Growth responses of riparian *Thuja occidentalis* to the damming of a large boreal lake

Bernhard Denneler, Yves Bergeron, Yves Bégin, and Hugo Asselin

Abstract: Growth responses of riparian eastern white cedar trees (*Thuja occidentalis* L.) to the double damming of a large lake in the southeastern Canadian boreal forest was analyzed to determine whether the shoreline tree limit is the result of physiological flood stress or mechanical disturbances. The first damming, in 1915, caused a rise in water level of ca. 1.2 m and resulted in the death of the trees that formed the ancient shoreline forest, as well as the wounding and tilting of the surviving trees (by wave action and ice push) that constitute the present forest margin. The second damming, in 1922, did not further affect the water level, but did retard the occurrence of spring high water levels, as well as reduce their magnitude. However, this did not injure or affect the mortality of riparian eastern white cedars. Radial growth was not affected by flooding stress, probably because inundation occurred prior to the start of the growing season (1915–1921) or was of too short duration to adversely affect tree metabolism (after 1921). It follows that (*i*) the shoreline limit of eastern white cedar is a mechanical rather than a physiological limit, and (*ii*) disturbance-related growth responses (e.g., ice scars, partial cambium dieback, and compression wood) are better parameters than ring width for the reconstruction of long-term water level increases of natural, unregulated lakes.

Key words: compression wood, eastern white cedar, flooding, ice scars, mortality, partial cambium dieback.

Résumé : La réaction des peuplements riverains de cèdre blanc (*Thuja occidentalis* L.) à la construction de deux barrages sur le lac Abitibi — un grand plan d'eau situé dans la région boréale méridionale de l'est du Canada — a été analysée afin de déterminer si la limite lacustre du cèdre blanc est déterminée par le stress physiologique dû à l'inondation ou par les perturbations riveraines. La hausse d'environ 1,2 m du niveau d'eau, engendrée par la construction du premier barrage en 1915, a causé la mort instantanée de tous les arbres qui formaient l'ancienne lisière de la forêt et provoqué des blessures et l'inclinaison des arbres survivants (formant la marge forestière actuelle), par l'action des vagues ou l'activité glacielle. La construction du deuxième barrage, en 1922, n'a pas augmenté significativement le niveau d'eau, mais a plutôt entraîné un retard et une baisse de magnitude des crues printanières, sans toutefois affecter la croissance des cèdres blancs riverains. La croissance radiale n'a pas été affectée par l'inondation, probablement parce que les crues printanières étaient déjà terminées avant le début de la saison de croissance (1915–1921), ou parce qu'elles étaient de trop courte durée pour nuire au métabolisme des arbres (après 1921). Il s'ensuit que (*i*) la limite lacustre du cèdre blanc est une limite mécanique liée à l'action des vagues et à l'activité glacielle, plutôt qu'une limite physiologique due à l'inondation, et (*ii*) que les paramètres de croissance reliés aux perturbations, tels les cicatrices glacielles, la formation de bois de compression et la mortalité partielle du cambium, sont de meilleurs indicateurs que la largeur des cernes de croissance, pour reconstituer l'augmentation à long terme du niveau d'eau de lacs naturels.

Mots-clés : bois de compression, cèdre blanc, cicatrices glacielles, inondation, mortalité, mortalité partielle du cambium.

Introduction

Flooding is generally recognized as the most important environmental factor limiting tree species occurrence on floodplains, where species are arranged along an elevation gradient reflecting flood tolerance (Beschel and Webber 1962; Bell and Del Moral 1977; Robertson et al. 1978; Metzler and Damman 1985). Flooding mainly affects trees through changes of soil properties resulting in physiological stress (Teskey and Hinckley 1977; Lugo and Brown 1984). Abrupt growth reduction and death of stressed trees are the predominant responses to both naturally (Broadfoot and

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Williston 1973; Tardif and Bergeron 1993; Astrade and Bégin 1997), and artificially (Harris 1975; Harms et al. 1980; Duever and McCollom 1987) prolonged flooding. However, short-term growth improvement (Conner et al. 1981; Stahle et al. 1992), and no-growth response (Johnson and Bell 1976; Mitsch and Rust 1984) were also observed. The severity of inundation-stress depends on the characteristics of the flood and on the tolerance level of the trees. The stress increases with inundation length and depth, and is more pronounced when flooding occurs during the growing season than in the dormant period (Brink 1954; Harris 1975; Teskey and Hinckley 1977; Harms et al. 1980).

Flooding is often accompanied by physical disturbances caused by wave action or ice push, which also affect shoreline trees. The main consequences of these riparian disturbances are wounding, tilting, and uprooting of the affected trees. Growth responses to such events were successfully used to analyze riparian disturbance dynamics in river environments (Hupp 1988; Desrosiers and Bégin 1992; Langlais and Bégin 1993), as well as on lakeshores (Bégin and Payette 1991; Tardif and Bergeron 1997*b*; Bégin 2000*a*, 2000*b*, 2001). Most of these studies took place in cold northern regions, where snow and ice considerably enhance the intensity and frequency of riparian disturbances in times of spring high water levels.

In this study, we examined growth responses of riparian eastern white cedar trees (*Thuja occidentalis* L.) to the double damming of Lake Abitibi, a large storage reservoir located in the southeastern boreal region of Canada. A first dam, the Couchiching Falls dam (CFD), was built in 1915 on the Abitibi River, ca. 15 km downriver from Lake Abitibi, and resulted in an abrupt 1.2 m rise of the water level (Christopherson 1915; Hudson's Bay Company 1915; Trudelle 1937; Lee 1974; Perron 1989; Asselin and Gourd 1995; Pollock 1995). The CFD was replaced in 1922 by another dam (Twin Falls dam (TFD)) built 20 km further down the Abitibi River (Pollock 1995). This second dam did not significantly affect the water level of Lake Abitibi, but it caused a major change of hydrological regime, retarding the occurrence and reducing the intensity of spring high water levels.

