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FLOODING EFFECTS ON TREE-RING FORMATION OF RIPARIAN EASTERN WHITE-CEDAR (*THUJA OCCIDENTALIS* L.), NORTHWESTERN QUEBEC, CANADA

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ABSTRACT

Tree-ring formation of eastern white-cedar (*Thuja occidentalis* L.) at a boreal lake in northwestern Quebec, Canada, was monitored using manual band dendrometers to (i) retrace cambial activity phases, (ii) evaluate the effects of flooding on radial growth, and (iii) analyze the relationships with meteorological factors. The daily circumferential activity of four trees at each of two sites, a riparian and an upland site, was recorded during the growing season of 1996, a year with an extreme spring flood. First cambium cell divisions occurred near June 9, followed by a distinct and sustained upward trend in the stem basal area until mid-July that reflected the earlywood formation. The strongly synchronous circumferential activity at both sites suggests no adverse flooding effect on growth of the riparian trees, which is explained by the rapid retreat of the water just before growth initiation in early June. The following month until mid-August was characterized by strong short-term fluctuations caused by alternating drought and rain periods and a slight downward trend of the basal area for six of the eight banded white-cedars. The dendrometers of two trees, the closest to the lake, showed a slight upward trend probably reflecting latewood formation. Pearson correlation with meteorological data indicated that precipitation was positively related to the daily changes in basal area of all trees except during the period of earlywood formation, which probably resulted from the high soil moisture after spring snow-melting. Mean and minimum air humidity were positively related and maximum temperature negatively related to the daily variations in stem circumference during the whole monitoring period, emphasizing the importance of the internal water status on stem size.

Keywords: Dendrometer, flood, basal area increment, Lake Duparquet, eastern white cedar, tree growth phenology, water table.

RÉSUMÉ

La formation des cernes annuels du cèdre blanc (*Thuja occidentalis* L.) en marge d'un lac boréal du Nord-ouest du Québec au Canada a été suivie au moyen de dendromètres circonférentiels manuels. L'étude avait pour but de (i) retracer les phases d'activité cambiale, (ii) d'évaluer les effets des inondations sur la croissance radiale et (iii) d'analyser l'influence de certains facteurs météorologiques. Les variations diurnes de la croissance ont été suivies chez quatre arbres dans deux sites, l'un en milieu riverain, l'autre supra-riverain durant la saison de croissance de 1996, une année de forte inondation. Les premières divisions cellulaires du cambium se sont produites le 9 juin et elles ont été suivies d'un accroissement soutenu de la surface terrière des tiges jusqu'à la mi-juillet, ce qui correspond à la formation du bois initial. Les dendromètres révèlent une croissance synchrone des arbres des deux sites, ce qui indique que l'inondation n'aurait que peu d'effets sur la croissance des arbres inondés. Cette absence de réponse pourrait être causé par l'abaissement du niveau du lac avant le déclenchement de la croissance en juin. À partir de la mi-juillet jusqu'au début d'août, la croissance connaît des variations reliées surtout à des épisodes d'assèchement des sols alternant avec des périodes de pluie. En août le

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[†] This paper was submitted in memory of Bernhard Denneler who died in January 2007.

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taux de croissance a considérablement diminué; il s'agit de la période de formation du bois final. Les corrélations de Pearson avec des données météorologiques suggèrent que les précipitations sont le principal facteur influençant la croissance durant la formation du bois final, alors qu'en période de formation du bois initial, le sol demeure humide et les précipitations ont peu d'effet. La moyenne et le minimum journaliers de l'humidité de l'air sont positivement corrélés à la croissance, alors que la température maximale journalière a une relation inverse avec l'activité des dendromètres. Il apparaît clairement que l'eau est le facteur prédominant de la croissance des arbres dans le milieu étudié.

Mots clés: Dendromètre, inondation, surface terrière, Lac Duparquet, cèdre blanc, phénologie de la croissance, nappe phréatique.

INTRODUCTION

Flooding usually represents a severe stress to trees, which results in reduced annual radial growth and, if inundation is prolonged or chronic, in death for almost all tree species (Broadfoot and Williston 1973; Tang and Kozlowski 1982; Kozlowski *et al.* 1991). However, the growth response highly depends on flood characteristics, species tolerance and tree size (Kozlowski 1984). Temporary inundation can have no effect at all on growth (Green 1947; Johnson and Bell 1976; Mitsch and Rust 1984) or even increase radial increment if flooding is of short duration or occurs during the dormant period (Broadfoot and Williston 1973; Teskey and Hinckley 1977; Kozlowski *et al.* 1991). Nevertheless, growth response of riparian trees to flooding was successfully used to reconstruct historical changes in lake levels (Stockton and Fritts 1973; Bégin and Payette 1988; Bégin 2000).

Although flooding may not systematically affect ring widths, rate of wood-cell divisions may be affected, creating intra-annual secondary growth variations in flooded trees. Studies focusing on the effects of flooding on intra-annual radial growth, *i.e.* on tree-ring formation, are rare. Conner *et al.* (1981) and Conner and Day (1992) detected distinct growth reduction from inundation stress in swamp trees growing under different flooding regimes. In contrast, Langdon *et al.* (1978) found that diameter increment of a typical swamp species was positively related to higher water levels. However, these studies were done in the southern USA with a much more temperate climate relative to the higher latitudes of the boreal forests where the flooding effects on the tree-ring formation might differ.

