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Continuous earlywood vessels chronologies in floodplain ring-porous species can improve dendrohydrological reconstructions of spring high flows and flood levels

S. Kames [a,b], J.C. Tardif [a,*], Y. Bergeron [c]

[a] Centre for Forest Interdisciplinary Research (C-FIR), University of Winnipeg, 515 Avenue Portage, Winnipeg, Manitoba R3B 2E9, Canada
[b] Department of Botany, University of Manitoba, Winnipeg, Manitoba, Canada
[c] NSERC-UQAT-UQAM Industrial Research Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, QC J9X 5E4, Canada

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SUMMARY

Plants respond to environmental stimuli through changes in growth and development. Characteristics of wood cells such as the cross-sectional area of vessel elements (hereafter referred to as vessels) may store information about environmental factors present at the time of vessel differentiation. The analysis of vessel characteristics therefore offers a different time resolution than annual ring width because vessels in tree rings differentiate within days to a few weeks. Little research has been conducted on the sensitivity of earlywood vessels in ring-porous species in response to flooding. The general objectives of this study were to determine the plasticity of earlywood vessel to high flows and spring flooding in floodplain black ash (*Fraxinus nigra* Marsh.) trees and to assess the utility of developing continuous earlywood vessel chronologies in dendrohydrological reconstruction. In contrast, most dendrohydrological studies until now have mainly used vessel anomalies (flood rings) as discrete variables to identify exceptional flood events. The study area is located in the boreal region of northwestern Québec. Vessel and ring-width chronologies were generated from *F. nigra* trees growing on the floodplain of Lake Duparquet. Spring discharge had among all hydro-climatic variables the strongest impact on vessel formation and this signal was coherent spatially and in the frequency domain. The mean vessel area chronology was significantly and negatively correlated to discharge and both the linearity and the strength of this association were unique. In floodplain *F. nigra* trees, spring flooding promoted the formation of more abundant but smaller earlywood vessels. Earlywood vessels chronologies were also significantly associated with other hydrological indicators like Lake Duparquet's ice break-up date and both ice-scar frequency and height chronologies. These significant relationships stress the utility of developing continuous vessels chronologies for hydrological reconstructions prior to instrumental data. Continuous earlywood vessel chronologies may also be useful in determining the impact of altered hydrological regime in floodplain habitat regulated by spring floods. Future research should involve quantifying the impact of high flows and flooding on other cell constituents and also determining the plasticity and utility of continuous anatomical series in floodplain diffuse-porous species.

1. Introduction

Tree growth is limited by a large range of external factors (Fritts, 1976; Schweingruber, 1996). Such factors may include light and water availability, air and soil temperature as well as soil nutrient level. In addition, exposure to disturbance agents such as heavy winds, avalanches, forest fires and insect outbreaks may also negatively affect tree growth (Schweingruber, 1996). Vegetation growing in swamps or around lake or river systems may also have to cope with constant or periodic water stress which may be one of the most severe stresses a tree can be exposed to (Kozlowski, 1985, 1997; Kozlowski and Pallardy, 2002). Flooding induces chemical changes in soils such as immediate and drastic decreases in gas exchanges between the soil system and the atmosphere since gas diffusion rates are 10,000 times reduced in water (Ponnamperuma, 1984; Armstrong and Drew, 2002; Jackson and Colmer, 2005). The resulting depletion of soil oxygen content does,

* Corresponding author at: Centre for Forest Interdisciplinary Research (C-FIR), University of Winnipeg, Department of Environmental Studies & Science, 515 Portage Avenue, Winnipeg, Manitoba R3B 2E9, Canada. Tel.: +1 204 786 9475.
E-mail address: j.tardif@uwinnipeg.ca (J.C. Tardif).

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among others, inhibit root respiratory processes (Kozlowski, 1985, 2002). Shoreline trees may also be subjected to physical damages caused by wave action, floating debris and ice push (Tardif and Bergeron, 1997b; Denneler et al., 2008a,b; Ballesteros-Cánovas et al., 2015).

Thus, even though the capacity of a tree to deal with flooding depends on its age and both morphological and physiological adaptations to flooding, prolonged flood periods that fall into the growing season often negatively affect tree growth (Armstrong et al., 1994; Kozlowski, 1997; Jackson and Colmer, 2005). Flooding may cause the production of smaller sized rings (Stockton and Fritts, 1973; Wendland and Watson-Steger, 1983). However, since drought stress and other factors can also lead to the formation of narrow rings (Woodcock, 1989; Corcuera et al., 2004; Girardin and Tardif, 2005), many dendrohydrological studies have incorporated additional proxy records when reconstructing past flood events. In addition to ring width, Nicault et al. (2014) have incorporated tree-ring densities and stable isotope ratios ($\delta^{13}C$ and $\delta^{18}O$) in their paleohydrological reconstructions in northern Québec. Boucher et al. (2011) using a generalized additive model (GAM) relied on both earlywood density measurements as continuous variables and ice-scar dates as a discrete variable. Floating ice blocks and flood debris can injure the vascular cambium of trees and datable tree scars have been used to provide information on fluctuating water levels (Tardif and Bergeron, 1997b; Lemay and Bégin, 2008; Denneler et al., 2008b; Boucher et al., 2009, 2011). Recently, river erosion dynamics have also been reconstructed based on decreases in lumen area of fibers in European ash (*Fraxinus excelsior* L.) rings after root exposure due to sediment loss (Hitz et al., 2008). Sediment depositions could also be dated given that ring-porous stem wood of green ash (*Fraxinus pennsylvanica* Marsh.) developed into diffuse-porous wood upon burial (Sigafoos, 1964; Cournoyer and Bégin, 1992). This response may however be associated with the ability to develop adventitious roots following burial (Copini et al., 2015).

Wood anatomical anomalies have also been observed in tree rings from ring-porous species [pedunculate oak (*Quercus robur* L.), bur oak (*Quercus macrocarpa* Michx.), white ash (*Fraxinus americana* L.) and *F. pennsylvanica*)] exposed to floods but not buried by sediments (Yanosky, 1983; Astrade and Bégin, 1997; St. George and Nielson, 2002, 2003; Sass-Klaassen et al., 2010; Wertz et al., 2013; Therrell and Bialecki, 2015; Ballesteros-Cánovas et al., 2015). Years with exceptional spring floods were successfully identified through tree rings containing earlywood vessels with abnormally small lumen areas (herein referred to as flood rings) whereas no consistent response in ring widths was observed (Yanosky, 1983; Astrade and Bégin, 1997; St. George and Nielson, 2002, 2003). Experimental flood experiments have also revealed that flooding at the time of vessel development lead to reduce vessel lumen area in species from the genus *Fraxinus* and *Quercus* (Sass-Klaassen et al., 2010; Copini et al., 2015; Tardif unpublished data).

Vessels of ring-porous species may not only store hydrological information but also unique climate signals (García-González and Eckstein, 2003; Fonti and García-González, 2004; Tardif and Conciatori, 2006; Fonti et al., 2006). For example, earlywood vessels may be influenced by precipitation at the time of their development as indicated by the positive correlation between the cross-sectional earlywood vessel lumen area of *Q. robur* and spring precipitation (García-González and Eckstein, 2003). Tardif and Conciatori (2006) observed positive associations between the mean cross-sectional vessel area of red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.) with May temperature. However, the associations of vessels and climate have been reported to be very weak (Fonti and García-Gonzáles, 2004; García-González and Fonti, 2006; Tardif and Conciatori, 2006). Also, since abnormally small cross-sectional earlywood vessel areas have been observed as a response of ring-porous species to flooding (Yanosky, 1983; Astrade and Bégin, 1997; St. George and Nielson, 2002, 2003; Sass-Klaassen et al., 2010; Wertz et al., 2013; Therrell and Bialecki, 2015), severe drought periods (García-González and Eckstein, 2003), insect defoliation (Huber, 1993; Asshoff et al., 1998–1999; Blank and Riemer, 1999; Thomas et al., 2006) and forest fires (Kames et al., 2011) a careful interpretation of earlywood vessel signals must be exerted.

