

Dynamics of eastern larch stands and its relationships with larch sawfly outbreaks in the northern Clay Belt of Quebec

Martin-Philippe Girardin, Jacques Tardif, and Yves Bergeron

Abstract: Climate change, fires, and insects outbreaks can affect eastern larch (*Larix laricina* (Du Roi) K. Koch) stand dynamics. To determine which of these factors had the greatest influence on stand dynamics, we sampled four wetlands dominated by larch on the margin of Lake Duparquet in the northern Clay Belt of Quebec. The ages of seedlings, saplings, and trees were determined in twelve 400-m² plots. Increment cores were taken at breast height to determine past disturbance episodes related, among others, to larch sawfly (*Pristiphora erichsonii* (Hartig)) activity. Stem analysis was conducted using larch and black spruce (*Picea mariana* (Mill.) BSP) for identification of post-disturbance releases in height growth. Analyses at the stand and cluster levels showed that larch age structures were characterized by many unsynchronized establishment periods. In addition, a seedlings bank not much older than 10 years characterized many plots. Two larch sawfly outbreak episodes (1895–1912 and 1955–1962) identified by tree-ring and stem analysis were associated with larch establishment. A smaller outbreak in the late 1970s could also have contributed to the initiation of establishment in one stand. Our results suggest that the length (severity) of an outbreak may be a critical factor in explaining the different patterns of establishment observed in these stands. During a severe outbreak, larch establishment may occur mainly from surviving stems (increased seed production), whereas during a mild outbreak, larch establishment may occur from increased survival of pre-established seedlings and saplings. Further studies on the distribution of gaps within larch stands may provide better information on the pattern of mortality (gap dynamics) during an outbreak and may help to better understand larch establishment in these stands.

Résumé : Quatre tourbières entourant le Lac Duparquet, Ceinture d'Argile du Québec, ont été échantillonnées avec l'objectif d'identifier les facteurs (changements climatiques, feux et (ou) épidémies d'insectes) influençant le plus fortement la dynamique des peuplements de mélèze laricin (*Larix laricina* (Du Roi) K. Koch). L'âge des semis, des gaules et des arbres a été estimé dans 12 quadrats de 400 m². Des carottes ont été récoltées à 1,3 m du sol afin d'identifier les périodes de perturbation associées à la ténthède du mélèze (*Pristiphora erichsonii* (Hartig)). Une analyse de tiges a aussi été réalisée sur le mélèze et l'épinette noire (*Picea mariana* (Mill.) BSP) afin d'identifier les périodes de reprise de croissance en hauteur associées aux perturbations. L'analyse des structures d'âge à l'échelle des peuplements et des groupements ont démontré plusieurs périodes de recrutement non-synchronisées. De plus, plusieurs quadrats comportaient une banque de semis établis au cours des dix dernières années. Deux épisodes épidémiques de la ténthède du mélèze (1895–1912 et 1955–1962) identifiés suite à l'analyse des cernes de croissance et des tiges ont été associés au recrutement. Une faible épidémie à la fin des années 1970 aurait également pu contribuer à une période de recrutement à l'intérieur d'un site. Nos résultats indiquent que la longueur (sévérité) des épidémies pourrait être un facteur critique permettant d'expliquer les patrons d'établissement observés à l'intérieur des peuplements. Lors d'une épidémie sévère, l'établissement du mélèze proviendrait des tiges ayant survécues (augmentation de la production de graines) alors que durant une épidémie modérée, l'établissement proviendrait de semis et de gaules ayant survécu. Des études plus approfondies sur la distribution des trouées pourraient nous renseigner davantage sur les patrons de mortalité (dynamique des trouées) durant les épidémies. Elles permettraient aussi de mieux comprendre l'établissement du mélèze à l'intérieur des sites étudiés.

Introduction

Eastern larch (*Larix laricina* (Du Roi) K. Koch) is a tree species characteristic of many North American wetlands (Nairn

et al. 1962; Heinselman 1970; Schooley and Pardy 1981; Bergeron et al. 1982; Martineau 1985; Johnston 1990). Because it can tolerate high soil moisture and acidity, as well as low soil temperature, larch is generally most abundant in

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M.-P. Girardin¹ and J. Tardif. Centre for Forest Interdisciplinary Research, University of Winnipeg, 515 Portage Avenue, Winnipeg, MB R3B 2E9, and Groupe de recherche en écologie forestière interuniversitaire (GREFi), Université du Québec à Montréal, C. P. 8888, succursale Centre-Ville, Montréal, QC H3C 3P8, Canada.

Y. Bergeron. Groupe de recherche en écologie forestière interuniversitaire (GREFi), Université du Québec à Montréal, C. P. 8888, succursale Centre-Ville, Montréal, QC H3C 3P8, Canada.

¹Corresponding author (e-mail: mgirardi@io.uwinnipeg.ca).

wetlands, although scattered trees may occur in surrounding uplands (Bergeron et al. 1982; Johnston 1990; Girardin et al. 2001a). Larch forms pure stands in many parts of the boreal zone but also forms mixed stands with eastern white-cedar (*Thuja occidentalis* L.) and black spruce (*Picea mariana* (Mill.) BSP) (Kenkel 1986; Johnston 1990; Girardin et al. 2001a). As with most stress-tolerant species, larch is not a good competitor and may be successional replaced on sites where it grows with more shade-tolerant species (Johnston 1990; Jardon et al. 1994a). Thus, like many tree species, disturbance is important for the persistence of larch on most sites. Although fire is an important agent of disturbance controlling the structure and dynamics of many forests in the boreal zone, on wetland sites, where larch is most often abundant, it is likely to be less important (Curtis 1959; Rowe and Scotter 1973; Vitt and Bayley 1984; Johnston 1990). Therefore, disturbances caused by insect outbreaks or changes to site hydrology may have more important effects on the dynamics of larch stands (Harper 1913; Coppel and Leius 1955; Lejeune 1955; Denyer and Riley 1964; Rose and Lindquist 1980; Bonkougou et al. 1983; Martineau 1985; Jardon et al. 1994a).

