

Sensitivity of Vessels in Black Ash
(*Fraxinus nigra* Marsh.) Tree Rings
to
Fire and Hydro-Climatic Variables

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ABSTRACT

Plants respond to environmental stimuli through changes in growth and development. Woody tissues store long-term environmental information since permanent morphological characteristics are the result of a combination of environmental and genetic factors that influenced wood formation. 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 offers therefore a different time resolution than ring-width because vessels in tree rings differentiate within days to a few weeks. Little information exists upon the reaction of cross-sectional vessel lumen area in ring-porous species in regards to disturbances such as forest fires and flooding. The general objectives of the thesis were thus to assess how forest fires and flooding could influence ring-width and vessel production in black ash (*Fraxinus nigra* Marsh.). The study area is located in the boreal forest of northwestern Quebec. Vessel and ring-width chronologies were generated from a *F. nigra* population growing on the floodplains of Lake Duparquet and from a nearby non-floodplain control population. The first chapter of this thesis describes earlywood vessel anomalies in *F. nigra* trees from the control site and in relation to post-fire tree-ring formation. Large reductions in cross-sectional earlywood vessel lumen areas were observed in the year following the documented 1923 forest fire. A similarly large and synchronized size decrease in cross-sectional earlywood vessel lumen area was not observed in other years and is likely related to direct injury of the trees or to alterations in environmental conditions

associated with fire. The second chapter of this thesis was undertaken to determine the impact of climate and spring flooding on earlywood vessel characteristics. Vessel and width chronologies were related to current and previous year's climatic conditions. The mean vessel area chronology developed from the floodplain trees was most strongly and negatively related to spring discharge whereas no control chronologies were associated with spring discharge. Until this study, anomalies in vessels were mainly used to identify discrete flooding events. The association between floodplain vessel characteristics and spring discharge was unique as well as the strength of this association for boreal tree species. The linear nature of this relationship also makes it possible to use vessels characteristics in floodplain *F. nigra* for dendrohydrologic reconstructions prior to instrumental data.

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1.0 General Introduction

1.1 Dendrohydrology and Climate Change

The global mean surface temperatures has been estimated to have increased by $0.76^{\circ}\text{C} \pm 0.19^{\circ}\text{C}$ from 1850 to 2005 (Trenberth et al. 2007). The greatest warming trends regarding surface air temperatures have been observed since 1979 in the Northern Hemisphere during the months of December to May (Trenberth et al. 2007). Temperature over landmasses have warmed at the highest rate but the ocean temperatures have also increased, up to thousands of meters in depth, and the increase in ocean surface temperature has affected atmospheric circulation patterns (Trenberth et al. 2007). Apart from increases in atmospheric and ocean surface temperatures, global warming is evident from the melting of polar and glacial ice and rising sea level (Bates et al. 2008). In order to comprehend these and other trends associated with climate change, paleoclimatic data are needed for the reconstruction of past climate patterns and the development of future models. Climate data that extend historical records have been partly obtained through the analysis of precisely dated tree rings (e.g. Fritts 1976; Hughes et al. 1982; Briffa et al. 1990; Cook 1995; Schweingruber 1996). Tree rings are formed through the activity of the vascular cambium, a secondary meristematic tissue located between the phloem and xylem which is observed in the stems, branches and main roots (Nultsch 2001; Pallardy 2008). Since the cambial activity may be strongly influenced by climatic factors which are displayed in tree-ring parameters, the correlation between annual wood features and climatic conditions can be used to extend historical climate data.

The analysis of precisely dated tree rings can not only provide climatic information but also information that is related to hydrologic events, for example, lake water level fluctuations (Stockton and Fritts 1973), river flows (Wendland and Watson-Stegner 1983; Meko and Graybill 1995; Clague et al. 2003; Boucher et al. 2006) and flooding events (Tardif and Bergeron 1997*a, b*; Bégin 2000; Tardif et al. in press) which defines the field of dendrohydrology. Such analysis of tree rings may provide useful hydrological data which are needed for example to develop flood risk assessments (Knox 2003).

Hydrometeorological data often do not cover sufficiently long time spans that allow for an assessment of the probability of extreme floods occurring in the future (Knox 2003).

Therefore, paleohydrologic data, which may be derived from dendrochronological methods, may be incorporated into flood frequency analyses. The modeling of future flood events is especially important in the context of climate change, for example, in order to understand how global warming may alter hydrological processes (Huntington 2006). The observed increase in temperature has already affected the hydrological cycle since processes by which water moves, such as evaporation, are positively correlated to temperature (Huntington 2006 and references therein; Trenberth et al. 2007). Significant melting of snow cover, glaciers and ice caps in many regions has led to changes in freshwater storages and has contributed to increases in sea level and changes in runoff (Bates et al. 2008). Decreases in frozen ground volume have affected the stability of land surfaces and alterations in precipitation patterns are also evident in many parts of the globe (Bates et al. 2008). On a very general scale, areas that had been dry become drier while areas that had been wet become wetter (Dore 2005). For example, the southwestern U.S. (Cook et al. 2007) and many other regions in the world, including the Sahel, the

Mediterranean, southern Africa and large parts of southern and western Asia have become drier (Trenberth et al. 2007). High latitude regions in the Northern Hemisphere have overall experienced increases in precipitation (Huntington 2006 and references therein). In Canada, the annual temperature has increased by more than 1.3°C since 1948, with highest increases observed in the Yukon and the Northwest Territories (Warren and Eggington 2008). During the past 50 years Canada has experienced an increase in precipitation of approximately 12% with largest increases observed in several areas of southern and eastern Canada (Zhang et al. 2000; Warren and Eggington 2008). However, since precipitation patterns vary more spatially than temperature, they are more problematic to predict, and require regional hydrologic data for the development of models (Gregory et al. 2006; Trenberth et al. 2007).

Changes in lake and river water levels and associated flood events are related to precipitation patterns. Since these changes may affect the activity of the vascular cambium, the dendrohydrological analysis of riparian trees may be used to reconstruct changes in regional precipitation. Tree rings of trees growing near river beds, peat bogs or on lakeshores may all provide paleohydrological data (Schweingruber 1996).

Fluctuating water levels can leave distinct datable evidence in the wood which may include changes in ring-widths (Stockton and Fritts 1973; Stockton 1975; Fritts 1976; Tardif and Bergeron 1993; Tardif 1996) and growth alterations such as wood anatomical anomalies (Sigafos 1964; Yanosky 1983; Astrade and Bégin 1997; St. George and Nielsen 2000, 2002, 2003; St. George et al. 2002), the development of scar tissues (Hupp

1988; Tardif and Bergeron 1997*b*; Bégin 2000, 2001), reaction wood (Lepage and Bégin 1996) or new roots or stems (Sigafos 1964; Hupp 1988).

The dendrohydrological analysis of precisely dated tree rings offers the potential to reconstruct floods if the magnitude and/or duration is sufficient to affect cambial activity whose sensitivity to fluctuating water levels may differ among species. For example, lake water level fluctuations have been reconstructed through tree-ring chronologies of white spruce (*Picea glauca* (Moench) Voss) showing abnormally small tree rings as a result of flood induced stress (Stockton and Fritts 1973). Such a relation to flooding can be made since tree rings of floodplain trees growing on moist alluvial sites usually exhibit little yearly variation except if growth reductions occur due to high magnitude floods (Yanosky 1982*a*) or floods of exceptionally long duration (Astrade and Bégin 1997 for diffuse-porous species). However, temperature and temperature induced drought stress may also lead to narrow rings (Woodcock 1989*a*; Cook 1995; Orwig and Abrams 1997; Corcuera et al. 2004*a, b*; Girardin and Tardif 2005). Therefore, hydrologic events may not be unambiguously reconstructed from tree-ring-widths in regions with greatly varying water and temperature stresses (Bégin 2001). In addition, a single high magnitude flood may cause unusually small tree rings to be formed for a number of years resulting in a series of narrow rings which might also be seen as multiple flood events, complicating the identification of single or several floods (Yanosky 1982*a*). Other problems of dating floods may arise through dating via usage of age determination of sprouts originating from trees whose aerial parts were severely damaged during flooding (Sigafos 1964). Since sprouting may occur only a year following a flood, an annual identification of the

flood event is not possible (Yanosky 1983). In addition, other events such as windthrow might also account for sprouting and need to be considered when establishing flood records (Yanosky 1983).

Because of the potential limitations that may be encountered using tree-ring widths alone to reconstruct floods, it has been suggested that geomorphic disturbances that accompany such events be used to precisely date floods (e.g. Yanosky 1983; Bégin 2001). On a population level, hydrologic events such as floods of given frequencies and/or magnitudes influence forest stand dynamics, species composition and distribution by altering sediments and exposing vegetation to mechanical and physiological stresses (e.g. Yanosky 1982*a, b*; Bégin and Payette 1991; Cournoyer and Bégin 1992; Tardif and Bergeron 1992, 1997*a*, 1999). Therefore, flood occurrences, intensities and frequencies on floodplain sites can be reconstructed through the analysis of tree regeneration patterns, such as the number of successfully established seedlings (Sigafos 1964; Tardif and Bergeron 1999).

Other alternatives of gaining information about floods can be obtained from datable tree scars since flood debris may impose mechanical damage to trees and shrubs and remove parts of the bark and injure the underlying wood tissue (Schweingruber 1996).

Conversely, an absence of such erosion scars in floodplain trees may suggest drier conditions with lower water levels (Bégin 2001). Similarly, spring flood levels in colder regions can be reconstructed from ice scars resulting from ice-push injuries (Eggington and Day 1977; Bégin and Payette 1990; Tardif and Bergeron 1997*b*; Bégin 2001). The

mechanical stress of wave actions may cause trees to tilt and to form reaction wood (Schweingruber 1996; Lepage and Bégin 1996). In black spruce (*Picea mariana* (Mill.) BSP), years, in which high water levels persisted following ice break-up, easily identifiable compression wood was formed (Lepage and Bégin 1996).

Changes in river flows can be dated by analyzing sediment deposition and erosion patterns, both of which may induce changes in wood anatomy (Schweingruber 1996). For example, buried parts of the ring-porous stem wood of green ash (*Fraxinus pennsylvanica* Marsh.) develops into diffuse-porous (Cournoyer and Bégin 1992). The main erosion periods of river flows cause sediment loss which can be identified through suppression patterns originating from abrupt growth declines in tree rings of several tree species, including *F. pennsylvanica*, silver maple (*Acer saccharinum* L.), and balsam poplar (*Populus balsamifera* L.) (Bégin et al. 1991) as well as black poplar (*Populus nigra* L.) (Fantucci 2007). Erosion has also caused alterations in wood anatomy of exposed roots of *F. pennsylvanica* (Sigafos 1964) and European ash (*Fraxinus excelsior* L.) (Hitz et al. 2008). Other anatomical anomalies of vessel characteristics observed in stem wood have been described as flood rings (Yanosky 1983; Astrade and Bégin 1997; St. George and Nielson 2000, 2002, 2003) which will be discussed further below (section 1.5.3).

1.2 Wood Formation in Ring-porous and Diffuse-porous Angiosperms

Ring-porous and diffuse-porous species have been shown to react differently to environmental influences such as climate (e.g. Eckstein and Frisse 1982; Villar-Salvador

et al. 1997; Corcuera et al. 2004b) or floods (Astrade and Bégin 1997). The classification into ring-porous, diffuse-porous or intermediate stages therein is based on the size and location of vessels within a tree ring of stem wood (Panshin and de Zeeuw 1980). In diffuse-porous species, such as *Acer*, *Populus* and *Betula*, vessels formed during different months of the year cannot be distinguished based on their size but rather on their relative position within a tree ring (Panshin and de Zeeuw 1980; Pallardy 2008). Diameters of vessels range approximately from 50 to 100 μm (Zimmermann 1982). In contrast, in ring-porous species such as *Quercus*, *Fraxinus* and *Ulmus*, vessels have a bimodal distribution, with large-sized vessels of 200 to 500 μm in diameter being produced in the spring and smaller-sized vessels formed in the summer (Panshin and de Zeeuw 1980; Zimmermann 1982; Woodcock 1989b; Pallardy 2008). The bimodal vessel distribution allows for an optical distinction of wood formed early on in the year, termed the earlywood zone and one formed later on in the year, called the latewood zone.

Since vessels make up most of the water-conducting system of a hardwood tree, the different vessel formation patterns in the stem (e.g. cross-sectional vessel lumen area and density) in diffuse-porous versus ring-porous species imply different strategies to conduct water which is linked to the species water requirements and water supplied by the environment (Sperry and Sullivan 1992; Sperry et al. 1994; Tyree et al. 1994; Sperry 2003). As water conductivity increases proportionally to the 4th power of a vessel radius (Hagen-Poiseuille law), larger diameter vessels as found in ring-porous species conduct water much more efficiently than those in diffuse-porous species (Sperry and Sullivan 1992; Tyree et al. 1994). However, larger-sized vessels are also more vulnerable to

cavitation (Sperry and Sullivan 1992; Sperry et al. 1994; Hacke and Sperry 2001). Comparisons of conductivity values in stem segments of ring-porous and diffuse-porous species under normal operating xylem pressures showed an abrupt loss in hydraulic conductivity with increasing negative pressure for ring-porous species while diffuse-porous species showed a gradual decline (Hacke et al. 2006). This is attributed to the fact that, at normal operating xylem pressures, ring-porous species lose more vessel area to cavitation than diffuse-porous species. However, the remaining functional vessels in ring-porous species still conducted more water than those of diffuse-porous species, which might be an adaptive strategy that enables ring-porous species during their growing season to better exploit water resources than diffuse-porous species (Hacke et al. 2006).