The objective of this study was to assess how fluctuating water levels and climate could influence tree-ring production in *Fraxinus nigra*. To achieve this objective, both tree-ring and vessel chronologies were developed from wood samples collected in trees growing along the floodplain of Lake Duparquet in northwestern Québec. It was hypothesized that floodplain trees would produce more earlywood vessels with a reduced cross-sectional mean area in response to spring high flows and flood levels. Further, the earlywood vessel chronologies were expected to be more strongly associated with spring flooding than the earlywood width. The utility of developing continuous earlywood vessels chronologies in dendrohydrological reconstruction was also assessed by comparing vessel chronologies with a wide array of hydrological data including spring discharge from various unregulated rivers (in various watersheds), ice-scar data and ice break-up dates for Lake Duparquet. No studies have assessed the usefulness of developing long continuous vessel chronologies in ring-porous species for dendrohydrological investigations and this necessity was recently emphasized (Therrell and Bialecki, 2015).

2. Materials and methods

2.1. Study area

The study area is located approximately 550 km north of Montréal in the Lake Duparquet region of north-western Québec (48°28′N, 79°17′W; Fig. 1). The overall region is part of the Northern Clay Belt of Ontario and Québec where rocky hills surrounding Lake Duparquet contain glacial till and lacustrine clay deposits (Veillette, 1994). The nearest weather station to the study area with at least 50 years of data is located in La Sarre, 42 km north of Lake Duparquet. Between 1971 and 2000 the mean annual temperature was 0.7 °C (Environment Canada, 2015). The total annual precipitation in this region was 889.8 mm of which snowfall accounted for 27.7%. Lake Duparquet is a large 50 km^2 unregulated lake that drains northward via the Duparquet River to James Bay. Observational data indicated that spring ice-breakup and subsequent flooding occurred generally between mid-April and mid-May (Tardif and Bergeron, 1997b; Denneler et al., 2008b, 2010; Mongrain, 2014).

The study area is situated in the mixedwood boreal forest in the balsam fir-white birch domain where both forest fires and insect outbreaks constitute the main disturbances. Riparian forests, however, also experience disturbances due to their exposure to periodic spring flood events (Tardif and Bergeron, 1997b, 1999; Denneler et al., 1999). On Lake Duparquet geomorphological shore types and elevation gradients are the major determinants for the distribution of species (Tardif and Bergeron, 1992, 1999; Denneler et al., 1999).

2.2. Sample collection and preparation

The five *F. nigra* stands sampled by Tardif and Bergeron (1992, 1999) were revisited in August 2006 to update tree-ring chronologies (Fig. 1). These sites are positioned on the floodplain of Lake Duparquet (approximate elevation 260 m above sea level). While *F. nigra* was the dominant tree species on each of these sites, the

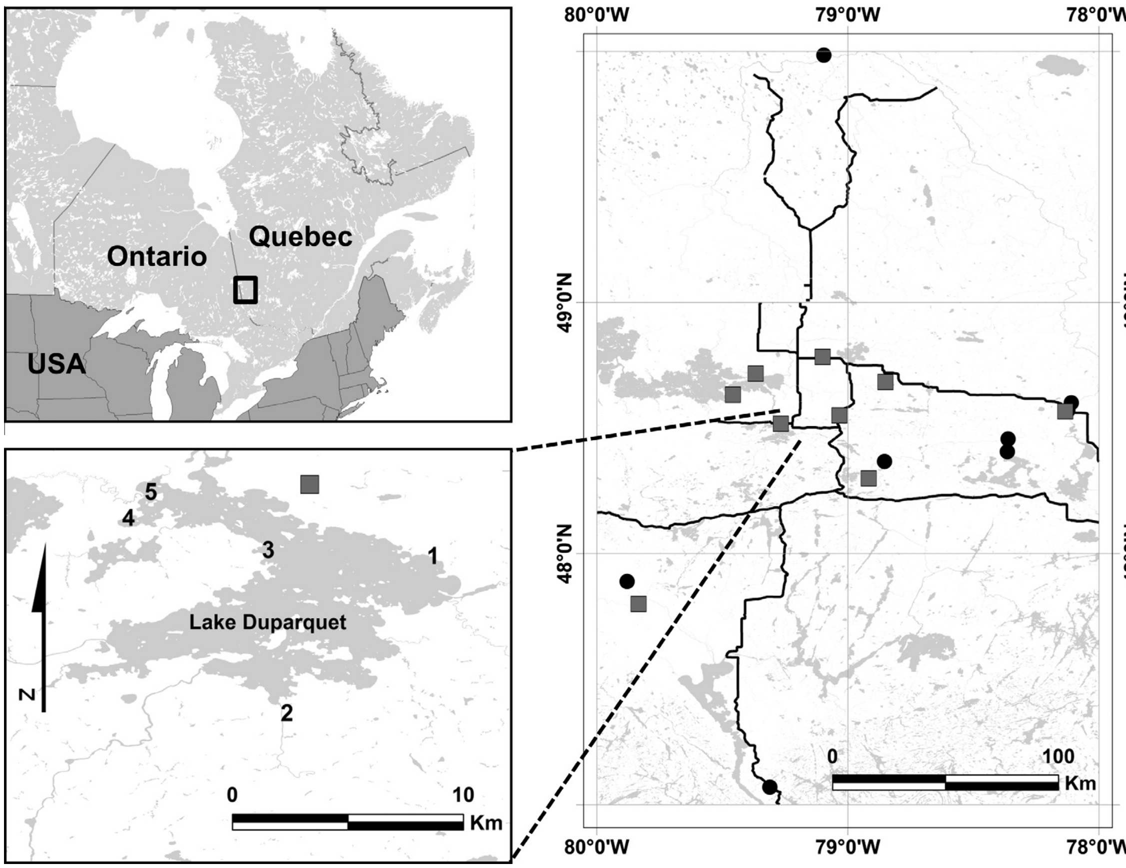

Fig. 1. Map showing the location of Lake Duparquet in northeastern Canada (upper left) with location of the five sampled floodplain sites (lower left): (1) on a sand bar, (2) beside mouth of river, (3) in a bay with a bog, (4) far from any river or bog and (5) on a river delta. The grey square represents the Lake Duparquet meteorological station that was in operation from 1981 to 1994. The right panel indicates the location of the hydrological stations (black circles) and of the closest meteorological stations (grey square) in relation to Lake Duparquet.

coexisting vegetation types differed according to elevation and drainage (Tardif and Bergeron, 1992, 1999). For each floodplain site 12 *F. nigra* trees were sampled. In all sites, wood samples were extracted from *F. nigra* trees as close to the base as possible using 5-mm diameter increment borers. In cases where the base of the stems was partly rotten, cores were taken at a higher height. Two cores were collected from each tree and along radii that were at least 90° to each other. After the cores had been extracted they were immediately deposited into labeled straws to avoid breaking during the transport to the laboratory. Subsequent tree-ring procedures (mounting, gluing, sanding) followed standard methods (Tardif and Bergeron, 1997a; Kames et al., 2011). Visual crossdating was achieved using both the list method and the reference *F. nigra* chronologies previously developed for the region (Tardif and Bergeron, 1997a). After cross-dating, annual tree-ring widths for all cores were measured to a precision of 0.001 mm with a VELMEX UniSlide measuring system and the program COFECHA (Holmes, 1999) was used to validate cross-dating and tree-ring measurements.

2.3. Image analysis

Many wood samples were partly rotten and not suitable for image analysis. A subset of trees was therefore selected based on wood quality. In total, 20 *F. nigra* trees were retained from two floodplain sites (Fig. 1, sites 2 and 3). The image analysis procedures used to measure the number and the cross-sectional area of vessels were similar to those described in Tardif and Conciatori (2006) and Kames et al. (2011). Each core was first clean with pressurized air to remove dust from vessels and then rubbed with white chalk to increase the contrast between vessel elements and the other wood cells. The prepared surfaces were scanned with a Polaroid DMC digital camera connected to a Nikon SMZ stereomicroscope to generate color images at a 25× magnification and a resolution of 1600 × 1200 pixels. Each ring image was analyzed with the program WinCell Pro Ver. 2004a (Régent Instruments Inc., 2005). In this study, earlywood, latewood and total tree-ring width and area were measured as well as the number and cross-sectional area of all vessels with an area above a threshold value of 800 μm^2. In cases where vessels were not properly identified by the program, manual corrections were made to the image. Incomplete vessels occurring at the ring boundary were excluded from the analysis as well as vessels from tree rings of very young cambial age (i.e. juvenile wood close to the pith) which exhibit a rather diffuse-porous vessel pattern. The distinction between earlywood and latewood vessels was determined qualitatively based on vessel size and location in the ring (Fonti and García-Gonzáles, 2004; Tardif and Conciatori, 2006) since in *Fraxinus* species tree rings contain large earlywood vessels followed by much smaller latewood vessels (Panshin and de Zeeuw, 1980; Yanosky, 1983; Tardif, 1996).