In the late 19th and the early 20th century, larch forests were seriously threatened by a severe outbreak of the larch sawfly (*Pristiphora erichsonii* (Hartig)) that destroyed most mature stands in eastern North America (Coppel and Leius 1955; Muldrew 1955; Ives and Nairn 1966; Turnock 1972; Marie-Victorin 1995). In the late 20th century, numerous dendrochronological studies have been conducted to reconstruct past outbreaks (Arquillère et al. 1990; Jardon et al. 1994a, 1994b; Case 2000; Girardin et al. 2001b). Although sawfly populations are currently at endemic levels, outbreaks of this insect remain a potential threat to these forests (Arquillère et al. 1990; Cloutier and Filion 1991; Tailleux and Cloutier 1993; Jardon et al. 1994a, 1994b; Girardin et al. 2001b). While relationships between larch growth reductions, increasing mortality rates, and the occurrence of larch sawfly outbreaks are well described (Harper 1913; Beckwith and Drooz 1956; Ives and Nairn 1966; Jardon et al. 1997a), few studies have examined the impacts of sawfly outbreaks on stand dynamics (Turnock 1954; Bonkougou et al. 1983). This lack of information is even more substantial when the dynamics of wetland stands of the Canadian boreal forest is considered.

A previous study of larch radial growth in the northern Clay Belt region indicated two severe larch sawfly outbreaks during the last 100 years (1895–1912 and 1955–1962) (Girardin et al. 2001b). These were inferred from the occurrences in larch of characteristic rings associated with larch sawfly outbreaks (missing and light latewood rings) (Harper 1913). Growth comparison with a nonhost species also indicated possibilities of less severe outbreaks for the early 1920s, late 1930s, and late 1970s (Girardin et al. 2001b). Although insect surveys (ministère de l'Énergie et des Ressources, Québec, rapports annuels 1937–1982) indicate moderate sawfly outbreaks for these periods, the low presence of characteristic rings made it difficult to confirm them in the studied area. Outbreaks of the larch casebearer (*Coleophora laricella* Hübner) might have taken part in these growth suppressions, notably in the 1970s (Benoit and Blais 1988). However, its effect on larch stand dynamics would be less important than

that of the sawfly. Larch mortality resulting from the casebearer has only been reported in some areas of the United States (Wilson 1977). Nevertheless, it may weaken the trees and make them susceptible to other causes of mortality (Kulman 1971).

The objective of this study was to document the dynamics of four larch stands in the boreal forest of the northern Clay Belt of Quebec. We mainly wanted to assess the impacts of larch sawfly outbreaks on larch establishment and age distribution. Therefore, we expected to find larch establishment cohorts associated with the severe outbreaks of 1895–1912 and 1955–1962.

Methods

Study area

The study area is part of the northern Clay Belt of Quebec and Ontario, which resulted from the maximum extension of the postglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). Mean annual temperature is 0.8°C, and total precipitation varies from 800 to 900 mm (Environment Canada 1993). The mean frost-free period is 64 days, but frost can occur at any time of the year (Atmospheric Environment Service 1982).

The wetlands sampled were located on the margins of Lake Duparquet, 700 km north of Montreal in the Abitibi region of southwestern Quebec (48°28'N, 79°17'W; Fig. 1). Lake Duparquet covers a 50-km² area and drains northward from Duparquet River towards James Bay. Lake Duparquet is also one of the few lakes in the region that has not been regulated, which makes it a unique study site (Tardif and Bergeron 1997).

Sampling design

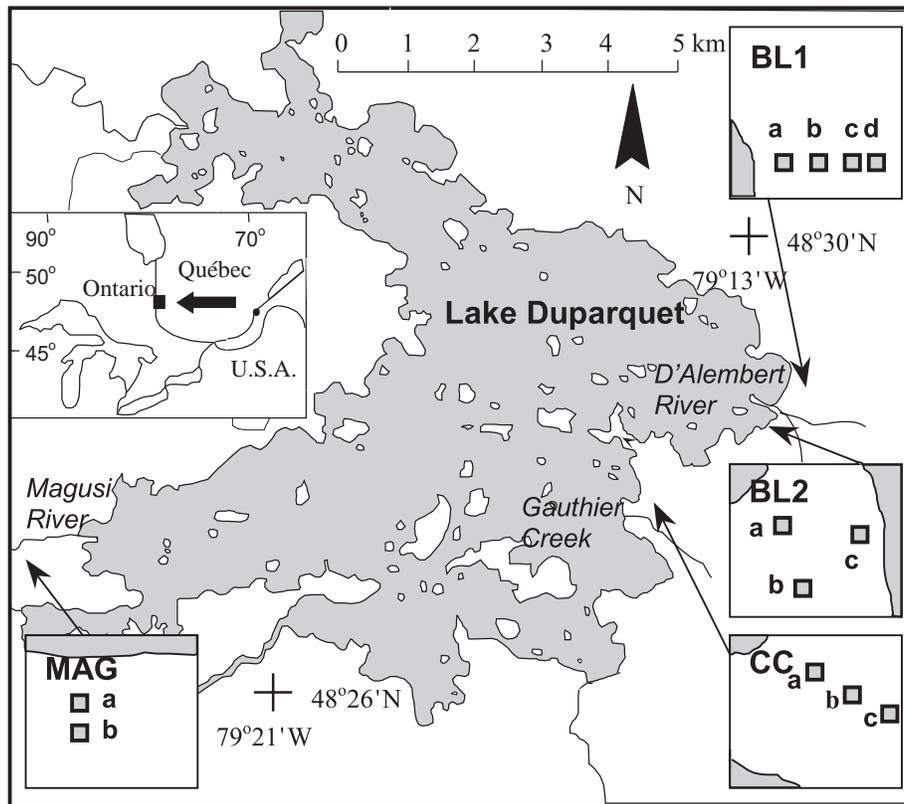
In the summer of 1999, three stands located on the shore of Lake Duparquet and one stand beside the Magusi River were sampled (Fig. 1). These stands were identified as BL1, BL2, CC, and MAG. In each of them, 400-m² plots (20 × 20 m) were established along a transect perpendicular to the waterbodies. A total of twelve 400-m² plots were established in the four stands.

In the first stand (BL1), four plots (BL1a, BL1b, BL1c, and BL1d) were sampled. These plots covered the inferior limit of larch distribution to the superior limit (Fig. 1). The second stand (BL2), which was characterized by the presence of both a lake and a river gradient, had one plot beside the lake (BL2a), one beside the river (BL2c), and one at the most elevated part of the gradient (BL2b). The third stand had one plot beside the lake (CCa), one in middle part of the wetland (CCb), and one at the elevated part (CCc). The fourth stand (MAG) had only two plots, one located at the inferior limit (MAGa) and one at the superior limit of larch distribution (MAGb). No lethal fires have been reported since the mid-19th century around these stands (Bergeron 2000).