In this study, we monitored the circumferential activity of eastern white-cedar (*Thuja occidentalis* L.; Farrar 1995) bordering a natural lake in the southwestern boreal area of Quebec, Canada. Spring of 1996 was characterized by extremely high water levels that inundated the riparian trees up to 1 m, enabling us to analyze the effect of flooding on the intra-annual tree-ring formation of white-cedar with the perspective of using flood-induced changes in ring width of this common species for the reconstruction of past floods. Because trees are in dormancy when spring floods occur, they may not react to water surplus. By studying their intra-annual growth in relation to a flooding event, we expect obtaining information on the processes by which a response may register in tree-rings increments. We compared the daily circumferential activity of shoreline trees flooded in spring 1996 to that of nearby upland trees not affected by flooding. We hypothesized that spring flooding would delay the initiation of the cambial activity and, hence, the formation of the first tracheids relative to the upland trees. In summer, however, the riparian trees could eventually make up for the later start of the growth period by benefiting from elevated soil moisture that prevents drought-caused slowdown or even cessation of cambial growth. As a consequence, flooding and drought may induce changes in both total secondary growth or changes in earlywood to latewood ratios. We focused on three objectives to (i) delimit the growing period of white-cedar, (ii) isolate an eventual flooding effect by comparison of the circumferential activity between the two sites, and (iii) determine the meteorological factors influencing the daily circumferential activity.

METHODS

Study Site

Lake Duparquet (48°28′N; 79°17′W) is a large (~40 km^2) water body located about 600 km northwest of Montreal, Quebec. The slopes of the surrounding rolling, rocky hills are mainly covered by glacial tills, which are often overlain by proglacial lacustrine clay deposits in the landscape depressions (Bergeron *et al.* 1983; Veillette 1994). Lake Duparquet has never been regulated and, hence, has a natural hydrological regime.

Cold winters and warm summers characterize the continental climate of the region. From 1971 to 2000, mean annual temperature and precipitation at La Sarre, the closest meteorological station (about 40 km to the north), were 0.7°C and 890 mm (Environment Canada: http://climate.weatheroffice.ec.gc.ca/climate_normals/), respectively. Mean monthly temperatures vary between −18.2°C (January) and 16.9°C (July), and snowfall amounts to 28% of the total annual precipitation. It is not unusual for snowpacks to reach 1 m in depth and to persist into early May. Mixedwood forests dominate the area of Lake Duparquet, the late successional stages being mainly composed of balsam fir (*Abies balsamea* (L.) Mill.) and white birch (*Betula papyrifera* Marsh.), which are accompanied by white spruce (*Picea glauca* (Moench) Voss) and eastern white-cedar (Bergeron and Bouchard 1983). The latter species occurs over a wide range of soil moisture contents (Collier and Boyer 1989) and develops a shallow, widespread root system (Johnston 1990). Along the shores of Lake Duparquet, the fire-sensitive white-cedar is very common and can attain ages up to *ca.* 900 years (Archambault and Bergeron 1992; Denneler *et al.* 1999).

The monitoring site was selected on the northern shore of Lake Duparquet. This location has never been affected by human impacts. Several healthy eastern white-cedar trees were found. Trees were selected to respect the minimum size of at least 15 cm in diameter at breast height (DBH = 1.5m) within and above the riparian zone and their growth compared to assess flooding effects. The topography of the monitoring site forms a slight terrace within the riparian zone whose slope falls relatively steeply down to the lake (Figure 1). The forest established after the last fire dating at A.D. 1760 (Bergeron 1991; Dansereau and Bergeron 1993), and the species found surrounding the site were trembling aspen (*Populus tremuloides* Michx.), white birch, and white spruce in the open upper canopy with white-cedar and balsam fir in the sub-canopy.

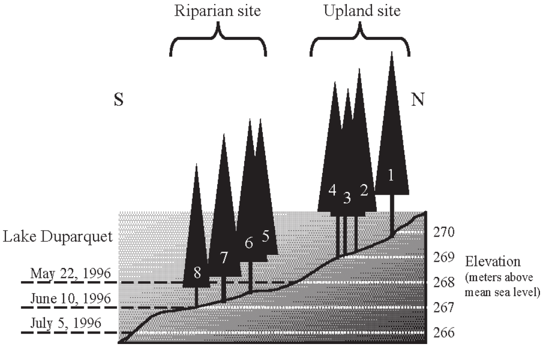

Figure 1. Design of the intra-annual circumferential activity monitoring by manual band dendrometers on eastern white-cedar. Four upright trees were chosen at each of two sites, the upland site at least 1 m above the maximum high water level (numbers 1 to 4), and the riparian site at the immediate shore (numbers 5 to 8), respectively. The water level of Lake Duparquet is indicated for three dates.

Dendrometer and Environmental Data

Monitoring the stem radial activity by band dendrometers is non-invasive and furnishes data with high temporal resolution (Kozlowski 1971; Telewski and Lynch 1991; Schweingruber 1996). In spring 1996, we thus installed manual band dendrometers at breast height on the smoothed stems of four upright eastern white-cedars (D5–D8) within the riparian zone close to the shore (subsequently called the riparian site; Figure 1) and on the same number of trees that were a few meters uphill and at least 1 m above the maximum high water limit (D1–D4; subsequently called the upland site). The upland site is characterized by soils that were not disturbed by water. Elevation above water level and distance from the shoreline in early July 1996 were <170 cm and <10 m for the riparian group of trees, but >300 cm and >16.5 m for the upland group (Table 1). The stem diameters ranged from 15.6 to 38.0 cm DBH

Table 1. Descriptive statistics of the dendrometer trees at the riparian and upland sites.

	Dendrometer Trees									
	Upland Site					Riparian Site				
Statistic	D1	D2	D3	D4	Mean ± SD	Mean ± SD	D5	D6	D7	D8
Elevation (cm)[a]	394	317	310	306	331.8 ± 41.7	136.8 ± 32.8	163	161	130	93
Distance (m)[a]	21.0	18.0	17.0	16.5	18.1 ± 2.0	8.0 ± 2.3	10.0	9.5	7.5	5.0
DBH (cm)	23.1	16.5	19.2	18.4	19.3 ± 2.8	23.6 ± 9.9	19.9	20.9	38.0	15.6
Establishment year	~1890	~1825	~1820	~1820	1839 ± 34.2	1835 ± 71.9	~1870	~1850	~1730	~1890
Sapwood width (mm)	18.3	11.9	10.0	9.0	12.3 ± 4.2	14.5 ± 1.3	14.1	15.9	15.1	13.0
Sapwood rings (n)	17	15	18	21	17.8 ± 2.5	20.8 ± 3.2	18	23	24	18
Flooding depth (cm)[b]	—	—	—	—	—	—	~30	~30	~70	~100
Flooding end	—	—	—	—	—	—	May 30	May 30	June 4	June 10

[a] with respect to the water level of July 5, 1996 (266.08 m a.s.l.).
[b] on May 22, 1996.

