Decreased fire frequency and increased water levels affect riparian forest dynamics in southwestern boreal Quebec, Canada

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

Abstract: The relative importance of fire and flooding on the population dynamics of eastern white-cedar (*Thuja occidentalis* L.) and black ash (*Fraxinus nigra* Marsh.) was evaluated in eight old-growth riparian stands of southwestern boreal Quebec, Canada. Rising water levels and decreasing fire frequency since the end of the Little Ice Age (ca. 1850) were expected to have favoured an inland migration of the riparian forest fringe, with the flood-tolerant black ash colonizing the lower parts of the shore terraces and eastern white-cedar the upper parts. Black ash was found to be restricted to the riparian zone (<200 cm elevation), whereas eastern white-cedar trees did not occur below 100 cm above lake level. Gaps of postfire eastern white-cedar recruitment were noted in stands exposed to riparian disturbances, whereas relatively continuous recruitment occurred at protected sites. Black ash, more tolerant to flooding and ice push, invaded the shore terrace sites left vacant by eastern white-cedar. The riparian forest fringe surrounding Lake Duparquet is currently migrating upland and this trend is expected to continue as water levels continue to increase and fire frequency continues to decrease during the 21st century.

Résumé : L'importance relative de deux des principales perturbations de la forêt boréale, le feu et les crues, sur la dynamique des populations de thuya occidental (*Thuja occidentalis* L.) et de frêne noir (*Fraxinus nigra* Marsh.) a été évaluée dans huit peuplements riverains du sud-ouest de la forêt boréale du Québec (Canada). L'hypothèse était que l'augmentation des niveaux d'eau et la diminution de la fréquence de feux depuis la fin du Petit Âge Glaciaire (ca. 1850) auraient favorisé une migration vers l'intérieur des terres de la frange forestière riveraine, le frêne noir, tolérant aux inondations, colonisant les parties basses des terrasses et le thuya occidental les parties hautes. Le frêne noir était restreint à la zone riveraine (<200 cm au-dessus du niveau d'eau), tandis qu'aucun thuya occidental mature ne se trouvait sous 100 cm au-dessus du niveau d'eau. Des épisodes de faible recrutement ont été notés dans les peuplements de thuya occidental exposés aux perturbations riveraines, tandis que le recrutement était relativement continu dans les sites protégés. Le frêne noir, plus tolérant aux crues et aux poussées glacielles, a envahi les terrasses riveraines abandonnées par le thuya occidental. La frange forestière riveraine du lac Duparquet est présentement en migration vers l'intérieur des terres et la tendance devrait continuer suivant l'augmentation des niveaux d'eau et la diminution des fréquences de feu au XXI^{e} siècle.

Introduction

Forest dynamics have been recognized to be strongly influenced by natural disturbances such as fire, windstorm, ice push, insect outbreaks, and flooding (White 1979). In the boreal forest, fire is the main natural disturbance (Payette 1992), and frequent and intense crown fires generally result in a forest mosaic of even-aged postfire stands, whereas uneven-aged stands develop under less frequent and intense fire regimes (Frelich and Reich 1995). In areas characterized by severe fire regimes, fire-sensitive species are often relegated to landscape features acting as firebreaks such as wetlands, lakes, rivers, and cliff faces (Larson and Kelly 1991). For example, red pine (*Pinus resinosa* Ait.) and white pine (*Pinus strobus* L.) are restricted to such fire-protected habitats at the northern limit of their range (Flannigan and Bergeron 1998; Engelmark et al. 2000). Eastern white-cedar (*Thuja occidentalis* L.) has been shown to occur in greater abundance and to attain higher ages on lakeshores and islands (Ericsson and Schimpf 1986; Archambault and

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Bergeron 1992) as well as on cliff faces (Larson and Kelly 1991).

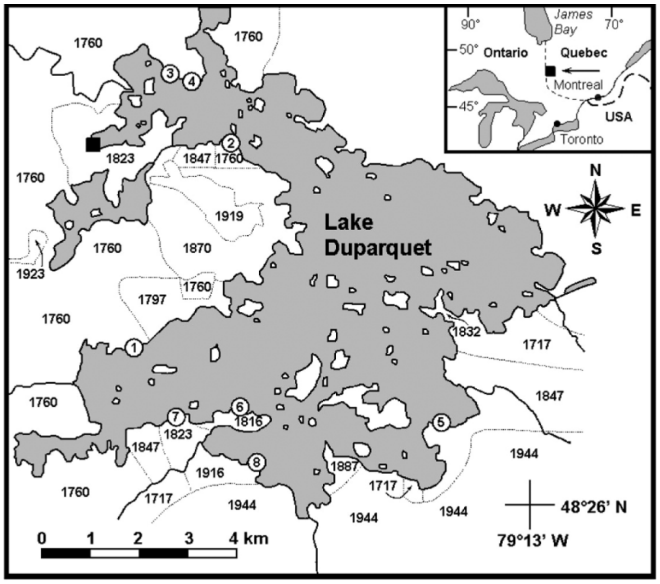
Although lake and stream margins are relatively well protected from fire (Kobziar and McBride 2006), they are exposed to periodic flooding, which is the main disturbance affecting bottomland forest dynamics (White 1979). Tolerance to flooding varies considerably according to species and tree size (Kozlowski 1984). Flood-related physical damage, caused by wave action and ice drift, is also an important tree mortality factor (Bendix and Hupp 2000; Denneler et al. 2008). Flooding can also have a beneficial effect on seed germination, seedling survival, and growth of seedlings and trees when soil moisture is increased during an otherwise dry summer (Cordes et al. 1997). However, survivorship of trees and, particularly, seedlings is adversely affected by long-lasting immersion (Hosner 1958).

Climate change acts directly upon vegetation and forest dynamics, but indirect effects through changes in the natural disturbance regimes might be even more important (Fleming 1996). Since the end of the Little Ice Age, a relatively cool period lasting from the 13th to 19th centuries (Grove 2001), the global average surface temperature has increased by 0.74 ± 0.18 °C between 1906 and 2005 (IPCC 2007). In eastern North America, the post-Little Ice Age temperature increase was coincident with increased precipitation and water levels (Groisman and Easterling 1994; Payette and Delwaide 2004) and decreased fire frequency (Cwynar 1977; Suffling et al. 1982). These changes in climate and natural disturbance regimes affected forest dynamics in different ways. In riparian forests, rising water levels due to climate change resulted in reduced tree growth, limited regeneration, and stand degradation due to excess soil moisture and erosion (Clark 1986). Shore disturbances such as ice push were more severe during periods of high spring water levels, injuring and killing shoreline trees and shrubs and favouring vegetative regeneration (Hupp 1988; Denneler et al. 2008). On the other hand, water level lowering caused by recent periods of low precipitation or by isostatic rebound allowed for downward expansion of shoreline shrub and tree populations (Cramer 1985; Bégin and Filion 1995).