Vegetation description

Among the 12 sampled plots, 6 were considered pure larch stands (BL2a, BL2b, BL2c and CCa, CCb, CCc). In these, the understory vegetation was dominated by *Kalmia angustifolia* L., *Andromeda glaucophylla* Link, *Myrica gale* L., *Ledum groenlandicum* Oed., *Cassandra calyculata* (L.)

Fig. 1. Map of Lake Duparquet showing the distribution of larch (*Larix laricina*) sample plots.



D. Don, *Smilacina trifolia* (L.) Desf., and a large proportion of the ground surface was covered by *Sphagnum* spp. Three plots (BL1a, BL1b, and BL1c) were mixed larch and black spruce stands. In these, the understory was dominated by *Alnus rugosa* (Du Roi) Spreng., *Ledum groenlandicum*, *Myrica gale*, and *Betula pumila* L., but the *Sphagnum* spp. cover was relatively low. The other plots (BL1d, MAGa, MAGb) were dominated by larch, black spruce, and white-cedar. The understory was mainly dominated by *Alnus rugosa*, *Ledum groenlandicum*, *Carex trisperma* Dewey, *Carex* spp., and *Sphagnum* spp. (a large percentage of the surface). For more details on stand vegetation, see Girardin et al. (2001a).

In this study, we have assumed that the position of the plots corresponded to a flood severity gradient and to changes in the water table depth. Although we have not measured the severity of the flood in each plot, the presence of indicative species can provide a reasonable qualitative scale (Kenkel 1986). As an example, the presence of black spruce and white-cedar inside a plot provide an indication of the water table depth, because their establishment is associated with a lower water table (larch being more tolerant to flooding) (Montague and Givnish 1996). Note that plots located on the edge of Lake Duparquet are the most affected by flooding (Denneler et al. 2000). Mean water table depths in larch-dominated stands of Lake Duparquet ranged from 16.5 to 25.0 cm during July and August (Girardin et al. 2001a).

Sampling

Diameter at breast height (DBH) and height of all tree stems (>5 cm DBH; live and recently dead (bark and branches

well preserved)) were measured in each plot with a DBH measuring tape and a Suunto clinometer. Diameter and height of larch saplings (<5 cm DBH) and seedlings (<100 cm tall) were also measured, whereas for cedar and black spruce, only height was measured. For larch seedlings, stem diameter was measured at the base. To determine the age of all trees (larch, spruce, and cedar), an increment core was taken as close as possible to the ground level with a Pressler increment borer. If the wood was rotten at this height, a core was taken higher on the stem, and its height was measured to allow for age correction by regression analysis (Bergeron and Gagnon 1987; Tardif and Bergeron 1999). All larch seedlings and saplings were collected for age determination. For black spruce and white-cedar a subset was collected (at least 10 individuals per 10 cm height class (0–1 m) when possible), because the two species were present at high densities. No distinction was made between sexual and vegetative origin for spruce and cedar stems. As for larch, field observation did not show evidences of vegetative reproduction. It was mentioned by Johnston (1990) that layering is the dominant reproductive mode for larch along the northern limit of trees in Canada and Alaska, whereas farther south it is uncommon but may occur when branches are covered by fast-growing sphagnum moss.

In each plot, two or three cores were taken from dominant larch trees at DBH for construction of tree-ring chronologies, which were used to identify stand disturbance events (sensu Lorimer 1980; Tardif and Bergeron 1999). Furthermore, three dominant larch trees and three black spruce trees (inside and (or) aside the plots) were felled, and cross sections were taken at 0.1 m below ground, ground level, 0.5 m

above ground, and each following metre to determine height-growth releases following stand disturbances (Zarnovican 1985; Bergeron 2000).

Age determination and development of larch chronologies

The cores and the cross sections (ground level and higher) from the saplings and the sampled trees were prepared following the standard procedures proposed by Swetnam et al. (1985). Trees (dead or living) were visually cross-dated using the method described by Yamaguchi (1991). In addition, the cores taken at DBH were measured using a Velmex Uni Slide measuring stage (0.001-mm accuracy) and the cross-dating was validated using COFECHA program (Holmes 1983).

Larch trees growing in wet sites have wide root systems, rarely deep, with no taproot (Johnston 1990) or a J-shaped stem as described in DesRochers and Gagnon (1997) and Kneeshaw and Claveau (2001). However, as the moss layer deepens, new roots develop on the stem above the original root collar, and growth of old roots nearly ceases (Johnston 1990). This may create a “false root collar” and lead to underestimation of tree age (DesRochers and Gagnon 1997; Kneeshaw and Claveau 2001). To assess possible age underestimation of larch trees resulting from this phenomenon, a number of larch trees were cut below the moss surface (~10 cm, as close as possible to the water table) for comparison of age at and below ground level using cross-dating techniques (Bergeron 2000). Age determination of larch seedlings <10 cm in height was made by counting all terminal bud scars from the apex to the “root collar” (Menes and Mohammed 1995). To verify if the age determined by ring count reflected the true age, a number of larch seedlings 10–20 cm tall was also dated from both ring and terminal bud scars count.

These verifications permitted us to estimate that the error in age determination for larch varied from 0 to 4 years for trees established after 1890, and from 1 to 11 years for trees established before 1889. Older trees usually had high growth suppression in the early stage, which resulted in higher error. Determination of error was repeated with black spruce and white cedar, and age underestimation was estimated to be less than 10 years. To account for possible dating errors, the age structures of larch are presented in classes of 5-year intervals (Bergeron and Gagnon 1987; Bergeron and Brisson 1990). Because many spruce and cedar individuals are the results of layering, the age provided should be considered as the time of development of the aerial shoot, not the true age. The age structures of these two species are presented in classes of 10-year intervals.

A multiple age–DBH–height regression analysis was used to estimate the age of recently dead trees and live larch trees with decayed centres. The regression was computed using the stems (seedlings, saplings, and live trees) that could be aged via cross-dating and terminal bud scar counts. The large percentage of the variance explained by the regression model (adjusted $R^2 = 0.863$, $p < 0.001$, $n = 537$ individuals, $y_{(\text{age})} = 10.834(\text{DBH})^{0.5} + 24.352(\text{height})^{0.5} - 6.173$) justified its use in age determination.

For some trees where the collection of cores at the ground level was impossible because of rotten wood, cores were

taken higher on the trunk. For these, another regression model was used as a correction factor to adjust for the height of the cores (adjusted $R^2 = 0.838$, $p < 0.001$, $n = 537$ individuals, $y_{(\text{age})} = 32.553(\text{height})^{0.5} - 6.157$).