Three objectives were pursued in this study. First, determine the effect of the abrupt 1.2 m water-level rise on the riparian eastern white cedar fringe. We expected (*i*) high mortality of the shoreline white cedar; (*ii*) an abrupt growth decrease of the surviving trees; and (*iii*) an increased frequency of disturbance-related growth responses like ice scars and compression wood formation. Detecting growth responses to increased water levels could prove useful for the reconstruction of past climate-driven long-term water level increases of natural, unregulated lakes, as well as to forecast the effects on riparian forests of future waterlevel increases.

The second objective consisted in determining whether the change in hydrological regime caused by the second damming affected the shoreline eastern white cedars. Finally, the third objective was to evaluate whether the lower limit of the riparian eastern white cedar fringe around Lake Abitibi was controlled by flooding or by disturbances. Two alternative hypotheses were considered.

(*i*) Physiological limit owing to excessive flooding stress: physiological stress caused by prolonged flooding prevents eastern white cedar from occurring closer to the lake. Although riparian disturbances cause some damage and kill some trees, they are not the main factor limiting the occurrence of the species close to the lake.

(*ii*) Mechanical limit owing to severe disturbance regime: although flooding might affect riparian eastern white cedar, the species can endure high levels of flood-induced stress. However, mechanical disturbance caused by wave action and ice push attains high intensities at the shores of large water bodies like Lake Abitibi and prevents eastern white cedar from colonizing sites close to the lake.

Material and methods

Study area

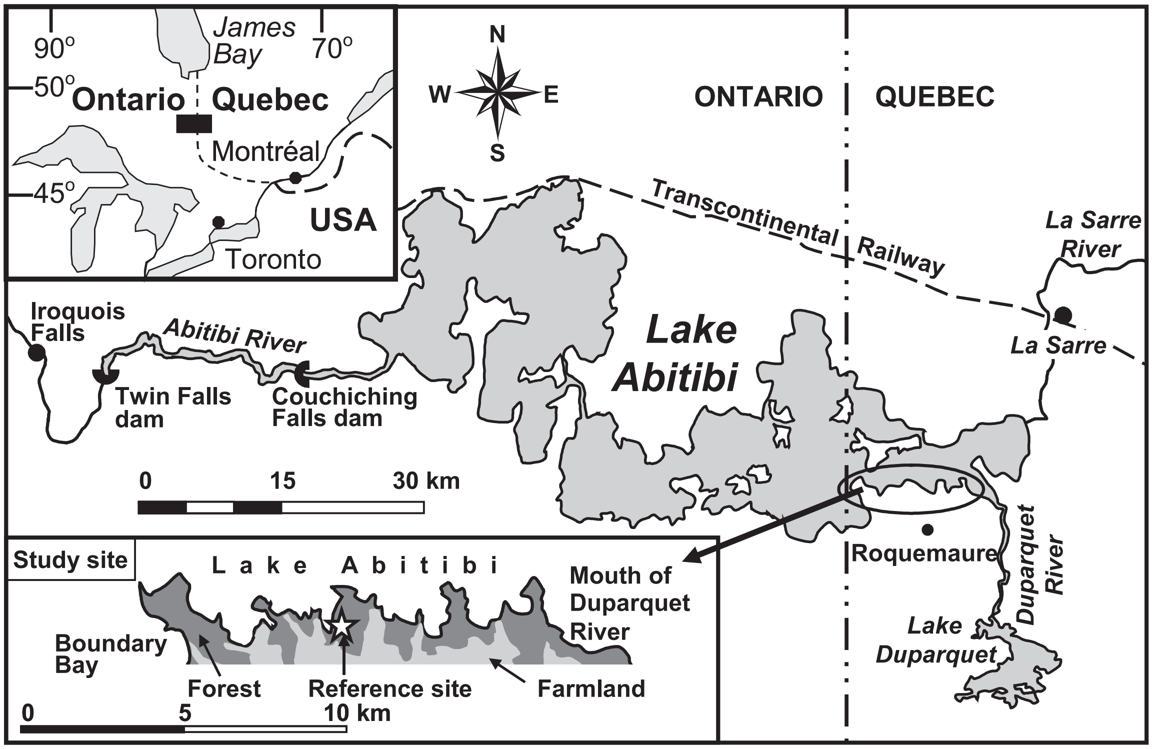
Lake Abitibi (48°40′N, 79°30′W; 264.7 m a.s.l.) is located approximately 600 km northwest of Montreal and 250 km south of James Bay, straddling the Quebec–Ontario border (Fig. 1). The Abitibi River drains the lake towards James Bay. Glacial till and rock outcrops prevail on the higher elevations of the fairly flat area (Bergeron et al. 1983), whereas landscape depressions are mostly covered by clayey deposits originating from the proglacial lakes Barlow and Ojibway (Veillette 1994). Mean annual temperature and total annual precipitation for the period 1971–2000 were 0.7 °C and 890 mm at La Sarre (ca. 10 km northeast of the lake), and 0.9 °C and 776 mm at Iroquois Falls (ca. 40 km west of the lake) (Environment Canada 2004).

The typical vegetation in this southern boreal area is a mixed forest with balsam fir (*Abies balsamea* (L.) Mill.), paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and white spruce (*Picea glauca* (Moench) Voss) dominating on mesic sites (Bergeron and Bouchard 1984). Tamarack (*Larix laricina* (Du Roi) K. Koch), black spruce (*Picea mariana* (Mill.) B.S.P.), black ash (*Fraxinus nigra* Marsh.), and balsam poplar (*Populus balsamifera* L.) occupy hydric sites (Bergeron et al. 1983; Tardif and Bergeron 1992; Denneler et al. 1999). Eastern white cedar, generally associated with late successional stages (Bergeron 2000), occurs on a wide range of organic and mineral soils (Bergeron et al. 1983; Denneler et al. 1999). This species tolerates extremely xeric and humid conditions, but is highly susceptible to fire because of its thin and inflammable bark (Johnston 1990). In areas characterized by severe forest fires (such as in northwestern Quebec), white cedar is thus most common on relatively protected sites such as lakeshores, islands, and cliff faces (Heinselman 1973; Ericsson and Schimpf 1986; Larson and Kelly 1991).