Many ring-porous species experience shorter growing seasons than diffuse-porous species (Lechowicz 1984; Hacke and Sperry 2001). In many ring-porous species, leaf unfolding occurs later than for diffuse-porous species (Lechowicz 1984 and references therein) and the larger conduits of ring-porous species cavitate earlier with the first fall frosts (Cochard and Tyree 1990; Sperry and Sullivan 1992; Sperry et al. 1994). Since most of their large diameter vessels are subject to freeze-thaw induced cavitation (Utsumi et al. 1996; Hacke and Sperry 2001), it has been suggested that ring-porous species rebuild a functional vascular system prior to leaf expansion in order to supply their leaves with water (Sperry and Sullivan 1992). Contrary to this hypothesis, Zasada and Zahner (1969), Atkinson and Denne (1988), Suzuki et al. (1996) and Fonti et al. (2007) have shown that only a few earlywood vessels if any are lignified and therefore functional at the time of leaf unfolding. Since leaves may be partly or even fully developed prior to the

termination of earlywood formation (Chalk 1930; Schmitt et al. 2000) photosynthates of the current year are possibly used for the last part of the earlywood growth.

Early stem growth is, however, largely built from carbohydrate reserves stored at the end of the previous growing season (Barbaroux and Bréda 2002); therefore, climatic conditions occurring during that period are linked to earlywood production (Nola 1996; Tardif 1996). In contrast to ring-porous species, diffuse-porous species rely much less on storage reserves of the previous year for wood production (Barbaroux and Bréda 2002; Barbaroux et al. 2003). In addition, many diffuse-porous species also produce their first flush of leaves earlier than ring-porous species as they are less cavitation prone and use vessels built in previous years (Lechowicz 1984; Aloni 1991; Sperry and Sullivan 1992). Furthermore, many diffuse-porous species produce many flushes of leaves during the growing season whereas many ring-porous species often only produce one flush of leaves (Lechowicz 1984 and references therein).

1.3 Effects of Climate on Vessel and Ring-Width Parameters

Environmental stresses often lead to a decline in ring-widths in ring-porous species (Tardif 1996; García-González and Eckstein 2003; Corcuera et al. 2004*a*; Eilmann et al. 2006; Tardif and Conciatori 2006). Earlywood and latewood width have been shown to relate to different climate variables (Nola 1996; Tardif 1996). Ring-width is highly correlated with latewood width of the same year which is generally more variable than earlywood width and therefore contributes more to total ring-width variability than earlywood width (e.g. Phipps 1982; Woodcock 1989*a, c*; Tardif 1996; Corcuera et al.

2004a). However, the effect of environmental stresses on total ring-width or latewood width of a given year will negatively influence the earlywood width production of the following year (García-González and Eckstein 2003; Corcuera et al. 2004a; Tardif and Conciatori 2006). This relationship is understandable given that in ring-porous species the earlywood is mostly produced from carbohydrate reserves stored in the previous growing season (Aloni 1991; Barbaroux and Bréda 2002).

In addition to ring-widths, vessel characteristics have been suggested to be useful for dendroclimatic analysis since vessels are produced at different times throughout the growing season, and might therefore contain unique short-term climate information not found in earlywood width, latewood width or total ring-width (Eckstein and Frisse 1982; Sass and Eckstein 1995; Woodcock 1989a; García-González and Eckstein 2003; Eckstein 2004; Fonti and García-González 2004; García-González and Fonti 2006; Fonti et al. 2007). Vessel formation is under hormonal as well as environmental control but the relative influence of each on wood formation is still poorly understood (Trewavas and Cleland 1983; Lachaud 1989; Savidge 1996, 2001; Arnold and Mauseth 1999; Han 2001). Few studies have compared signals of earlywood and latewood vessel characteristics with each other (e.g. Woodcock 1989a; Pumijumnong and Park 1999; Corcuera et al. 2004a, 2006). All of these four studies showed that the cross-sectional latewood vessel lumen areas showed a greater climatic variability than the cross-sectional earlywood vessel lumen areas and that water stress during the growth period generally decreased the cross-sectional latewood vessel lumen area.

Both, temperature and water seem to influence the cross-sectional earlywood vessel lumen area, however, which of these factors has a larger impact on vessel size is subject to discussion and might depend on the species water and temperature requirements, specific climate regions and microsite conditions (e.g. Villar-Salvador et al. 1997; García-González and Eckstein 2003; Corcuera et al. 2004*a*, 2006; Fonti and García-González 2004; Tardif and Conciatori 2006). However, the majority of studies indicate that the mean cross-sectional earlywood vessel lumen area decreases if temperature is high during (i) the previous growing season and subsequent winter and/or (ii) the spring of the current growing season (Eckstein and Frisse 1982; García-González and Eckstein 2003; Corcuera et al. 2006; Fonti and García-González 2004; García-González and Fonti 2006; Fonti et al. 2007).

1.4 Utility of Vessel Chronologies to Reconstruct Climate

Despite the development of new computer technologies and semi-automated image analysis, quantifying vessel characteristics such as frequency and area is a much more time consuming process than measuring ring-widths (Gartner et al. 2002; Eckstein 2004). In order to reconstruct climate, vessel analysis is only advantageous over ring-width analysis if vessels contain unique and significant climate information not stored in the width parameters, since the latter are much more quickly obtainable (Tardif and Conciatori 2006). Wimmer (2002) pointed out that different anatomical wood features are often interdependent; therefore, vessel chronologies might yield the same climatic results as width chronologies.

Based on the differing results involving vessel and ring-width parameters, the usefulness of vessel chronologies over ring-width chronologies to reconstruct climate in any climatic region is difficult to assess. General conclusions on the utility of vessels to reconstruct climate are further complicated by the fact that no uniform filtering procedures for selecting vessels exist, which affect the definition and selection of earlywood or latewood vessels (García-González and Fonti 2006; Tardif and Conciatori 2006). Moreover, studies of ring-porous species that analyzed vessels but excluded earlywood and latewood widths cannot conclude that unique climate information can be gathered from vessel chronologies since comparisons to width parameters are lacking (Woodcock 1989a; Pumijumong and Park 1999; Schume et al. 2004; Verheyden et al. 2005). However, studies that analyzed vessel variables and ring-widths, showing for example that cross-sectional earlywood vessel lumen areas contain unique climate information also stated that this variable was not very sensitive (Fonti and García-González 2004; Fonti and García-González 2008) or was found to be too weak to be used in dendroclimatological reconstruction (Tardif and Conciatori 2006).

1.5 Other Environmental Factors Affecting Vessel Formation

1.5.1 Earlywood Vessels as Indicators of Insect Defoliation

In ring-porous species insect defoliation has been associated with decreased latewood production during the year of defoliation and anomalous earlywood vessel production in the year following defoliation (Huber 1993; Blank 1997; Asshoff et al. 1998-1999; Blank and Riemer 1999; Thomas et al. 2006). In English oak (*Quercus robur* L.) insect defoliation led to the production of smaller cross-sectional earlywood vessel lumen areas,

whereas in Spanish Chestnut (*Castanea sativa* Mill.) both, smaller sized and less abundant earlywood vessels were observed (Huber 1993; Asshoff et al. 1998-1999; Thomas et al. 2006). Studies with defoliated sessile oak (*Quercus petraea* Liebl.) were somewhat contradictory regarding cross-sectional earlywood vessel lumen areas in stem and twig wood of three year old saplings (Huber 1993; Thomas et al. 2006). Stem wood showed earlywood vessels of reduced cross-sectional lumen area (Huber 1993) whereas the analysis of twig wood showed earlywood vessels of increased cross-sectional lumen area (Thomas et al. 2006).

1.5.2 Earlywood Vessels as Potential Indicators of Forest Fires

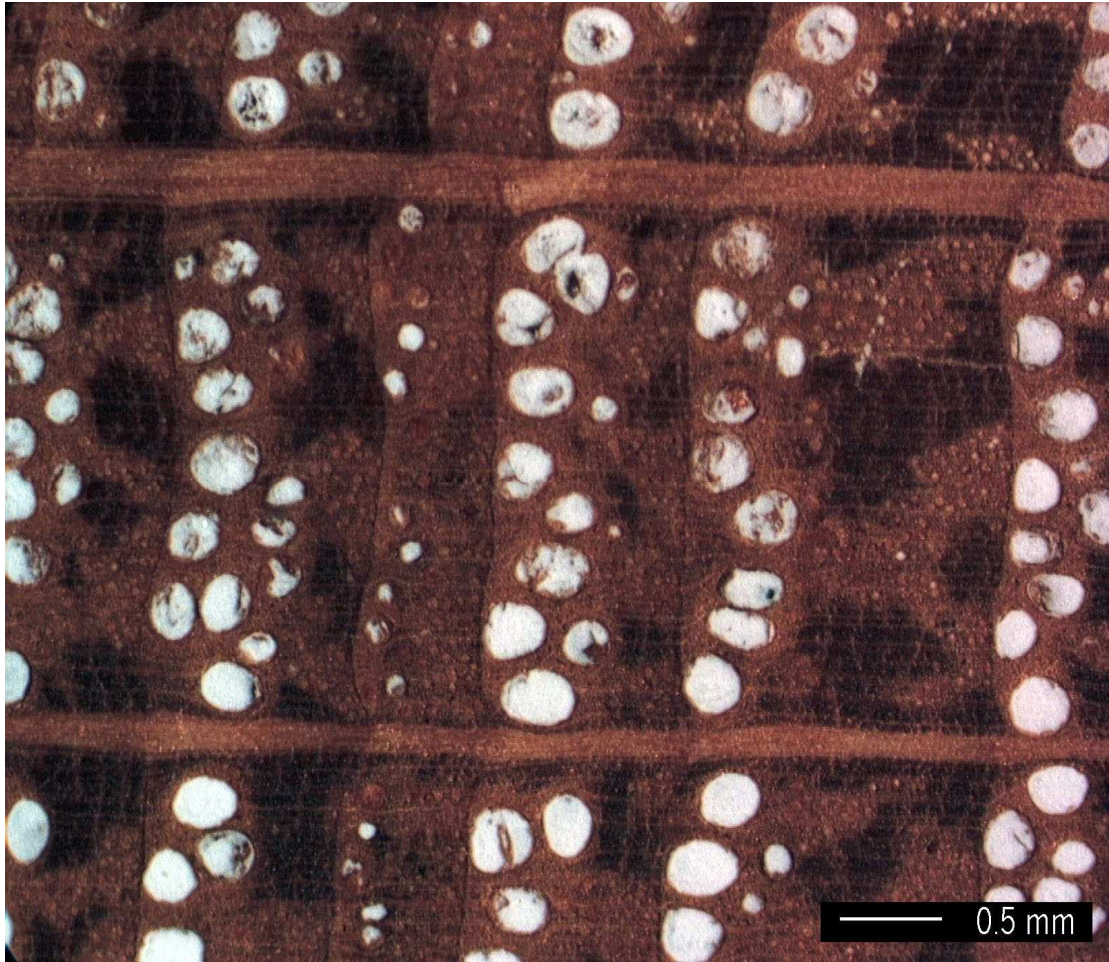
While fire scars have been described in several angiosperm species (e.g. Smith and Sutherland 1999, 2001; Guyette and Stambaugh 2004) little information exists upon the reaction vessels in ring-porous species in regards to forest fires. Schweingruber (1996, Figure 11.16d, e) reported deformed earlywood vessels produced by pubescent oak (*Quercus pubescens* Willd.) when exposed to fire during the earlywood production period. Recent studies have indicated that *C. sativa* trees bearing or not bearing fire scars reacted to forest fires by producing smaller cross-sectional earlywood vessel lumen area during the year of fire occurrence (Bigio et al. 2008). Smaller cross-sectional earlywood vessel lumen areas were also observed in unscarred *F. nigra* trees in the year following a forest fire (Kames et al. in press; Chapter 1). These studies indicate that cross-sectional earlywood vessel lumen areas may possibly be used as an additional tool in forest fire history reconstructions.

1.5.3 Earlywood Vessels as Indicators of Past Flooding

Cross-sectional earlywood vessel lumen area anomalies in ring-porous species have been best described and investigated in relation to geomorphic events such as flooding.

Changes in wood anatomy related to sediment deposition or erosion events have already been noted in section 1.1. A number of vessel anomalies have been detected in trees that were flooded during the growing season. For example, Sigafos (1964) and Cournoyer and Bégin (1992) noted in *F. pennsylvanica*, that the ring-porous nature of stem wood acquired a more diffuse-porous vessel pattern when stems were buried with sediments during a flood. In such tree rings, earlywood vessels were of decreased area whereas latewood vessels increased in size. In response to high spring magnitude flood events specific vessel anomalies were observed in the earlywood zones and tree rings showing these anomalies were termed flood rings (Yanosky 1983; Astrade and Bégin 1997; St.George and Nielson 2000, 2002, 2003; Sass-Klaassen 2008, 2009; Tardif et al. in press). These flood rings were characterized through earlywood vessels with abnormally small lumen in *Q. robur* (Astrade and Bégin 1997; Sass-Klaassen 2008, 2009), bur oak (*Quercus macrocarpa* Michx.) (St.George and Nielson 2000, 2002, 2003), white ash (*Fraxinus americana* L.), *F. pennsylvanica* (Yanosky 1983) and *F. nigra* (Tardif et al. in press). However, the majority of these studies has used vessels as pointer years to identify exceptional flood events (Yanosky 1983; Astrade and Bégin 1997; St.George and Nielson 2000, 2002, 2003; Sass-Klaassen 2008, 2009) or have only developed very short time series (Astrade and Bégin 1997).

Astrade and Bégin (1997) found a distinct flood ring in the moderately flood tolerant ring-porous *Q. robur*. Characteristic for this flood ring were one row of normal sized earlywood vessels followed by several rows of abnormally narrow earlywood vessels, as opposed to an expected additional row of regular sized earlywood vessels. Due to the additional rows of earlywood vessels the earlywood zone was greatly enlarged and a reduced latewood zone was observed. Similar to the above study, abnormally small earlywood vessels and a reduced latewood width characterized several flood rings found in the moderately flood tolerant *Q. macrocarpa* (St.George and Nielson 2000, 2002, 2003). In this case, flood rings were characterized by a reduction rather than an extension of the earlywood zone (Figure 1.1). Yanosky (1983) observed several different types of flood rings in the earlywood zones of up to 53 year old flood tolerant *F. americana* and *F. pennsylvanica* trees. As in Astrade and Bégin (1997) and St.George and Nielson (2000, 2002, 2003), most earlywood flood rings showed abnormally small earlywood vessels, however, the earlywood width varied greatly. No common response of the earlywood or latewood width can be assigned to the definition of a flood ring as these parameters varied greatly among (Yanosky 1983; Astrade and Bégin 1997; St.George and Nielson 2000, 2002, 2003) and within (Yanosky 1983) those studies. Nevertheless, the abnormally small vessel size observed in all earlywood flood rings might be the result of numerous different stresses that flooding imposes on tree growth and vessel development (see Section 1.6).