(diameter at breast height) and the approximate establishment date of the trees from *ca.* 1730 to *ca.* 1890; both mean size and age were slightly higher at the riparian site. The sapwood width varied between 9.0 and 18.3 mm and was composed of 15 to 24 tree rings (Table 1).

We used the manual band dendrometer from the *Agricultural Electronics Corporation* (AEC http://www.phytogram.com/manualband.htm), which measures variations of tree stem circumference using a steel band wrapped around the trunk and attached to a micrometer. The resolution of the readings was 10 µm. In order to increase reliability, three consecutive measurements were done by each dendrometer, and the data of the three readings were averaged. The daily measurements were always done at approximately the same time, between 16 and 19 h (EDT), to minimize the influence of diurnal stem shrinkage and swelling of the tree stems caused by transpiration water loss and water uptake (Daubenmire 1949; Kozlowski and Winget 1964; Kozlowski 1971; Herzog *et al.* 1995). The dendrometer readings were done in the late afternoon, at the expected time of the day when circumferential fluctuations are reduced.

The daily circumference increment data were compared to both hydrological and meteorological variables. From spring to autumn 1996, the daily water level fluctuations of Lake Duparquet (Figure 2) were measured manually using a calibrated stick driven in the lake bottom. Records of the fluctuations in spring and summer water levels of this lake exist only for 1989 to 1991 and 1996 to 1998 (Figure 2) (Tardif and Bergeron 1997). Water levels were measured using the same procedure. The spring flood of 1996 was by far the most extreme on record and represented an extraordinary event as revealed by the partial inundation of several buildings close to the lakeshore.

To determine depth of the groundwater table at the two monitoring sites, we dug a hole close to dendrometer trees D6 (riparian site) and D3 (upland site) and installed a 1-m-long piece of a drainage tube of 10-cm diameter in a vertical position. Before installing the drainage tubes, we measured the lower limit of the tree main roots horizon at *ca.* 15 cm (upland site) and *ca.* 20 cm (riparian site). Some roots, however, were observed down to 60 cm. The soil at both sites consisted of glacial till, but the riparian site contained more clay. Elevation above the lake level of the dendrometer trees and the upper end of the two drainage tubes was surveyed with a theodolite (WILD-T2, Heerbrugg, Switzerland). Elevation, lake level, and groundwater table data were transformed into elevation above sea level using the reference point 78L235 of Canada's vertical control data set (Geodetic Survey of Canada 1986). Hourly data of air temperature and air humidity were taken in 1996 from a weather station on Heron Island in Lake Dupar-

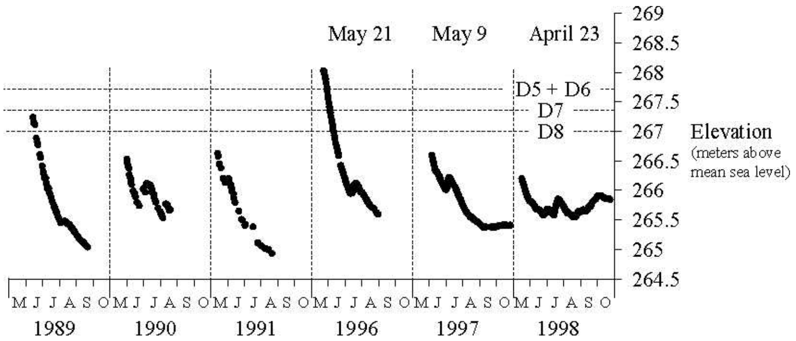

Figure 2. Seasonal water level fluctuations of Lake Duparquet between May and October of 1989 to 1991 (data from Tardif and Bergeron 1997) and 1996 to 1998. The first four years are manual records, whereas 1997 and 1998 represent daily means of a hydrograph placed on the bottom of the lake. The horizontal dashed lines indicate the position of the four banded eastern white-cedars from the riparian site (D5–D8). The date of the first ice-free day is given for 1996 to 1998.

quet, *ca.* 7.5 km southeast of the dendrometer sites. Because the precipitation gauge did not work correctly in 1996, we acquired the precipitation data from another weather station located at Rapide-Danseur, *ca.* 6.5 km to the north.

Data Treatment and Analysis

Stem circumferences, water level of Lake Duparquet, and depth to groundwater were recorded daily from mid-May to mid-August 1996 (except during four days in June) and sporadically during the second half of August (5 measurements in 2 weeks). The dendrometer data were corrected for thermal expansion and contraction of the Invar band (1μm m^{-1} °C^{-1}) and the brass tube (3μm °C^{-1}) (AEC http://www.phytogram.com/manualband.htm). All dendrometer, hydrological, and meteorological data were checked for outliers caused by lightning, animals, or other unknown reasons, but no aberrant values were detected. Because each dendrometer band needed some time after installation to adjust before it could accurately reflect changes in tree circumference, the measurements of the first eight days, during which the circumference decreased almost continually, were dropped. Thus, the analyzed measurement series start at May 31.

We transformed the daily circumference increments into basal area (BA) changes to allow comparison between the uneven sized trees (Conner *et al.* 1981; Conner and Day 1992) and set the value of June 9 as the starting point (Figure 3A). Furthermore, we transformed the tree BA increment curves into percentage to minimize the effect of age, vigor, and competition (Figure 3B; Daubenmire and Deters 1947; Tardif *et al.* 2001) and calculated the daily mean percentages for the two monitoring sites (Figure 3C).