Seasonal water-level fluctuations

Since instrumental water-level measurements only started in 1949 at Lake Abitibi (and thus well after double damming), data from Lake Dumoine (46°50′N, 77°55′W) were used to approximate the seasonal Lake Abitibi water-level fluctuations prior to damming. Lake Dumoine is not dammed, and is located ca. 250 km southeast from Lake Abitibi. It was the nearest lake with a sufficiently long and complete record of water levels (records available for all four seasons starting in 1968). Spring to autumn water-level

Fig. 1. Map of the Lake Abitibi area in the southern boreal region of Ontario and Quebec, showing the Couchiching Falls and Twin Falls dams. Enlarged detail shows the study area and the location of the reference site.



measurements were available for Lake Duparquet, located only 15 km south of Lake Abitibi (Fig. 1), for the periods 1989–1991 (Tardif and Bergeron 1997*b*) and 1996–1998 (Denneler et al. 2008). Comparison of the records from lakes Dumoine and Duparquet showed very similar seasonal patterns, confirming that Lake Dumoine could be used to reconstruct the natural hydrological regime of Lake Abitibi prior to damming. Maximum water levels generally occurred in May at Lake Dumoine, between the minima in March and September (Fig. 2*a*).

From 1915 to 1921, Lake Abitibi water levels were high in winter and spring when the CFD gates were closed, and low in summer and autumn when gates were open (Fig. 2*a*). Thus, although the spring water level was higher (by ca. 1.2 m), the seasonal hydrological regime was similar to the one prevailing prior to damming, with maximum water levels reached in May.

The seasonal Lake Abitibi water-level regime changed considerably in 1922 owing to the replacement of the CFD by the TFD. Gauge measurements for the period 1949–1997 indicate that the water level was lowered during winter and spring, whereas consecutive refilling of the reservoir resulted in relatively high water levels throughout summer and autumn (Fig. 2*a*). Maximum water levels were delayed by one month and occurred in June. This change in the seasonal pattern of Lake Abitibi water level is confirmed by the comparison of the mean monthly discharges, from 1922 to 1993, of the regulated Abitibi River with those of the naturally fluctuating Harricana River located ca. 90 km east of the study area (Fig. 2*b*).

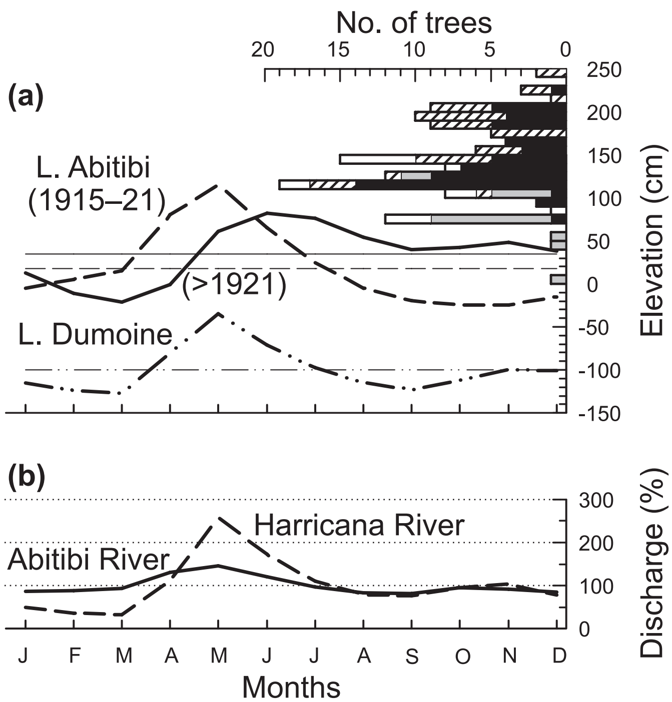
Study site

One large study site was selected on the south shore of Lake Abitibi (Fig. 1) instead of several small ones because preliminary observations showed that only a few shoreline trees of sufficient age to provide information about the 1915 water-level increase were preserved and still in situ. Stands of the study area are late-successional, the western and eastern parts of the site having burned for the last time in the 1760s and 1820s, respectively (Lefort et al. 2003). Eastern white cedar dominates the study site, with some balsam fir and white spruce, as well as scattered paper birch. To distinguish the effects of water-level changes from other environmental factors that might have influenced the growth of lakeshore trees, a large stand of eastern white cedar growing on the same soil type and located close to Lake Abitibi, but more than 5 m above the high water level, was selected as a reference site (Fig. 1).

Data collection

Along the ca. 35 km shoreline of the study area, cross-sections were sampled above the root collar of all dead white-cedar trees and snags that were still in situ, well preserved (i.e., with at least 50 tree rings to allow cross dating), and located less than 2.5 m above the present water level [measured using a WILD-T2 theodolite (WILD, Heerbrugg, Switzerland)]. Within the same area, samples were also taken from all living eastern white cedar trees with a dbh ≥ 10 cm, and an innermost tree ring dating back from at least 1885 (30 years before the first damming), to allow comparison of the growth patterns before and after dam-

Fig. 2. Riparian white cedar in relation to elevation above lake level and hydrological regime (Water Survey Division of Canada). (*a*) Horizontal bars, frequency distribution of eastern white cedars along the elevation gradient (lowest tree = 0 cm). The bars indicate dead trees on rock (filled bars; n = 61) and clay (grey bars; n = 17), and living trees on rock (hatched bars; n = 37) and clay (open bars; n = 14). Line graphs, mean monthly water-level fluctuations around the annual average (horizontal lines) of Lake Abitibi for the periods before 1915 (natural regime approximated from Lake Dumoine gauge measurements); 1915–1921 (estimation); and after 1921 (Lake Abitibi gauge measurements, 1949–1997). (*b*) Mean monthly discharges of the regulated Abitibi River and the natural Harricana River as a percentage of the average annual discharge from 1922 to 1993.



ming. Almost all sampled trees were located on headlands, because large bay shores lacked eastern white cedar, were affected by erosion, and were partially converted to farmland. The selected trees were either cored twice or, if coring indicated a nonrotten centre, two discs were sampled: one at dbh level to analyze radial growth and formation of compression wood, and one at stem base for ice-scar analysis. Altogether, 89 dead and 51 living riparian eastern white cedar trees were sampled. In addition, two cores from each of 18 eastern white cedar trees dating back from at least 1885 were sampled at the reference site.

