, 1931; Denyer & Riley, 1964; Gill, 1977). These adaptations serve as efficient exchange organs for the absorption of oxygen and diffusion of toxins out of the plant (ethanol, acetaldehyde and ethylene). However, Duncan (1954) reported that in an excessive drought, the alteration of these metabolic exchanges would cause growth reduction and sometimes death.

An interesting phenomenon observed in the Lake Duparquet area is the increase in larch mean sensitivity since about 1960. Year-to-year fluctuations in radial growth are more important, suggesting the existence of a stronger environmental signal. By comparing the 1915-1996 and 1962-1996 response functions, we clearly observed the more important influence of hydric factors during spring on the radial growth of larch, notably from the May river discharge and the May drought index. This is in contrast to the non-riparian site (CM), where no relationship was found with the May river discharge.

**FIGURE 7b.** Pearson correlation coefficients between *Larix laricina* residual chronologies and temperature, precipitation, Harricana River discharge and drought index for the 1915-1996 (solid bars) and 1962-1996 intervals (empty bars). The sites shown are CC, LS and CM. The dotted lines and the dashed lines indicate a significant relationship at $p < 0.05$ (non-corrected significant level) for the 1915-1996 and 1962-1996 analyses, respectively. Significant variables ($p < 0.05$) tested separately with the response function analyses are shown by an asterisk (1915-1996) and a circle (1962-1996). First and second response function models $r^2$ values are also indicated in order of analyses. Note that the increase in $r^2$ from the first to the second models is only attributed to a decrease in the degrees of freedom (this is due to a decrease in the time interval studied).
Conclusions

This study showed that sawfly outbreaks are an important component in growth trends in larch. Both flooding early in the growing season and hydric conditions at the end of the growing season also negatively influenced radial growth of larch in wetlands along the shore of Lake Duparquet. The hypothesized decrease in drought occurrence (Bergeron & Archambault, 1993; Bergeron & Flannigan, 1995) and increase in spring flooding (Tardif & Bergeron, 1997b) may also be responsible for the increase in larch mean sensitivity since the mid-twentieth century. This trend was not observed at our non-riparian site and thus may be related to an increase of inter-annual variability in Lake Duparquet water levels (Tardif & Bergeron, 1997b). Further studies on larch stand dynamics in relation to water levels will provide the information needed to confirm these hypotheses.

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Literature cited