Before assessing relationship between the trees' circumferential changes and the meteorological factors, we removed the intrinsic growth trend of the cumulative BA curves using first-order differencing (Chatfield 1989), which simply consists of a difference between successive values to obtain daily BA changes (Bormann and Kozlowski 1962; Tardif *et al.* 2001). However, the resulting first-order differences normally have unstable mean and variance with time caused by changes of both growth rates and swelling/shrinkage conditions during the growing season (Tardif *et al.* 2001). Also, biological response to the same environmental variable may change during the year as revealed by separate dendroclimatic analyses of earlywood and latewood chronologies (*e.g.* Tardif 1996). We arbitrarily divided the daily BA change series of the eight trees into three phases: beginning of tree growth to maximum BA (June 9 to July 15), mid-growth period until the start of growth rate decrease (July 16 to August 1), and period of growth rate decrease (August 2 to August 17). For each phase, Pearson's correlation coefficients were calculated between the tree's daily BA changes and the meteorological variables air temperature,

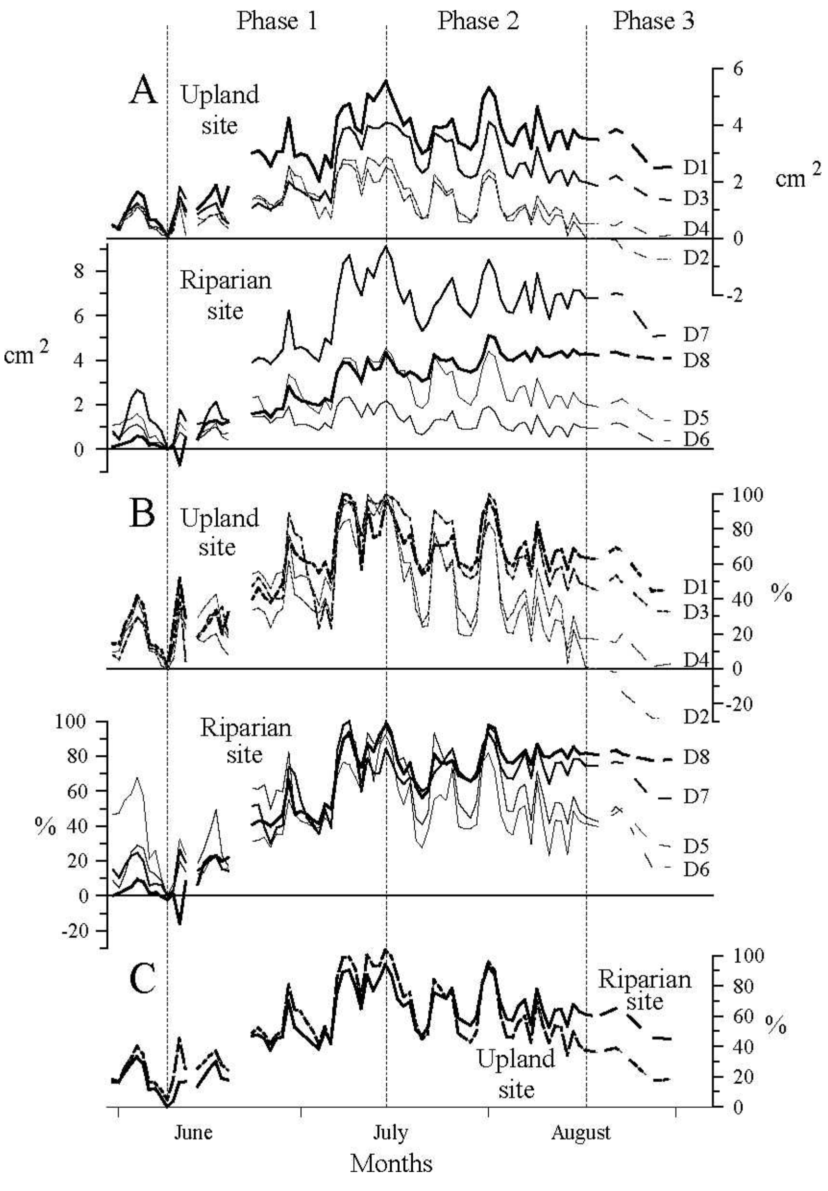

Figure 3. Daily basal area (BA) increment curves for the four eastern white-cedar trees at the upland (D1–D4) and riparian sites (D5–D8) from May 31 to August 31, 1996. Absolute (A) and relative (B) cumulative daily BA increment are presented for each tree separately but grouped by site. Mean cumulative daily BA increment in percentage (C) is given for each of the two sites. The vertical dashed lines delimit the three predetermined phases of cambial activity discussed in the text (June 9 to July 15, July 16 to August 1, and August 2 to17, respectively).

air humidity (for first-order differences of the daily maxima, means, and minima), and rainfall (daily sums). To better highlight the main meteorological factors associated with the daily BA changes, principle component analysis (PCA) was conducted on correlation coefficients between all trees per period and meteorological factors using the program CANOCO 4.02 (ter Braak and Smilauer 1998). The meteorological variables entering the ordination were restricted to those with at least six significant correlation coefficients.

Ring-Width Analysis

To better evaluate if flooding in 1996 influenced radial growth of riparian eastern white-cedar, ring widths of the monitored trees from the two sites were compared. Therefore, in spring 1997 two cores were taken perpendicularly at breast height on each tree equipped with a dendrometer. The cores were mounted on wooden supports and sanded. The ring widths were measured to the closest 0.001 mm with a Velmex UniSlide micrometer. Correct dating of the tree rings was verified by visual and statistical cross-dating applying the programs ITRVIEW (Grissino-Mayer *et al.* 1996) and COFECHA (Grissino-Mayer 2001). The software ARSTAN (Cook and Holmes 1986) was used to eliminate the low-frequency variations in the measurement series by 32-year spline detrending and to build tree chronologies by averaging the two index series of each tree. Pearson's correlation coefficients were calculated between each pair of tree chronologies using the routine MAT of the Dendrochronology Program Library (Grissino-Mayer *et al.* 1996).