Growth substratum and elevation above lake level were noted for each sampled individual to take into account the possible influence of different site conditions on growth patterns. Only two different substrata were found within the study site: glaciolacustrine clay and basaltic rock (Anonymous 1995), each influencing root system development of eastern white cedar in a different way. Clay deposits were characterized by poor soil aeration restricting the root system to the topmost, organic soil layer, whereas trees found on basaltic rock outcrops were deeply rooted within cracks. To compensate for daily lake-level fluctuations, elevation above lake level was measured as elevation above the lowermost individual (considered to be at 0 m).

Cross-dating and chronology development

Ring widths of all samples were measured with a Velmex UniSlide micrometer (0.001 mm precision; Velmex Inc., Bloomfield, N.Y.). Raw measurement curves were statistically cross-dated with two master chronologies from nearby Lake Duparquet (Archambault and Bergeron (1992), AD 1185–1987; Tardif and Bergeron (1997*a*), AD 1417–1987) using the program COFECHA (Grissino-Mayer 2001). A total of 78 dead and 51 living riparian trees were successfully cross-dated and used in the analyses.

Ice scars and compression-wood sequences were dated for the 41 trees from which discs were sampled. Ice scars are partially or completely overgrown wounds on the lake side of the stems caused by the abrasive action of drifting ice, whereas compression wood is composed of tracheids rich in lignin formed on the downhill side of tilted coniferous trees (Kaennel and Schweingruber 1995). Partial cambium dieback (Larson et al. 1993) was discovered on the lake side of some of the cross-sections during sample preparation and was thus included in the analyses to determine whether its formation was related to the damming of Lake Abitibi.

To evaluate the effects of Lake Abitibi water-level changes on radial growth of eastern white cedar, ring-width chronologies were developed for the reference site and five subsets of the riparian sample, formed by combining each growth substratum type with 50 cm segments of the elevation gradient. Two chronologies were developed for trees growing on clay (CL2, 50–100 cm of elevation; CL3, 100–150 cm) and three for trees rooted in rock (RC3, 100–150 cm; RC4, 150–200 cm; RC5, 200–250 cm). The ring-width series were standardized by fitting a negative exponential, a negative linear trend, or a horizontal line (whichever provided the best fit) using the program ARSTAN (Cook and Holmes 1986; Holmes et al. 1986) to eliminate growth trends due to physiological aging of the trees.

Data analysis

Frequency distributions of tree mortality, ice scars, compression wood, and partial cambium dieback were calculated to detect differences attributable to the construction of the CFD in 1915 and the TFD in 1922. Results are presented for the entire riparian site because preliminary analyses revealed similar frequency distributions for the eastern, central, and western parts of the study site.

Pearson's product–moment correlation coefficients were calculated between the reference chronology and each riparian chronology using 25-year segments lagged by 5 years. In addition, mean annual sensitivity curves were computed for all six chronologies. Sensitivity is a measure of the high-frequency variation of tree-ring series reflecting causal environmental factors (Kaennel and Schweingruber 1995). According to Yanosky (1982), increased tilting and wounding of riparian trees caused by a higher exposure to disturbances, such as wave action and ice push following a rise in water level, should result in increased ring-width variability and, hence, sensitivity.

To compare the riparian series to the Lake Abitibi reference chronology, the growth indices of the reference chronology were subtracted from those of each individual riparian series for each year from 1848 to 1995. Normalized departures were obtained using the program OUTBREAK (Holmes and Swetnam 1996). The threshold for a significantly positive or negative departure was set at ±1.645 SD and relative frequency of significant departures was compiled for each riparian chronology.

Results

The riparian eastern white cedar trees growing on clay were restricted to elevations below ca. 1.5 m, whereas those on rock were most common between 1 m and 2 m (Fig. 2*a*). Median elevation of trees found on clay was 80 cm for dead individuals and 115 cm for living ones. The corresponding values for trees found on rock were 140 cm (dead) and 185 cm (alive). Higher elevations for trees growing on rock might reflect their higher exposure to wave action and ice push owing to their position on more exposed headlands.

Seasonal fluctuations of the Lake Abitibi water level resulted in temporary flooding of the riparian eastern white cedar (Fig. 2*a*). Prior to damming, only the trees closest to the lake (≤50 cm of elevation), two dead individuals, might have been shortly flooded by spring high water levels. After damming, those trees were flooded for long periods in winter and spring (CFD), or from spring to autumn (TFD). Since all trees within the second elevation segment (50–100 cm) were found above 75 cm, they were only flooded in April and May (CFD) or for a short period in June (TFD). The trees within the third elevation interval (100–150 cm) were only flooded for short periods of time in cases of extraordinarily high water levels. Although the trees within the uppermost two elevation classes (150–200 and 200–250 cm) were not directly affected by the high water levels, the rising water table might have reached their root systems.

Tree mortality, wounding, and tilting

The frequency distribution of dead riparian eastern white cedars indicates a period of high mortality between ca. 1890 and 1914 (Fig. 3). However, as bark and an unknown number of growth rings were missing from those trees, mortality could not be dated precisely. The dramatic reduction in mortality after 1914 suggests that most dead trees with an outermost ring dating between 1890 and 1914 were in fact killed by the 1915 rise in lake level. No peak in tree mortality was associated with the second damming of the lake in 1922.