In the boreal forest of southwestern Quebec, the long-term trend towards higher temperatures and precipitation was accompanied by a distinct decrease in fire frequency since the mid-19th century (Bergeron and Archambault 1993). Dendroclimatological analysis of drought-sensitive eastern white-cedars on Lake Duparquet rock outcrops indicated moisture deficits during the Little Ice Age followed by increasing summer precipitation during the late 19th and 20th centuries (Archambault and Bergeron 1992). Ice scarring frequency and maximum ice scar height on eastern white-cedar stems bordering Lake Duparquet revealed increasing ice push activity related to an approximately 1 m rise in spring high water levels since 1850 (Tardif and Bergeron 1997). The increased severity of the Lake Duparquet flooding regime also caused a change in the regeneration pattern of riparian black ash (*Fraxinus nigra* Marsh.) from sexual towards vegetative reproduction (Tardif and Bergeron 1999).

The eastern white-cedar and black ash fringe bordering Lake Duparquet, being exposed to both fire and flooding, offers a unique model to study the indirect effects of climate change on boreal forest ecosystems. Previous observations suggested that this fringe might not be in equilibrium with the present water level, since mean stem size within the riparian zone was considerably larger than in more elevated sites (Denneler et al. 1999). The same study also provided evidence for recent black ash invasion of the lower parts of the shoreline terraces, also observed by Tardif and Bergeron (1999).

Fig. 1. Time-since-fire map of Lake Duparquet (after Dansereau and Bergeron 1993) showing the location of the eight study stands (numbered circles).



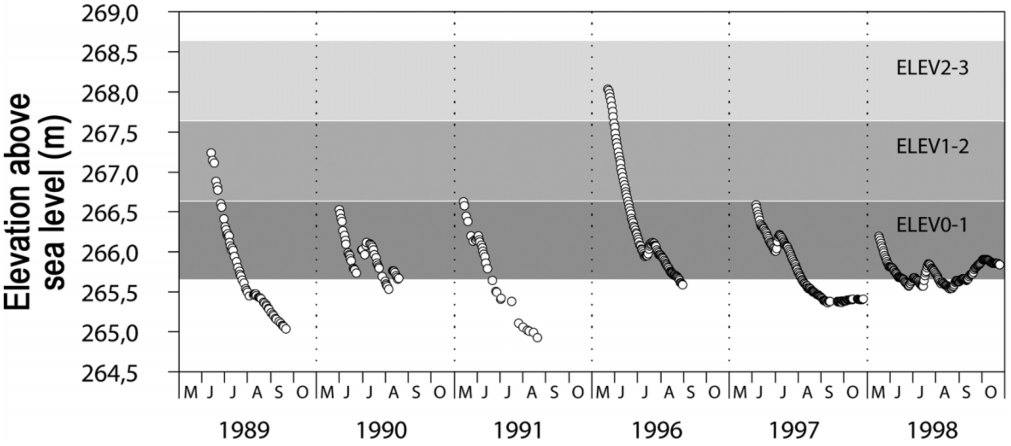
In this study, the population dynamics of lakeshore eastern white-cedar and black ash forests were examined in relation to fire frequency and long-term water level changes. Rising water levels and decreasing fire frequency since the mid-19th century were expected to have favoured an inland migration of the riparian forest fringe, with the flood-tolerant black ash colonizing the lower parts of the shore terraces and eastern white-cedar the upper parts. Differential responses of eastern white-cedar and black ash were expected due to differences in tolerance to shade, drought, and disturbances such as fire, flooding, and ice push (Johnston 1990; Wright and Rauscher 1990).

Methods

Study area

Lake Duparquet (48°28′N, 79°17′W) is located in the Abitibi-Témiscamingue region approximately 600 km northwest of Montreal and embedded within the slightly undulating landscape of the Canadian shield (Fig. 1). Clayey deposits originating from proglacial Lakes Barlow and Ojibway cover most areas below 300 m elevation (Veillette 1994), whereas hilltops (>300 m) are covered with glacial till or left bare as rock outcrops (Clayden and Bouchard 1983). Meteorological data for the period 1961–1990 were obtained from the La Sarre weather station located approximately 40 km north of the study area (Environment Canada 1993). Mean annual temperature is 0.8 °C and mean temperatures of the warmest and coldest months (July and January) are 16.8 and –17.9 °C, respectively. Total annual precipitation is 856.8 mm, of which 25% falls as snow.

Fig. 2. Seasonal water level fluctuations of Lake Duparquet between May and October of 1989–1991 (after Tardif and Bergeron 1997) and 1996–1998 (this study). The first 4 years represent manual measurements, whereas 1997 and 1998 are daily means from a hydrograph installed at the bottom of Lake Duparquet. The shaded areas indicate the position of the three elevation intervals ELEV0–1, ELEV1–2, and ELEV2–3.



The study area is located at the southern border of the boreal forest within the balsam fir – white birch domain (Saucier et al. 1998). Mature stands on mesic sites are characterized by balsam fir (*Abies balsamea* (L.) Mill.) and white birch (*Betula papyrifera* Marsh.) along with white spruce (*Picea glauca* (Moench) Voss) and eastern white-cedar. Tamarack (*Larix laricina* (Du Roi) K. Koch), black spruce (*Picea mariana* (Mill.) BSP), eastern white-cedar, black ash, and balsam poplar (*Populus balsamifera* L.) dominate the hydric sites surrounding Lake Duparquet (Denneler et al. 1999). Eastern white-cedar occurs on a wide variety of organic and mineral soils, tolerates a wide range of soil moisture regimes, reproduces best on rotten wood, is shade tolerant and thus associated with late successional stages, and develops a shallow but widespread root system (Johnston 1990). The shade- and drought-intolerant black ash typically occupies rich but poorly drained sites in bogs or along rivers and lakeshores where it is exposed to seasonal flooding (Wright and Rauscher 1990).

Lake Duparquet covers approximately 40 km^2 (Fig. 1) and drains north in James Bay through Duparquet River, Lake Abitibi, and Abitibi River. Lake Duparquet has never been dammed, although the downstream part of Duparquet River (approximately 15 km north) has been transformed into an outgrowth of Lake Abitibi after the construction of a dam in 1915 (Denneler et al. 2008). The size and flow of the Lake Duparquet outlet did not appreciably change, however, as revealed by photographs dating back from the early 1920s (Alain Boutin, personal communication (1999)). Hence, water level fluctuations of Lake Duparquet still follow a natural regime and the limited available gauge measurements indicate considerable year-to-year variations with respect to annual amplitude and maximum spring flood level (Fig. 2).