↑
1826 flood ring

Figure 1.1. Bur oak (*Quercus macrocarpa*) tree rings magnified 30x. The flood ring produced by the 1826 Red River flood is marked by an arrow and is characterized by earlywood vessels of abnormally small cross-sectional area and a marked reduction in earlywood width. Source: Courtesy of S. St. George, image taken by F. Conciatori.

1.6 Possible Reasons for Abnormal Earlywood Vessel Development

The smaller cross-sectional vessel lumen area observed in years of spring floods of high magnitude may be related to changes in hormonal concentrations. In submerged parts of the plant, flooding leads to increased concentrations of ethylene and auxin (Tang and Kozlowski 1984; Yamamoto and Kozlowksi 1987; Aloni 1991). Auxin is a key factor in regulating tracheary element formation (Uggla et al. 1996, 1998; Tuominen et al. 1995, 1997) and increases in both, auxin and ethylene have been related to decreased cross-sectional lumen area of tracheary elements (Yamamoto et al. 1987; Aloni et al. 1998; Tuominen et al. 1995; Junghans et al. 2004) and increased number of tracheary elements (Yamamoto et al.1987; Eklund and Little 1996). However, a cambial derivative that differentiates to become part of a vessel undergoes a complex sequence of developmental events until its programmed cell death (Larson 1994). Besides auxin and ethylene, cytokinin, brassinosteroids, xylogen, CLE peptides and HD-Zip genes have been shown to be involved in tracheary element differentiation (Little and Savidge 1987; Aloni 1991, 2007; Moritz and Sundberg 1996; Woodward and Bartel 2005; Turner et al. 2007 and references therein; Nilsson et al. 2008). Since the interactions of these factors and their modes of action are not fully understood, the contribution of these factors in influencing the number and size of tracheary elements during flood stress cannot be excluded.

Large forest fires commonly burn vegetation and litter which results in higher amounts of precipitation reaching and infiltrating the soil following fires (Neary and Ffolliott 2005). Hence, during the beginning of the growing season following a forest fire, trees growing in burned areas may be stressed by excess water availability. Decreases in soil water table

depth indirectly caused by forest fires or directly by lake spring flood events may cause diebacks of the root system resulting in an insufficient water supply to the shoot system (Andersen et al. 1984; Armstrong and Drew 2002; Kozlowski and Pallardy 2002). As the development of normal sized vessels partly depends on a sufficient cellular water uptake (Ray and Green 1972; Samuels et al. 2006), the smaller vessel area observed following years of forest fires or during years of flooding may be related to a lower water supply to the shoot system.

Crown damages due to forest fires and defoliation associated with forest fires and insect outbreaks may both require trees to re-foliate which has been suggested to decrease the storage carbohydrate pool of the current growing season (Blank 1997; Asshoff et al. 1998-1999; Blank and Riemer 1999; Sutton and Tardif 2005). This decrease in storage carbohydrates has further been suggested to be related to the smaller vessel area observed in the year following the defoliation (Blank 1997, Asshoff et al. 1998-1999; Blank and Riemer 1999; Kames et al. in press).

1.7 Autecology of Black Ash (*Fraxinus nigra* Marsh.)

Fraxinus nigra is a medium-sized, broadleaved hardwood species which belongs to the Oleaceae (Baas et al. 1988; Sims et al. 1990; Wright and Rauscher 1990). In Canada, its distribution ranges from western Newfoundland to southeastern Manitoba (Wright and Rauscher 1990). In these regions, *F. nigra* grows where the annual precipitation total ranges from 510 to 1140 mm, the average January temperatures is -18° to 0°C and the

average July temperature is 18° to 21°C. Further, in these regions 80 to 180 days are annually without frost and 76 to 254 cm of annual snowfall occurs.

Fraxinus nigra may form pure stands but is commonly found in conjunction with American elm (*Ulmus americana* L.) and red maple (*Acer rubrum* L.) and to a lesser extent with northern white-cedar (*Thuja occidentalis* L.), balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (P. Mill.) B.S.P.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), yellow birch (*Betula alleghaniensis* Britt.) and tamarack (*Larix laricina* (Du Roi) var. *alaskensis* (W. Wight) Raup) (Rudolf 1980; Sims et al. 1990; Wright and Rauscher 1990).

Fraxinus nigra prefers shallow or deep organic soils but also grows well on sandy soils underlain by clay that impedes drainage of water. Its shallow root system is intolerant of severe drought and adapted to mesic and hydric sites along streams, rivers, and lakes (Sims et al. 1990; Wright and Rauscher 1990). It can also be found in swamps or in depressed areas characterized by slow surface drainage patterns (Rudolf 1980). These sites are often flooded for several weeks in spring which is well tolerated by *F. nigra* given that sufficiently aerated soils are provided by moving to semi stagnant water bodies (Rudolf 1980). On sites most exposed to flooding, changes in regeneration pattern from sexual towards vegetative reproduction was observed and a higher percentage of stump sprouting than on less flooded sites may be observed (Tardif and Bergeron 1999). Seedlings show slower growth rates than sprouts in their first years of growth and are less tolerant to drought and flooding than stump sprouts (Sims et al. 1990). Further

adaptations to flooding disturbance regimes are seen in seeds that may remain dormant up to eight years (Sims et al. 1990).

Fraxinus nigra is a ring-porous species with distinct ring boundaries showing earlywood vessels that can easily be distinguished from latewood vessels based on the larger vessel size in the earlywood (Figure 1.2). Typically, 2 to 4 rows of earlywood vessels can be observed per ring, while latewood vessels may be solitary or in multiples of 2 to 3 (Panshin and de Zeeuw 1980). In comparison to other ring-porous species, *F. nigra* shows few to moderately few earlywood vessels which are approximately 150-200 μm in diameter (Panshin and de Zeeuw 1980). Fibers are usually observed in close vicinity to earlywood vessels (Panshin and de Zeeuw 1980).

1.8 Former Tree-Ring Studies in the Lake Duparquet Region

In the past 150 years, the Lake Duparquet region in the southeastern boreal forest has experienced changes in precipitation patterns and fire regimes that are likely to be caused by climate warming due to shifts in atmospheric circulation patterns following the end of the Little Ice Age (Girardin et al. 2001; Bergeron et al. 2002). In this region, fire is the most important forest disturbance (Bergeron 1991, 1998). In the Lake Duparquet region, the historical data on the fire regimes were extended using dated fire scars and results showed a significant increase in the length of the fire cycle, causing changes in vegetation patterns (Bergeron 1991; Bergeron and Dansereau 1993; Bergeron et al. 2002). This lengthening of the fire cycle is thought to be a result of decreased drought occurrences caused by increases in precipitation (Bergeron and Archambault 1993;

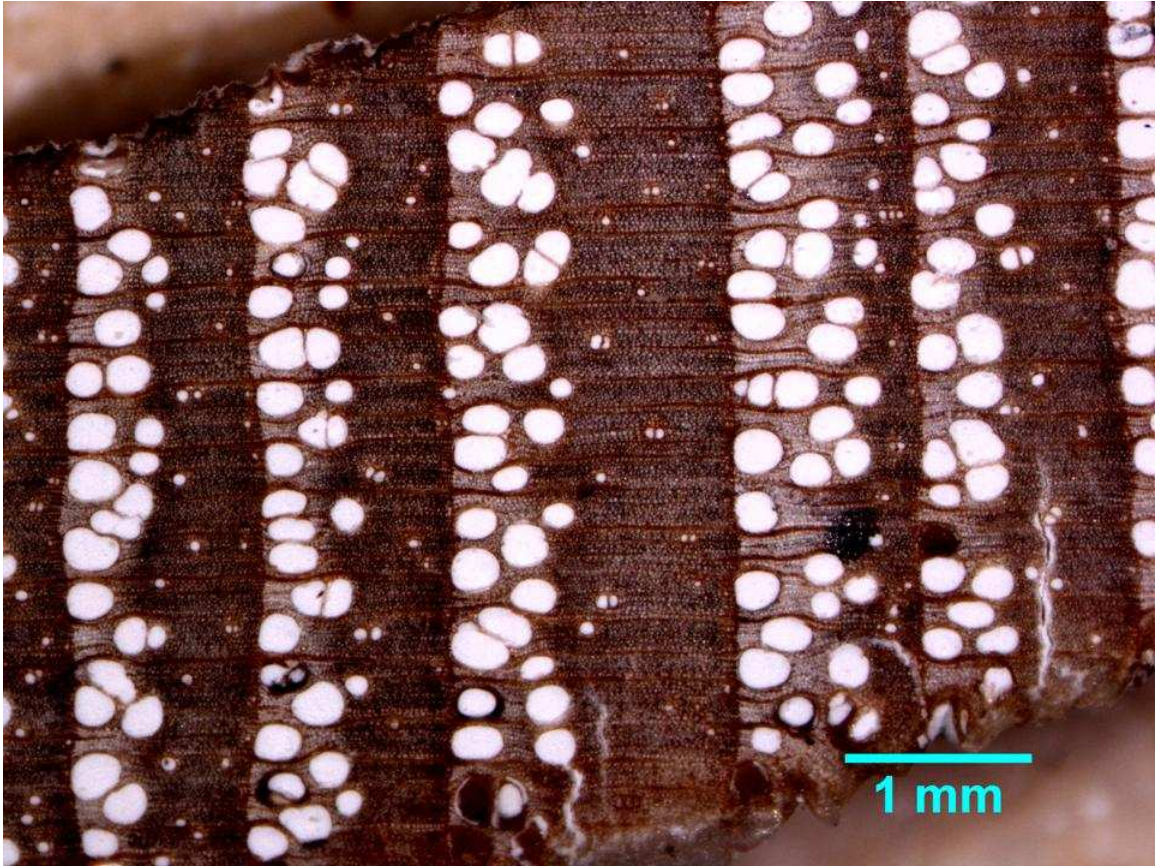


Figure 1.2. *Fraxinus nigra* tree rings magnified 20x showing distinct zones of earlywood with large sized vessels and slightly darker coloured latewood zones with smaller sized and less dense vessels. Vessels and cracks in the wood appear white since the core was rubbed with chalk.

Bergeron and Flannigan 1995).

Heavier annual precipitation as well as warmer winter and spring temperatures have also been suggested to have caused earlier spring melts and substantially more frequent major ice floods observed in the 20th century compared to the end of the Little Ice Age period (Tardif and Bergeron 1997b). In comparison to the end of the Little Ice Age, the spring lake water level has increased by a meter since 1915 which also influenced riparian forest stand dynamics (Tardif and Bergeron 1997b, 1999; Denneler et al. 2008). Since 1850, *F. nigra* has invaded the lower shore terraces thereby replacing the less flood tolerant *T. occidentalis* (Denneler et al. 2008). Contrary to what might have been expected, spring flooding has not had a negative effect on latewood width and ring-width increment of floodplain *F. nigra* (Tardif and Bergeron 1993). Since the negative relationship of earlywood width with spring lake water levels was too weak for flood reconstructions, it was suggested to investigate earlywood vessel characteristics as event indicators of high spring floods (Tardif 1996). *Fraxinus nigra* trees growing in the lake Duparquet region may be especially useful for flood reconstructions since they have been shown to frequently reach ages of 200 years (Tardif and Bergeron 1999). Anomalous earlywood vessels produced in other *Fraxinus* species during years of high spring floods (Yanosky 1983) further suggested to investigate the relationship of vessel characteristics in *F. nigra* with spring floods.

Recent work has allowed for the comparison of reconstructions of Lake Duparquet spring floods using chronologies of ice-scar frequency and maximum ice-scar height with

earlywood vessel area chronologies (Tardif et al. in press). The ice-scar chronologies were strongly negatively associated with the earlywood vessel area chronology. This result indicates that in years of well recorded ice-floods, lake water levels tend to be high during the earlywood vessel production period. The two approaches may however be used in conjunction with each other, since ice-scar as well as vessel chronologies each identified years of high discharge which were not captured by the other one.

1.9 Objectives and Hypotheses

The first chapter of this thesis describes earlywood vessel anomalies in *F. nigra* trees that survived a severe forest fire in year 1923 (Dansereau and Bergeron 1993). It was hypothesized that these earlywood vessel anomalies were associated with post-fire tree-ring development. In the second chapter the overall objective was to better understand the linkages between vessel production in *F. nigra* and the growing conditions associated with fluctuating water levels caused by spring floods. In addition, this study aimed at assessing the potential of earlywood vessel variables to reconstruct long-term hydrological changes and at addressing the utility of developing continuous vessel chronologies for hydrologic reconstructions. This is the first study to develop long continuous vessel chronologies from floodplain trees that investigates whether changes in vessel characteristics are only confined to years of high magnitude flood events. To achieve these objectives, tree-ring and vessel chronologies were developed from wood samples collected from *F. nigra* trees growing in both flooded and unflooded control sites from the Lake Duparquet region, northwestern Quebec. In addition to the traditional measurements of earlywood, latewood and total ring-width, the number of vessels and the

cross-sectional vessel area above $800 \mu\text{m}^2$ were measured in the earlywood and latewood. The comparison of the chronologies from both flooded and unflooded sites helped to assess how well the flooding signal is recorded by *F. nigra* trees.

It was hypothesized that during years with prolonged spring and early summer flooding

(1) floodplain trees would produce smaller earlywood vessels than trees not exposed to flooding,

(2) an increased number of earlywood vessels would be observed in floodplain trees compared to control trees

(3) the earlywood vessel chronologies would better reflect the spring and early summer flooding signal than earlywood width chronologies,

(4) no signal related to spring flooding would be recorded in latewood vessels or latewood width since the time of spring flooding is not concurrent with the latewood production interval, and that

(5) no unique climate information other than flood events would be contained in earlywood or latewood vessels that cannot be obtained from ring-width parameters.