Response in annual growth to flooding was analyzed for eight years with extreme spring high water levels of Lake Duparquet. Beside 1996, the years 1922, 1934, 1947, 1959, 1976, 1979, and 1984 were considered. In these years, Lake Duparquet attained the highest spring water levels in the 20th Century as evidenced by an ice-scar chronology (Tardif and Bergeron 1997), and it was supposed that the banded riparian trees were flooded as in 1996. The individual ring-width index of the year preceding the spring flood was subtracted from that of the flooding year and the resulting differences were subsequently averaged over all trees from the same site. The between-site differences of this mean growth response to flooding were then tested for significance using the GLM Repeated Measures procedure of SPSS 11.5 (SPSS Inc., Chicago, Illinois).

RESULTS

Basal Area Increment (BA)

The short-term fluctuations of the cumulative daily BA increment curves of the eight eastern white-cedars were very similar, but their seasonal trends differed (Figure 3A). For the upland site until August, the rank order of the BA corresponded to the tree's diameter (Table 1); D1 had the greatest increase and D2 the least. But at the riparian site, D8, the smallest tree, accumulated relatively more basal area than the larger trees D5 and D6. As the growing season progressed, the curves of the two trees that were flooded until June 10, 1996 (D7 and D8) diverged from the falling curves of the less flooded trees D5 and D6 (Figure 3A, B).

Several distinct periods of BA increment were common to both sites (Figure 3C). An initial BA increase was observed during the first few monitoring days followed by a decrease to values less than those noted on May 31, the designated starting point. The period from June 9 to July 15 was characterized by fluctuating but increasing BA values at both sites, suggesting a similar growth rate. During the second half of July, both curves, but particularly that of the upland trees, decreased dramatically, recovered, decreased again, and recovered once more to values near those of July 15. Afterwards, the mean cumulative BA increment curves for the trees at the two sites started to diverge. By end of August, mean BA of the upland white-cedars had decreased to only 13% of the maximum values, whereas mean BA of the riparian trees varied around 60% before dropping to 45% in the last days of August (Figure 3C).

Relationship with Hydrological and Meteorological Data

The day after the ice on Lake Duparquet had disappeared in 1996 (May 21), all banded eastern white-cedars of the riparian site were flooded up to *ca.* 30 cm (D5 and D6), *ca.* 70 cm (D7), and *ca.* 100 cm (D8), and the stems remained flooded until May 30 (D5 and D6), June 4 (D7), and June 10 (D8), respectively (Table 1, Figure 4D). The groundwater table at the riparian site was 36 cm below the surface (267.17 m above mean sea level) when measured for the first time on June 8 (Figure 4D). Thus, the upper 20 cm, representing the main root horizon, were already aerated for

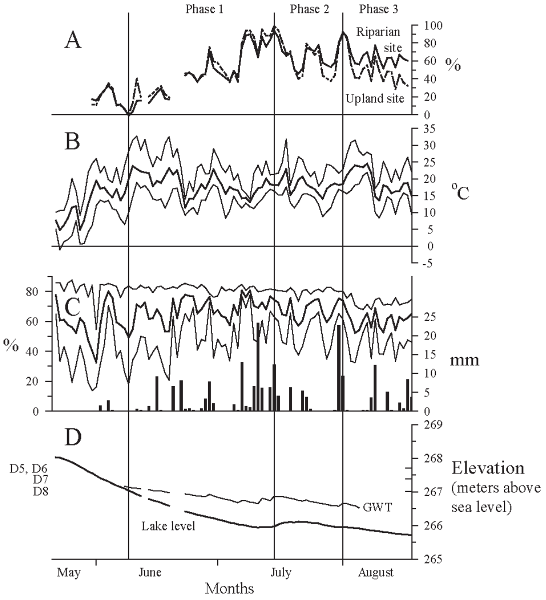

Figure 4. Comparison of the 1996 mean daily basal area (BA) increment with selected meteorological and hydrological variables. (A) Mean cumulative daily BA increment in percentage for the riparian (bold line) and the upland site (dashed line). (B) Maximum, mean, and minimum air temperature. (C) Maximum, mean and minimum air humidity (line graphs) as well as rainfall (vertical bars). (D) Water level of Lake Duparquet and depth of the groundwater table (GWT) at the riparian site, both transformed into elevation above sea level. After August 6, the groundwater level remained below 1 m (266.53 m a.s.l.). Elevation of the banded trees at the riparian site (D5–D8) is indicated. The period covered is from May 22, the second day after disappearance of the ice cover on the lake, to August 17. The vertical lines delimit the three phases of cambial activity discussed in the text (June 9 to July 15, July 16 to August 1, and August 2 to 17, respectively).

tree D6. If we assume for the other three trees the same span of time between the end of flooding and the aeration of the upper root horizon as for D6, *i.e.* about 5 days, the adverse effect of flooding should end around June 4 (D5 and D6), June 9 (D7), and June 15 (D8) for the four riparian trees. Both lake and groundwater levels had a small secondary peak in mid-July after a period of abundant rainfall (Figure 4C, D). On August 7, the groundwater level for the riparian site decreased below 1 m. At the upland site, the groundwater table was never within the 1-m deep drainage tube over the whole measurement period.