Stand selection

Stand selection was restricted to shoreline sections having a terrace-like topography because a former study revealed particularly large individuals of eastern white-cedar on this type of riparian zone (Denneler et al. 1999). Such large eastern white-cedars were expected to predate the last forest fire reported for the area because of their relatively fire-protected position close to the lake, thus providing an opportunity to reconstruct riparian tree limit changes due to long-term water level fluctuations.

Eight sampling points were chosen around Lake Duparquet. The sampling points were selected so as to maximize shore terrace breadth, favour places where large eastern white-cedar individuals were present, and avoid areas with visible human impact (Fig. 1). The eight study stands differed with time since the last fire and exposure to wave activity. The fetch, i.e., the distance from the opposite lakeshore in the direction of the prevailing winds (northwest), was used to quantify exposure. Stands 1, 3, and 4 are south oriented and thus considered well protected. Stand 5 is the most exposed with a fetch of 4.9 km, whereas stands 2, 6, 7, and 8 have moderate wind exposure with fetches varying from 1.1 to 2.4 km (Table 1). Four stands were burned for the last time in 1760 during one of the most devastating fires ever to happen in the area (Dansereau and Bergeron 1993), three stands were burned in the first half of the 19th century, and one stand was burned in 1916 (Table 1; Fig. 1).

From each shoreline sampling point, a 10 m wide transect was set up perpendicular to the lake shore, up to 3 m above lake level, resulting in lengths varying between 13 and 30 m (Table 1). The transects were subdivided into three 1 m elevation plots for population dynamics analyses. The lowest plot, between 0 and 1 m (ELEV0–1), consisted of the rocky shore and riparian shrub belt and was flooded during most of spring and summer (Fig. 2). The highest plot (ELEV2–3), in contrast, was within the upland forest, above the mean high water level identified at approximately 2 m above lake level by small erosion taluses and the upper limit of deposited driftwood. The lower part of plot ELEV2–3, however, can be shortly flooded during extraordinarily high spring floods like that of 1996 (Fig. 2). Plot ELEV1–2 corresponded to an intermediate position with respect to flooding and represented the transition zone between the shrub belt and the forest. Thus, elevation reflected not only a flooding gradient but also a light availability gradient from the open riparian shrub belt to the closed upland forest.

Data collection

Within all plots, diameter at breast height (DBH) (1.3 m high) was measured for all individuals with DBH > 1 cm

Table 1. Descriptive statistics for the eight study stands located on the shores of Lake Duparquet.

	Stand No.[a]								
	1	3	4	8	7	2	6	5	Lake[b]
Length (m)	15	16	25	17	13	17	26	30	19.9±6.2
Fetch to the northwest (km)	0.0	0.0	0.0	1.1	1.9	2.4	2.4	4.9	1.6±1.7
Last forest fire[c]	1760	1760	1760	1916	1823	1760	1816	1847	—
Plot size (m^2)									
ELEV2–3	24.5	45.3	74.4	34.0	15.4	51.1	21.9	—[d]	38.1±20.5
ELEV1–2	95.0	92.5	137.3	68.2	66.8	71.0	180.9	161.3	109.1±44.8
ELEV0–1	35.2	26.5	43.4	72.1	55.9	51.1	59.6	139.3	60.4±34.9

Note: All transects started from the same reference water level (265.65 m).

[a] The stands are presented, from left to right, in order of increasing exposure to riparian disturbances (fetch to the northwest).

[b] Composite information from the eight study stands (mean ± 1 SD).

[c] The fire years were taken from Dansereau and Bergeron (1993).

[d] Stand 5 is located on a small peninsula with a maximum elevation of only approximately 1.5 m above lake level.

(trees). Living and in situ dead trees of all species were considered, although black spruce was later omitted from the analyses because only one individual was found. If the trunk of a dead tree was no longer present, such as for trembling aspens (*Populus tremuloides* Michx.) cut by beaver (*Castor canadensis* Kuhl, 1820), diameter of the uppermost part of the stump was measured. Each living eastern white-cedar and black ash was cored as close as possible to stem base. Because many eastern white-cedar trunks had rotten, hollow centres, a core was taken higher up on the stem to get as close as possible to the pith. Height above ground and stem diameter at coring level were measured to allow later estimation of germination date (see following section). Two samples were also taken at different heights on the trunks of 16 randomly chosen eastern white-cedars with intact centres to calculate a sampling height correction factor for age. An analogous sampling procedure was employed for dead tree individuals, with the difference that cross sections were sampled instead of cores. Elevation above lake level was measured for each eastern white-cedar and black ash tree using a WILD-T2 theodolite (WILD, Heerbrugg, Switzerland) taking into account water level fluctuations that occurred during fieldwork. The trees of all other species were assigned to either one of the three elevation zones (ELEV0–1, ELEV1–2, and ELEV2–3).

All living individuals <1 cm DBH (regeneration) were sampled within a 2 m wide transect oriented perpendicular to the lakeshore and set up in the middle of each 10 m wide transect. These transects were subdivided into 1 m × 2 m plots, and elevation above lake level (rounded to the nearest 5 cm) was measured at the centre of each plot, i.e., in 1 m steps along the transects. All individuals within the same plot were assigned the same elevation. After identification of species and regeneration mode (sexual or vegetative), each individual was aged directly in the field by counting the number of terminal bud scars. When terminal bud scars were not clearly visible, the number of tree rings at the root collar was counted. Some samples with particularly narrow tree rings were brought to the laboratory where the number of rings was counted under a dissecting microscope. If the two dating methods yielded different values, the higher age was retained for further analyses.

Estimation of germination age

Age correction of eastern white-cedar trees was necessary for samples without pith (pith correction) and when sampling height did not correspond to stem base (sampling height correction). The number of missing tree rings was visually estimated when the innermost ring of the sample was very close to the pith (<1 cm). In all other cases, pith correction was based on the estimation of the distance from the innermost tree ring to the pith. Three different methods were applied to estimate the missing sample length. For cross sections with concentric tree rings and a hollow centre, the missing part was considered to equate half the diameter of the hole. For incomplete cross sections and cores, the arc of the innermost tree ring was used to calculate the distance to the pith using the equation proposed by Duncan (1989). In this approach, the relation between length (L_A) and height (H_A) of the arc is used to calculate the missing radius (R):

$$[1] \qquad R = L_A^2/8H_A + H_A/2$$

When the inner tree rings were not arched, the missing radius was calculated as the difference between half the stem diameter at coring height (D) and the length of the core (L_C):

$$[2] \qquad R = D/2 - L_C$$

For either of the three methods, the number of tree rings to add was obtained by dividing the estimated length of the missing radius by the mean ring width of the 20 innermost tree rings.