To estimate the age of the white cedar and black spruce stems (seedlings, saplings, and trees) that were not cored, the process described for larch was repeated using an age–height regression model (white-cedar: adjusted $R^2 = 0.596$, $p < 0.001$, $n = 88$ individuals, $y_{(\text{age})} = 57.238(\text{height})^{0.5} - 17.279$; black spruce: adjusted $R^2 = 0.609$, $p < 0.001$, $n = 180$ individuals, $y_{(\text{age})} = 31.796(\text{height})^{0.5} + 2.615$). For the cores collected higher on the trunk, the same equations were used to adjust for the height.

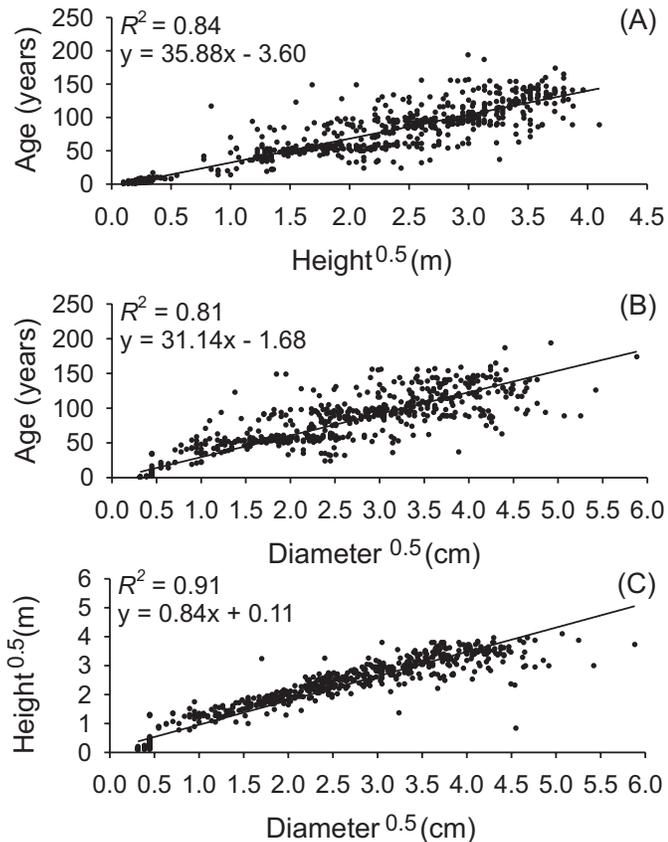
Data analysis

Stand dynamics were studied using age-frequency and cumulative age distributions (Zar 1999). The ages of both live and recently dead trees were included in the analyses. Similarities in age-class distribution among 400-m² plots were examined using complete clustering analysis (farthest neighbour) computed from the chi-square distance matrix of the $\log_{10}(y + 1)$ transformed age distribution. This method of clustering offers the advantage of excluding every pair of zeros in the quantification of the object descriptor relationships (Legendre and Legendre 1998). Following this analysis, the plots showing similarities in age distributions were grouped together for further analyses. Throughout this paper, these groups of plots are identified as cluster types I, II, III, and IV. The use of two types of grouping in the analysis (stands and clusters) permitted us to verify that the establishment periods identified are not restricted to one stand or one plot in particular. The use of clusters also simplified the interpretation of the plot data.

To examine the effects of disturbances on stand age structure, larch age-frequency distributions were compared with the larch radial growth patterns. This helps to assess whether initial stem recruitment was related to past disturbance events, which were observed as tree growth releases and suppressions (sensu Lorimer 1980; Glitzenstein et al. 1986; Tardif and Bergeron 1999). After measuring and cross-dating larch cores and cross sections taken at DBH (samples from the stem analyses that were located within the plots were also used), a spline function (giving a 50% frequency response of 45 years) was applied to each measured series to produce standardized tree-ring series. The spline function mainly removes age- or size-related trends in tree growth (Cook and Peters 1981). Biological persistence contained in the tree-ring data was also removed (autoregressive modelling) from the standardized series to produce residual tree-ring series (Holmes 1983). The residual tree-ring series were grouped together based on the results of the cluster analysis conducted on the larch age-frequency distribution. To combine the dendrochronological data for each cluster type, biweighted means of the residual series were computed with ARSTAN (Holmes 1983; Cook 1985) to produce the residual chronologies. Therefore, one residual chronology will be shown per cluster type.

The growth release and the suppression periods were recorded for each residual tree-ring series following Holmes (1999). We considered trees to exhibit a release at a given year when ring width was at least 50% greater than the mean

Fig. 2. Age–height (A), age–diameter (B), and height–diameter (C) regressions for larch stems. DBH and height data were converted using a square-root transformation.



ring width of the 10 previous years (program parameters: jolt release factor of 1.5 and 10-year moving average (Holmes 1999)). This increase in ring width also had to be maintained for 10 years. We considered trees to exhibit suppression at a given year when ring width was at least 50% lower than the mean ring width of the 10 previous years (program parameters: jolt suppression factor of 1.5 and 10-year moving average). This reduction in ring width also had to be maintained for 10 years. The percentages of trees in growth releases and suppressions are presented for each cluster type. These analyses were conducted with the program JOLTS (Holmes 1999) on the residual tree-ring series.

Results

Age-frequency distribution

As indicated by the R^2 of the regression models (Fig. 2), a high goodness of fit was observed between the square-root transformed diameter and the age of larch ($p < 0.01$) (Fig. 2B). Relationships between larch height and age, as well as larch height and radial growth, were also strong ($p < 0.01$) (Figs. 2A and 2C). As shown in Fig. 3, the distribution of the estimates is similar to the age-frequency distribution of trees cored at ground level, except for BL1 (age-class 1961–1965).

Among the stands, five periods of larch establishment can be observed (Fig. 3). The first period occurred mostly in CC

in the mid-19th century and lasted about 40 years. The second period was mainly observed in BL2. It started in the late 19th century, peaked in the early 20th, and ended in the 1910s. The third period of establishment occurred between 1936 and 1960. It was observed in stand BL1 and CC. A fourth establishment period was observed in stand MAG and lasted from 1976 to 1980. Finally, establishment has also been occurring in the decade prior to the sampling season and mainly consisted of seedlings (Fig. 3). As for black spruce and white-cedar age distributions, the results showed that most of the individuals became established in mid-20th century (Fig. 3). In three plots, either species outnumbered larch (Table 1).