Due to the large data set produced, numerous data quality control procedures were used. For example, ring-width measurements obtained from the program WinCell Pro were plotted and compared to those obtained from direct tree-ring measurement of the cores using the Velmex system. This procedure assured that the captured tree-ring images had been assigned the correct calendar years thus reducing operator errors.

2.4. Chronology developments

After completion of data quality control, ring-width and vessel measurements were used to generate 15 tree-ring variables. These variables were earlywood (EW), latewood (LW) and total ring width (RW), total cross-sectional area of vessels in the earlywood (TVAE) and in the entire ring (TVATR), number of vessels in the earlywood (NE) and in the entire ring (NTR), mean cross-sectional vessel area in the earlywood (ME) and in the entire ring (MTR), mean cross-sectional area of the 25% largest vessels in the earlywood (25E) and in the entire ring (25TR), density (density defined as number of vessels divided by area) of vessels in the earlywood (dE) and in the entire ring (dTR), porosity of the earlywood (pEW) and of the entire ring (pTR). As both, earlywood vessel fraction and lumen fraction are highly correlated to wood porosity (Ding et al., 2008) the porosity of the earlywood in this study was defined as the total cross-sectional earlywood vessel area divided by the earlywood area while porosity of the entire ring was defined as the total cross-sectional vessel area divided by the ring area. These ratios can also be considered equivalent to earlywood and total conductive area (Woodcock, 1989).

In order to reduce the possible effect of stem eccentricity, average values of the two cores were calculated for all variables. García-González and Fonti (2008) demonstrated that climatic signals of cross-sectional earlywood vessel areas in sessile oak (*Q. petraea* (Mattuschka) Liebl.) and Spanish chestnut (*Castanea sativa* Mill.) were improved when values of two cores were pooled rather than used individually. Averaging the 25% largest vessel area was taken from García-González and Fonti (2006) who showed that the mean vessel area of larger sized earlywood vessels may contain climatic information that differs from those of smaller sized earlywood vessels. For all above procedures the software package SYSTAT v.11 (Systat Software Inc., 2004) was used.

To produce chronologies, each of the time-series was standardized using a cubic spline function with a 50% frequency response of 60 years. Following standardization, autoregressive modeling was performed to remove autocorrelation, if present. In presence of temporal autocorrelation, the overestimation of the number of degrees of freedom has for consequences that non-significant results might be falsely identified as significant (Legendre and Legendre, 1998). In this study, standard chronologies were used when temporal autocorrelation was found to be non-significant and residual chronologies were used when temporal autocorrelation was found significant. In order to further enhance the common signal, all chronologies were developed using a biweight robust mean. To evaluate the statistical quality and the signal strength of each of the 15 chronologies, the expressed population signal (EPS), the percent variance of the first principal component (PC1) and the mean correlations between trees (Rbt) were calculated. The quality of a chronology is thought to be sufficient if an EPS value of 0.85 has been reached (Wigley et al., 1984). For all above procedures the program ARSTAN Windows (v. 4.0a; Cook, 1985) was used.

All 15 chronologies from Lake Duparquet were subjected to principal components analysis (PCA) using CANOCO v. 4.52 (ter Braak, 1994) to assess their intercorrelation structure. The PCA was carried out using the chronology time span of 1915–2005. In order to decrease the emphasis that chronologies of higher variance have on the separation of the descriptors in the PCA space, all chronologies were equally weighted by using a correlation input. The broken stick model was also used to determine the number of meaningful components to interpret (Legendre and Legendre, 1998).

2.5. Climatic and hydrological data

Monthly climate data for the study area were obtained using the BioSIM weather generator (Régnière and Bolstad, 1994; Régnière et al., 2014) for the period 1914–2005. At any time, the best four weather stations closest to floodplain site 3 (Fig. 1) were used to develop monthly total precipitation and monthly mean temperature. It should be noted that the choice of the best four climatic stations for any given year is made from the list of available stations which vary in time due to station operation time (Régnière et al., 2014). In this study, the closest station for any given year was located on average 30 km (±20 km SD) from Lake Duparquet. In addition, the daily temperature and precipitation data generated from BioSIM were used to calculate the Canadian Drought Code. These daily drought indices were averaged to produce monthly indices for May to September over the time span 1915–2005. This index rates the moisture content of deep organic layers by taking into account stored moisture content, evapotranspiration and precipitation (Girardin and Tardif, 2005).

Hydrological data were acquired from the Water Survey of Canada (2015). Daily and monthly discharge data for the unregulated Harricana River (Harricana River watershed) were obtained. Lake Duparquet (Abitibi River watershed) is located approximately 85 km west of the Harricana River (Fig. 1). A former study had shown good agreement between Harricana River spring discharge and Lake Duparquet spring water level (Tardif and Bergeron, 1997b). In addition, hydrological data specific to Lake Duparquet were also used for comparison. These included both ice-scar frequency and maximum height from Tardif and Bergeron (1997a), a short-term water-level series from Denneler et al. (2010) and observational ice break-up dates from Mongrain (2014). Additionally, discharge data were obtained from another six unregulated hydrological stations distributed in an approximately 60,000 km^2 territory (Table 1; Fig. 1).

The associations between the first two principal components (PCs) and tree-ring chronologies with the climatic and hydrological variables were determined using Spearman rank correlations

Table 1
Name and location of the hydrological stations used to assess the spatial coherence in the correlation structure between the mean vessel area chronology (ME) and discharge data. The distance to Lake Duparquet is indicated as well as the drainage area and the operation period. All rivers are unregulated. The Harricana River discharge data was pooled into a single time series given the absence of difference in discharge for the overlapping period. The hydrological stations are also indicated in Fig. 1.

Station Name	Id	Distance (km)	Latitude	Longitude	Drainage area (km^2)	Period
Turgeon River	04NA003	~165	49°59′	79°5′	11,200	1968–2001
Harricana River	04NA002	~85	48°34′	78°7′	3680	1914–1933
Harricana River	04NA001	~85	48°36′	78°6′	3680	1933–2005
Kinojevis River	02JB013	~32	48°22′	78°51′	2590	1965–2005
Kinojevis River	02JB003	~67	48°27′	78°21′	1680	1936–1966
Kinojevis River	02JB004	~67	48°24′	78°21′	984	1938–1972
Blanche River	02JC008	~80	47°53′	79°52′	1780	1968–2005
Kipawa River	02JE015	~156	47°4′	79°18′	NA	1962–2005

unless indicated. Associations of both, PCs and tree-ring chronologies with hydro-climatic data were determined from April of the year prior to ring formation to August of the year of ring formation and for the time period 1915–2005. Hydro-climatic data included monthly mean temperature, monthly total precipitation, monthly drought code and monthly mean discharge data. Seasonal and annual scale analyses were also conducted. Other hydrological flood proxy specific to Lake Duparquet included ice-scar chronologies (frequency and maximum height; Tardif and Bergeron, 1997b) and dates of ice break-up from 1968 to 2014 (Mongrain, 2014). Wavelet Coherence (WTC) was also calculated from the Continuous Wavelet Transform (CWT) of selected time series to determine their local correlation in time frequency space (Grinsted et al., 2004). In these analyses, the estimation of the significance level was determined from 10,000 Monte Carlo iterations.

3. Results

The chronology statistics indicated that both ring-width and vessel chronologies (Fig. 2) had a high common signal (Table 2). Among all chronologies, earlywood width showed to be the least reliable with an Rbt value of 0.21 and an EPS value of 0.84. All other chronologies had much higher values with EPS values above 0.90 indicating a high amount of shared variance. Among the vessel chronologies ME, MTR, 25E and 25TR recorded the highest values for percent variance in PC-1, EPS and Rbt (Table 2).