2.0 Anomalous Earlywood Vessel Lumen Area in Black Ash (*Fraxinus nigra* Marsh.) as Potential Indicators of Forest Fires¹

2.1 Abstract

Earlywood, latewood, total ring width and cross-sectional earlywood vessel lumen areas were measured in 21 *Fraxinus nigra* trees located in the southern boreal region of Quebec, Canada. Two of the trees survived a severe fire in 1923 during which almost no latewood was produced. In 1924 both trees produced rings with a strong decrease in the size of the largest earlywood vessels. This synchronized size decrease in cross-sectional earlywood vessel lumen area was not observed in other years and is likely a response of the trees to either direct injury or changes in environmental conditions associated with fire. Vessel characteristics in ring-porous species have the potential to be used in conjunction with other indicators of fire to extend fire history reconstructions on a spatial scale.

Keywords: cross-sectional earlywood vessel lumen area, Fraxinus nigra, ring-porous, forest fire

¹ The content of this chapter formed the basis for a scientific publication: Kames, S., Tardif, J.C., Bergeron, Y. in press. Anomalous Earlywood Vessel Lumen Area in Black Ash (*Fraxinus nigra* Marsh.) as Potential Indicator of Forest Fires. *Dendrochronologia* 0:00.

2.2 Introduction

Numerous studies have confirmed that size and/or density of vessels in tree rings from ring-porous species are influenced by environmental factors (e.g. Woodcock, 1989a; Villar-Salvador et al., 1997; García-González and Eckstein, 2003; Tardif and Conciatori, 2006). In ring-porous species, earlywood and latewood vessels can be easily distinguished from each other based on their size difference (Panshin and deZeeuw, 1980; Woodcock, 1989b). Since these vessels are produced at different times throughout the growing season, they may also record short-term environmental information not found in other measurements such as earlywood width, latewood width or total ring width. For example, cross-sectional earlywood vessel lumen area in *Castanea sativa* Mill. trees were reported to record unique temperature signals that could be used for dendroclimatic reconstructions (Fonti and García-González, 2004; García-González and Fonti, 2006). In numerous studies, vessel anomalies in ring-porous species have been successfully used to identify discrete environmental events. For instance, cross-sectional earlywood vessel lumen area in *Quercus robur* L. were shown to be of abnormally small size following a severe winter-spring drought (García-González and Eckstein 2003). Further, earlywood vessels of decreased cross-sectional lumen area were produced in *Quercus* and *Castanea* species (*Q. robur*, *Q. petraea* Liebl., *C. sativa*) in the year following defoliation events (Huber, 1993; Asshoff et al., 1998-1999). Compared to the previous examples, cross-sectional earlywood vessel lumen anomalies in ring-porous species have been best described and investigated in relation to dendrogeomorphic events. Reconstruction of high magnitude flood events was achieved by identification of earlywood vessels with abnormally small lumen areas using both *Quercus* species (*Q.*

robur, *Q. macrocarpa* Michx.) and *Fraxinus* species (*F. americana* L., *F. pennsylvanica* Marsh., *F. nigra* Marsh.) (Yanosky, 1983; Astrade and Bégin, 1997; St. George and Nielson, 2000, 2003; Tardif et al. in press). Furthermore, decreases in cross-sectional vessel lumen area and changes in vessel distribution may be used to date sediment deposition events as ring-porous stem wood of *F. pennsylvanica* developed into diffuse-porous wood upon burial with sediments (Cournoyer and Bégin, 1992).

Although fire scars have been described in several angiosperm species (e.g. Smith and Sutherland, 1999, 2001; Guyette and Stambaugh, 2004) little information exists upon the reaction of cross-sectional vessel lumen area in ring-porous species in regards to disturbances such as forest fires. Schweingruber (1996, Figure 11.16d, e) reported deformed earlywood vessels produced by *Quercus pubescens* Willd. when exposed to fire during the earlywood production period. Bigio et al. (2008) observed slight decreases in earlywood vessel size and an increase in earlywood vessel density in tree rings of *C. sativa* trees that were produced in the year during which the trees endured a moderate intensity surface fire. We describe here earlywood vessel anomalies in *F. nigra* trees growing in northwestern Québec and associated with post-fire tree-ring development. We present evidence that fire occurrence can affect earlywood vessel production in the following year. Implications for fire history studies and dendroclimatic studies using vessel characteristics are discussed.

2.3 Materials and Methods

2.3.1 Study Area

The study site is located south of Lake Monsabrais (48°27'N, 79°25'W) near Lake Duparquet in the southern part of the boreal forest of northwestern Quebec in the Abitibi region, about 550 km north of Montreal (Tardif and Bergeron, 1997). The overall region is part of the Northern Clay Belt of Ontario and Québec (Veillette, 1994). The study area is located in the mixedwood boreal forest in the balsam fir-white birch domain where both forest fires and insect outbreaks constitute the main disturbances (Bergeron et al., 1983, 2002). The area was burned by two large forest fires in 1760 and 1923 (Dansereau and Bergeron, 1993). The nearest weather station 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 0.75° C (Environment Canada, 2008). The total annual precipitation in this region was 889.8 mm of which snowfall accounted for 27.7 %.

2.3.2 Data Collection and Chronology Development

At the Monsabrais sampling site, 21 living *F. nigra* trees were cored twice near the base with a 5 mm increment borer. After crossdating, tree-ring widths were measured to a precision of 0.01 mm with a VELMEX measuring system. The program COFECHA was used to validate crossdating quality and width measurements (Holmes 1999). The Roquemaure chronology from Tardif and Bergeron (1997) and the Monsabrais chronology developed from the nineteen youngest trees were also used to assess that no false/missing rings occurred in the Monsabrais series during the period for which only two trees existed. After this initial phase, samples were prepared for image analysis as described in Tardif and Conciatori (2006). Images were generated at a 25x magnification and a resolution of 1600 x 1200 using a Polaroid digital microscope camera coupled to a

Nikon SMZ800 stereomicroscope. Colour images were analyzed with the program WinCell Pro (version 2004a, Régeants Instruments Inc. 2005) in which the minimum cross-sectional lumen vessel area was set to $800 \mu\text{m}^2$ which captured all earlywood vessels. Very young rings which were curved due to their proximity to the pith were excluded from the image analysis since those exhibit a rather diffuse-porous vessel pattern. For each ring, earlywood vessel numbers and cross-sectional earlywood vessel lumen areas as well as total ring area were recorded. The distinction between earlywood and latewood was based on the change in vessel size (Fonti and García-González, 2004; Tardif and Conciatori, 2006) since the bimodal vessel distribution of larger sized earlywood and smaller sized latewood vessels can easily be made in *Fraxinus* species (Panshin and deZeeuw, 1980; Yanosky, 1983; Tardif, 1996). On each ring image, the ring area of each tree ring was delimited and green markers were included that approximately separated earlywood vessels from latewood vessels. For each ring, earlywood and latewood widths were also measured twice along two radial files and the new ring width measurement series were used to cross-validate with those obtained initially with the Velmex measurement system. This procedure also helped to delimit within each ring the earlywood and latewood vessels. From these measurements, the following variables were generated: earlywood width (EW), latewood width (LW), total cross-sectional earlywood vessel lumen area (TVAE), mean cross-sectional earlywood vessel lumen area (ME), density of the earlywood vessels (dE) defined as number of earlywood vessels divided by earlywood area and porosity of the earlywood (pE). As earlywood vessel fraction and lumen fraction both 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.

2.4 Results

2.4.1 Indications of Exposure to Forest Fire

The age distribution of the 21 black ash trees indicated that most of the trees originated during or after 1923 with most of them immediately following 1923 (Fig. 2.1). In our study area, the year 1923 corresponded to one of the two largest forest fires of the past 250 years and our study site was located within the 1923 burned area delimited by Dansereau and Bergeron (1993). The date of the 1923 fire was determined using both fire scars and stand initiation age and the area burned was precisely delineated using aerial photographs taken in 1926 (Dansereau and Bergeron, 1993). *Fraxinus nigra* is considered to be sensitive to fire (Grimm, 1984) and heavily sprouts following forest fires (Heinselman, 1981; Tardif, unpublished observations). Many of the trees cored originated from stump sprouts which were presumably initiated after the 1923 fire. Since in several cases the pith was not cored, an exact age determination was not possible, although it was estimated from the rather diffuse-porous vessel arrangement and stronger ring curvature in young tree-rings that for most cases the pith was only missed by one to two years. Two of the sampled *F. nigra* trees survived the 1923 fire (Fig. 2.1). Even though described as sensitive to fire (Grimm, 1984), individuals of *F. nigra* may survive forest fires as a few trees growing on the Lake Duparquet floodplain endured a fire in 1944 (Tardif and Bergeron, 1999).

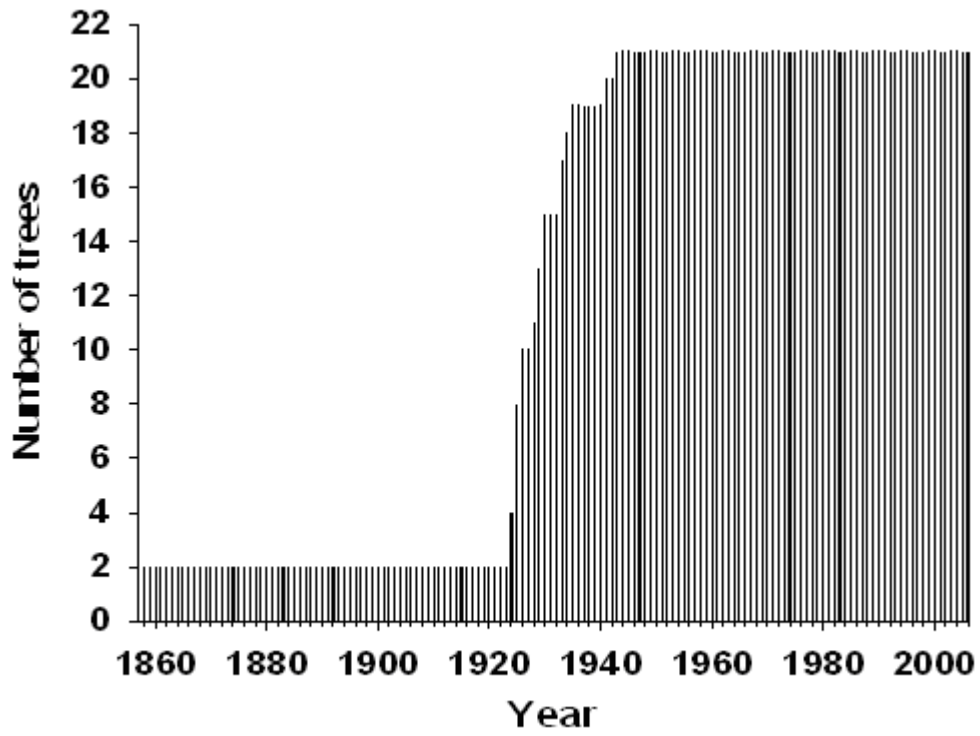


Figure 2.1 Age distribution for all 21 *Fraxinus nigra* trees sampled at the Monsabrais site.

2.4.2 Forest Fire and Tree-ring Characteristics

The raw data of the two *F. nigra* trees that survived the 1923 forest fire indicate that the year 1923 corresponded to a sharp decrease in ring-width, as almost no latewood was produced (Figs. 2.2a, 3 upper and lower left panels) with little change in earlywood width (Fig. 2.2b). This pulse-type response in ring-width and latewood-width is followed by a period of suppression that lasts for approximately 15 years (Fig. 2.2a). Intriguingly, in 1924 both trees produced rings with a strong decrease in the mean and total cross-sectional earlywood vessel lumen area as seen from the raw data (Fig. 2.2c, d) and the ring images (Fig. 2.3 upper and lower left panels). A less prominent increase in earlywood vessel density and almost no change in earlywood porosity occur in the same year (Fig. 2.2e, f). The decrease in cross-sectional earlywood vessel lumen area had no equivalent in other years except in 1966 in only one tree which thereafter shows growth suppressions until the early 1980s and both earlywood width and total earlywood cross-sectional vessel area never recovering (Figs. 2.2b, d, 2.3 upper right panel). No such reduction in vessel characteristics was observed in 1966 in the 19 remaining Monsabrais trees.