Figure 4 compares the mean cumulative daily BA increment results to the meteorological and hydrological data. The initial swelling of the stems in early June was preceded by a distinct increase in air temperature of about 10°C from 5–10°C to 15–20°C (Figure 4B) and paralleled an increase in air humidity and some rainfall (Figure 4C). This was followed by an abrupt decrease in BA during a short dry and cool period. The initiation of a period of generally increasing basal area at both sites coincided with the longest hot period of the whole summer with maximum temperatures above 30°C (Figure 4B). Towards the end of June, minimum humidity as well as precipitation started to increase. The 37 days from June 9 to July 15 were a wet period with 114 mm of rainfall (*i.e.* 12.8% of the annual mean) when 65% of the days had measurable precipitation. However, rainfall was initially low and the decreasing lake and groundwater levels suggest greater losses *versus* additions to soil moisture levels. Maximum cumulative basal area was attained around mid-July when heavy rainfall occurred almost daily. The subsequent strong fluctuations in stem circumference coincided with a series of alternating wet and dry periods (Figure 4).

Mean and minimum air humidity, maximum temperature, and precipitation were the only meteorological factors showing at least six significant correlation coefficients with the trees' daily BA changes and, hence, entered the PCA (Figure 5). The first principal component explained 67.6% and the second explained most of the remaining variation in the data (25.9%). PCA clearly separated the three time periods analyzed (Figure 5). During the early phase (June 9 to July 15), the daily BA changes correlated positively with mean and minimum air humidity as well as precipitation but negatively with maximum air temperature. However, none of the correlations with precipitation were significant ($p > 0.199$). This meteorological variable, however, became most important in controlling the daily BA fluctuations during the second phase lasting from July 16 to August 1. During the third phase (August 2 to 17), mean and minimum air humidity as well as maximum temperature exerted the strongest control on stem circumference. In spite of the diverging trends observed for this period in the curves of the cumulative mean daily BA

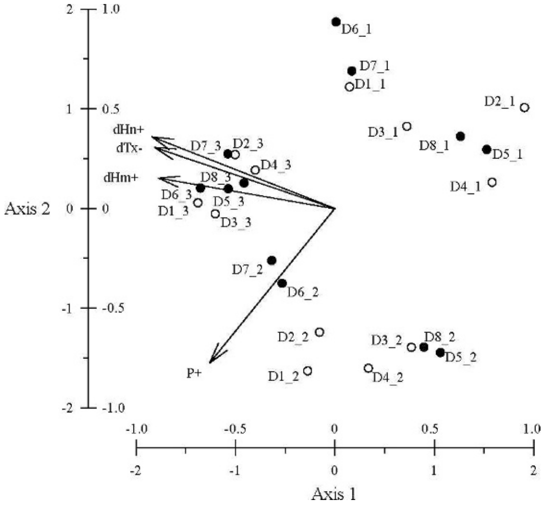

Figure 5. Principal component analysis of the Pearson correlation coefficients between the meteorological variables and the daily BA changes of the upland trees (D1 to D4: open circles) and the riparian trees (D5 to D8: filled circles). The ordination diagram shows the position of the descriptors (axes scales inward) and the trees (axes scales outward) along the first two axes. The descriptors are precipitation (P) as well as the daily changes (=first-order differences) in mean air humidity (dHm), minimum air humidity (dHn), and maximum air temperature (dTx). The plus/minus signs designate positive/negative influence of the corresponding variable. The number after each tree code refers to the three predetermined phases of cambial activity: June 9 to July 15 (1), July 16 to August 1 (2), and August 2 to 17 (3).

changes (Figure 3C), PCA did not separate the riparian from the upland trees, indicating similar growth-weather relationships at the two monitoring sites (Figure 5).

Annual Growth

The standard chronologies of the eight dendrometer trees showed similar variations (Figure 6) and all cross-correlated significantly for the period 1905 to 1998 ($p < 0.01$; Table 2). The index series of the upland trees were generally more closely related among each other (mean $r = 0.646$) than were those of the riparian site (mean $r = 0.587$). The individual nearest to the lake, D8, showed the lowest mean correlation coefficient with the other trees. Ring width of 1996, the year of monitoring, was relatively small for most of the trees (Figure 6). Growth response to flooding, based on the eight years with the highest spring water levels in the 20th Century, was significantly different between the two sites ($F = 33.217$, $p = 0.001$; Table 3). The riparian white-cedar generally showed a less extreme growth reduction or a more distinct growth release in flooding years compared to the upland trees. Flooding seems to have a positive effect on their annual growth.

DISCUSSION

Initiation of Radial Increment and Flooding

Radial movement of the tree stem is not only caused by xylem cell divisions, but also by several other influences such as diurnal and periodic swelling and shrinkage of the extensible tissues driven by changing water potential in xylem, phloem and periderm (Kozlowski and Winget 1964; Kozlowski 1971; Hinckley and Bruckerhoff 1975; Keeland and Sharitz 1993; Herzog *et al.* 1995). It is thus difficult to determine exactly the date of the onset of the xylem cell divisions by mean of dendrometer measurements. Earlier studies showed that a first swelling of the stem in early spring may be confused with the beginning of cambial growth as a result of rehydration of the living tissue (Fraser 1956; Kozlowski and Peterson 1962; Kozlowski and Winget 1964). The time lag between the recovery of cell turgor and the cambium activation of eastern white-cedar was found to vary from a few days (Bannan 1955) to several weeks (Tardif *et al.* 2001). However, our dendrometers were installed too late (end of May 1996) to register this initial swelling that starts in late April (as shown by our subsequent dendrometer readings in 1997) (Tardif *et al.* 2001).