The 16 eastern white-cedar trees with an intact centre that were sampled at two different heights along the stem were used to calibrate the sampling height correction. The regression of the mean width of the 20 innermost tree rings of the lower sample against the age difference of the two samples standardized for a 10 cm height difference resulted in a highly significant relationship ($R^2 = 0.66$, $P = 0.0001$, $n = 16$):

$$[3] \qquad \log_e(y) = 2.304 - 2.775x$$

where x is the mean width of the 20 innermost tree rings and y is the number of years per 10 cm height difference on the stem. Thus, to calculate the number of missing rings due to sampling height, the mean width of the 20 innermost tree rings was used as the independent variable in eq. 3, and the resulting y value was then multiplied by sampling height in decimetres. Finally, estimated germination year was obtained by adding the number of missing years determined by one or both of the correction methods to the measured number of tree rings.

Sampling height and pith corrections rarely had to be applied to black ash trees. When needed, the number of missing rings due to sampling height was estimated visually (+1 year if sampling was not done directly at stem base), and pith correction was done visually or by the Duncan (1989) method.

Since the age of most (92%) eastern white-cedar trees had to be estimated, tree age distributions are presented in 20-year classes. To compensate for the unequal size of the plots and to allow comparisons between stands, the frequencies of each size and age class were converted to number of stems per 0.01 ha.

Ring-width measurement and crossdating

The cores and cross sections were prepared using standard dendrochronological procedures (Fritts 1976). Ring width of all samples was measured with a Velmex UniSlide micrometer (precision of 0.001 mm) to insure exact dating because eastern white-cedar produced complacent rings with few pointer years, and incomplete as well as missing rings were expected to occur in both species. Ring width measurements allowed crossdating of the samples taken from the dead trees, and crossdating accuracy was tested statistically using the program COFECHA (Holmes et al. 1986).

Statistical analyses

Tree species population dynamics are typically analyzed using static and cumulative age distributions that usually follow one of two models: the negative exponential or the power function (Hett and Loucks 1976; Tardif and Bergeron 1999). The negative exponential model assumes constant recruitment and mortality rate over time. Such distributions are typical of uneven-aged but stable forest stands with sustained seedling input (Leak 1965). The power function model, however, is more appropriate if the chance of survival increases with time. For both models, the *y*-intercept and the slope of the regression indicate initial recruitment and mortality rate, respectively.

In this study, riparian population dynamics were characterized by computing age structures for eastern white-cedar and black ash. Frequency distributions were calculated for each stand separately as well as for all stands together, i.e., at the scale of Lake Duparquet. The complete data set, including trees (DBH ≥ 1 cm) and regeneration (DBH < 1 cm), was used in the analyses.

The negative exponential and the power function models were both used to evaluate which best described the observed cumulative frequency distributions of eastern white-cedar and black ash at the lake scale. The linear regressions were calculated separately for each of the three elevation zones using SPSS (SPSS Inc. 1997). However, the lowest riparian zone (ELEV0–1) was discarded for eastern white-cedar and the upland zone (ELEV2–3) for black ash because both species were too rare within the corresponding plots. Dead trees were excluded from the calculation of the cumulative frequency distributions. Nevertheless, they are shown in the age structure profiles and were used to discuss the results.

Results

Stand species composition and diameter distribution

Very few seedlings or trees were found in the lowest elevation interval (ELEV0–1), with most stems being small and from broadleaf species, predominantly black ash (Fig. 3). Conifers in the lowest elevation interval were only present in stand 5, where seedlings of eastern white-cedar and white spruce were found. Intermediate elevation plots (ELEV1–2) were mostly dominated by conifers, particularly eastern white-cedar, although some broadleaf species were also present, even dominating in stands 5 and 6 where black ash and balsam poplar were common (Fig. 3). In all of the intermediate-level plots, the largest individuals were eastern white-cedars and trembling aspen stumps cut by beavers. Upland forest plots (ELEV2–3) were dominated by balsam fir and eastern white-cedar, although the latter species did not reach as large diameters as within the upper riparian zone. Only the youngest stand (stand 8, last fire in 1916) showed a mixed balsam fir and white birch forest (Fig. 3).

Composite age distribution along the elevation gradient

With the exception of only three 1-year-old seedlings, eastern white-cedar was not found closer to Lake Duparquet than 100 cm above water level (Fig. 4). The composite age distributions between 100 and 300 cm showed a distinct trend towards lower ages with increasing elevation (Fig. 4). Almost all trees older than 300 years were found between approximately 120 and 160 cm. Above 200 cm, only a few individuals dated more than 150 years and most trees located between 220 and 255 cm were 80 years old. The lower limit of occurrence of eastern white-cedar changed through time (Fig. 4). Between the early 15th and mid-18th centuries, it lowered by 21 cm, going from 129 to 108 cm. It then rose back 32 cm to reach its present position at 140 cm. However, many seedlings less than 5 years in age presently occur down to 65 cm (Fig. 4).

Black ash was restricted to the interval between 50 and 200 cm above lake level and hence occupied lower elevations on the lakeshore terraces compared with eastern white-cedar (Fig. 4). The highest ages, up to approximately 200 years, were attained between about 70 and 150 cm, whereas only a few trees were found above this elevation. Recruitment was very poor below 115 cm but abundant above. Dead black ash trees were slightly more frequent close to the lake. Since the mid-18th century, the lower limit of occurrence of black ash advanced 23 cm towards the lake, from 83 cm to its present position at 60 cm.

Lake-scale age distribution

The age structure profiles of eastern white-cedar for the two upper elevation intervals showed differences with respect to mortality rate and maximum age (Fig. 5A). At ELEV1–2, ages of more than 600 years were attained and (almost) continuous recruitment started at the end of the 16th century. The second half of the 18th century was characterized by a relatively low number of trees. This period also corresponds to the start of continuous eastern white-cedar recruitment within ELEV2–3 (Fig. 5A), although the oldest (dead) tree at this elevation dated back to ca. 1575. The age structures for the two elevation intervals corre-

Fig. 3. Size structures of all species for each stand and elevation interval (ELEV0–1, ELEV1–2, and ELEV2–3). The size classes used are seedlings and sprouts with stems <1 cm DBH (S), trees by 5 cm DBH classes from 1 cm up to 50 cm (1–10), and a last class for stems ≥51 cm DBH. The number of stems within the first size class of all plots was divided by 10. The category "other species" contains the less frequent white birch, balsam poplar, and willows (*Salix discolor*, *Salix heterophylla*, *Salix lucida*, and *Salix rigida*). The stands are presented, from A to H, in order of increasing wind exposure. The year of the last forest fire is given in parentheses.