2.5 Discussion

2.5.1 Forest Fire and Ring Characteristics

The strong decrease in ring-width from 1922 to 1923 and the following longer lasting period of suppression (Fig 2.2a, b) observed beyond the drought periods of the early 1920s (Girardin et al., 2004, 2006) suggests that both trees may have been physically damaged in 1923. While no signs of fire scars or oxidation of the wood were visible,

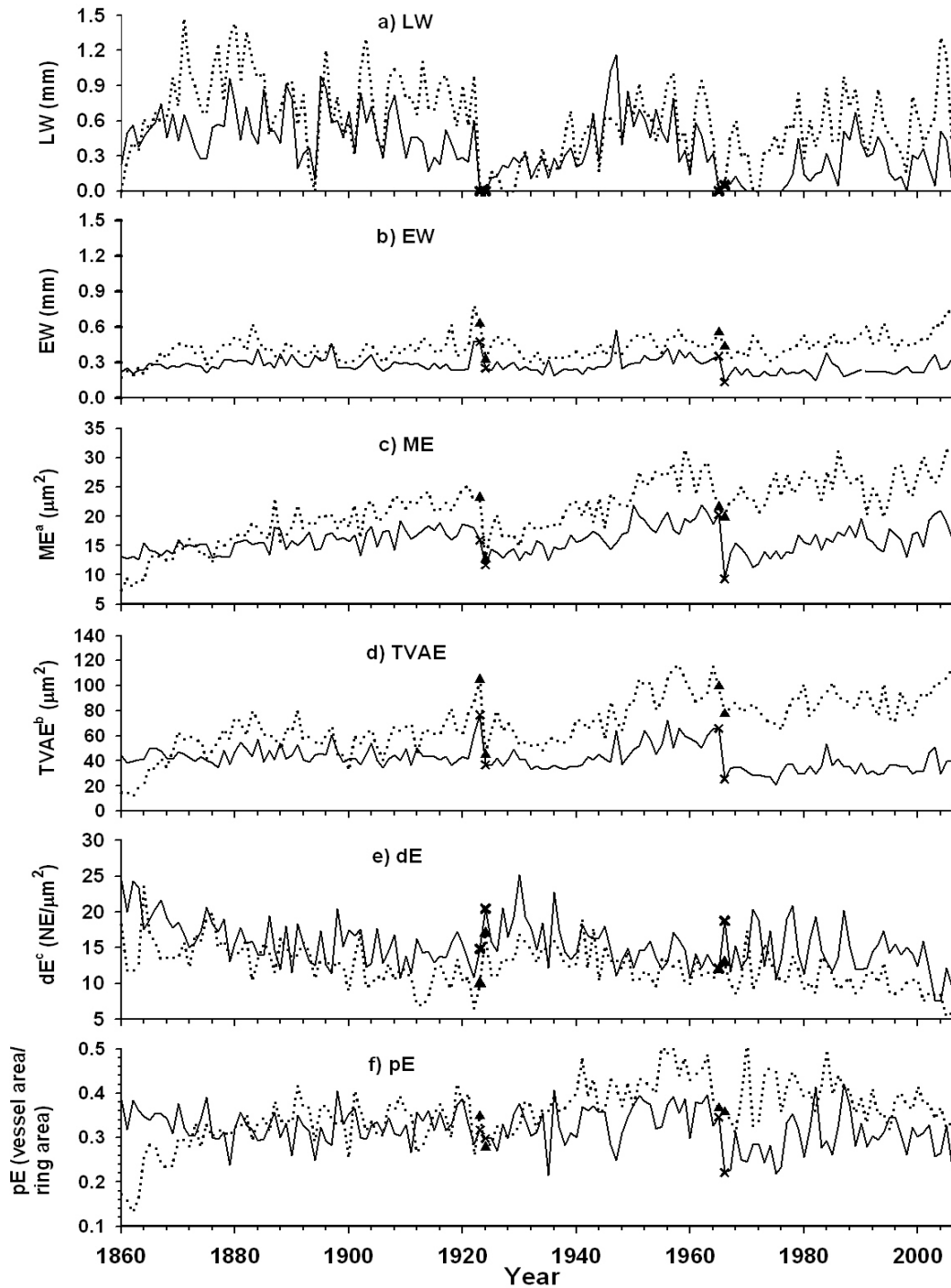


Figure 2.2 Unstandardized time series of the two oldest *Fraxinus nigra* trees for the period 1860-2006. Chronologies for tree #1 are represented by a solid line while chronologies for tree #2 correspond to a dotted line. The symbol x marks the years 1923, 1924, 1965 and 1966 for tree #1 while a triangle marks the same years for tree #2. Variables are as follows: a) latewood width (LW), b) earlywood width (EW), c) mean cross-sectional earlywood vessel lumen area (ME), d) total cross-sectional earlywood vessel lumen area (TVAE), e) earlywood vessel density (dE) and f) porosity of the earlywood (pE). ^a x 1000; ^b x 10000; ^c x 0.000001

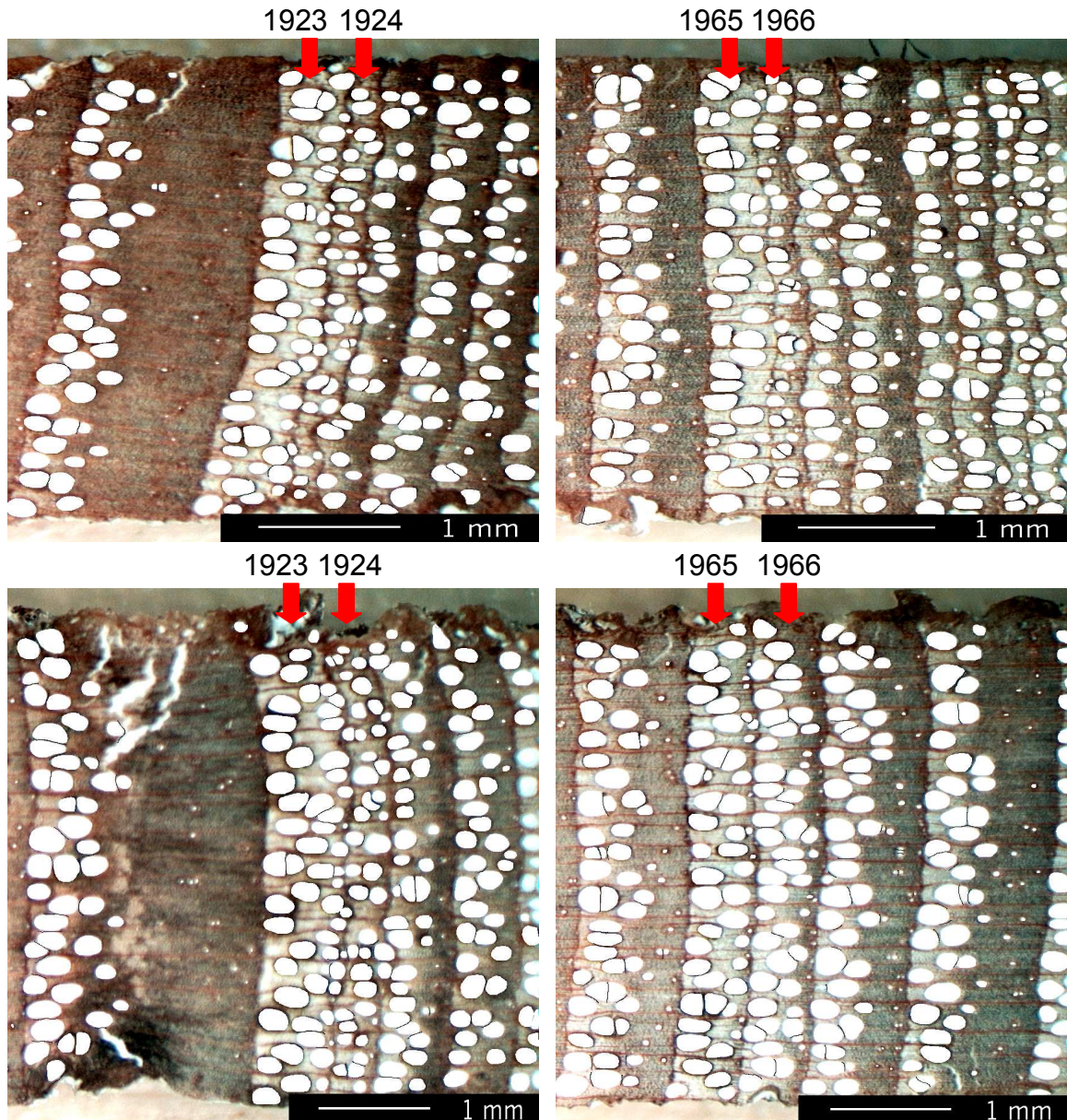


Figure 2.3 Tree rings in *Fraxinus nigra* for the two oldest trees magnified 25x. Vessel lumens were highlighted with white colour to increase contrast. Adjacent vessels were separated with black lines. Cracks in the wood appear white as cores were rubbed with chalk. Upper left panel) Tree #1 core 1a and lower left panel) tree #2 core 2a. In both images, the complete tree rings for the period 1922 to 1926 (from left to right) are seen. Arrows are pointing at the rings of the years 1923 and 1924. The ring 1924 is characterized in both rings by earlywood vessels of small cross-sectional lumen area. Upper right panel) Tree #1, core 1a and lower right panel) tree #2, core 2a. In both images, the complete tree rings for the period 1964 to 1968 (up to 1971 in tree #1) are seen. Arrows are pointing at the rings of the years 1965 and 1966. Many earlywood vessels of greatly decreased lumen area can be seen in the ring of 1966 in tree #1. In contrast, the earlywood vessels of tree #2 are of no unusual size in the ring of 1966.

localized cambial death as a result of overheating during the 1923 fire cannot be excluded, and neither can the loss of branch and shoot material. However, similar to Monsabrais trees, Bigio (personal communication 2008) also observed a decrease in mean cross-sectional earlywood vessel lumen area the year following a fire in an unscarred *C. sativa* tree located within a burned area. Unlike other studies with angiosperms (Smith and Sutherland, 1999, 2001; Bravo et al., 2008) no darkening of the sapwood in the year of the fire or the subsequent year was observed in Monsabrais trees however the wood of the rings 1923 and 1924 appears lighter colored (Fig. 2.3a, b). Smith and Sutherland (2001 and references therein) observed that cambial injuries associated with fire caused the sapwood to darken due to an increased production of phenolic compounds which counteract pathogenic attack. In *F. nigra*, no darker coloration of the sapwood was observed indicating that no enhanced production of phenolic compounds occurred. Such discolorations, however, usually do not extend throughout the whole transverse sectional plane (Smith and Sutherland, 2001) and in *F. nigra* trees, the use of cores makes it difficult to determine whether the absence of discoloration in the wood was observed throughout the stem.

In the Lake Duparquet region most fires tend to occur in mid-May to mid-June (Y. Bergeron, unpublished data). In the study area, fires may thus occur at the end of the earlywood production interval given that by the beginning of June *F. nigra* trees have fully developed leaves (Tardif, personal observation). Leaf development in ring-porous species implies that a functional vascular system has been rebuilt to supply water to the foliage (Sperry et al., 1994). The fire in 1923 could have therefore not affected earlywood

width in 1923. However, auxin is an important regulator of vessel differentiation (Sundberg et al., 2000 and references therein) and the loss of branch and shoot material during 1923 might have led to lowered auxin concentrations throughout the year 1924 as auxin is produced mainly in young buds and leaves. According to the six-point hypothesis, auxin concentrations are highest near the sources of production which are buds and developing leaves (Aloni and Zimmermann, 1983). Since developing wood cells near auxin sources are exposed to high concentrations of auxin, they differentiate faster than those located near the stem base, resulting in a gradual basipetal increase in vessel size and a decrease in vessel density (Aloni and Zimmermann, 1983). However, the negative association of vessel size and auxin concentrations only seems to be true for a certain auxin concentration range (Doley and Leyton, 1968; Zakrewski, 1991). Studies with stem segments of ring-porous *Fraxinus* and *Quercus* species have shown increases in cross-sectional vessel lumen area in response to exogenously applied auxin until a threshold concentration was reached (Doley and Leyton, 1968; Zakrewski, 1991). Therefore, suboptimal auxin concentrations in 1924 might have triggered decreased earlywood vessel lumen area throughout the 1924 ring (Fig. 2.3). Also, according to Aloni (1991) earlywood vessels of ring-porous species are built from carbohydrate reserves stored at the end of the previous growing season. It is therefore possible that an insufficient amount of carbohydrate reserves was accumulated in 1923 given the high drought stress and providing that the fire caused a substantial amount of foliage loss. Lowered carbohydrate reserves might therefore be partly responsible for the reduction in cross-sectional earlywood vessel lumen area in 1924.

As an alternate hypothesis, it is also possible that *F. nigra*, which commonly grows on moist soils, might have been exposed to a decrease in soil water table depth following the 1923 fire event. Large forest fires commonly burn vegetation and litter leading to higher amounts of precipitation that reach and infiltrate the soil following fires (Neary and Ffolliott, 2005). In our site, it cannot be excluded that the 1923 forest fire may have affected the timing of snow melt resulting in a larger amount of water available in the spring over a shorter period. At this time, it cannot be ruled out that the decrease in cross-sectional mean earlywood vessel lumen area observed throughout the year 1924 (Fig. 2.3a, b) might not be a response to excess water availability as has already been observed with other ring-porous species (Yanosky, 1983; Astrade and Bégin, 1997; St. George and Nielson, 2000, 2003).

The reduction in cross-sectional earlywood vessel lumen area and porosity in one of the trees in 1966 could be likely due to local site factors or other endogenous disturbances as none of the other 20 *F. nigra* trees at the Monsabrais site shared such a decrease in cross-sectional earlywood vessel lumen area in 1966 (data not shown). In addition, from a first visual inspection of cores of an additional 60 *F. nigra* trees growing on the floodplains of Lake Duparquet, none presented vessel anomalies in 1966.

2.5.2 Vessel Characteristics in Relation to Possible Other Disturbance Factors

In the Monsabrais area, the early 1920s were characterized by a drought period (Girardin et al., 2004). As severe winter-spring drought events were associated with a reduction in cross-sectional earlywood vessel lumen area in *Q. robur* (García-González and Eckstein,

2003) the possibility cannot be excluded that the decrease in mean cross-sectional earlywood vessel lumen area in 1924 was the result of water stress. However, drought periods of similar severity to those of the early 1920s such as the 1910s, the early 1930s and the mid 1950s (Girardin et al., 2004) did not cause such a pronounced change in vessel size which led us to suggest the investigation of cross-sectional vessel lumen area as a possible additional feature for fire history reconstructions. Decreases in earlywood vessel size and reductions in latewood width have also been detected in ring-porous species following defoliation events (Huber, 1993; Asshoff et al., 1998-1999). We speculate however that the reduction in the cross-sectional earlywood lumen vessel area in trees of Monsabrais have not been caused by severe insect outbreaks since floodplain trees growing within 15 km from our site showed no anomalous earlywood vessels or latewood width development in the years 1923, 1924 or 1925.

2.5.3 Implications for Dendrochronological Studies

From a dendroclimatic point of view, studies using vessel characteristics to reconstruct past climate conditions need to consider the potential effect of forest fires on vessel size in addition to other disturbances such as insect defoliation. Signals interpreted as being associated with droughts might actually come from that of disturbance events and the quality of dendroclimatic reconstructions might suffer due to improper identification of the signal. Brown and Swetnam (1994) suggested the use of other ring characteristics in addition to fire scars in order to reconstruct fire history since the use of other fire associated ring characteristics allowed for a more complete fire reconstruction. The observed decrease in the size of the cross-sectional earlywood vessel lumen areas in the

year following an intense fire may be useful to identify the exact year and may contribute to a more precise spatial reconstruction of forest fires. However, since the decrease in vessel lumen area can be triggered by several environmental factors, fire history reconstructions may not be solely based on changes in vessel size but require additional indicators to identify forest fires such as the regeneration pulse observed in subsequent years, as well as fire scars. Further, due to the observed variability in cross-sectional earlywood vessel lumen area, we suggest such studies to include the analysis of many trees to eliminate the possibility of mistaking an endogenous with an exogenous disturbance signal.