The beginning of a general upward trend (7 of 8 trees) of the mean cumulative daily BA increment curves on June 9, 1996, suggests that cell division started that day. Such a long lasting upward trend has been recognized to reflect wood increment (Belyea *et al.* 1951; Fraser 1956). Growth seems to have started at about the same time in 1997 (Tardif *et al.* 2001). Both years were characterized by a period of high air temperatures in early June that might have activated the cambium. Several studies provided evidence for such a triggering effect of high spring temperatures

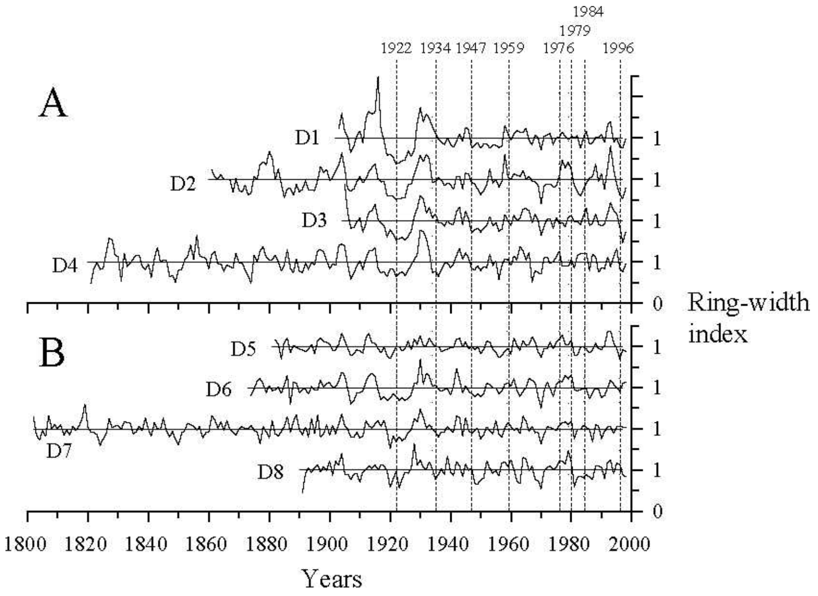

Figure 6. Standard ring-width chronologies for each of the eight dendrometer trees ordered by elevation and grouped by the upland (A) and riparian (B) site. The vertical dashed lines indicate years with extreme spring water levels of Lake Duparquet in the 20th Century.

for the initiation of radial growth (Daubenmire 1950; Turner 1956; Ahlgren 1957; Fraser 1958), whereas others point instead to the predominance of day length (*e.g.* Daubenmire 1949). Except for D8, the onset of tree growth is synchronous among riparian and upland trees, suggesting a control by air temperature and day length. Similar observations were made in southern USA where growth of swamp tree species starts independently from the flooding regime (Conner *et al.* 1981; Conner and Day 1992). However, at Lake Duparquet the sustained rise in basal increment that started in all trees was delayed for two days in D8, the tree that was flooded for the longest time (until June 10) (Figure 3A and B). This could indicate that above tolerance limits, tree growth may be delayed by flooding.

Intra-Annual Radial Increment and Flooding

Phase 1. The early period from June 9 to July 15, 1996, was characterized at both sites by a constant and almost linear upward trend with some distinct short-term decreases. This increase

Table 2. Cross-correlation matrix of the eight tree standard chronologies for the period 1905 to 1998 (n = 94 years).

	Upland Site				Riparian Site			
	D1	D2	D3	D4	D5	D6	D7	D8
D2	0.653	—						
D3	0.666	0.732	—					
D4	0.526	0.572	0.727	—				
D5	0.417	0.599	0.546	0.416	—			
D6	0.544	0.665	0.665	0.610	0.650	—		
D7	0.545	0.553	0.586	0.521	0.551	0.644	—	
D8	0.308	0.558	0.382	0.285	0.486	0.527	0.665	—
Mean	0.523	0.619	0.615	0.522	0.524	0.615	0.581	0.459

Note: All correlations were significant ($p < 0.01$).

Table 3. Annual growth response of the monitored white-cedar to major flooding of Lake Duparquet. The result of the GLM Repeated Measures procedure indicates significantly different growth response to flooding between the two sites (F = 33.217, p = 0.001). Signs indicate that growth rings were negatively or positively affected by flooding and that the riparian site was more affected (−) or less affected (+) than the upland site.

Flooding Year	Index Difference[a] (mean ± SD)		
	Upland Site (n = 4)	Riparian Site (n = 4)	Between-site Difference[b]
1922	−0.138 ± 0.042	0.028 ± 0.157	0.166
1934	−0.385 ± 0.192	−0.161 ± 0.063	0.224
1947	−0.311 ± 0.107	−0.006 ± 0.067	0.305
1959	−0.238 ± 0.235	0.030 ± 0.095	0.268
1976	0.067 ± 0.177	0.110 ± 0.047	0.044
1979	0.074 ± 0.138	0.047 ± 0.192	−0.027
1984	0.160 ± 0.106	0.020 ± 0.057	−0.140
1996	−0.308 ± 0.123	−0.093 ± 0.124	0.215
All	−0.135 ± 0.020	−0.003 ± 0.041	0.132

[a] ring-width index of the flooding year minus the index of the preceding year.

[b] mean of the riparian site minus mean of the upland site.

in BA reflected earlywood formation, which normally constitutes the main part of a conifer tree ring (Schweingruber 1988). In 1998, the earlywood-latewood transition also occurred about mid-July as evidenced by histological samples taken from the same trees (Denneler, unpublished data). Flooding probably did not influence the growth rate of the riparian trees during this phase; the relative circumferential expansion was very similar at both sites. This observation might be explained in two ways. First, dendroclimatic and other studies provide evidence that the earlywood part of a tree ring is formed principally with stored carbohydrates that were produced during the previous growing season, whereas the actual photosynthetic production is of minor importance (Wareing 1951; Fritts 1976; Tardif 1996). Second, the water retreated from the stem bases of the riparian trees no later than June 10 (at D8). Even if the soils were saturated for some more days, flooding probably occurred too early in the growing season to adversely affect the growth of eastern white-cedar, which is very tolerant of high soil moisture (Collier and Boyer 1989; Johnston 1990).