3.1. Correlation structure among chronologies

In general the vessel chronologies developed from the earlywood and the entire ring presented less year-to-year variability than latewood or total ring width (Fig. 2). Despite this lower variability, the earlywood vessel number and vessel area chronologies showed highly pronounced peaks and troughs over the period 1915–2005. Notable years in which earlywood vessel chronologies showed high deviations from the mean were observed in 1917, 1922, 1928, 1947, 1950, 1960, 1967, 1979, 1989 and 1996. In these years, tree rings showed a visually easily detectable pattern of increased number of earlywood vessels with dramatically reduced area while no consistent increases or decreases in EW or LW were observed (Fig. 2).

The PCA first and second components explained respectively 59.0% and 27.1% of the total variance (Fig. 3). The third component representing 9.9% of the total variance did not meet the broken stick model threshold of 12.5% and will thus not be presented. The PC-1 was mainly reflective of earlywood vessel chronologies while those related to widths (EW, LW, RW) and to lesser extends pTR and dTR had high loadings on PC-2. The vectors associated with the NE and NTR chronologies showed a near 180° angle with those of ME, MTR, pE, 25E and 25TR indicating that tree rings with a high number of earlywood vessels were characterized by small cross-sectional (Fig. 3). Such rings were also associated with low porosity/conductive area (pE, pTR) and high vessel density (dE, dTR). The yearly PC-1 scores also depicted low (high) values for vessels area (number) chronologies in years 1917, 1922, 1928, 1947, 1950, 1960, 1967, 1979, 1989 and 1996 (Fig. 3).

3.2. Associations between tree-ring chronologies and hydro-climatic data

Compared to vessel chronologies (area and number), the width chronologies (EW, LW, RW and PC-2) showed few, if any,

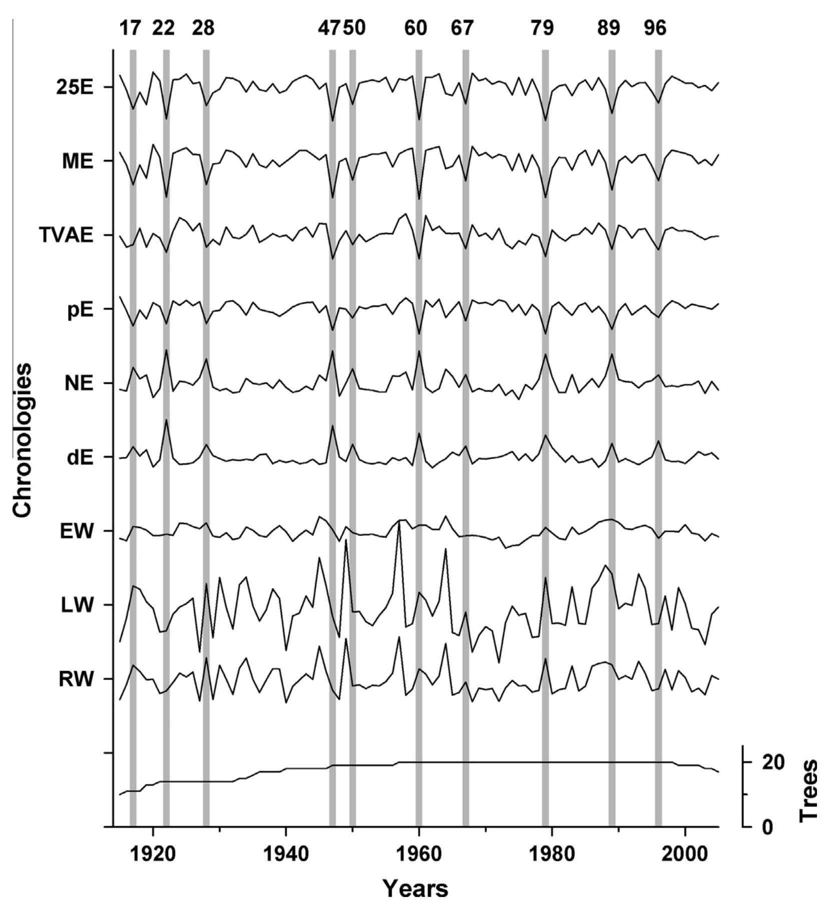

Fig. 2. The 15 chronologies developed from *Fraxinus nigra* trees growing on the floodplain of Lake Duparquet. The number of trees included is indicated at the bottom. Years for which anatomical show important deviations from their respective mean value are highlighted in grey. Chronologies are abbreviated as in Table 2.

Table 2
General statistics characterizing the standard (S) or residual (R) tree-ring widths and vessel chronologies generated from 20 trees from the Lake Duparquet. The chronologies cover the period 1890–2006. Abbreviations are as follow: first principal component (PC-1), expressed population signal (EPS); earlywood width (EW); latewood width (LW); total ring-width (RW), number of vessles in earlywood (NE) and in the entire ring (NTR); total cross-sectional area of vessels in the earlywood (TVAE) and in the entire ring (TVATR); mean cross-sectional vessel area in the earlywood (ME) and in the entire ring (MTR); 25E, mean cross-sectional vessel area of the 25% largest vessels in the earlywood (25E) and the entire ring (25TR); density of vessels in the earlywood (dE) and the entire ring (dTR); porosity of the earlywood (pEW) and of the entire ring (pTR).

	Mean[a]	Standard deviation	Auto-correlation[b]	Variance in PC-1 (%)[c]	EPS[c]	Intertree Correlation (Rbt)	Type[d]
EW (mm)	0.52	0.07	0.48	28	0.84	0.21	R
LW (mm)	0.56	0.36	0.12	45	0.92	0.36	S
RW (mm)	1.1	0.19	0.17	48	0.93	0.44	R
NE	38	0.14	0.12	57	0.96	0.53	S
NTR	43	0.15	0.11	59	0.96	0.54	S
TVAE (10^4 μm^2)	62	0.12	0.19	53	0.95	0.49	R
TVATR (10^4 μm^2)	64	0.12	0.22	52	0.95	0.49	R
ME (10^4 μm^2)	1.7	0.17	−0.05	67	0.97	0.64	S
MTR (10^4 μm^2)	1.5	0.17	−0.07	68	0.97	0.65	S
25E (10^4 μm^2)	2.6	0.15	−0.05	67	0.97	0.63	S
25TR (10^4 μm^2)	2.5	0.15	−0.06	68	0.97	0.64	S
dE (10^{-13} mm^{-2})	1.6	0.12	−0.01	42	0.92	0.35	S
dTR (10^{-13} mm^{-2})	0.99	0.19	0.11	40	0.91	0.33	S
pE	0.26	0.10	−0.06	52	0.95	0.47	S
pTR	0.15	0.19	0.02	55	0.96	0.51	S

[a] Calculated from measurement series.
[b] Calculated from standard chronologies.
[c] Calculated from the common period 1957–1998.
[d] Type of chronology used: Standard (S) or Residual (R).