The plots sampled are not of equal densities (Table 1). In general, plots located away from the water bodies (refer to Fig. 1) have higher total densities (BL2b, CCB, BL1c, BL1d, and MAGb), higher larch densities (BL2b, CCB, and BL1d), and higher spruce and cedar densities (BL1c, BL1d, and MAGb). Larch tree densities were generally lower in mixed stands. As for the larch basal area, high values were observed in plots BL2b, BL2c, CCA, and CCC. This pattern of distribution did not correspond to the environmental positioning along the water bodies.

Examination of the age structures formed by the cluster analysis show four distinctive age distributions (Fig. 4). In cluster type I, a majority of larch trees dated around mid-20th century (Fig. 5A). Some establishment also occurred around the 1990s. The oldest larch dated from the 1880s. In cluster type II, a majority of larch dated around late 19th and early 20th century (Fig. 6A). A small establishment period occurred from 1976 to 1980 in MAGa. The oldest dated from the 1810s. Cluster type III identifies two periods of important establishment (Fig. 7A). One period occurred from middle to late 19th century. The other period occurred in late 20th century and is much stronger than the one observed in cluster type I. The oldest larch tree in this cluster dated from late 1820s. Like in cluster type III, cluster type IV also shows two periods of important establishment: the early and late 20th century (Fig. 8A). However, the age distributions among the three plots that formed this cluster are not that similar, as shown by the relatively high distance value linking plot BL1d with plots MAGb and BL2a (Fig. 4). This is due to the absence of an early 20th century establishment in BL1d. It is important to note that the establishment peak in BL1d from 1961 to 1965 is mostly composed of tree estimates observed in Fig. 3. The oldest larch tree in this cluster is also the oldest observed at Lake Duparquet and dated around the 1800s. Again, the cluster analysis did not demonstrate a similarity or dissimilarity in age structures among the plots relatively to the positioning along the water bodies.

Identification of disturbances

Dates of major larch sawfly outbreaks are shown with each cluster residual chronology (Figs. 5B–8B). The grouping of tree-ring series in cluster was justified by the high correlation among series and the high percentage of explained variance in the first eigenvector of the principal components analysis (Table 2). Because of limited sample depth, the interpretation of the tree-ring data should not be made beyond the 1880s in cluster type III (Fig. 7B) and early 20th century in other clusters. As observed from the residual chronologies,

Fig. 3. Static (vertical bars) and cumulative age distribution (solid lines) of larch (5-year age-class), spruce, and cedar (10-year age-class) stems per hectare in (A) pure larch stands and (B) mixed-composition stands. For the larch static distribution, solid bars show the age frequency of living and recently dead trees estimated from the cores taken at ground level. Open bars show the age frequency of trees that were estimated or corrected with a regression model.

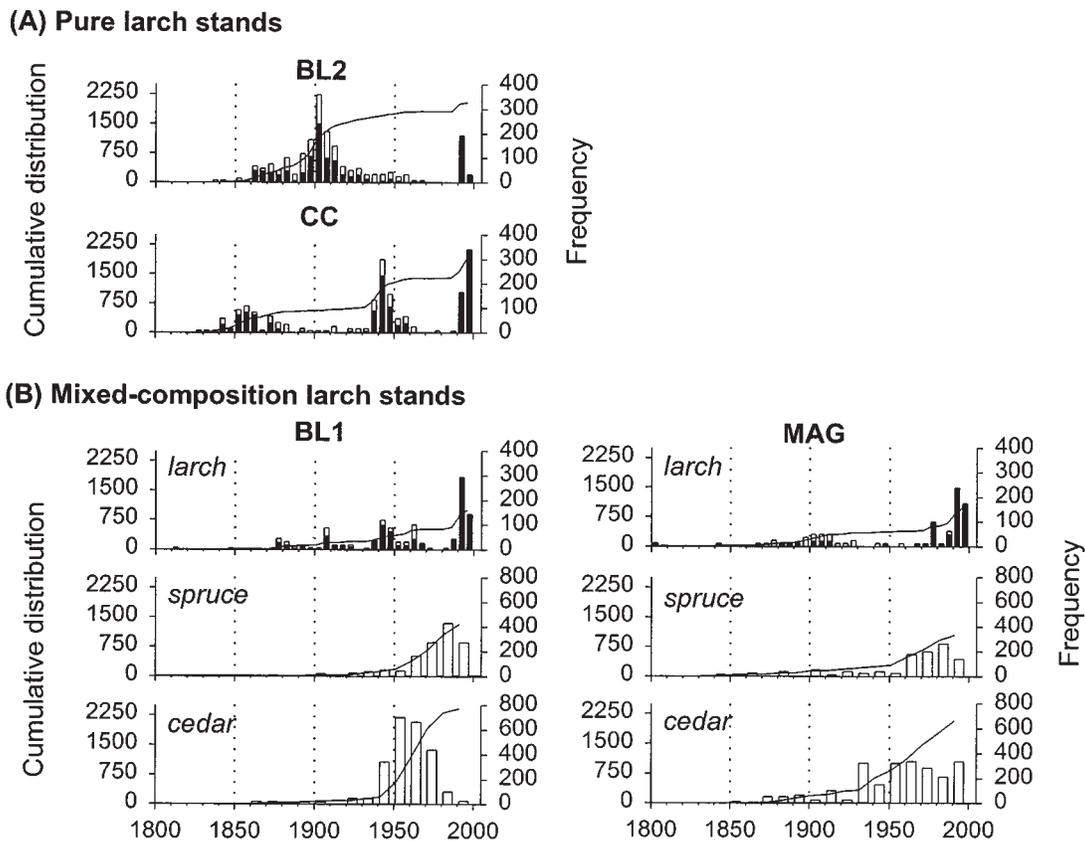


Table 1. Stand structures at four Lake Duparquet sites, Abitibi.