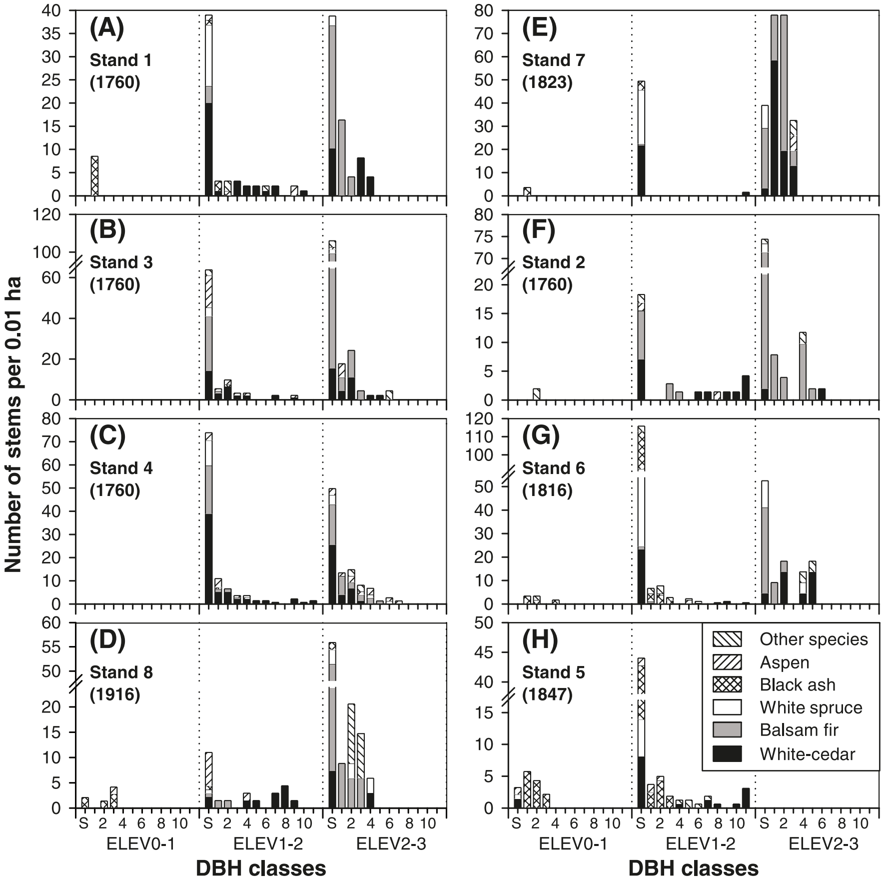
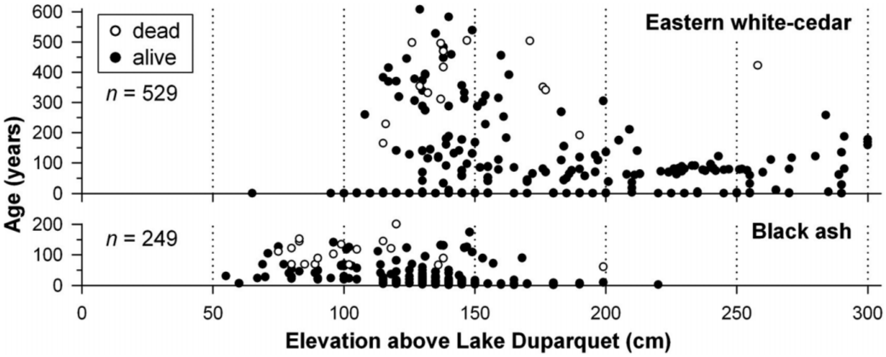


Fig. 4. Composite age distribution of living and dead stems of eastern white-cedar and black ash along the elevation gradient between 0 and 300 cm above water level.



sponded well to both the constant mortality and the decreasing mortality models (Table 2). The negative exponential function, however, yielded higher R^2 values. Mortality rate and initial recruitment were both significantly higher for ELEV2–3 than for ELEV1–2 (Table 2). The cumulative age distribution for ELEV1–2 showed a very high mortality rate from the first to the second 20-year age class followed by rather low mortality (Fig. 5A). Juvenile mortality was much less pronounced within the upper elevation interval.

Relative to eastern white-cedar, maximum age and mortality rate of black ash were much less different between the two elevation intervals where the species occurred (Fig. 5B). Continuous recruitment within ELEV1–2 began ca. 1825, when the oldest living tree established. Only one dead tree was found to be approximately 40 years older. The frequency distribution corresponded to that of an uneven-aged population with constant mortality, although the 20-year age classes between 1878 and 1938 were slightly underrepresented. Maximum age of black ash within ELEV0–1 was only slightly lower than within ELEV1–2.

Fig. 5. $\log_e$-transformed static age distributions of living and dead stems in 20-year classes for (A) the upper (ELEV2–3) and intermediate (ELEV1–2) elevation intervals for eastern white-cedar and (B) the intermediate (ELEV1–2) and lower (ELEV0–1) elevation intervals for black ash. The lines show the cumulative frequency distributions of the living stems. The years represent the median values of the 20-year classes.

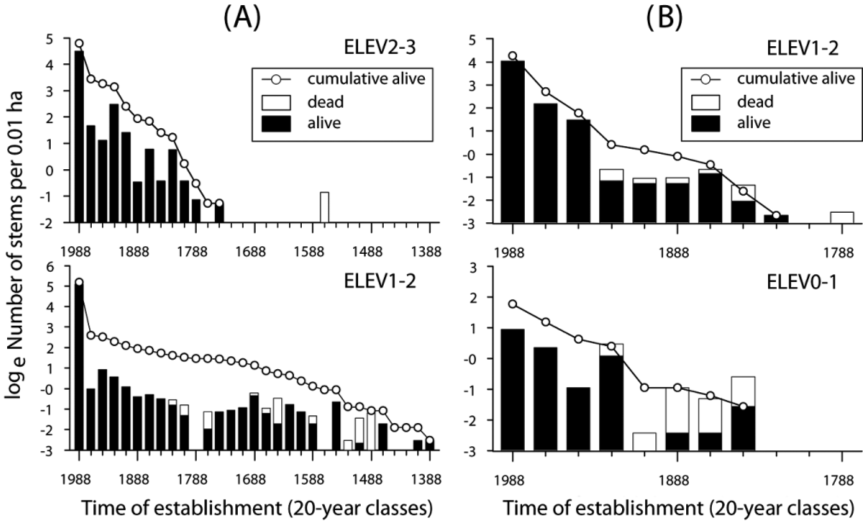


Table 2. Results of the linear regression analysis applied to the cumulative age distributions of black ash and eastern white-cedar.