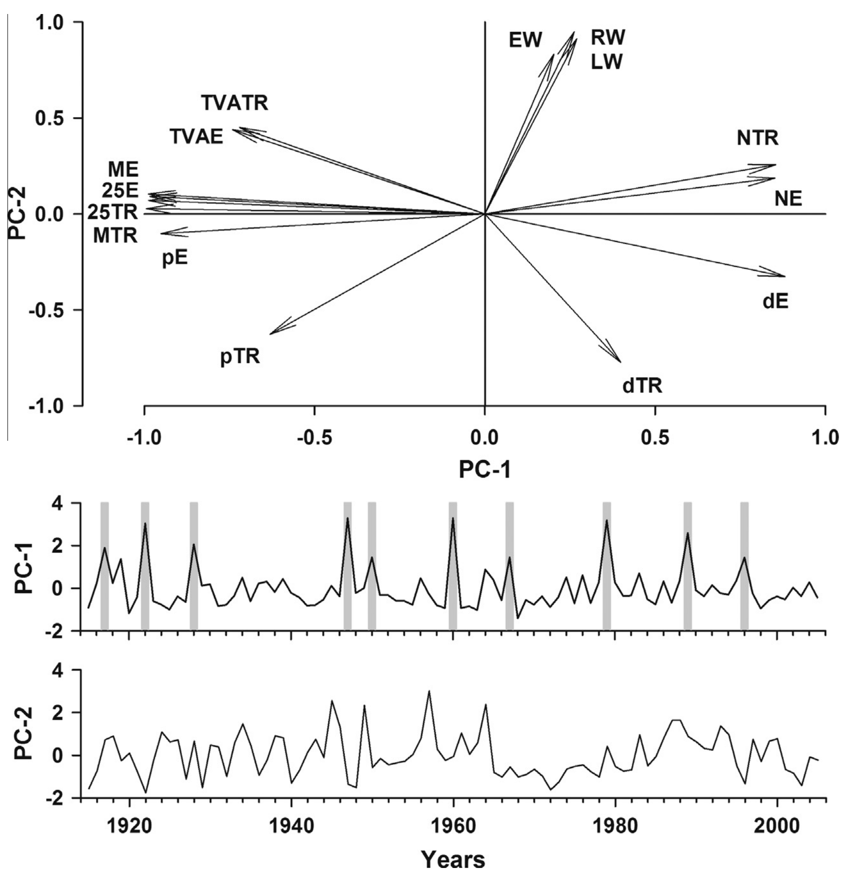

Fig. 3. Principal components analysis of the 15 tree-ring chronologies for the Lake Duparquet floodplain (top panel). The first two principal components axes are shown as well as a tree ring sequence from tree core S103–12b illustrating the changes in wood anatomy observed from 1975 to 1981 and including the flood ring of 1979. The reference period is 1915–2005. Chronologies are abbreviated as in Table 2. The bottom two panels show the year' scores associated with principal component 1 and 2 respectively. In PC-1, the year' scores that show important deviations from the mean value are highlighted in grey as in Fig. 2.

correlations with climate and hydrological variables (Fig. 4). Earlywood width was positively correlated with May (t) precipitation and negatively with both June (t) temperatures and drought code. All width chronologies (EW, LW, and RW) were also positively associated with June (t) discharge. In contrast to width, the number of associations between vessel chronologies and hydro-climatic variables was striking (Fig. 4). In the year prior to vessel formation, warm temperatures in July (t-1) were negatively correlated to

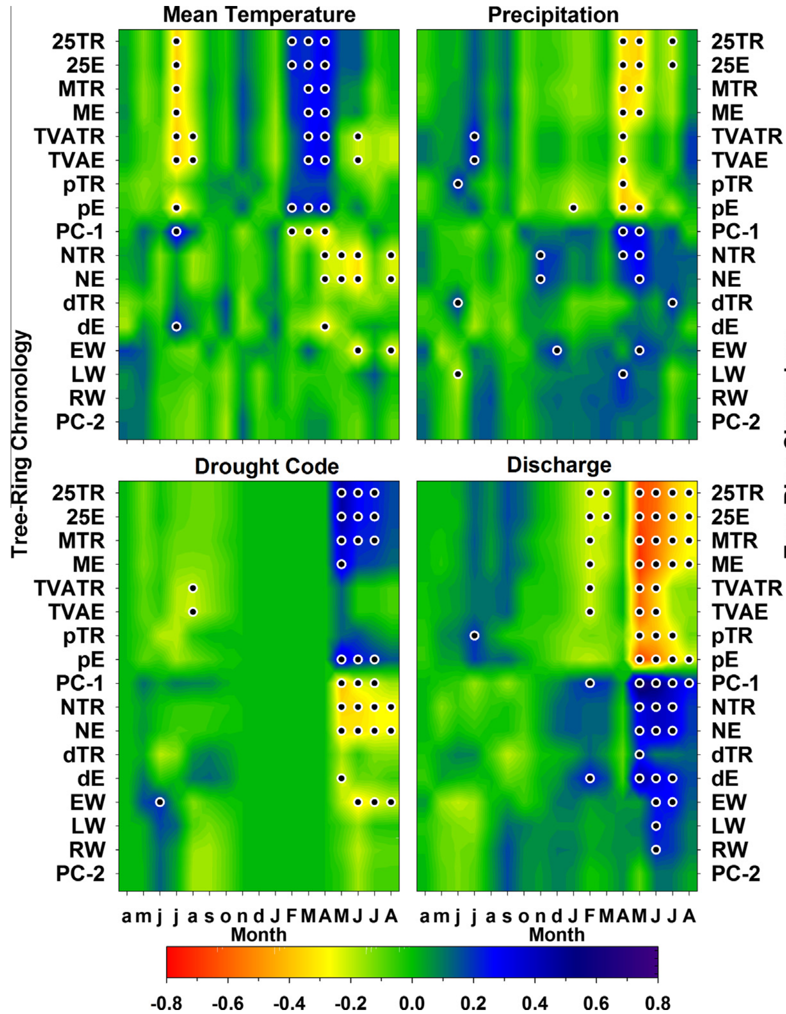

Fig. 4. Spearman rank correlation coefficients between the 15 *Fraxinus nigra* chronologies from the Lake Duparquet floodplain and mean monthly temperature (upper left), total monthly precipitation (upper right), mean monthly drought code (lower left) and mean monthly Harricana River discharge (lower right) from April of the year prior to ring formation to August of the year of ring formation and for the reference period 1915–2005. Darker blue indicates a positive correlation and darker red indicates a negative correlation. Significant ($p < 0.05$) correlations are denoted by black circles with white border. Chronologies are abbreviated as in Table 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

earlywood vessel area chronologies (25E, ME, TVAE, pE) with the inverse association with PC-1 and dE. Strong coherency was also observed with late winter (t) temperatures (February to April) being positively correlated with vessel area chronologies (Fig. 4). The vessel area chronologies were also negatively associated with February (t) discharge while dE and PC-1 showed the inverse relationship. In addition, 25E and 25TR were negatively related to March (t) discharge (Fig. 4).

The strongest associations between vessel chronologies and climatic variables were observed in the months of April (t) and May (t) with correlations with discharge showing a one-month lag (May and June). April (t) mean temperature had a positive association with vessel area chronologies and the inverse association with vessel number (Fig. 4). In contrast April (t) precipitation had the opposite association with abundant precipitation favoring vessels with smaller area. Total precipitation in May (t) was also negatively correlated to vessel size with correspondent association with May (and subsequent months) discharge data. The opposite associations were found with the drought code indicating that in year with dryer conditions in May (and subsequent months), the earlywood vessels tend to be of larger area and less numerous (Fig. 4). Looking specifically at the correlation with PC-1, the results indicates that warm February (t) to April (t) conditions, wet April (t) and May (t) with low drought index, high discharge in May (t) and June (t) were all positively associated with numerous but smaller earlywood vessels. In contrast, dry conditions in May (t) and June (t) were associated with the production of larger but less numerous earlywood vessels (Fig. 4). The TVAE, TVATR, ME, MTR, 25E, 25TR, pE and pTR chronologies were negatively and significantly correlated to May (t) and June (t) discharge with Spearman rho ranging in May from −0.40 to −0.72 ($p < 0.001$, $n = 91$) and in June from −0.37 to −0.59 ($p < 0.001$, $n = 91$) (Fig. 4). Among these correlations, the strongest one was found between ME and May (t) discharge (Spearman rho = −0.72, $p < 0.001$, $n = 91$). Using the cumulative discharge above 125 m^3/sec from mid-April to mid-June slightly increase the overall correlation (Spearman rho = −0.74, $p < 0.001$, $n = 91$).

Furthermore, the strength of the correlations between vessel chronologies (ME, TVAE, PC-1) and hydro-climatic variables were maintained when using seasonal and annual data (Table 3). The strongest negative correlations were again observed between vessel chronologies and spring discharge. Total spring precipitation was also negatively correlated to vessel chronologies with mean spring temperature showing an inverse correlation (Table 3). Mean vessel area is maximized in warm spring years accompanied by limited precipitation and discharge. This negative association between

Table 3
Spearman correlations between selected vessel chronologies and seasonal hydroclimatic variables. The number of observation varies between 89 and 91. Significant correlations are indicated in bold and correspond to the following *p*-values: $^{*}p \leqslant 0.05$ and $^{**}p \leqslant 0.01$. ME: Mean earlywood vessel area, TVAE: Total earlywood vessel area, PC-1: First principal component, PC-2: Second principal component.