	BL2a	CCa	BL2c	CCc	BL2b	CCb	BL1a	BL1b	BL1c	MAGa	MAGb	BL1d
Larch												
No. of living stems/ha	1400	2025	1350	700	2325	2650	775	700	700	625	1300	2475
No. of dead stems/ha	150	200	250	25	575	150	0	50	75	50	25	25
% of dead stems	9.7	9.0	15.6	3.4	19.2	5.4	0.0	6.7	9.7	7.4	1.9	1.0
Tree density (ha)	675	975	1125	600	2150	725	425	225	600	350	325	175
Tree basal area (m ² /ha)	6.7	18.7	20.3	12.6	14.5	2.9	5.8	3.6	11.4	7.4	7.5	1.0
White-cedar												
No. of living stems/ha	—	—	—	—	—	—	—	—	—	175	4425	9775
Tree density (ha)	—	—	—	—	—	—	—	—	—	25	625	600
Tree basal area (m ² /ha)	—	—	—	—	—	—	—	—	—	0.3	6.3	5.0
Black spruce												
No. of living stems/ha	—	—	—	—	—	—	50	175	3275	600	1500	1825
Tree density (ha)	—	—	—	—	—	—	50	100	75	50	425	200
Tree basal area (m ² /ha)	—	—	—	—	—	—	0.1	0.9	0.9	0.4	5.2	1.4
Total no. of stems/ha	1550	2225	1600	725	3000	2800	825	925	4050	1450	7250	14 100

outbreaks identified by Girardin et al. (2001b) were also observed among the tree-ring series sampled in this study (Figs. 5B–8B). The two periods of growth suppression in early and middle 20th century were effectively reproduced. In addition, one can observe that the 1955–1962 outbreak did not produce important growth suppression in cluster type

III (Fig. 7C). Based on our criteria, less than 20% of the tree-ring series recorded a reduction in growth in 1956. In contrast, in cluster type I, more than 65% of the tree-ring series recorded growth suppression for that single year (Fig. 5C). In this cluster, trees also recorded important growth release few years later. This is not the case in cluster types III and IV

Fig. 4. Results of the complete clustering analysis conducted on the \log_{10} -transformed static age distribution of larch. As the distance increases in the linkage process (X axis), the similarities between the two linked plots (or groups of plots) decrease.

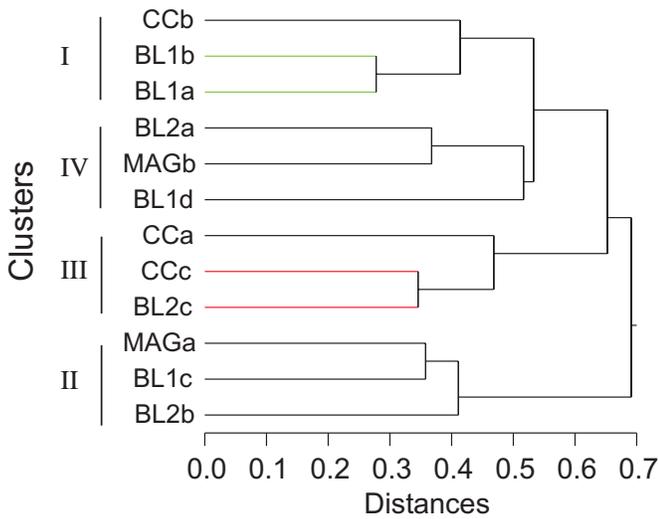


Fig. 5. Relationships between larch establishment and radial growth in cluster type I. (A) Static and cumulative age distribution (solid line; data divided by 10) of larch (live and recently dead) per hectare calculated from plots BL1a (open bars), BL1b (solid bars), and CCb (hatched bars). (B) Residual tree-ring chronology (solid line) and number of measured series (broken line). The number of series was divided by 50 to use only one scale. Periods of severe larch sawfly outbreaks (1895–1912 and 1955–1962; Girardin et al. 2001b) are shown by the solid triangles. (C) Relative frequency of trees in either a growth release (positive values) or growth suppression (negative values) at a given year. (D) Stem analysis for larch (solid lines) and black spruce (broken lines). Note that some of the trees analysed were collected aside the plots.

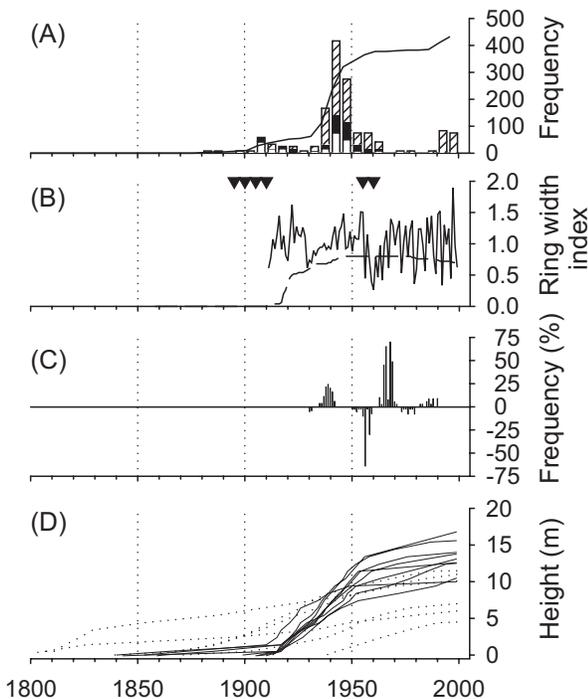
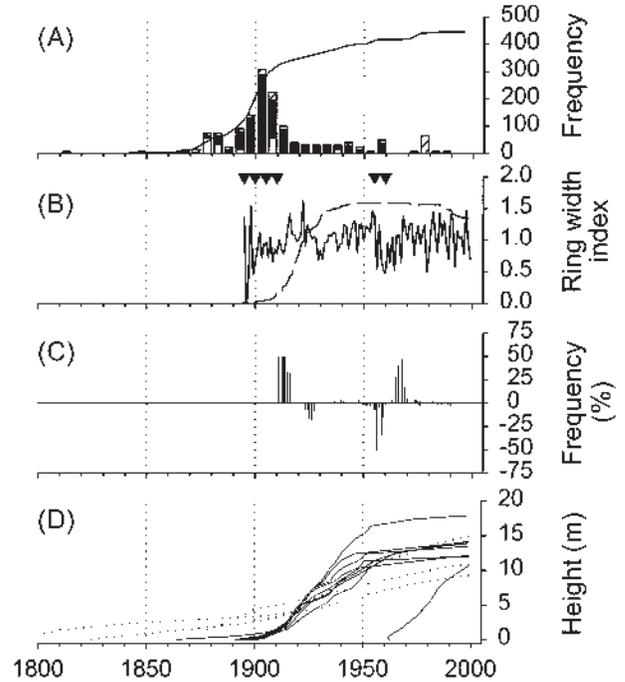


Fig. 6. Relationships between larch establishment and radial growth in cluster type II (plots BL1c (open bars), BL2b (solid bars), and MAGa (hatched bars)). Definitions are as in Fig. 5.