	Black ash		Eastern white-cedar	
Statistic	ELEV0–1	ELEV1–2	ELEV1–2	ELEV2–3
Negative exponential model				
n	8	9	31	13
R^2 adjusted	0.941	0.944	0.907	0.967
Intercept	1.890a	3.922b	3.414a	4.685b
Slope	–0.025a	–0.038a	–0.009a	–0.024b
Power function model				
n	8	9	31	13
R^2 adjusted	0.863	0.917	0.788	0.802
Intercept	5.217	10.039	9.103	9.988
Slope	–1.287	–2.254	–1.543	–1.832

Note: All linear regressions were significant at $P < 0.0006$. Values of intercept and slope of the negative exponential model sharing the same letter do not differ significantly between the two elevation intervals for the same species ($P < 0.05$); *n* is the number of age classes in the cumulative distribution.

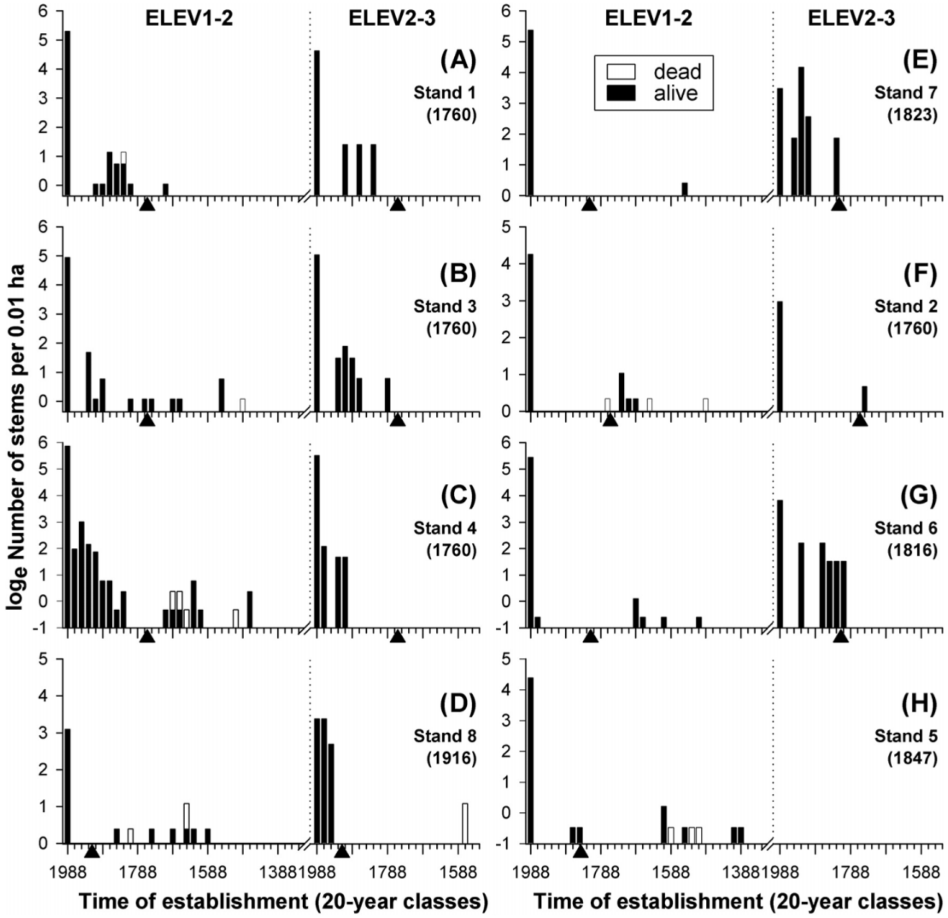
However, since several of the oldest sampled trees were dead, continuous recruitment started as late as the 1920s. Although the negative exponential function and power function models for population dynamics were both highly significant, the constant mortality model explained slightly more variation (Table 2). Initial recruitment was significantly higher in the upper than in the lower riparian zone.

Stand age distribution

Eastern white-cedar at low elevations grew considerably older than within the upland forest in almost all stands (Fig. 6). Maximum age of the living trees varied between approximately 600 years (stand 5) and 300 years (stand 1) for ELEV1–2 but only between 250 years (stand 2) and 60 years (stand 8) for ELEV2–3. The age distributions of eastern white-cedar at the stand scale showed considerable deviations from constant mortality and recruitment population dynamics as observed at the lake scale. The first 20-year age class was dominant in 14 out of 15 plots, whereas the next two age classes (21–60 years) were devoid of trees in all but two ELEV1–2 plots (Fig. 6). The age distributions of the ELEV1–2 plots were characterized by episodic recruitment phases occurring at different moments but without distinct peaks (Fig. 6). The three stands that were well protected from riparian disturbances (stands 1, 3, and 4) showed considerably more recruitment within the riparian zone (Figs. 6A–6C). In all other stands, almost no postfire eastern white-cedars occurred, although recent recruitment was present (Figs. 6D–6H). The lack of postfire recruitment within the riparian zone of three of the wind-exposed stands (stands 6, 7, and 8) contrasts with the relatively abundant regeneration within the upland forest at the same sites (Figs. 6D, 6E, and 6G).

The stand age distributions of black ash are shown in Fig. 7 for the two elevation intervals where the species occurred (ELEV0–1 and ELEV1–2). Three stands were omit-

Fig. 6. $\log_e$-transformed static and cumulative age distributions of living and dead eastern white-cedar stems in 20-year classes for the intermediate (ELEV1–2) and upper (ELEV2–3) elevation intervals. The stands are presented, from A to H, in order of increasing wind exposure. The fire year of each stand is given in parentheses and as triangles on the abscissa.



ted because the species was either completely absent (stand 2) or only one stem was found within the whole sampling area (stands 3 and 4). Very few living stems of black ash were encountered in stands 1, 7, and 8, and they were almost all restricted to the first two 20-year age classes (Figs. 7A–7C). Black ash was most numerous and attained the highest ages at the most exposed stands (Fig. 7D and 7E). Differences in stand age structures between elevation zones were relatively small, with the notable exception of the first age class that was devoid of trees in all but one plot at ELEV0–1, whereas it was predominant in all plots but one at ELEV1–2.