	Fall (SON)	Winter (DJF)	Spring (MAM)	Summer (JJA)	Annual (S-A)
Harricana discharge					
ME	0.087	−0.103	**−0.582****	**−0.445****	**−0.407****
TVAE	0.015	−0.092	**−0.452****	**−0.285****	**−0.365****
PC-1	−0.065	0.112	**0.559****	**0.484****	**0.426****
PC-2	0.108	0.050	−0.005	0.089	0.075
Mean temperature					
ME	0.114	0.023	**0.353****	−0.001	0.197
TVAE	0.090	−0.079	**0.316****	**−0.265***	0.049
PC-1	−0.139	−0.039	**−0.349****	−0.028	**−0.227***
PC-2	−0.022	−0.084	0.066	−0.081	−0.095
Total precipitation					
ME	−0.005	−0.188	**−0.440****	−0.079	**−0.256***
TVAE	0.006	−0.058	**−0.224***	0.121	−0.027
PC-1	0.037	**0.215***	**0.486****	0.125	0.317*
PC-2	0.027	0.132	0.169	0.109	0.163

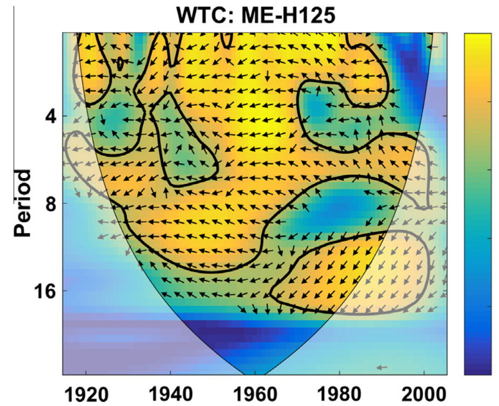

Fig. 5. Wavelet coherence between the mean vessel area chronology (ME) and the Harricana River cumulative discharge above 125 m^3/sec from mid-April to mid-June. A high degree of dependence is observed between the two variables. The relative phase relationship is shown as arrows with the significant sections showing anti-phase (arrows pointing left).

spring high flows and vessel development was also coherent over a large territory. Vessel chronologies (ME and PC-1) were significantly and negatively correlated with unregulated May discharge data from seven hydrological stations distributed within an area approximatively 60,000 km^2 (Table 4; Fig. 1). In addition to the spatial domain, high coherence was also observed in the frequency domain (Fig. 5). Wavelet coherence analysis revealed significant anti-phase correlation between ME and both Harricana May discharge (not presented) and cumulative discharge above 125 m^3/sec from mid- April to mid-June. The significant region in the figure indicates that ME largely mirrors the discharge data (Fig. 5).

3.3. Earlywood mean vessel area and Lake Duparquet's hydrology

The Harricana River hydrograph and Lake Duparquet water level measured during the growing season of 1989–1991 indicate that long lasting high river flows in the spring months were associated with lasting high flood level (Fig. 6). This was the case in the spring of 1989 with the lake water level on June 20th being about 1.25 m above that recorded in 1990 and 1991. In 1989, the long lasting flood affected vessel development in *F. nigra* trees (Fig. 6). Similarly to 1989, the years 1917, 1922, 1928, 1947, 1950, 1960, 1967, 1979, and 1996 previously identified as years with low ME values largely corresponded to years with high spring discharge with the exception of 1950 and 1996 (Fig. 7 upper panel). Of these years, 1979, 1989 and especially 1996 corresponded to a late ice break-up date (Fig. 7, upper panel, inverted bars). As a general trend, the ME chronology was negatively associated with the Lake Duparquet break-up date (Spearman rho = −0.36, n = 39, p < 0.01); the latter being positively associated with May discharge (Spearman rho = 0.48, n = 47, p < 0.01; Fig. 8). Among all years, the year 1974 stand out as one being characterized by both a late ice break-up date and high discharge but vessel area while reduced was not dramatically decreased (Fig. 7 upper panel). The years 1890 and 1909 given their departure from the ME chronology's mean may also be of high magnitude spring floods. From 1890 to 1910 the sample depth ranged from 3 to 10 trees (Fig. 7 lower panel). With EPS values of 0.85 being attained with 3 trees and 0.97 with 10 trees indicating strong signal strengths at both sample depths. The strong decrease observed in the mean vessel area of all three trees in 1890 (Fig. 7) was also from trees that originated in 1864 precluding that the small vessel areas observed in 1890 were related to an age (juvenile) effect.

In contrast to the associations with ice break-up date and discharge, those between ME and both ice-scar frequency and maximum scar height were weaker (Fig. 7 middle panel). Many years of abundant ice scars however corresponded to reduce ME values i.e., 1890, 1917, 1922, 1947, 1967 and 1979. A significant negative correlation was observed between ME and both ice-scar frequency and maximum height (respective Spearman rho = −0.33 and −0.57; n = 101; p < 0.001). The Harricana River May discharge was positively associated with both ice-scar frequency and maximum ice-scar height (Fig. 8). Further analysis of the association between the discharge data and ME indicated that their association was largely linear (Fig. 8). Mean earlywood vessel area was also the flood proxy with the strongest relationship to discharge. Using discharge as the dependent variable, adjusted r square values of 0.60 and 0.67 were obtained following stepwise multiple regressions (Table 5) using ME, TVAE and ice-scar frequency as independent variables (respectively for May mean discharge and cumulative discharge above 125 m^3/sec from mid-April to mid-June, n = 76, p < 0.001).

Table 4
Spearman correlation between the May discharge of seven unregulated rivers located up to 165 km from Lake Duparquet and both mean earlywood vessel area chronology (ME) and first principal component (PC-1). The significant correlations are indicated in bold. The location of the hydrological stations is provided in Table 1 and Fig. 1.

Station	Station ID	Period	*n*	Coefficient		*p*-value	
				ME	PC-1	ME	PC1
Turgeon River	04NA003	1969–2001	33	**−0.437**	**0.351**	0.011	0.045
Harricana River	04NA001/2	1915–2005	91	**−0.719**	**0.684**	<0.001	<0.001
Kinojevis River	02JB003	1938–1966	29	**−0.653**	**0.663**	<0.001	<0.001
Kinojevis River	02JB004	1939–1972	34	**−0.620**	**0.636**	<0.001	<0.001
Kinojevis River	02JB013	1968–2004	42	**−0.766**	**0.764**	<0.001	<0.001
Blanche River	02JC008	1968–2005	46	**−0.665**	**0.637**	<0.001	<0.001
Kipawa River	02JE015	1963–2005	32	**−0.536**	**0.403**	0.002	0.022

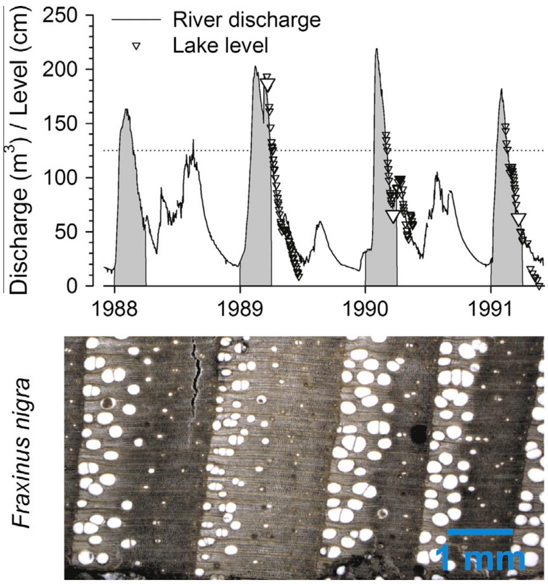

Fig. 6. Daily discharge of the Harricana River from March 1st 1988 to August 31st 1991 (top graph). The grey zones indicate the April to June period. The black triangles indicate actual measurement of Lake Duparquet water level. The white triangles refer to the water level on June 20th. It should be noted that in 1989 *F. nigra* trees closest to the lake still had their lower trunk flooded until early July. The dotted line indicates the 125 m^3/sec threshold value. The bottom picture refers to the tree rings that developed during the same time frame.

4. Discussion

4.1. Chronology statistics and intercorrelation patterns

The lower interannual variability of EW compared to LW and RW is in accordance with a previous *F. nigra* study (Tardif, 1996). This trend was also reported in numerous ring-porous species (Fonti and García-González, 2004; Corcuera et al., 2004; Tardif and Conciatori, 2006) and appears to be a characteristic inherent to ring-porous species. In accordance with other studies, LW and RW chronologies also contained a stronger common signal than the EW chronology (Tardif, 1996; Fonti and García-González, 2004; Tardif and Conciatori, 2006). Vessel chronologies in floodplain *F. nigra* trees also showed strong common signal strength and this was further highlighted in the coherent response to the hydro-climatic variables affecting Lake Duparquet spring water levels. On the floodplain, rings with high vessel density (dE) and high number of vessels (NE) tended to contain very small sized vessels with low total vessel area. These rather "diffuse-porous" earlywood vessel patterns were most pronounced in years of high magnitude spring flood.