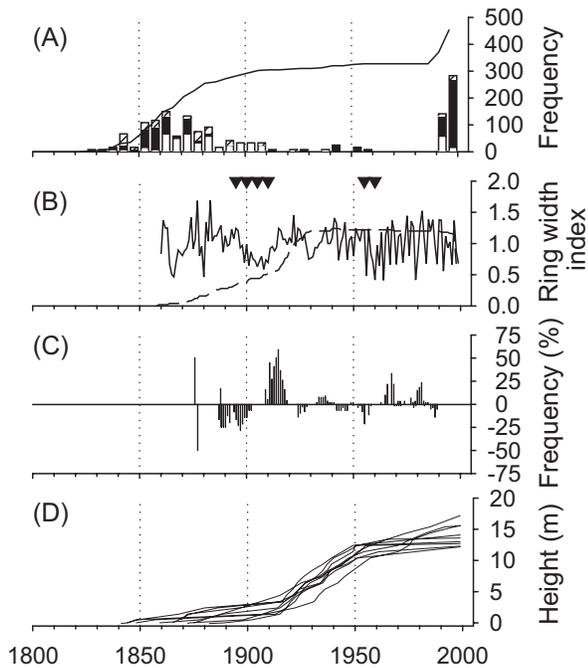


(Figs. 7C and 8C). Some growth suppression was also recorded in mid-1920s. It is, however, minor as less than 25% of the series was affected.

In addition to the radial growth releases observed in cluster type I, important height growth releases were identified following the 1895–1912 outbreak, this time on all larch trees studied (Figs. 5D–8D). Before the 1910s, most trees were restricted to a height growth rate of less than 0.4 m/decade. After the outbreak, the height growth rate abruptly increased to about 2 m/decade, until mid-20th century where it started to slow down. Note that in cluster type I, the decrease is less important than in other clusters. In addition, some trees also recorded a growth release in the late 1960s and 1980s (Figs. 7 and 8). For most of these trees, the release only lasted a few years. As for black spruce, there was only a small increase in height growth at the end of the 19th century in some trees and during the early part of 20th century in others (Figs. 5D, 6D, and 8D). However, in contrast to larch growth releases, spruce releases were less pronounced (less than 0.6 m/decade). As with larch, a reduction in spruce height growth started in the second half of the 20th century.

Figures 5–8 demonstrate that the magnitude of an establishment period is relatively proportional to the percentage of trees affected by growth reductions and releases. The establishment peak observed in cluster type I notably coincide with important radial growth suppressions a few years later, followed by growth releases (Figs. 5A–5C). Clusters where little or no establishment was observed did not have such important growth suppressions and releases (Figs. 6–8). Furthermore, the figures highlighted a disagreement in the timing between establishment and outbreak. The establishment periods observed in mid-20th century (Figs. 3, 5, and 8) and in the late 1970s (Fig. 6) occurred before and during the outbreak. On the other hand, the establishment period observed

Fig. 7. Relationships between larch establishment and radial growth in cluster type III (plots BL2c (open bars), CCa (solid bars), and CCc (hatched bars)). Definitions are as in Fig. 5.



in the early 20th century occurred during and after the outbreak (Figs. 3 and 6).

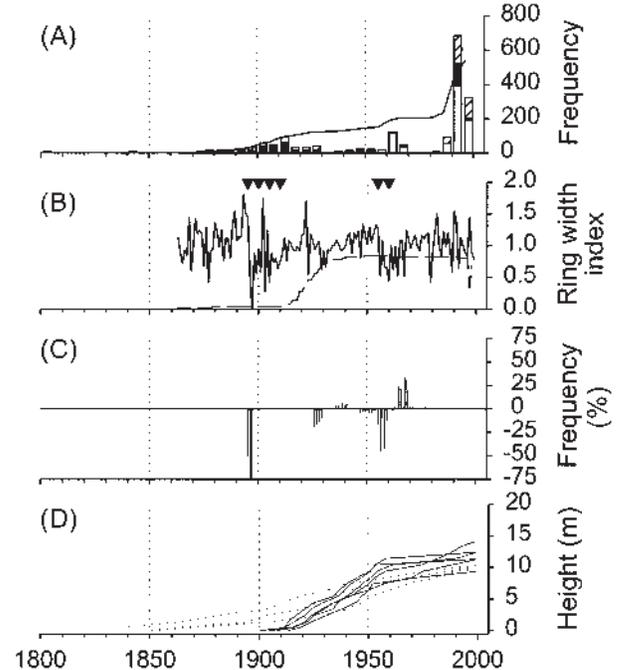
Discussion

Role of disturbances

Age-class distribution results support the hypothesis that larch dynamics is predominantly controlled by major stand disturbances. The age-distribution curves observed in our study are unlike the classic inverted “J” shape distribution that are found in stable populations and characterized by declining tree density with increasing age or size (Lorimer 1980; Oliver and Larson 1990; Tardif and Bergeron 1999). Moreover, we found many discontinuities in larch establishment (Fig. 3), which is common among tree species whose regeneration depends on catastrophic events that open the forest canopy (Bergeron and Gagnon 1987; Bergeron and Brisson 1990; Morin 1994).

The high variability in age structure among stands and among clusters suggests that the larch sawfly outbreaks of 1895–1912 and 1955–1962 were responsible for the creation of canopy gaps. The height-growth releases that were observed in surviving larch stems and black spruce stems are indications that the canopy was reduced, allowing more light to the surviving trees. The smaller outbreak of the late 1970s may also have affected the larch stand dynamics, notably in stand MAG. The effect of sawfly defoliation on larch mortality has been studied, notably by Beckwith and Drooz (1956) and Ives and Nairn (1966) during the mid-20th century outbreak. During this outbreak, Beckwith and Drooz (1956) found that the larch sawfly killed a small fraction of the larch in their plots (i.e., <30%) and that the amount of affected trees varied spatially. The effect of intense sawfly defoliation on larch population dynamics may notably be similar to the

Fig. 8. Relationships between larch establishment and radial growth in cluster type IV (plots BL1d (open bars), BL2a (solid bars), and MAGb (hatched bars)). Definitions are as in Fig. 5.



impact that the spruce budworm has on the dynamics of balsam fir (*Abies balsamea* (L.) Mill.) in stands surrounding Lake Duparquet. In these stands, tree mortality resulting from the budworm outbreaks is distributed in patches instead of being uniformly distributed over the entire landscape (Kneeshaw and Bergeron 1998, 1999).