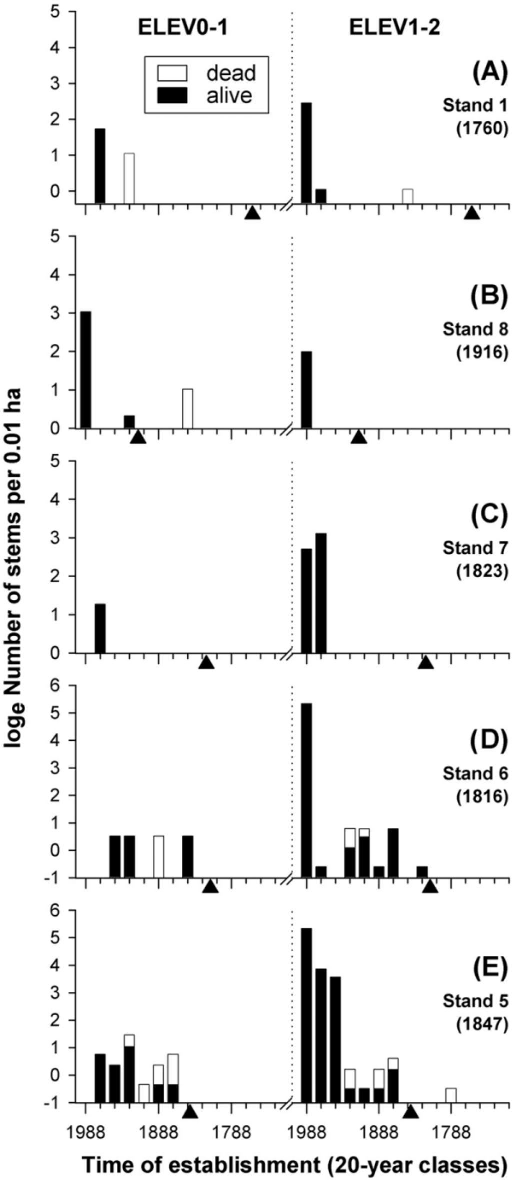
Discussion

Species composition

Species composition and relative importance changed considerably from the shore of Lake Duparquet to the upland forests. The lowest sites were clearly dominated by black ash, a flood-tolerant species forming almost pure stands on the floodplains of the lake (Denneler et al. 1999; Tardif and Bergeron 1999). In most of the sampled shore terrace stands, however, black ash occurred only sparsely, and more or less closed populations were only found on the two deepest terraces (stands 5 and 6) with balsam poplar and trembling aspen as companion species. Black ash occurrence was limited to the riparian area, below approximately 2 m above the water level, which roughly corresponds to the mean maximum high water level of the lake. Flood tolerance, combined with a capacity to reproduce vegetatively by stem sprouting, allowed black ash to persist in the highly disturbed riparian habitat. On the other hand, shade intolerance (Wright and Rauscher 1990) might explain the species' absence from upland forests, where interspecific competition for light is more intense.

Several tree species were found within the upper riparian zone (between 1 and 2 m above lake level), although eastern white-cedar was clearly dominant, with many large and old individuals. Trembling aspen was more abundant within the open riparian zone than within the closed upland forest. Many large trembling aspen trees had been cut by beavers, stimulating root suckering. Since beavers can be active quite far from the lakeshore (Bordage and Filion 1988), sucker age did not significantly change with elevation (data not shown). Balsam fir was rarely found and white spruce trees were even completely absent within the flooded area, although a few trees of the latter species were found within the flooding zone at other locations along the perimeter of Lake Duparquet (Denneler et al. 1999). Nevertheless, white spruce seedlings were abundant and occurred in almost every stand, indicating successful reproduction at the border of Lake Duparquet, relying on wind-dispersed seeds from

Fig. 7. $\log_e$-transformed static and cumulative age distributions of living and dead black ash stems in 20-year classes for the lower (ELEV0–1) and upper (ELEV1–2) riparian zones. The stands are presented, from A to E, in order of increasing wind exposure. The fire year of each stand is given in parentheses and as triangles on the abscissa.



nearby adult trees (Asselin et al. 2001). Survivorship of balsam fir and white spruce seedlings, however, was low compared with upland stands (data not shown). Possible reasons for the high mortality of 1-year seedlings close to the lake could be intolerance to flooding or summer drought (Frank 1990; Nienstaedt and Zasada 1990).

Balsam fir and, to a lesser degree, eastern white-cedar dominated the upland forest plots, whereas the two pioneer species trembling aspen and paper birch were rarely found. This species composition reflects an advanced stage of succession because stand initiation dated more than 150 years in all but one stand. In this stand (stand 8, which burned for the last time in 1916), paper birch codominated together with balsam fir. White spruce regeneration occurred in all stands, but trees were restricted to stands 4, 6, and 8.

Upland population dynamics subject to fire

Population dynamics of eastern white-cedar above the riparian zone was found to be strongly influenced by forest fire. Almost no eastern white-cedar trees established before the last fire in any stand (Fig. 6). The significantly higher mortality rate compared with that observed in the lowland was thus largely due to the elimination of the prefire population. Eastern white-cedar was present in the upland forests of all eight stands. Postfire establishment was sometimes delayed up to 50 years (150 years for stand 4). A delay of approximately 120 years was observed in a study on postfire species dynamics along a chronosequence in the area of Lake Duparquet (Bergeron 2000). The presence of surviving seed trees in the nearby riparian zone might have accelerated postfire re-invasion in some of the studied stands (Asselin et al. 2001).

Black ash was not present in the upland forest, as the species is intolerant to shade and is thus outcompeted by balsam fir and eastern white-cedar (Wright and Rauscher 1990). Intolerance to drought and fire probably also have a role to play in the species' absence from the upland stands.

Lowland population dynamics subject to flooding and fire

The age distribution of eastern white-cedar within the riparian zone provided evidence for a reduced impact of fire disturbance relative to the upland forest. Trees of this fire-sensitive species predating the last fire event were found in all stands within ELEV1–2. Black ash, also intolerant to fire, is limited to riparian habitats. Since fire probability has been shown to depend significantly on soil moisture (Clark 1989), the relatively humid soils of the riparian zone would have resulted in conditions unfavourable to burning. The oldest eastern white-cedar individuals were found in stand 5, a small peninsula particularly well protected from fire. Kobziar and McBride (2006) showed that large riparian zones are particularly effective as firebreaks, an assertion supported here by black ash dominance in the two largest riparian zones (stands 5 and 6). Nevertheless, the maximum age of 608 years found for eastern white-cedar in this study does not represent the maximum natural life span of the species, as much older individuals have been found on xeric rock outcrops on the islands of Lake Duparquet (approximately 900 years; Archambault and Bergeron 1992) and on the cliff faces of the Niagara escarpment in southern Ontario (>1650 years; Larson 2001). This somewhat reduced longevity might have been caused by a still higher exposure to fire on mainland shores compared with the relatively small islands where chance to be spared by fire is higher.