4.2. Chronologies and hydro-climatic factors

In this study, few hydro-climatic variables were associated with tree-ring width chronologies in comparison to anatomical ones. The absence of a significant negative association between the EW and May (t) discharge was unexpected. Tardif (1996) did report a weak but significant negative relationship between the EW of *F. nigra* trees and discharge. Site specific signal may be at the origin of this difference as the trees analyzed by Tardif (1996) pertained to another location on the floodplain characterized by its lower elevation and greater flooding duration (Fig. 1, site 5 versus sites 2 and 3, respectively; Tardif and Bergeron, 1992, 1999). The strength of the correlation between the standard ring-width chronology developed in both studies (Spearman rho = 0.56, $p < 0.001$, $n = 74$) also support this site-variation hypothesis.

Alternatively coring height may also be involved with Tardif (1996) coring higher along the stem than in this study. In studies using vessel chronologies for hydrological reconstructions it may be indicated to extract cores as close to the tree base as possible. St. George et al. (2002) found that vessel flood signatures in

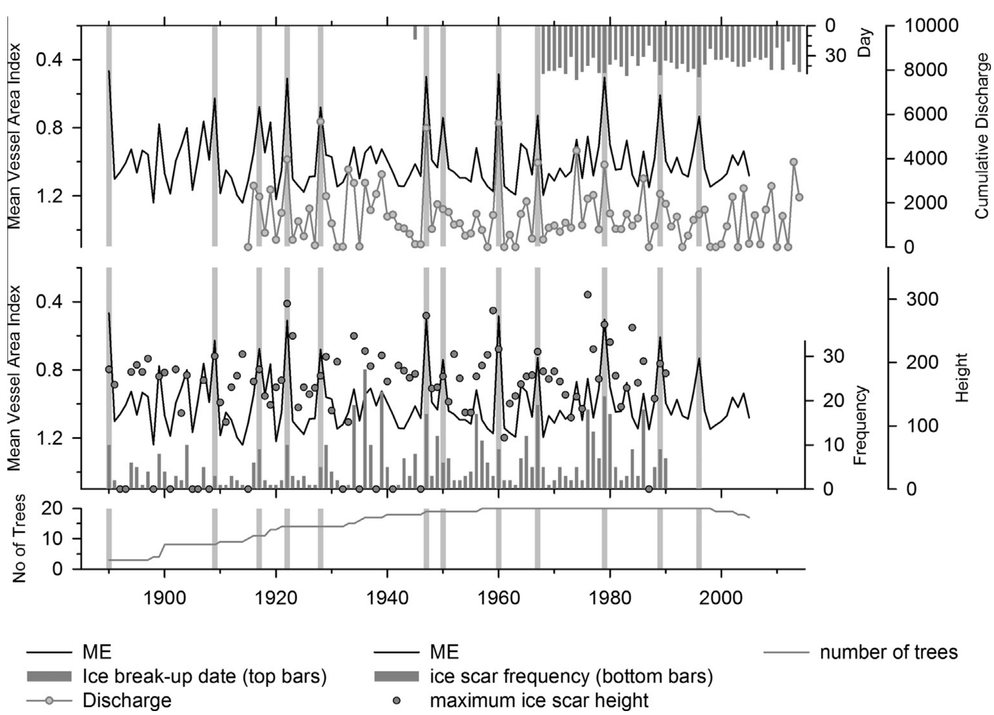

Fig. 7. Lake Duparquet ice break-up date (number of days after April 1st), mean earlywood vessel area (ME), cumulative Harricana River discharge above 125 m^3/sec from mid-April to mid-June with Lake Duparquet's ice scar frequency and maximum ice scar height (adapted from Tardif and Bergeron, 1997b). The number of *F. nigra* trees included in the ME chronology is also indicated. The ME chronology values are inverted to ease making comparison. The vertical pale grey bars indicate the years for which anatomical variables were shown to strongly depart from their mean values (see Figs. 2 and 3). The legends pertain respectively to the top, middle and bottom sub-figure.

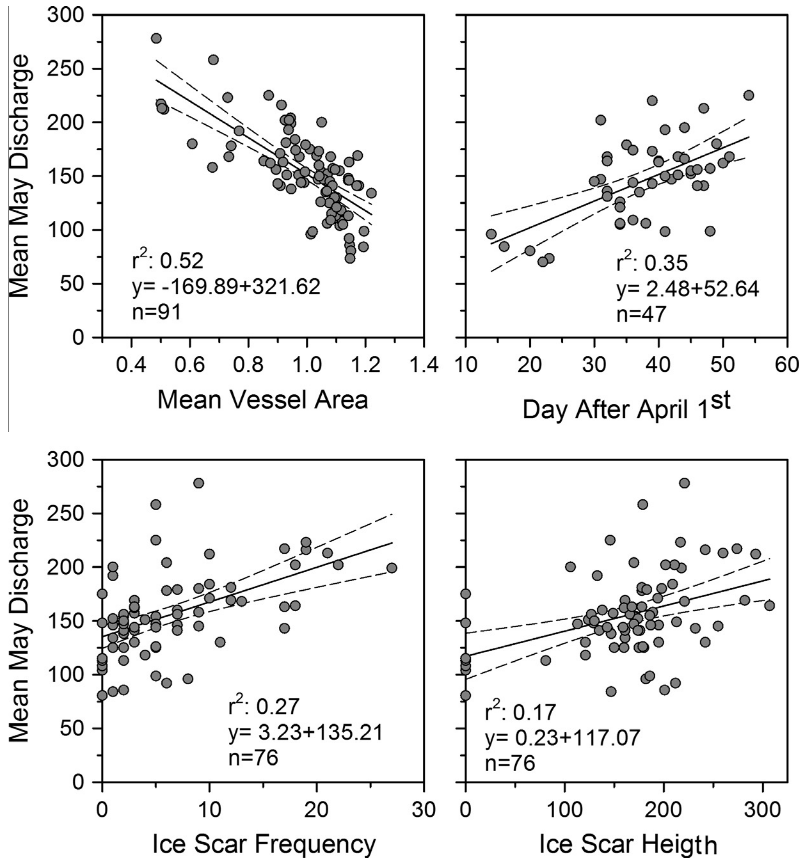

Fig. 8. Relationships between mean May discharge (m^3/sec) and mean earlywood vessel area (ME, top left), Lake Duparquet ice break-up date corresponding to the number of days after April 1st (top right), ice scar frequency (bottom left) and maximum ice scar height (bottom right) for Lake Duparquet. Included are the regression model equations and the r^2 values adjusted for degrees of freedom. The dashed lines represent the 95% confidence intervals.

Table 5
Summary of the forward stepwise regression models used to predict the Harricana discharge. The period of analysis is 1915–1990 ($N = 76$) and the entry level for each independent variable is indicated in parenthesis for each model. The model adjusted *r*-squares are respectively 0.604 and of 0.671. ME: Mean earlywood vessel area, TVAE: Total earlywood vessel area, Scar Freq: Ice-scar frequency.

Effect	Coefficient	Std error	Std coefficient	Tolerance	*t*	*p*-value	Cumulative *r*-square
A- Haricanna mean May discharge							
CONSTANT	333.677	24.938	0.000	–	13.380	0.000	–
ME (1)	−73.955	28.458	−0.331	0.326	−2.599	0.011	0.540
TVAE (2)	−114.309	34.831	−0.374	0.406	−3.282	0.002	0.585
SCAR FREQ (3)	1.385	0.542	0.222	0.702	2.557	0.013	0.619
B- Haricanna cumulative discharge above 125 m^3/sec from mid-April to mid-June							
CONSTANT	7,832.153	788.361	0.000	–	9.935	0.000	–
ME (1)	−3,569.080	899.639	−0.460	0.326	−3.967	0.000	0.628
TVAE (2)	−3,077.855	1,101.089	−0.290	0.406	−2.795	0.007	0.654
SCAR FREQ (3)	45.230	17.119	0.209	0.702	2.642	0.010	0.684

Q. macrocarpa were mostly present in the lower stem wood close to the ground whereas the flood signatures were lost if cores were taken higher along the stem. Aloni (1991) stated that in flooded stems numerous narrow vessels form below the water surface while those formed above the water surface were wider. Experimental studies with ring-porous saplings (Tardif, unpublished data; Copini et al., 2015) also support these observations.