The frequency distributions of ice scars, partial cambium dieback, and compression wood showed two distinct periods of disturbance (Fig. 4). Very few of these disturbance-related growth responses dated before 1915. A small peak of ice scars and compression wood was recorded in the early 19th century and some reaction wood was also formed between 1855 and 1885. Wounding and tilting became much more common after the transformation of Lake Abitibi into a reservoir in 1915.

The frequency of tilting events (i.e., initial years of compression wood sequences) increased only slightly after damming and showed small peaks around 1917 and in the 1940s (Fig. 4*d*). However, the number of tilting events after 1915 was probably underestimated because repeated tilting of a single tree was impossible to detect in long-lasting compression-wood sequences. Mean length of the reaction-wood sequences increased significantly (independent-samples *t*-test with unequal variances: $t = -5.243$; df = 44.730; $P < 0.001$) from 5.0 ± 5.0 years between 1800 and 1914 ($n = 37$ sequences) to 21.4 ± 19.1 years between 1915 and 1995 ($n = 40$ sequences). This may partly be explained by differences in tree age. In the 19th century, young, thin, flexible stems rapidly returned to a stable upright position after the loss of balance caused by minor but frequent impacts, such as heavy snow loads. Decades later, stems had increased in size and remained unbalanced, forming compression wood for longer periods after having been tilted by major events such as ice push.

Radial growth

All five riparian chronologies were significantly ($P < 0.0001$) correlated with the Lake Abitibi reference chronology for the period 1848–1995 (CL2, $r = 0.669$; CL3, $r = 0.643$; RC3, $r = 0.580$; RC4, $r = 0.700$; and RC5, $r = 0.638$). The chronologies showed similar patterns during the pre-damming period: relatively high index values around 1860, followed by reduced growth in the 1870s, and a distinct growth reduction prior to 1907 (Figs. 5*b*–5*g*). Few significant normalized departures of the riparian series from the reference chronology were recorded before 1915 (Fig. 6).

During the CFD operational period (1915–1921), all riparian chronologies showed growth reductions in 1916 and 1919 (Figs. 5*c*–5*g*). The similar pattern obtained for the Lake Abitibi and Lake Duparquet reference sites (Fig. 5*b*) suggests that these abrupt growth reductions were not caused by flooding. In addition, growth reductions of the late 1910s were not as important as those that occurred in the late 1840s or around 1907, during the pre-damming period. The riparian series even showed positive normalized departures relative to the reference chronology, particularly in 1919 (Fig. 6).

After the second damming of the lake in 1921, ring-width indices of all chronologies increased considerably and remained at high values compared to the pre-damming period (Fig. 5). The growth rise lasted until the 1930s at the reference site, whereas it continued until the 1940s and was more pronounced at that riparian sites. Significant negative departures from the reference chronologies were distinctly more common after the second damming of Lake Abitibi in 1921 than during the pre-damming period (Fig. 6). Positive deviations were most frequent around 1940 and in the late 1950s, whereas peaks of negative departures were observed around 1930 and after 1985. Recent negative departures were particularly pronounced for the drought sensitive rock outcrop chronologies (Figs. 6*a*–6*c*) that all experienced a decreasing growth trend (Figs. 5*c*–5*e*) in contrast to the Lake Abitibi reference chronology and clay chronologies that showed growth increases. Notably, the Lake Duparquet reference chronology (from xeric sites) showed a growth decrease in recent years.

Pearson's correlations between the Lake Abitibi reference chronology and each of the five riparian chronologies were mostly significant and showed similar variations (Fig. 7).

Fig. 3. Mortality of eastern white cedars bordering Lake Abitibi (n = 76). Filled bars indicate exact mortality dates, whereas grey bars represent minimum year of death (owing to missing outermost rings). Vertical broken lines indicate the dates of construction of the Couchiching Falls dam (CFD) and Twin Falls dam (TFD), in 1915 and 1922, respectively.