Until now, it remained unclear what factors could have contributed to the patchy distribution of larch establishment in our forested wetland stands. Beckwith and Drooz (1956), nevertheless, reported that larch mortality in mid-20th century generally occurred along exposed edges of stands or on mineral soils. Also, according to Ives and Nairn (1966), older trees would be more affected by mortality, as immature larch would be able to withstand several years of severe defoliation before succumbing.

Recruitment, establishment, and growth

In the Lake Duparquet region, larch sawfly outbreaks are likely to play an important role in the initiation of stand recruitment. A main effect of larch sawfly outbreaks on larch stand dynamics would be to allow an increase in the survival rate of the seedling bank after reduction of the tree cover. In this study, seedlings from the seedling bank were younger than 10 years (about 6 years of age). Larch is shade intolerant, but it was observed that the seedling bank is periodically renewed under shade conditions (Duncan 1954; Logan 1966; Johnston 1973; Brown et al. 1988) (seeds produced every 3–6 years; Duncan 1954; Payette et al. 1982; Johnston 1990). After reduction of the tree cover, the seedlings benefit from an increase in light availability, which results in an abrupt height growth release (Figs. 5–8). These newly established individuals will eventually become dominant and will, with the other surviving saplings and trees, assure the production of seeds. Note that larch can bear viable seeds on trees as

Table 2. Larch residual tree-ring chronologies statistics for Lake Duparquet, Abitibi.

Larch tree-ring statistics	Cluster type				All series
	I	II	III	IV	
Chronology length (years)	1910–1998	1894–1999	1858–1999	1862–1998	1858–1999
No. of measured series	40	79	62	42	233
% of missing rings	0.87	0.47	1.09	0.93	0.81
Mean sensitivity	0.38	0.33	0.29	0.35	0.28
SD	0.33	0.29	0.27	0.30	0.25
First-order autocorrelation	–0.02	0.02	0.09	–0.01	0.08
Correlation among all series	0.65*	0.53*	0.50*	0.47*	0.50 [†]
Variance in first eigenvector (%)	66.5*	55.5*	51.7*	49.9*	52.2 [†]

*To maximize the number of series analysed, a common interval time span of 1930–1996 was chosen.

[†]Analysis of all series together had to be conducted on the common interval time span 1917–1996 as the number of series entered in the analysis could not exceed the number of years. No. of series in the common interval analyses are, respectively, 28, 57, 55, 30, and 59.

young as 12 years of age (Johnston 1990) and that seed production is maximized under full light conditions (Nelson 1950). Depending on the density of this new developing tree cover, a number of recruits may survive to fill the remaining gaps, until light becomes insufficient for any new establishment. Such conditions synchronously induce a decrease in seed production (Nelson 1950) and in height growth from established individuals (Figs. 5–8).

Although the concordance between establishment and outbreak may be present, the pattern of sawfly outbreak followed by larch establishment may not always be observed. Results tend to show that middle and late 20th century establishment peaks occurred before and during the outbreaks, whereas the early 20th century establishment peak occurred during and after the outbreak. The different patterns of establishment observed may emerge from the variability in the length and severity of the outbreaks. These factors could be critical in determining if establishment will originate from surviving stems (increase seed production) or from increased survival of the seedling bank. Because of higher seedlings and saplings survival rates, regeneration during a shorter outbreak (1955–1962; Girardin et al. 2001b) may not depend as much on seed production.

When mature trees are severely defoliated for many years (1895–1912; Girardin et al. 2001b), the sawfly larvae fall to the ground and consume all or most of the pre-established individuals (Duncan 1954; Nairn et al. 1962; Ives and Nairn 1966). In such condition, larch stand re-establishment can only depend on the production of seeds from surviving individuals, which would explain the delay between the date of outbreak and the establishment peak. However, a further investigation on this matter is needed, because tree age underestimation may have contributed to this disparity (Wong and Lertzman 2001; Kneeshaw and Claveau 2001). The presence of a high water table; the absence of a deep buried stem, a J-shaped stem, or a deep rooting system; and the shade intolerance of larch strongly suggest that the age underestimation error may not be as important in larch as it was reported in balsam fir (Kneeshaw and Claveau 2001).

Impacts on mixed stands

In Girardin et al. (2001a), it was speculated that black spruce or white-cedar would gradually replace larch in mixed

wetlands of Lake Duparquet. The present results clearly show that both stands BL1 and MAG have evolved from being larch dominated to cedar–spruce–larch stands around the 1950s. This replacement is most important in plots located away from the water bodies. Although a large number of larch seedlings were found in the understory, most of them should undergo mortality because of their inability to survive under the spruce and cedar shade (Johnston 1990; Montague and Givnish 1996). In these stands, it is probable that the larch sawfly has contributed to this decline in larch population by killing the dominant trees. Thus, although in most larch stands the sawfly outbreaks may initiate stand establishment, in such stands, the sawfly may accelerate the normal successional pathway under which pioneer species get replaced by more shade-tolerant species (Johnston 1990; Jardon et al. 1994b).

Conclusion

Our results showed that larch sawfly outbreaks are a major factor controlling the dynamics of larch stands in wetlands of the northern Clay Belt boreal forest. Some of Lake Duparquet's larch establishment was associated with the 1895–1912, 1955–1962, and possibly late 1970s sawfly outbreaks. The results of this study also support the hypothesis that the larch sawfly outbreaks, instead of inducing tree mortality across entire larch populations, operate at a smaller scale by creating small canopy gaps. This lead to the discontinuous age-class distributions observed among the plots and stands. In addition, results show a disparity between the timing of an outbreak and the post-recruitment period. The most severe outbreak recorded (1895–1912) was associated with a recruitment peak during and after the outbreak, whereas the less severe outbreaks (1955–1962 and the late 1970s) were associated with a recruitment peak that would have occurred few years before. From our present knowledge of the sawfly and larch dynamics, we suggest that, depending on the length of the outbreak, recruitment may origin from either pre-established seedlings, or greater seed production among surviving trees. This extended period of establishment after an outbreak could also have originated from the underestimation of the age of older larch trees. However, this bias is mainly associated with shade-tolerant species and thus may

have little effect on larch trees. Further studies should be conducted in the area to characterize the size of canopy gaps and their spatial distribution. It would notably be interesting to determine what factors (e.g., tree age or density, topography, water table, plant species assemblage, needle chemistry, etc.) favour the creation of these gaps in the larch stands of Lake Duparquet.

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