There is some evidence that forest fires did not always stop at the upper limit of the riparian zone, as reported elsewhere (Everett et al. 2003). Indeed, reduced eastern white-cedar recruitment within the riparian zone during the second half of the 18th century (Fig. 5A) was probably related to the 1760 fire, when four of the eight study stands burned for the last time. In stand 1, for example, only one eastern white-cedar, almost leaning to the ground but still alive, predated the 1760 fire. Eccentric tree rings and the presence of compression wood starting in 1761 suggest that tilting was related to the fire event. Probably the fire front advanced close to the lakeshore and killed all eastern white-cedars but this one, which was consecutively tilted by a falling tree or by stronger winds after canopy opening. Several of the trees that established during the 19th century germinated on the rotten part of this tilted tree. In other stands (4–8), old eastern white-cedars, although present, all predate fire by at least a decade, suggesting that the lethal crown fires decreased in intensity while getting closer to the lake and transformed into low-intensity surface fires that killed the young but not the older trees. The resulting canopy opening could have stimulated the reproduction of the shade-intolerant black ash that quickly recolonized stands 5 and 6 following fires in 1847 and 1816, respectively. Elsewhere, the absence of nearby mature trees prevented black ash from colonizing sites affected by surface fires.

The lake-scale composite cumulative frequency distribution representing the riparian eastern white-cedar metapopulation was well fitted by the constant mortality model. At the stand scale, however, important deviations from this model were observed for most of the plots. Many stands (2, 5–7) approximated bimodal age structures with very old and very young stems and almost none in between. The presence of old trees could be explained by burning by surface rather than crown fires that would have killed the young but not the older trees. Regeneration failure is probably due to unsuitable conditions due to wind exposure and riparian disturbances (Johnson 2000). This is supported by the presence of black ash in sites 5 and 6, a species more tolerant than eastern white-cedar to ice push disturbance. Relative basal area of eastern white cedar on shore terraces of Lake Duparquet has been shown to be highest on sites well protected from the dominant northwestern winds (Denneler et al. 1999).

Both composite cumulative frequency distributions of black ash followed a negative exponential function. However, whereas initial recruitment was significantly higher for the upper than for the lower riparian zone, mortality rates did not differ significantly. Nevertheless, the higher exposure to riparian disturbances at low elevations not only resulted in a slightly lower maximum age but also in a period of high mortality that lasted from the late 19th century to about 1920. Many of the smaller black ash trees were probably killed by the extreme spring flood of 1922 (Tardif and Bergeron 1997). This would also explain the consecutive increase in the number of trees stimulated by stem sprouting.

As for eastern white-cedar, black ash population dynamics at the stand level differed considerably from the constant mortality model. High exposure to riparian disturbances on the relatively short shore terraces of stands 2, 7, and 8 only allowed black ash to recruit and survive sporadically as indicated by rare and mostly young individuals. In stands 5 and 6, however, black ash reproduced more continuously and attained higher ages, probably because the impacts of wave action and ice push were reduced by larger riparian zones. Competition for light in the relatively protected stands 1, 3, and 4, where riparian eastern white-cedars were common, could have restricted black ash occurrence. Except for stand 8, recent recruitment (<20 years in age) occurred only in the upper riparian zone. This points to recent problematic regeneration of black ash close to the lakeshore. In addition, seedlings younger than 5 years were sparse and 1-year-old seedlings were even absent within the whole riparian zone of all stands. This regeneration failure might be due to several years of poor seed production (Wright and Rauscher 1990) or to exceptional flooding events.

Long-term water level changes

Riparian eastern white-cedar populations along the exposed parts of the perimeter of Lake Duparquet are not in equilibrium with the actual water level. Based on the composite age distribution of eastern white-cedar along the elevation gradient (Fig. 4), three periods can be distinguished. The lake level was relatively high during the 15th century and eastern white-cedar did not occur closer to the lake than 129 vertical centimetres. Between approximately 1500 and 1850, i.e., during the Little Ice Age known as a relatively cool and dry period (Grove 2001), eastern white-cedar migrated downward to the lake by 21 cm as the lake level receded. Since then, the tree limit progressively drove back by 32 cm, reacting to the post-Little Ice Age water level increase of Lake Duparquet. This is, however, considerably less than the increase of the spring flood levels, which has been estimated at about 100 cm by Tardif and Bergeron (1997) for the same period using changes of the maximum ice scar height on eastern white-cedar stems bordering Lake Duparquet. However, this 100 cm increase of the spring flood level was restricted to a few years with extreme water levels since the 1920s. The floods of most other years were at least half a metre lower, within the frame of what is reported here. The main effect of the recent water level rise was likely neither uprooting of old trees nor inhibition of seed germination but rather prevention of seedling establishment and survival below approximately 130 cm. Since eastern white-cedar successfully recruits on protected parts of the lake perimeter, seedling dieback was likely caused by physical damage due to drifting ice and timber during the increasingly frequent high spring floods rather than by flooding stress that affects the seedlings in the same way everywhere around the lake.

Black ash also reacted to the post-Little Ice Age water level increase of Lake Duparquet. Since about 1850, the flood-tolerant black ash started to invade the riparian zone of the shore terraces in greater numbers (Figs. 4 and 5), replacing eastern white-cedar.

Conclusion

Eastern white cedar is in disequilibrium with the current Lake Duparquet water level and has been migrating upland since the end of the Little Ice Age due to its poor tolerance to flooding and ice push disturbance. The migration of the species is, however, limited by its susceptibility to fire, more frequent on upland sites. Black ash, a species tolerant to flooding and ice push disturbance, recently colonized the riparian sites abandoned by eastern white-cedar. The migration of black ash toward higher elevations is, however, limited by intolerance to shade, drought, and fire.

Scenarios exploring future climate trends suggest that temperature and precipitation will continue to rise during the 21st century (IPCC 2007). The water level of Lake Duparquet will thus likely continue to rise, resulting in increased frequency and amplitude of extreme spring floods. Fire frequency in the Canadian boreal forest is expected to stay low or even continue to decrease during the 21st century (Bergeron et al. 2006), and thus, the migration pattern identified in this study for the eastern white-cedar and black ash riparian fringe is expected to continue.

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