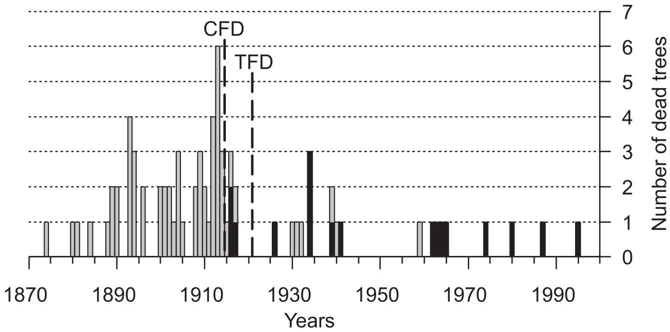
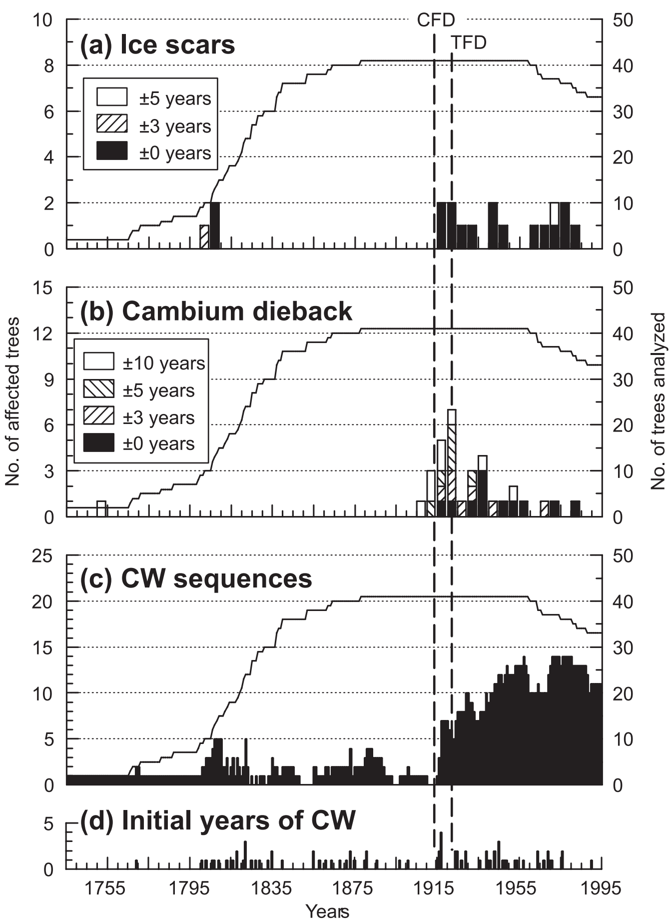
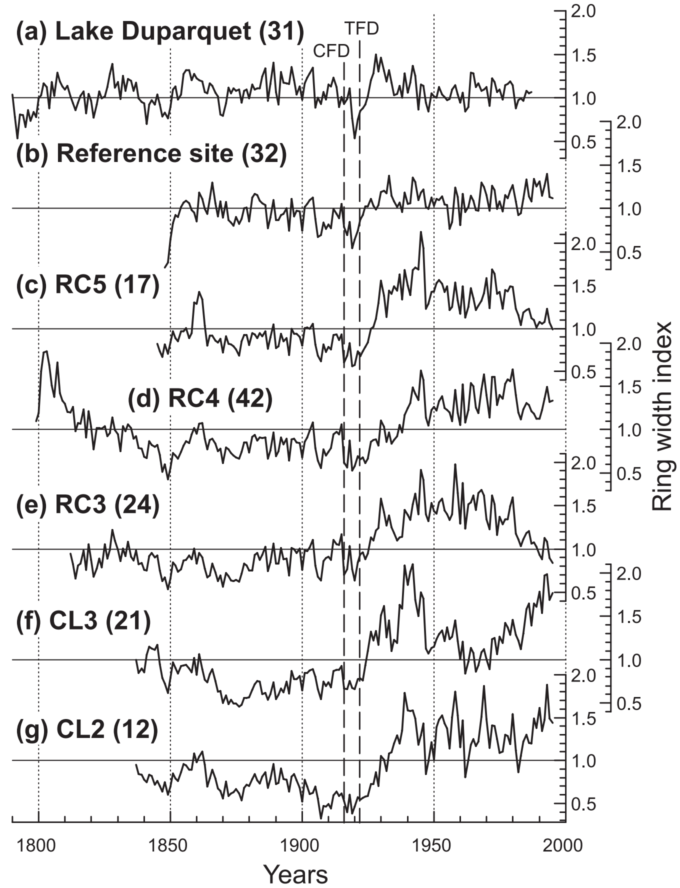


Fig. 4. Frequency distributions of (a) ice scars in 5 year classes, (b) partial cambium dieback (year of the last complete tree ring) in 5 year classes, and (c) sequences and (d) initial year of compression wood for a subset of trees covering the period 1885–1945 (n = 41). Dating accuracy is given for ice scars and cambial dieback. CFD, Couchiching Falls dam; TFD, Twin Falls dam. Line graphs show the number of trees analyzed.



The generally high coefficients in the late 19th and early 20th centuries were followed by a decrease to lower values in the 1940s, reflecting the diverging growth trend of the riparian chronologies relative to the reference chronology in the 1930s and 1940s.

Fig. 5. Standard eastern white cedar chronologies from (a) xeric sites from Lake Duparquet, (b) Lake Abitibi reference site, and (c–g) Lake Abitibi riparian sites. The graphs only show those parts of the curves that are composed of at least 10 series. Maximum number of series is indicated between parentheses. CFD, Couchiching Falls dam; TFD, Twin Falls dam.



Mean sensitivity of the six standard chronologies, ranging from 0.13 to 0.18 (Table 1), was relatively low but similar to values obtained for other eastern white cedar chronologies in the area (Archambault and Bergeron 1992; Tardif and Bergeron 1997a). Mean annual sensitivity did not show any long-term trend, but rather three isolated peaks around 1898, 1920, and 1960, and relatively low values in the mid 1850s, the 1920s, and the early 1950s (Fig. 8a). Mean annual sensitivity values were slightly higher for riparian series compared with the Lake Abitibi reference chronology, although trends were similar (Figs. 8b–8c). Year-to-year variation was particularly high between 1915 and 1945 for the rock outcrop chronologies and for the periods 1860–1900 (CL3) and 1915–1965 (CL2) for the clay chronologies.

Discussion

Tree response to increased water level

According to historical data sources, the water level of Lake Abitibi prior to 1915 was ca. 1.2 m lower than today. Thus, the older eastern white cedars that form the present-day forest limit were at that time in the forest interior and

Fig. 6. Relative frequencies of significant normalized positive and negative departures from the Lake Abitibi reference chronology for the five riparian chronologies. CFD, Couchiching Falls dam; TFD, Twin Falls dam.