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3.0 Sensitivity of Vessels in *Fraxinus nigra* Marsh. to Climatic and Hydrologic Variables

3.1 Abstract

Little research has been conducted on the sensitivity of earlywood vessels in ring-porous tree species in response to flooding. Dendroclimatic studies have also yielded contrasting results regarding the utility of vessel chronologies for climate reconstructions. The impact of flooding and climate on vessel characteristics in black ash (*Fraxinus nigra* Marsh.) was studied in the boreal region of northwestern Quebec. Both, the floodplain vessel and width chronologies and those developed from unflooded control trees were related to current and previous year's photosynthetic periods. Vessel chronologies were associated with climate variables to which the EW was related, but also showed unique correlations with climate. On the floodplain, spring discharge had the strongest impact on vessel formation among all environmental variables whereas spring discharge was unrelated to control vessel chronologies. In floodplain trees, flooding promoted the formation of more abundant and smaller earlywood vessels. Among all chronologies, the mean vessel area chronology showed the strongest association with spring discharge and was exceptionally high for boreal tree species. Previous dendrohydrologic studies used vessel anomalies to identify exceptional flood events. However, the linear relationship between the mean vessel area chronology and spring discharge stress the utility of developing of continuous vessel chronologies for hydrologic reconstructions prior to instrumental data periods.

Keywords: earlywood vessels, dendrohydrology, dendroclimatology, ring-porous, Fraxinus nigra

3.2 Introduction

Tree growth is limited by a large range of external factors (Fritts 1976; Schweingruber 1996). Such factors include light and water availability, air and soil temperature and soil nutrient content (Schweingruber 1996). In addition, exposure to disturbance agents such as heavy winds, avalanches, forest fires and insect outbreaks may negatively affect tree growth (Schweingruber 1996). However, 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 and references herein). The resulting depletion of soil oxygen content does not only inhibit root respiratory processes (Kozlowski 1985, 2002), it also initiates changes in soil microbial communities which may result in denitrification (Kozlowski 1997). In addition, the decreased soil oxygen content may negatively affect mycorrhizal communities, many of which are strongly aerobic and crucial for tree survival or growth (Gadgil 1972; Reid and Bowen 1979; Kozlowski 1982 and references therein; Stenström 1991; Linderman 1994). Thus, even though the capacity of a tree to deal with flooding depends on its age and adaptations to flooding, prolonged flood periods that fall into the growing season often negatively affect tree growth (Kawase 1981; 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*a, c*; Cook 1995; Orwig and Abrams 1997; Corcuera et al. 2004*a, b*; Girardin and Tardif 2005), many dendrohydrological studies have incorporated further variables in order to reconstruct floods. For example, 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 (Eggington and Day 1977; Bégin 1990, 2000, 2001; Bégin and Payette 1991; Lepage and Bégin 1996; Tardif and Bergeron 1997*b*). Recently, river erosion dynamics have 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 since ring-porous stem wood of green ash (*Fraxinus pennsylvanica* Marsh.) developed into diffuse-porous wood upon burial (Sigafos 1964; Cournoyer and Bégin 1992).

Wood anatomical anomalies have also been observed in tree-rings from ring-porous species [English 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 2000, 2002, 2003; Sass-Klaassen 2008, 2009). Years with exceptional spring floods were successfully identified through tree-rings containing earlywood vessels with abnormally small lumen areas whereas no consistent response in ring-widths was observed (Yanosky 1983;

Astrade and Bégin 1997; St. George and Nielson 2000, 2002, 2003; Sass-Klaassen 2008, 2009).

Vessels of ring-porous species may not only store hydrologic information but also unique climate signals (Woodcock 1989*a, c*; García-González and Eckstein 2003; Fonti and García-González 2004; Eilman et al. 2006; Tardif and Conciatori 2006; Fonti et al. 2007). 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 Garcia-Gonzales 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 2000, 2002, 2003; Sass-Klaassen 2008, 2009), severe drought periods (García-González and Eckstein 2003) and insect defoliation (Huber 1993; Blank 1997; Asshoff et al. 1998-1999; Blank and Riemer 1999; Thomas et al. 2006) a careful interpretation of earlywood vessel signals must be exerted.

In the Lake Duparquet area, past spring floods associated with ice-break-up were reconstructed using ice-scarred trees (Tardif and Bergeron 1997*a*). Earlywood vessel

anomalies in ring-porous *F. nigra* trees were also observed during major ice-floods (Tardif et al. in press) whereas the earlywood width was too weakly related to spring floods for flood reconstructions (Tardif 1996). No studies have assessed the usefulness of continuous vessel chronologies to climate or periodic spring flood events in *F. nigra* trees.

The overall objective of this study was to assess how fluctuating water levels and climate could influence tree-ring production in *F. nigra*. To achieve this objective, both tree-ring and vessel chronologies were developed from wood samples collected in trees growing at flooded and unflooded (control) sites in the Lake Duparquet region of northwestern Quebec. It was hypothesized that only trees originating from floodplains would produce more earlywood vessels with a reduced cross-sectional mean area in response to high spring floods. Further, the earlywood vessel chronologies were expected to be more strongly associated with spring flooding than the earlywood width. No reaction of latewood features (vessels or width) to spring waterlogging was expected since the time of flooding is not concurrent with the latewood production interval. The comparison of chronologies from both flooded and control will help to assess how well the flooding signal was recorded by *F. nigra* trees and it will also allow evaluating the usefulness of continuous vessel chronologies for hydrological reconstructions. As the water availability on the two study sites differs throughout the year, it was further hypothesized that earlywood and latewood vessels of floodplain and unflooded trees contain different climatic signals due to their different exposure to water and drought stresses.

3.3 Materials and Methods

3.3.1 Study area

The study area is located approximately 550 km north of Montréal in the Lake Duparquet region of north-western Quebec (48°28'N, 79°17'W; Figure 3.1). 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 (Bergeron et al. 1983; Veillette 1994). The nearest weather station to the study area is at Duparquet (Figure 3.1) however, the closest weather station with 46 years of data is located in La Sarre, 42 km north of Lake Duparquet. Between 1971 and 2000 the mean annual temperature was 0.75° C (Environment Canada 2008). The total annual precipitation in this region was 889.8 mm of which snowfall accounted for 27.7 %.

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 (Bergeron et al. 1983, 2002). 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; Denneler et al. 1999). Non riparian *F. nigra* stands from the surrounding Haute Pleine Hébecourt close to Lake Duparquet were also described by Bergeron et al. (1983).

3.3.2 Sample Collection and Preparation

The five geomorphologically distinct *F. nigra* stands initially sampled by Tardif and

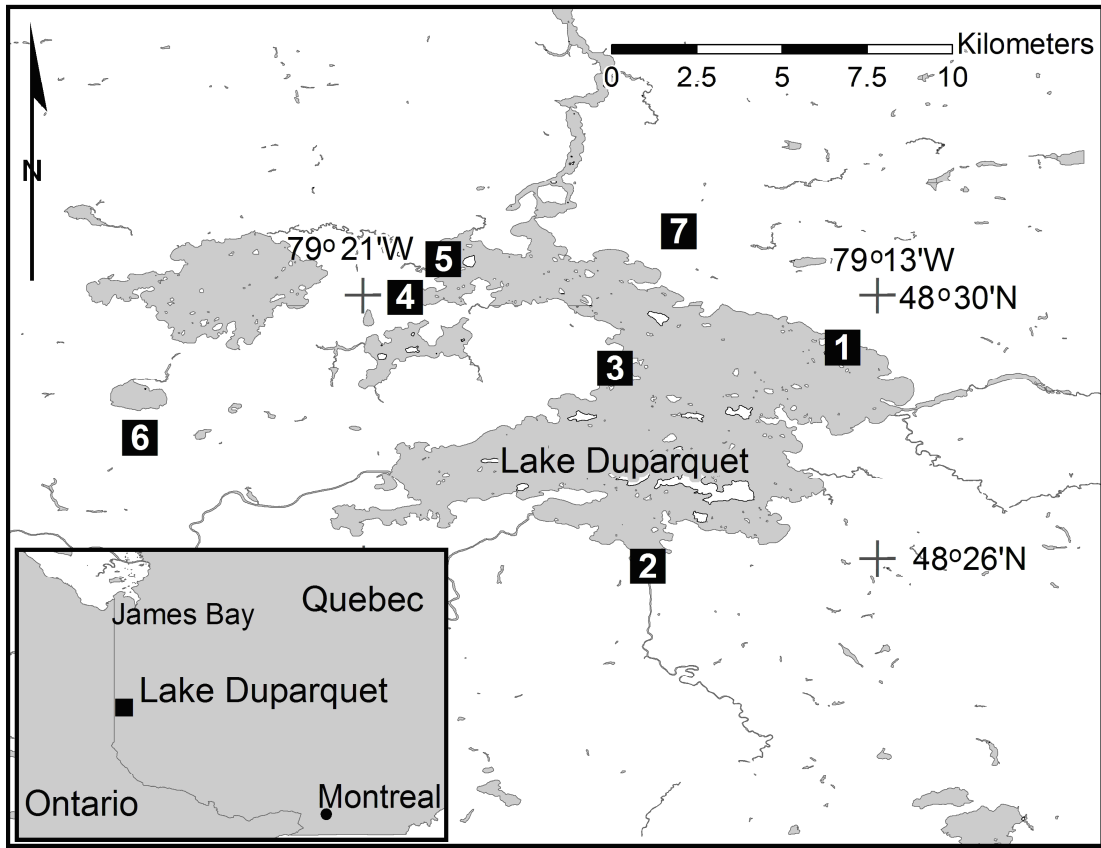


Figure 3.1. Map of Lake Duparquet showing the location of the sampled floodplain sites (1-5), the control site (6) and the nearest weather station (7).

Bergeron (1992) were revisited in August 2006 to update chronologies developed in 1989 (Figure 3.1). These sites are positioned on the floodplains of Lake Duparquet (approximate elevation 260 m above sea level). While *F. nigra* was the dominant tree species on each of these sites, the coexisting vegetation types differed according to elevation and drainage (Tardif and Bergeron 1992). For each floodplain site 12 *F. nigra* trees were sampled. An additional 27 *F. nigra* trees were sampled from an unflooded site (48° 27'N, 79° 25'W) located south of Lake Monsabrais about six km east of Lake Duparquet (approximate elevation 300 m above sea level, Figure 3.1). Since these trees are not exposed to lake flood events they served as a control.

In all sites, wood samples were extracted from *F. nigra* trees as close to the base as possible using five mm diameter increment borers. In cases where the base of the stems were 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 procedures in the laboratory consisted of careful mounting and gluing of cores on wooden supports to ensure a correct alignment of cells (Pilcher 1990). After air drying, all cores were carefully sanded at the 80, 180, 220, 320, 400 and 600 sandpaper grit levels according to the method described in Stokes and Smiley (1968). The date of ring formation was determined through a simplified crossdating technique similar to that described by Yamaguchi (1990) in which ring-width pattern matching is based on the listing of unusually small or large rings rather than the use of skeleton plots. In many floodplain trees, very large rings were observed, including

those in 1945, 1949, 1957, 1964, and 1975 while extremely small rings were found in 1915, 1927, 1940, 1968 and 1972. In control trees, exceptionally large rings occurred, for example, in 1938, 1939, 1945, 1949, 1951 and 1956 whereas narrow rings were produced in 1860, 1894, 1924, 1925 and 1998.

3.3.3 Tree-Ring Measurements

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 to identify measurement errors. COFECHA log transforms measurement series to reduce unequal variance, standardizes chronologies using a 32-year spline function, and constructs a master chronology (Holmes 1999). Each standardized individual series is then correlated up to a -10 and +10 year lag to the master chronology from which temporarily the series being tested has been removed (Holmes 1999). Through this comparison, possible misdated series segments and measurement errors could be identified and were corrected if the subsequent visual verification agreed with those flagged by COFECHA.

3.3.4 Image Analysis

Many wood samples from floodplain and control trees were partly rotten and were not suitable for image analysis which requires vessels to be clearly visible and undistorted. A sub-selection of trees was therefore done based on wood quality. In total, 20 floodplain trees were retained from two floodplain sites, one located beside the river Mouilleuse and

the second located in a bay beside a bog (Figure 3.1, sites 2 and 3). Of the 27 trees sampled from the control site, 21 were subjected to image analysis.