Phase 2. After mid-July, precipitation became a significant factor in controlling the stem circumference changes in both study sites, suggesting reduced soil moisture. This water depletion effect was found to be slightly stronger for the upland trees because of the closer positive association of rainfall with their circumferential variations and the more pronounced reductions of their mean cumulative daily BA increments during dry periods. The trees closest to the lake, D7 and D8, showed the least pronounced contractions during dry periods indicating a lower drought stress. They might have benefited from higher soil moisture from the prolonged flooding earlier in the year.

Phase 3. During the entire monitoring, but particularly during the third period covering the first half of August, mean and minimum air humidity were strongly positively related and maximum air temperature negatively related to the circumferential changes at both monitoring sites (Figure 5). These associations point to the importance of short-term fluctuations in stem circumference because of changes in the internal water balance. Diurnal swelling and shrinkage of the tree stems have been documented in many studies from the earliest dendrometer records to recent works (Friedrich 1897; Kozlowski and Winget 1964; Braekke and Kozlowski 1975; Kramer and Kozlowski 1979; Herzog *et al.* 1995). Shrinkage during the daytime of the elastic water conduction system and, hence, stem circumference is caused by increasing water deficit, which is created by the time lag between transpiration loss and water absorption through the roots

(Kramer and Kozlowski 1979; Hinckley and Lassoie 1981; Herzog *et al.* 1995; Zweifel *et al.* 2000). Prevailing water absorption during night, in turn, results in rehydration and, hence, a slight swelling of the stem. Changes of the internal water balance of longer durations have similar effects on stem circumference as the diurnal variations. Dry periods of several days cause a water stress resulting in stem shrinkage, particularly when drought coincided with high temperatures, whereas the contrary is observed after rainfall (*e.g.* Kozlowski and Winget 1964). The positive correlations of the daily BA changes with mean and minimum air humidity as well as the negative correlation with maximum air temperature indicate a high vapor pressure deficit during dry and hot periods. This resulted in transpiration water loss that surpassed water absorption from the soil and, hence, a contraction of the tree stems. The changing vapor content in the air could also have caused hygroscopic expansion and contraction of the bark although this effect has been shown for seedlings only and may be of minor importance (Lövdahl and Odin 1992).

The end of the seasonal cambial activity of the growing season is difficult to determine by dendrometer monitoring because of the small diameter of the latewood cells (Deslauriers *et al.* 2003). The slow but sustainable BA increment of the two trees closest to the lake between mid-July and mid-August, however, might reflect latewood formation. Histological samples taken from the monitored trees two years later showed that tree-ring formation in 1998 was completed around the same time, *i.e.* mid-August (unpublished data). The contemporary contraction of the other six stems does not mean that cambial activity of these trees had stopped but rather that the shrinkage caused by internal water stress exceeded the expansion from cell formation and elongation. It was therefore not possible to test our hypothesis that growth of riparian white-cedar benefited from a lower drought stress later in the season because of higher soil moisture. We can only indirectly deduce that there might be such a beneficial effect of flooding on growth of the riparian trees because in the years with highest spring water levels, annual growth of the riparian trees responded relatively positively to flooding compared to the upland trees. In the absence of any between-site difference of both initiation and rate of radial growth in the early growing season, this growth difference must be related to the late growing season, *i.e.* to latewood formation. It would thus be interesting to analyze the effect of flooding on the earlywood to latewood ratio of the tree rings.

CONCLUSION

We infer that the extreme spring flood of 1996 had no important adverse effect on the radial growth of riparian eastern white-cedar at Lake Duparquet. In other words, the excessive water did not exert a physiological stress on the trees. However, this does not mean that white-cedar is insensitive to water availability. Dendroclimatic analysis of the same species from xeric sites revealed that high precipitation in the early growing season has a positive effect on annual growth, whereas dry periods are negatively related to radial increment (Archambault and Bergeron 1992; Kelly *et al.* 1994). Thus, white-cedar is stressed by a lack of water, whereas excessive water at the beginning of the growing season does not seem to adversely affect its cambial growth.

This inference seems to contradict evidence for reduced radial increment caused by flooding stress observed for many species (*e.g.* Broadfoot and Williston 1973; Conner *et al.* 1981; Duever and McCollom 1987; Conner and Day 1992; Kozlowski *et al.* 1991). However, most of these studies were done south of the boreal forest where flooding generally occurs later in the year and the growing season starts earlier compared to the northern regions. In the boreal forest region, floods precede the growth period. Several studies have shown that radial growth of temporarily flooded trees does not decrease, but sometimes even increases if the flooding is of short duration or pre-dates the growing season (Broadfoot and Williston 1973; Johnson and Bell 1976; Teskey and Hinckley 1977; Mitsch and Rust 1984; Kozlowski *et al.* 1991). Nevertheless, dendroclimatic studies of black ash (*Fraxinus nigra* Marsh.) in floodplains (Tardif and Bergeron 1993) and tamarack (*Larix laricina* (Du Roi) K. Koch) in alluvial fens (Girardin *et al.* 2001) at Lake Duparquet revealed a negative impact of high spring water levels on tree growth. These two species, however, grow on lower elevations than the white-cedar trees analyzed for this study and are thus flooded for a longer period. This might explain why they had a flooding signal in their ring-width pattern.

Monitoring of eastern white-cedar by band dendrometers provided useful information about the period of cambial activity in 1996 and its control by meteorological and hydrological factors. The principal aim of this study was to evaluate how flooding in the late spring of 1996 influenced cambial activity of eastern white-cedar. Recording of the intra-annual changes in stem circumference of riparian trees did not reveal any adverse effect of flooding on the timing of growth initiation nor on the extent or duration of earlywood formation when compared to upland trees. Thus, secondary growth of eastern white-cedar was not apparently affected by flooding, which might be explained by both the early retreat of the water before growth initiation and the use of stored carbohydrates from the preceding year for the formation of the earlywood. Therefore, it might be difficult to reconstruct past floods using radial increment analysis of this species. However, further studies are needed to elucidate flooding effects on the cambial activity of riparian tree species, particularly on latewood formation that could benefit from higher soil moisture after flooding.

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