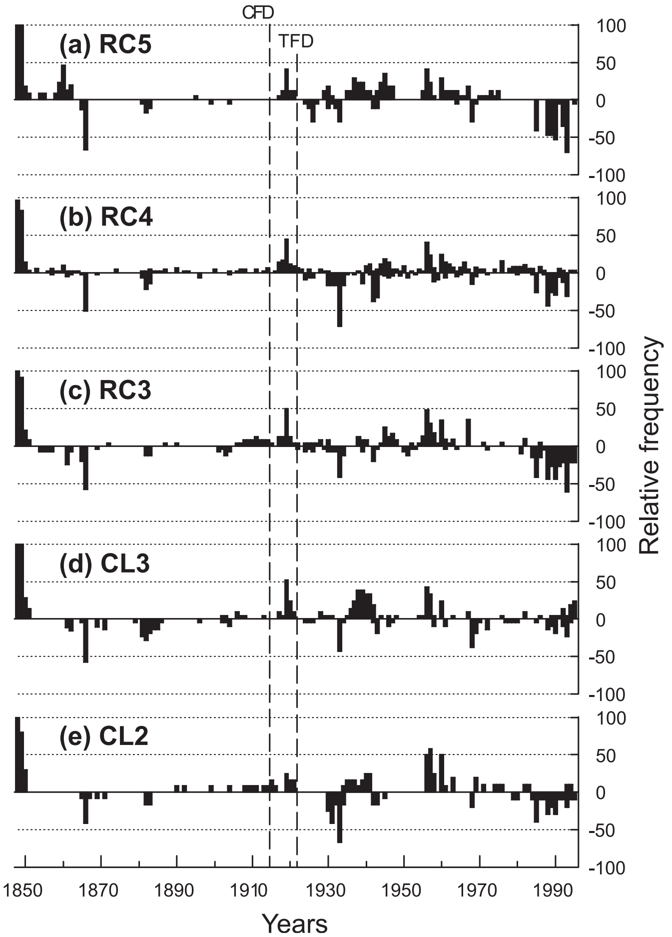
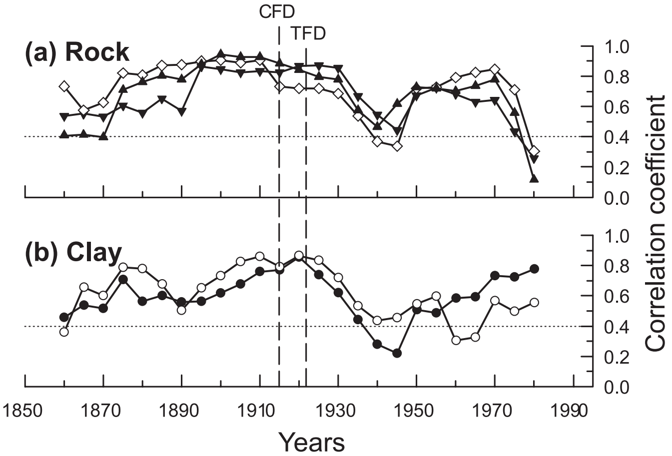


Fig. 7. Pearson's correlations between the Lake Abitibi reference chronology and each of the five riparian chronologies. The correlation coefficients were calculated using 25-year segments lagged by 5 years. The curves are grouped by growing substratum: rock (RC3, filled upside-down triangles; RC4, open diamonds; RC5, filled triangles) and clay (CL2, filled circles; CL3, open circles). The broken lines indicate the significance level ($P = 0.05$). CFD, Couchiching Falls dam; TFD, Twin Falls dam.



out of reach of the riparian disturbances caused by wave action and ice push. Damming of the lake in 1915 resulted in the quick death of all trees that constituted the former riparian zone, whereas the surviving trees at higher elevations were injured and tilted. This is well documented by an abrupt increase in the frequencies of ice scars, cambium dieback, and compression wood after 1915. Although relatively protected from wave action, large bays were nonetheless severely affected by erosion because of their poorly resistant clayey substrate. Unstable slopes noticed during fieldwork indicate that this process is still in progress.

Since all but one partial cambium dieback events dated from 1915 or later, and since dieback only occurred on the lake-facing side of the stems, it was assumed that the phenomenon was closely related to the increased water level due to damming. Eastern white cedar is radially sectored with respect to xylem hydraulic pathways (Larson et al. 1994), hence root loss on one side of a tree causes the subsequent death of cambium and shoots on the same side, as observed for old individuals growing on the cliffs of the Niagara escarpment in Ontario (Larson et al. 1993). The same process might have been at the origin of partial cambium mortality observed on the shores of Lake Abitibi owing to erosion of the lakeside roots.

Compared with the reference site, radial growth of the riparian eastern white cedars did not show any response to the damming of Lake Abitibi in 1915. Growth reductions recorded after 1915 reflected regional climate patterns rather than flooding stress. The limited dendrometric data available for eastern white cedar in the southern boreal forest indicate that tree-ring formation starts in late May (B. Denneler, unpublished data, 1998) to early June (Tardif et al. 2001). It therefore seems that the eastern white cedar trees growing close to the lake (50–100 cm of elevation) were still in dormancy when flooding occurred (from April to early June during the CFD period, from 1915–1922), and thus less affected than if flooding had occurred during the growing season (Broadfoot and Williston 1973; Teskey and Hinckley 1977).

Tree response to delayed and lower spring floods

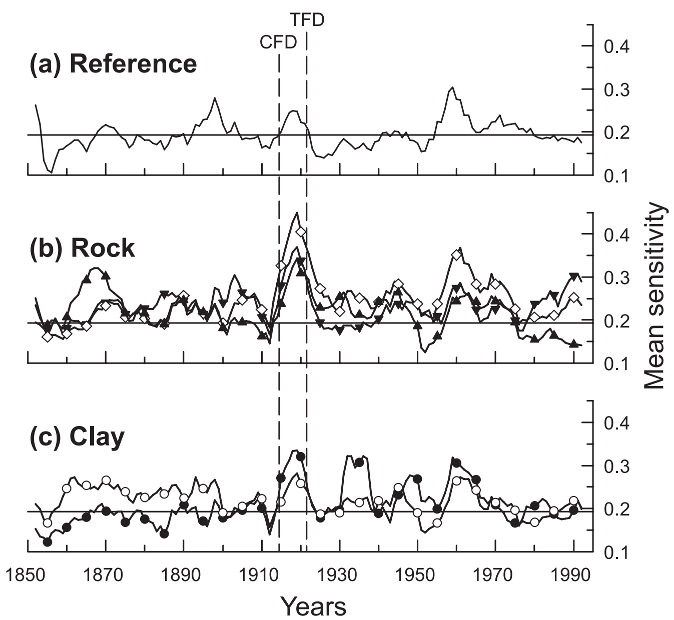
The main consequence of the replacement in 1922 of the CFD by the TFD was an alteration of the hydrological regime characterized by delayed and lowered maximum spring water levels and relatively high water tables during summer and autumn. Riparian eastern white cedars, however, did not show any growth response to these changes. Lower peak water levels might explain the absence of a signal in mortality and disturbance-related growth response. Compared with the Lake Abitibi reference chronology, the riparian chronologies registered a slightly delayed growth release in the 1920s, temporarily lowered correlation coefficients, and a higher number of trees with significant growth departures. However, these differences did not change along the elevation gradient, as would be expected if they were related to flooding. Thus, the differences between the reference and the riparian sites were rather due to the relative change in position of the trees from the closed forest interior to the lakeshore forest limit after destruction of the former riparian forest following damming in 1915. The sustained increase in growth rate of the riparian trees, starting in the 1920s, could

Table 1. Descriptive statistics of the six Lake Abitibi eastern white cedar ring-width chronologies.