To measure the number and the cross-sectional area of vessels, cores were 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 25x magnification and a resolution of 1600 x 1200 pixels. On each ring image, the ring area of each tree ring was delimited and green markers were included that approximately separated earlywood vessels from latewood vessels (Figure 3.2 left panel). The program WinCell Pro Ver. 2004a (Régent Instruments Inc. 2005) was used for image analysis which measures the size and x-y positioning of each vessel and marker. In order to allow the data for earlywood vessels to be separated from those of latewood vessels, the x-coordinates of earlywood vessels, markers and latewood vessels were used. To properly do this analysis, tree rings had to be positioned during image capturing in such a way that the ring boundary was as parallel as possible to the image boundary so that latewood vessels occupied a higher x-positioning than earlywood vessels (Figure 3.2 left panel). The distinction between earlywood and latewood vessels was determined qualitatively based on vessel size and location in the ring (Fonti and Garcia-Gonzales 2004; Tardif and Conciatori 2006) since in *Fraxinus* species tree rings contain large earlywood vessels followed by much smaller latewood vessels (Panshin and deZeeuw 1980; Yanosky 1983; Tardif 1996). Prior to image analysis, the color of all images was increased in magenta

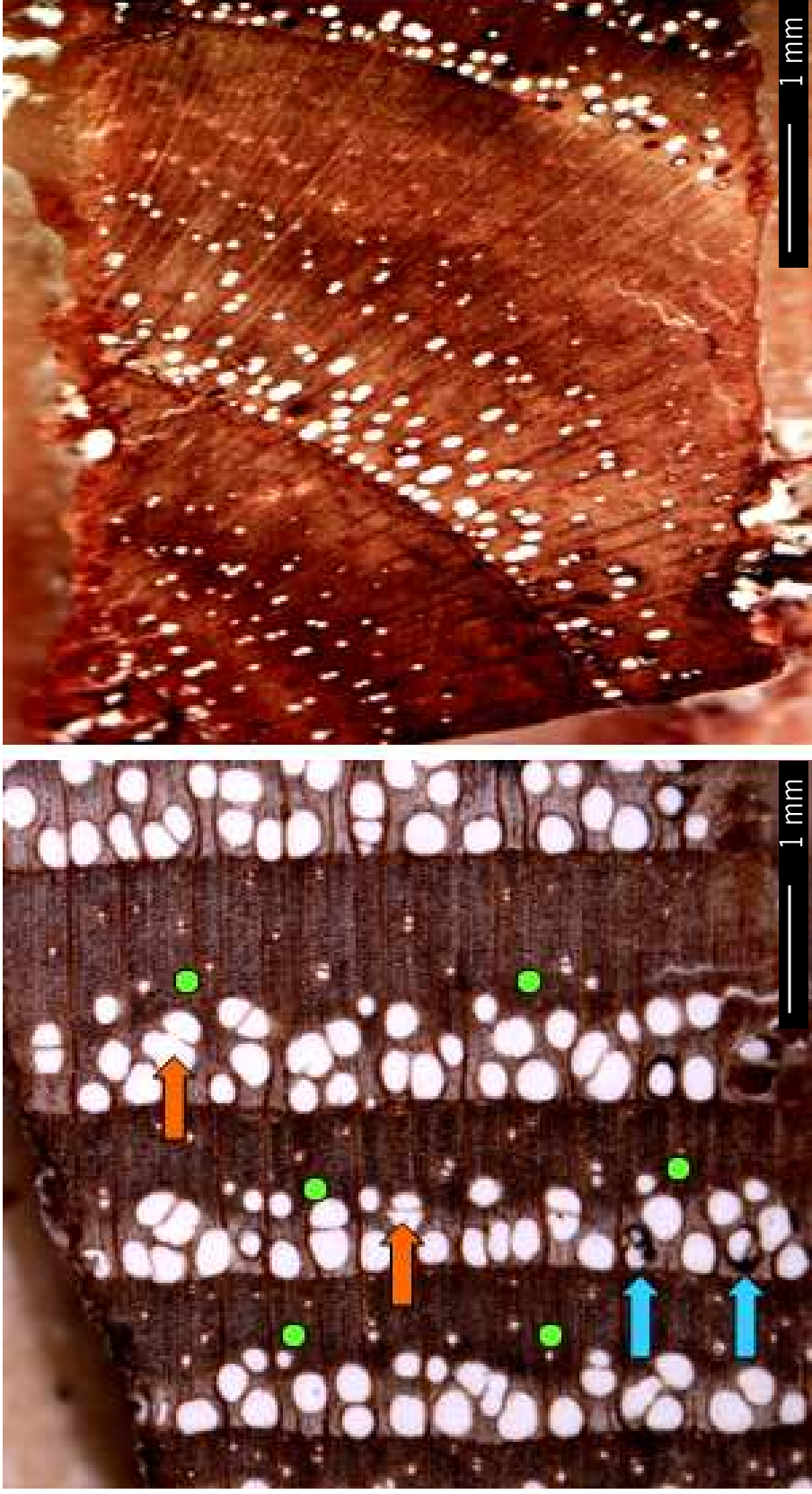


Figure 3.2. Images of *Fraxinus nigra* trees rings at a magnification of 20x. In the left panel ring images are aligned parallel to the image boundary. Earlywood and latewood vessels are separated through green dots. Blue arrows point to examples of adjacent vessels that require manual separation through black lines prior to image analysis. Red arrows point to examples of vessels that need to be manually highlighted with white color prior to image analysis. The right panel shows tree rings of very young cambial age with more diffuse-porous vessel patterns.

which did not affect the appropriate selection of white colored vessels but which allowed the program to better distinguish the green markers from other wood cells. For this procedure, the program Adobe Photoshop v. 5.0 Limited Edition (Adobe Systems Inc. 1998) was used.

Color classes were developed to allow for recognition of vessels and markers. Vessel measurements included the number and cross-sectional vessel area above a threshold of $800 \mu\text{m}^2$ to exclude non vessel cell types. In cases where vessels were not automatically identified by the program, they were highlighted manually and adjacent vessels were separated using black lines to ensure every vessel was recognized as such. Measurements of incomplete vessels occurring at the ring boundary were manually excluded from the analysis. Since tree rings of very young cambial age (i.e. close to the pith) exhibit a rather diffuse-porous vessel pattern, they were omitted from the analysis (Figure 3.2 right panel).

Path analysis was also selected in WinCell Pro to obtain both earlywood and latewood width measurements for each ring image and along two radial files at the upper and lower portions of the image. The obtained earlywood and latewood widths values were averaged to yield the earlywood and latewood width for each ring and the sum of the two yielded the ring-width. These ring-width measurements and those obtained from direct tree-ring measurement of the cores using the Velmex system were plotted and visually compared for data quality control purposes i.e., to verify that the captured ring images had been assigned correct calendar years. In years in which the two measurements

deviated largely, ring images were first compared to wood samples to ensure that captured images had been assigned a correct calendar year. If non-concordance occurred, images were re-analyzed.

Due to the large data set produced, numerous data quality control procedures were used. In addition to ring width comparisons (see above), scatter plots of total ring width and ring area were also compared. Another procedure included the verification that each ring image contained only two green markers to approximate earlywood and latewood vessel positioning. Despite the artificial reddish coloring of the wood and the fact that color classes had been developed to distinguish markers, other wood cells and the periphery of vessels in several rings also contained green color elements. Thus, for rings in which more than two markers appeared in the WinCell Pro output, additional color classes were developed and rings were reanalyzed.

3.3.5 Chronology Developments

After the initial data quality control was completed, ring-width and vessel measurements were used to generate 15 tree-ring variables for each of the control and floodplain sites. Three of these variables were determined from width measurements: 1) earlywood width (EW), 2) latewood width (LW) and 3) total ring-width (RW) (note: for variables generated from trees originating from the control site, the capital letter C will precede the variable abbreviation whereas the abbreviation will be preceded by the capital letter F for variables originating from floodplain trees). These 3 ring-width variables together with total ring area were also used to determine earlywood area and latewood area as both

these variables were needed to calculate density and porosity (see variables 9 to 12 below). For each ring, the earlywood area (latewood area) was calculated through multiplying the ring area by the earlywood width (latewood width) and dividing the obtained value by ring-width. The 12 other variables were obtained from vessel measurements and included 1) the total cross-sectional area of vessels in the earlywood (TVAE), 2) the total cross-sectional area of vessels in the entire ring (TVATR), 3) the number of vessels in the earlywood (NE), 4) the number of all vessels in the entire ring (NTR), 5) the mean cross-sectional vessel area in the earlywood (ME), 6) the mean cross-sectional vessel area of all vessels in the entire ring (MTR), 7) the mean cross-sectional area of the 25% largest vessels in the earlywood (25E), 8) the mean cross-sectional area of the 25% largest vessels in the entire ring (25TR), 9) the density (density defined as number of vessels divided by ring area) of vessels in the earlywood (dE), 10) the density of vessels in the entire ring (dTR), 11) the porosity of the earlywood, and 12) the porosity 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.

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 *C. sativa* were improved when values of two cores were pooled

rather than used individually. The variables total vessel area and number of vessels were calculated for each ring and then averaged on a tree level. For the variable mean vessel area, the number of vessels in each ring was multiplied by the mean vessel area and ring values from two cores ring were afterwards averaged. Prior to averaging the 25% largest vessel area was calculated on a core level and subsequently averaged. This variable was calculated since García-González and Fonti (2006) 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 the variables density and porosity the number and total vessel area respectively obtained from each core were first added before they were divided by the summed ring area of the according year obtained from both cores. For all above procedures the program SYSTAT v.11 (Systat Software Inc. 2004) was used. A further data quality control following data manipulation consisted of verifying that the summed values of earlywood and latewood vessel number and total vessels areas, respectively, yielded the values for the entire ring.

To produce chronologies, each of the 15 measurement time-series generated from each of the control and flooded site was standardized using a cubic spline function with a 50% frequency response of 60 years. This procedure removes low-frequency variations associated with age-related trends or stands dynamics (Cook and Peters 1981; Cook et al. 1990a) which may influence vessel size (Corcuera et al. 2004a; Tardif and Conciatori 2006) and ring widths. The calculation involves dividing the observed measured value by the expected value obtained from the cubic spline function the measurements are thus transformed into a dimensionless index, thereby retaining only high-frequency variation.

Following standardization, autoregressive modeling was performed to remove autocorrelation, if present. Autocorrelation occurs if one value in a time series at time (t) is correlated to another value at time (t + x) (Fritts 1991). In presence of autocorrelation, the number of independent observations is reduced and if autocorrelation is not removed, it will lead to a false number of degrees of freedom in subsequent statistical analyses (Legendre and Legendre 1998). Overestimation of the number of degrees of freedom due to the presence of temporal autocorrelation has for consequences that non-significant results might be falsely seen as significant (Legendre and Legendre 1998). As a consequence, standard chronologies were used when temporal autocorrelation was found to be non-significant and residual chronologies were used when temporal autocorrelation was significant. In order to further enhance the common signal, all chronologies were developed using a biweight robust mean which assigns weights to the indices at a specific time t to identify and eliminate statistical outliers (Cook et al. 1990b). For all above procedures the program ARSTAN Windows (v. 4.0a; Cook 1985) was used.

To evaluate the statistical quality of each of the 15 standardized or residual time series per site, the mean sensitivity, expressed population signal (EPS), percent variance of the first principal component and between tree correlations were calculated using ARSTAN Windows (v.4.0a). The mean sensitivity assesses the mean change from one ring value to the following (Fritts 1976). The highest possible mean sensitivity index value of 2 indicated that every second ring would have a value of 0 while the lowest mean sensitivity index value of 0 would signify that there would be no difference between ring measurement values. The EPS scales the common signal by the total chronology variance

and thus contains similar information as the correlation among trees or the percent variance common to all trees (Briffa and Jones 1990). The EPS measures how representative the obtained chronology is compared to a theoretical chronology with an infinite number of trees (Wigley et al. 1984). A value of 0.0 indicates no correlation, while a value of 1.0 indicates a perfect correlation. The quality of a chronology is thought to be sufficient if a value of 0.85 has been reached (Wigley et al. 1984).

3.3.6 Climatic and Hydrologic Data

Both, daily and monthly climate data were obtained from the BioSIM weather generator (Régnière and Bolstad 1994; Régnière 1996) for the period 1914 to 2005. The climate variables obtained from the BioSIM weather generator include precipitation, minimum, mean and maximum temperature, and monthly snow cover. Daily data from four weather stations closest to a reference point were used to develop daily climate data at site 3 (Figure 3.1) (48°28'50"N, 79°17'21"W). During the procedure, adjustments are made for differences in latitude, longitude, and elevation between the study site and the weather stations. Since the availability of climate data at each station varied over time, stations closest to the study site were more highly weighted in the calculation of the climate data. From 1914 to 2005, the distance of the weather stations to the study site ranged from 276 km (Station Stonecliffe 46°11'30"N, 77°52'44"W) to 4 km (Station Duparquet 48°31'12"N, 79°16'12"W). Stations most highly weighted were on average 32 km and 58 km away from the study site whereas those less highly weighted were on average at 58 km and 74 km distance from the study site.

To validate climate data of the BioSIM weather generator, mean monthly temperature and total monthly precipitation were compared to climate data obtained from the La Sarre weather station (Environment Canada 2008). This weather station is located within 42 km north of Lake Duparquet and recorded 46 years of data (1951-1997 and 2 months of the year 2004) with few missing values. Correlations of the two datasets showed good agreement. Mean Spearman's rank correlation between monthly mean temperature from the two data set was $r=0.96$ ($n=12$) with the highest correlation obtained for the month of December (Spearman $r=0.98$, $p=0.000001$) and the lowest for the month of July (Spearman $r=0.89$, $p=0.000001$). For total precipitation, a mean Spearman's correlation of $r=0.86$ ($n=12$) was found with the month of May showing the strongest agreement (Spearman $r=0.92$, $p=0.000001$) and December showing the lowest value (Spearman $r=0.79$, $p=0.000001$).

In addition, the daily temperature and precipitation data from BioSIM were used to calculate the Canadian Drought Code as in Girardin et al. (2004). These daily drought indices were averaged to produce monthly indices for May to September over the time span 1915-2005. The Canadian Drought Code was originally developed by Turner (1972) and Van Wagner (1987) and is used as part of the Canadian Forest Fire Behaviour System to assess forest fire danger. The index rates the moisture content of deep organic layers by taking into account stored moisture content, evapotranspiration and precipitation (Girardin and Tardif 2005).

Hydrologic data were acquired from the Water Survey of Canada (2008). Daily and monthly discharge data for the Harricana River for the period 1915-2005 were obtained. The Harricana River is located approximately 80 km east of Lake Duparquet and drains an area of 3680 km². A former study had shown that good agreement was observed between spring Harricana River discharge and spring Lake Duparquet water level (Tardif and Bergeron 1997a). Discharge data for the Harricana River came from two gauge stations: Station 1 (48°34'11" N, 78°7'24" W) covered the time period of October 1914 to July 1933 and station 2 (48°36'2" N, 78°6'34" W) covered the time period January 1933 to September 2005. For station 2 no data were available from September 1998 through February 1999 which were also not estimated. Both stations are approximately 4 km apart. An examination of the overlapping monthly data of the 7 months (January to July) recorded by both gauge stations in the year 1933 showed an almost 100% agreement with ranked data yielding a Spearman $r=1.0$. No adjustments were thus made to account for the relocation of the Harricana gauge station.

3.3.7 Chronologies and Associations to Climatic and Hydrologic Data

All 15 chronologies originating from each site (control and floodplain) were subjected to principal components analysis (PCA) using CANOCO v. 4.52 (ter Braak 1994). An extra PCA included all 30 chronologies generated from trees growing on control and floodplain sites. All 3 PCAs were carried out using the chronology time span of 1915-2005.