In the present study, the mean and total vessel area (vessel number) chronologies showed a strong decrease in size (increase in number) in response to high May (t) and to lesser extent high June (t) discharge. This signal was also spatially coherent over hundreds of km^2 and across watersheds. In contrast the relationships with July (t) and August (t) discharge were much weaker and likely related to autocorrelation in the discharge data. The strong control played by spring flooding on vessel development is also consistent with mean vessel area being positively associated with May–June–July (t) drought code and negatively with April–May (t) precipitation. Abundant precipitation in April–May (t) may cause spring floods to be of higher magnitude and of prolonged duration. The importance of ice freeze-up, total snow accumulation and spring precipitations on the Lake Duparquet spring flood level (Tardif and Bergeron, 1997b) and high-boreal lakes flood level in general (Lemay and Bégin, 2008) have been well documented. All these results converge toward revealing the major role played by flood magnitude and/or duration on tree-ring development in floodplain *F. nigra* trees.

The most important factor influencing vessel number, vessel density and especially mean and total vessel area of floodplain

F. nigra trees was flooding in the spring which presumably occurred during the onset of cambial activity and vessel differentiation. In the Lake Duparquet's region, the development of first annual vessels is not likely to start prior to the end of April. In northeastern Minnesota, Ahlgren (1957) reported that *F. nigra* trees started radial growth between the first to the third week of May. In southeastern Ontario wood formation in *F. nigra* was also initiated at the beginning of May (Fraser, 1958). The importance of synchrony between earlywood vessel development and flooding was further confirmed in experimental studies. For example, experimental flooding of dormant juvenile 2-year old *F. pennsylanica* saplings for three weeks did not result in an apparent reduction of earlywood-vessel size compared to control trees whereas flooding during the onset of earlywood formation did induce a clear reduction in vessels size. No apparent reduction in vessel size was detected when flooding occurred in June at a time earlywood vessel development and leaf expansion were completed (Tardif, unpublished data). Copini et al. (2015) reported similar results with four-year-old *Q. robur* saplings.

The large decrease in earlywood mean vessel area observed in this study was also consistent with observations made for *F. americana*, and *F. pennsylvanica* (Yanosky, 1983), *Q. macrocarpa* (St. George and Nielson, 2003) and *Q. robur* (Astrade and Bégin, 1997; Sass-Klaassen et al., 2010; Copini et al., 2015). A unique feature in *F. nigra*'s response to flooding was the production of more numerous earlywood vessels when compared to dendrohydrological studies investigating *Quercus* species. The production of smaller but numerous vessels in *F. nigra* tress during spring flooding may constitute an adaptation to reduce cavitation and embolism (López et al., 2014) while still allowing water transport to shoot growth. Results from studies conducted with *Q. macrocarpa* (St. George and Nielson, 2003) and *Q. robur* (Sass-Klaassen et al., 2010; Copini et al., 2015) suggest that in these species the reduction in vessel area is not accompanied by an increase in vessel number. Therrell and Bialecki (2014) however presented microphotographs of annual flood rings in *Quercus* species displaying a wide range of anatomical anomalies and a quantitative classification of these anomalies in relation to flooding characteristics remains to be completed.

4.3. Utility of continuous vessel chronologies in hydrological reconstructions

In this study, the linear relationships between vessel chronologies and May discharge suggest that changes in vessel size and number are largely proportional to flood magnitude (height and duration). This signal was also spatially coherent across a large region of the northeastern Canadian boreal forest. No threshold discharge value above which vessels area (number) ceased to decrease (increase) was observed. Vessels may therefore not only be discrete event recorder for high magnitude floods as previously indicated (Yanosky, 1983; Astrade and Bégin, 1997; St. George and Nielson, 2002, 2003; St. George et al., 2002; Sass-Klaassen et al., 2010; Wertz et al., 2013; Therrell and Bialecki, 2015) but they also serve as a continuous proxy for hydrological records. The development of continuous ME chronologies may be best suited to reconstruct lake water levels or river discharge. It may also be a good marker to document the impact of hydrological changes on tree growth in riparian zone. As previously discussed, both (i) the synchrony between the timing of spring flooding (and its duration) and earlywood vessel development and (ii) the flood level itself in relation to stem coring height are key elements to consider when using earlywood vessels as a flood indicator. As previously observed in experimental studies (Tardif unpublished data; Copini et al., 2015) flooding of the stem needs to occur during the narrow period of earlywood development (usually 2–4 weeks) for trees to record the event. In absence of such synchrony, investigations aimed at assessing the impact of flooding on other anatomical parameters such as fiber's secondary wall thickness may be considered. More work is also needed to assess if developing continuous vessel chronologies is only valid for trees (diffuse-and/or ring- porous species) growing in close proximity to water bodies where they are exposed to spring flooding. In tree species rarely flooded, it may be that developing continuous vessel chronology also be of little utility.

One of the advantages that vessel chronologies have over dendrohydrological methods that use variables such as ring width, sprout and/or recruitment pulses to date flood years lies in the unequivocal flood signal. The correlations between ME and discharge observed in this study were also extremely high if compared to vessel or RW associations with climate obtained from the same or similar climatic regions (Tardif, 1996; Tardif and Bergeron, 1997a; Girardin and Tardif, 2005; Tardif and Conciatori, 2006). In boreal regions, ice-scar height and/or frequency chronologies have been used frequently to reconstruct spring floods (e.g. Tardif and Bergeron, 1997b; Denneler et al., 2008b; Boucher et al., 2009, 2011). Ice scars are however not a perfect flood proxy as for example years with *in situ* ice melting and little wind may induce an underestimation of spring water levels as well as years in which the flood magnitude is greatly increased due to abundant spring precipitation occurring after ice break-up (Tardif and Bergeron, 1997b). In addition, developing ice-scar chronologies requires sampling a high number of trees and scar tissues may not be externally visible thus requiring more extensive field work like felling of trees and subsequent sectioning of the stem. In some circumstances however parameters such as ice scar, cambium dieback and compression wood may be better than ring width alone to reconstruct long-term water level (Denneler et al., 2008b).

Results indicated that vessel chronologies could nicely complement ice-scar chronologies or other flood proxies when feasible for more complete hydrological reconstructions. Significant negative correlations between the floodplain ME chronology and both ice-scar frequency and maximum height chronologies were observed. In years of major ice-floods, Lake Duparquet level is often high and flooding long enough to overlap with earlywood formation and cause a decrease in the cross-sectional earlywood vessel area of floodplain *F. nigra* trees. In contrast the dissimilarity between proxies could be used to identify specific hydro-climatic contexts as both proxy types contain distinct information on flood initiation, magnitude and duration. Evaluating how wood anatomy in other ring-porous, diffuse-porous and coniferous species changes in response to flooding may be quite valuable in complementing current dendrochronological methods (see Ballesteros-Cánovas et al., 2015) use in lake level and flood reconstructions. In this context, the successful use of vessels number in cativo trees (*Prioria copaifera* Griseb.), a diffuse-porous tropical evergreen, to reconstruct the Atrato River level in Columbia (López et al., 2014) sounds promising.

5. Conclusions

The descriptive statistics of earlywood vessel chronologies developed from Lake Duparquet's floodplain *F. nigra* trees showed stronger common signal than ring-width chronologies and a greater sensitivity and response to spring flood conditions. Spring flooding during earlywood development promoted the formation of rings with numerous vessels of small mean and total cross-sectional area. In contrast to previous studies which mainly used vessel anomalies as indicators of high magnitude flood events (flood rings), the present study stresses the utility of developing continuous earlywood vessel chronologies which in *F. nigra* were linearly related with spring discharge. This association was exceptionally strong and coherent both spatially and in the frequency domain. Floodplain species such as *F. nigra* may be particularly useful in dendrohydrological reconstructions as they are annually exposed to variable spring flood events and thus do not solely record high magnitude events. Further studies are required that investigate the potential utility of vessel chronologies in other floodplain (ring- and diffuse- porous) species in dendrohydrological reconstructions.

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