		Riparian sites*				
	Reference site	CL2	CL3	RC3	RC4	RC5
Chronology length	1834–1995	1808–1995	1806–1995	1750–1995	1637–1995	1796–1995
Number of trees / radii	18/32	6/12	11/21	12/24	23/42	9/17
Missing rings (%)	0.02	0.05	0.00	0.09	0.04	0.00
Mean ring width (mm)	0.76	0.76	0.54	0.55	0.47	0.66
Mean sensitivity	0.13	0.14	0.13	0.14	0.18	0.13
Standard deviation	0.19	0.36	0.39	0.30	0.36	0.34
First-order autocorrelation	0.61	0.86	0.89	0.82	0.80	0.88
Common interval analysis (1885–1945)						
Number of trees / radii	18/32	6/12	11/21	12/24	22/41	9/17
Signal-to-noise ratio	10.60	4.37	13.98	4.27	5.55	8.54
Variance in first PCA vector (%)	43.41	58.79	62.55	40.62	36.14	55.47
Expressed population signal	0.914	0.814	0.933	0.810	0.847	0.895
Intercore correlation	0.38	0.46	0.57	0.28	0.21	0.51
Intertree correlation	0.37	0.42	0.56	0.26	0.20	0.49
Intratree correlation	0.61	0.85	0.80	0.76	0.72	0.92

*The five chronologies are combinations of soil (CL, clay; RC, rock) and elevation classes (2, 50–100 cm; 3, 100–150 cm; 4, 150–200 cm; and 5, 200–250 cm).

Fig. 8. Mean annual sensitivity curves for the Lake Abitibi reference and riparian chronologies. The curves for the riparian sites (*b* and *c*) are grouped by growth substratum: rock (RC3, filled upside-down triangles; RC4, open diamonds; RC5, filled triangles) and clay (CL2, filled circles; CL3, open circles). The curves were smoothed using a running mean of 7 years. To ease comparison, the horizontal line in all three graphs represents the mean value of the reference site (0.193). CFD, Couchiching Falls dam; TFD, Twin Falls dam.



thus be explained by increased light for trees now located at the margin of the lake. The absence of any response in radial growth to flooding, in spite of the delayed high water levels, might be explained by the relatively short-lasting inundations that did not affect radial growth (Broadfoot and Williston 1973; Teskey and Hinckley 1977; Mitsch and Rust 1984).

Reconstruction of natural water level increases

Since radial growth of riparian eastern white cedars did not clearly reflect the abrupt 1.2 m rise in the water level of Lake Abitibi in response to the 1915 damming, ring-width measurements of this common, but quite complacent, species would be inefficient to reconstruct climate-driven long-term water level increases of natural, unregulated lakes. Indeed, the relatively low magnitude and speed of a natural water-level rise compared with damming of a reservoir such as Lake Abitibi results in a noisy trend owing to year-to-year water level fluctuations. Moreover, the root systems of affected trees have time to adapt to the slowly changing environmental conditions, thus tempering the growth response.

On the other hand, the use of growth responses to riparian disturbances could successfully be used to reconstruct water level increases, because death, wounding, and tilting represent clear and distinct events that are relatively easy to date. Indeed, frequency and maximum height of ice scars have been used to reconstruct long-term changes of high lake levels over the last centuries in boreal Quebec (Bégin and Payette 1988, 1991; Payette and Delwaide 1991; Tardif and Bergeron 1997*b*; Bégin 2000*a*, 2000*b*, 2001).

Factors controlling the lower limit of the white cedar fringe

Analysis of the growth responses of riparian eastern white cedars to the first damming of Lake Abitibi in 1915 revealed a strong disturbance signal. The intensified disturbance regime resulted in tilting, wounding, and uprooting of several trees, whereas the radial growth patterns did not provide clear evidence for a flooding stress. However, because of missing bark and the outermost tree rings on the dead trees, as well as the loss of low-elevation trees that were already decomposed or had been displaced at the time of sampling, determination as to whether the cause of the mortality peak of ca. 1915 was attributable to excessive flooding stress or to mechanical disturbances, was prevented. The latter explanation seems more probable, however, because (*i*) eastern white cedar tolerates extremely humid conditions (Johnston

1990) and can survive prolonged inundation, and (*ii*) trees sampled at slightly higher elevations (50–100 cm) did not register any flooding stress. Consequently, although eastern white cedar can withstand high levels of flooding stress and thus colonize sites very close to the lake, the combined effects of wave action and ice push (reaching high intensities given the large size of Lake Abitibi), keep the lakeshore limit at higher elevations, where flooding does not affect radial growth. Therefore, we suggest that the shoreline limit of *Thuja occidentalis* is a mechanical rather than a physiological limit. Thus, the conceptual view that flooding tolerance represents the prime factor in the ordination of tree species along a flood-stress gradient (Beschel and Webber 1962; Bell and Del Moral 1977; Robertson et al. 1978; Metzler and Damman 1985) should be revised as it implies that the lower limit of species reaching the shoreline is necessarily a physiological limit. This might apply to large river floodplains in southern areas where periods of high water levels generally occur during the growing season, and ice push, as well as wave action are mostly absent, but not in northern boreal areas, where mechanical disturbances play a key role on exposed shores, whereas flooding-related physiological stress is limited to protected bays.

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