Principal components analysis is a special case of canonical correlation which finds a line of best fit through data lying in a multidimensional space (Legendre and Legendre 1998). The method rotates variables in a Euclidean space such that new ordination axes are

obtained which account for the maximum possible amount of variance (Legendre and Legendre 1998). Principal components analysis was therefore used to assess the intercorrelation structure among the 15 chronologies. 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 matrix (Legendre and Legendre 1998). As a cross-verification of the PCAs, Spearman rank correlations were calculated among all 15 chronologies per location as well as all 30 chronologies of both sites for the time span 1915-2005 through using Systat v. 11 (Systat Software Inc. 2004).

In addition, the associations between the first two principal components (PCs) and tree-ring chronologies and climatic and hydrologic variables were determined using Spearman rank correlations. The associations between tree-ring chronologies were investigated over the time period 1915-2005. Associations of both, PCs and tree-ring chronologies with climatic data were analyzed from April of the year prior to ring formation (1914-2004) to August of the year of ring formation (1915-2005). Climatic data included monthly minimum and maximum temperature, total monthly precipitation and monthly drought code. For all analyses involving hydrologic data, discharge data of the Harricana River for the period 1915-2005 were used.

3.4. Results

3.4.1 General Statistics and Tree-Ring Chronologies

3.4.1.1 Descriptive Statistics

Trees growing on control and floodplain have overall similar mean raw measurement values (Table 3.1). However, even though trees growing in both habitats showed roughly the same mean RW value, the proportion of EW in rings from trees from the control was on average lower than in those from the floodplain trees (38% and 48% respectively). The larger FEW compared to CEW also corresponded to more abundant yet smaller vessels resulting in an earlywood zone with a slightly lower vessel density and porosity (Table 3.1).

Mean sensitivity and standard deviations were higher in the floodplain vessel chronologies than in control vessel chronologies, indicating their higher interannual variations compared to the control ones (Table 3.1). For trees growing on the control, CLW and CRW achieved the highest values for percent variance in the first principal component (PC-1), expressed population signal (EPS) and intertree correlation. In addition, all control chronologies except C25E, CdE and CpE had EPS values above 0.85 indicating a high amount of shared variance. In contrast to the control, vessel chronologies from the floodplain shared the most variance. The floodplain vessel chronologies FME, FMTR, F25E and F25TR showed higher values for percent variance in PC-1, EPS and intertree correlation than the CLW and CRW of the control trees (Table 3.1). Further differences observed among trees growing on control and floodplain related to the autocorrelation of standard chronologies. Except for FEW, all floodplain tree-ring chronologies were less auto-correlated than control tree-ring chronologies (Table 3.1).

Table 3.1 General statistics characterizing the standard (S) or residual (R) tree ring widths and vessel chronologies generated from 21 and 20 trees from the control (C) and floodplain sites (F) respectively. The chronologies for control and floodplain site trees cover the periods 1857-2006 and 1890-2006, respectively and all statistics except those indicated were calculated for these respective time periods. Abbreviations are as follow: PC-1, first principal component; EPS, expressed population signal; EW, earlywood width; LW, latewood width; RW, ring-width; NE, number of earlywood vessels; NTR, number of earlywood and latewood vessels; TVAE, total cross-sectional vessel area of earlywood; TVATR total cross-sectional vessel area of earlywood and latewood; ME, mean cross-sectional vessel area of earlywood; MTR, mean cross-sectional vessel area of earlywood and latewood; 25E, mean cross-sectional vessel area of the 25% largest earlywood vessels; 25TR, 25% largest cross-sectional vessel area of the 25% largest vessels; dE, vessel density in the earlywood; dTR, vessel density in total ring; pE, porosity in the earlywood; pTR, porosity in the total ring.

	Mean ^a		Mean sensitivity		Standard deviation		Auto-correlation ^b		Variance in PC-1 (%) ^c		EPS ^c		Intertree correlation		Type ^d	
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
EW (mm)	0.39	0.52	0.13	0.08	0.13	0.07	0.44	0.48	28	28	0.85	0.84	0.21	0.21	R	R
LW (mm)	0.65	0.56	0.44	0.39	0.37	0.36	0.27	0.12	59	45	0.96	0.92	0.56	0.36	R	S
RW (mm)	1.0	1.1	0.27	0.21	0.25	0.19	0.30	0.17	60	48	0.96	0.93	0.56	0.44	R	R
NE	31	38	0.11	0.13	0.11	0.14	0.34	0.12	40	57	0.92	0.96	0.35	0.53	R	S
NTR	37	43	0.11	0.14	0.10	0.15	0.31	0.11	44	59	0.93	0.96	0.40	0.54	R	S
TVAE (10⁴ μm²)	55	62	0.12	0.14	0.12	0.12	0.42	0.19	38	53	0.91	0.95	0.32	0.49	R	R
TVATR (10⁴ μm²)	60	64	0.12	0.13	0.12	0.12	0.44	0.22	43	52	0.93	0.95	0.38	0.49	R	R
ME (10⁴ μm²)	1.8	1.7	0.08	0.20	0.08	0.17	0.41	-0.05	29	67	0.87	0.97	0.24	0.64	R	S
MTR (10⁴ μm²)	1.6	1.5	0.07	0.19	0.07	0.17	0.35	-0.07	27	68	0.86	0.97	0.22	0.65	R	S
25E (10⁴ μm²)	2.9	2.6	0.08	0.18	0.07	0.15	0.35	-0.05	26	67	0.84	0.97	0.20	0.63	R	S
25TR (10⁴ μm²)	2.6	2.5	0.07	0.18	0.07	0.15	0.34	-0.06	28	68	0.86	0.97	0.22	0.64	R	S
dE (10⁻¹³ mm⁻²)	1.8	1.6	0.09	0.10	0.08	0.12	0.16	-0.01	18	42	0.73	0.92	0.11	0.35	R	S
dTR (10⁻¹³ mm⁻²)	0.93	0.99	0.25	0.17	0.24	0.19	0.28	0.11	57	40	0.96	0.91	0.52	0.33	R	S
pE	0.31	0.26	0.07	0.12	0.07	0.10	0.19	-0.06	15	52	0.56	0.95	0.06	0.47	R	S
pTR	0.15	0.15	0.22	0.21	0.24	0.19	0.13	0.02	57	55	0.96	0.96	0.53	0.51	S	S

^aCalculated from measurement series.

^bCalculated from standard chronologies.

^cCalculated from the common period 1957-1998.

^dType of chronology used: Standard (S) or Residual (R).

3.4.1.2 Ring-width and Vessel Chronologies

Within the control and floodplain chronologies both LW and RW and to a lesser extent dTR and pTR shared common variability with peaks (e.g. 1945, 1949, 1979, 1993, 1999) and troughs (e.g. 1929, 1940, 1948, 1965, 1972, 1995) occurring in the same years (Figure 3.3).

The FEW showed somewhat lower year-to-year variation than the CEW (Table 3.1, Figure 3.3). The floodplain earlywood vessel chronologies (FNE, FTVAE, FME, F25E, FdE, FpE) and most of the floodplain total ring vessel chronologies (FNTR, FTVATR, FMTR, F25TR) presented much higher interannual variation than those of the control (Table 3.1, Figure 3.3). Both the floodplain earlywood vessel number and vessel area chronologies showed highly pronounced peaks and troughs over the period 1915-2005, which resulted in skewness values (γ) ranging from -1.5 to 2.3. The chronologies FdE ($\gamma = 2.3$), FdTR ($\gamma = 2.2$), FNE ($\gamma = 1.5$) and FNTR ($\gamma = 1.5$) showed the highest positive skew. The highest negative skews were observed for FME ($\gamma = -1.5$), FMTR ($\gamma = -1.5$), F25E ($\gamma = -1.5$), F25TR ($\gamma = -1.5$) and FpE ($\gamma = -1.3$). The highly negatively skewed chronologies FME, FMTR, F25E, F25TR and the positively skewed chronology FdE were also not normally distributed over the time period 1915-2005 according to the Kolmogorov-Smirnov test for normality (for FME $p=0.017$, $n=91$; for FMTR $p=0.027$, $n=91$; for F25E $p=0.013$, $n=91$; for F25TR $p=0.009$, $n=91$; for FdE $p=0.002$, $n=91$). Among the 12 vessel chronologies developed for the control six chronologies were skewed with skewness values ranging from -1.6 to 1.9 (CMTR $\gamma=-1.6$; CME $\gamma=-1.3$; C25TR $\gamma=-0.90$; CdTR $\gamma= 1.2$; CpTR $\gamma=1.2$; CNE $\gamma= 1.9$). Despite these skewness

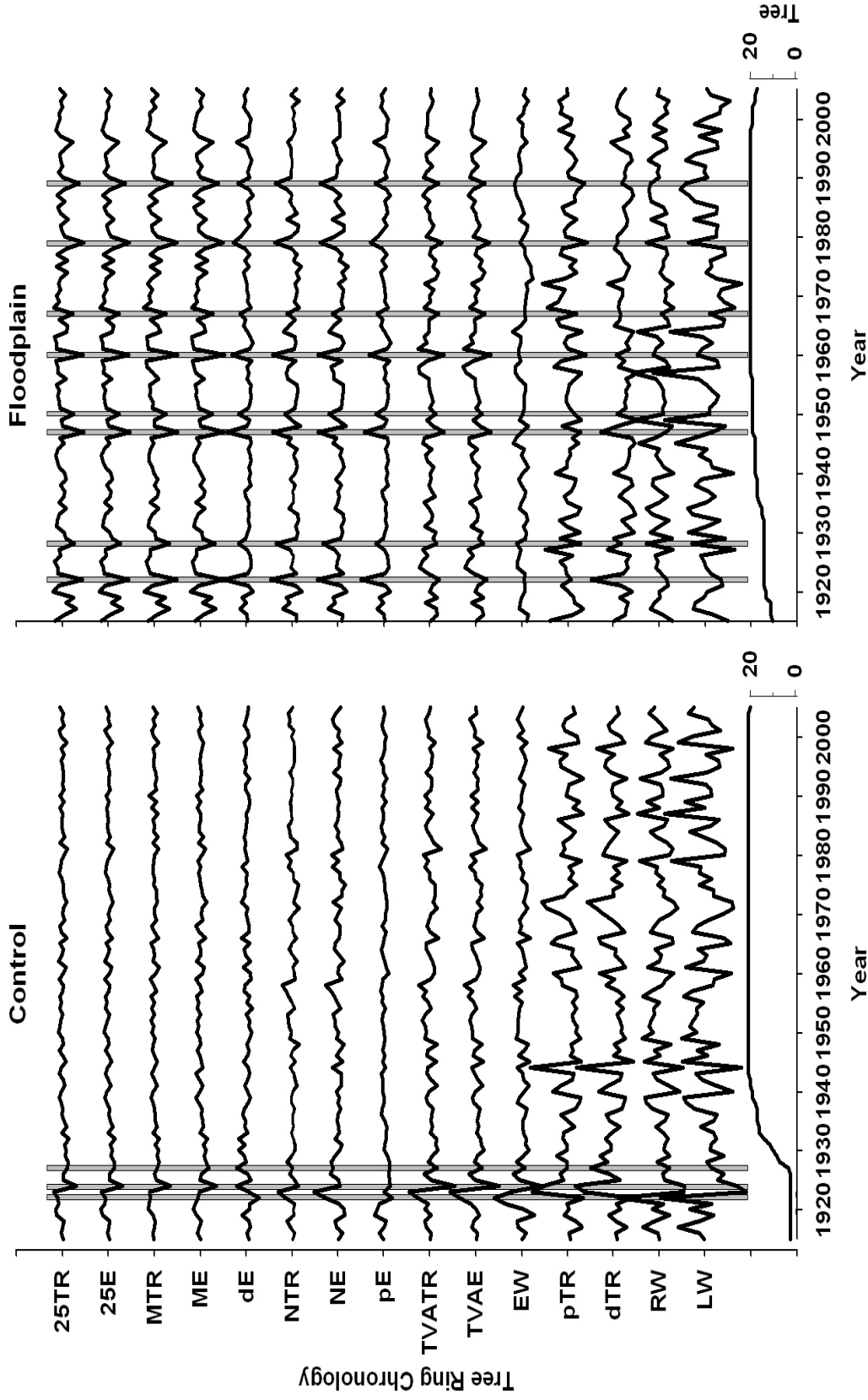


Figure 3.3. The 15 tree-ring chronologies for *Fraxinus nigra* growing on the control (left panel) and floodplain sites (right panel) with number of samples indicated at the bottom. Years in which 4 earlywood vessel chronologies deviated by 1.5 standard deviations are highlighted. Chronologies are abbreviated as in Table 3.1.

values, all of the chronologies were normally distributed according to the Kolmogorov Smirnov test (not presented). Years in which at least four out of six floodplain earlywood vessel chronologies showed deviations from the mean by at least 1.5 standard deviations were 1922, 1928, 1947, 1950, 1960, 1967, 1979 and 1989 (Figure 3.3). On the control, at least four out of six earlywood vessel chronologies deviated by at least 1.5 standard deviations from the mean in 1922, 1924 and 1927 (Figure 3.3).

3.4.2 Correlation Structure among Chronologies

The first two PCs of the PCA (Figure 3.4a) conducted with the 15 control chronologies explained respectively 46.6% and 24.2% of the variance. The first PC mainly reflected earlywood vessel characteristics (except for CNE and CpE) and CEW as indicated by their higher loadings on PC-1. Control latewood width, CRW, CdTR and CpTR had higher loadings on PC-2 than on PC-1 indicating that they also shared residual variance not common to earlywood related variables.

Rings with thick CEW were characterized by lower CdE as can be inferred from the inverse direction of the respective vectors showing an about 180° angle between CEW and CdE (Figure 3.4a). Control EW shared much variance with CTVAE, CTVATR, CNTR and to lesser extent CNE as can be seen from the proximity of the respective vectors (Figure 3.4a). These results indicate that rings with thicker CEW tended to be characterized by more abundant vessels and a larger total vessel area. The number of vessels (CNE, CNTR) shared more variance with CTVAE, CTVATR and CEW than with the mean vessel area (CME, CMTR, C25E, C25TR). These relationships are indicated

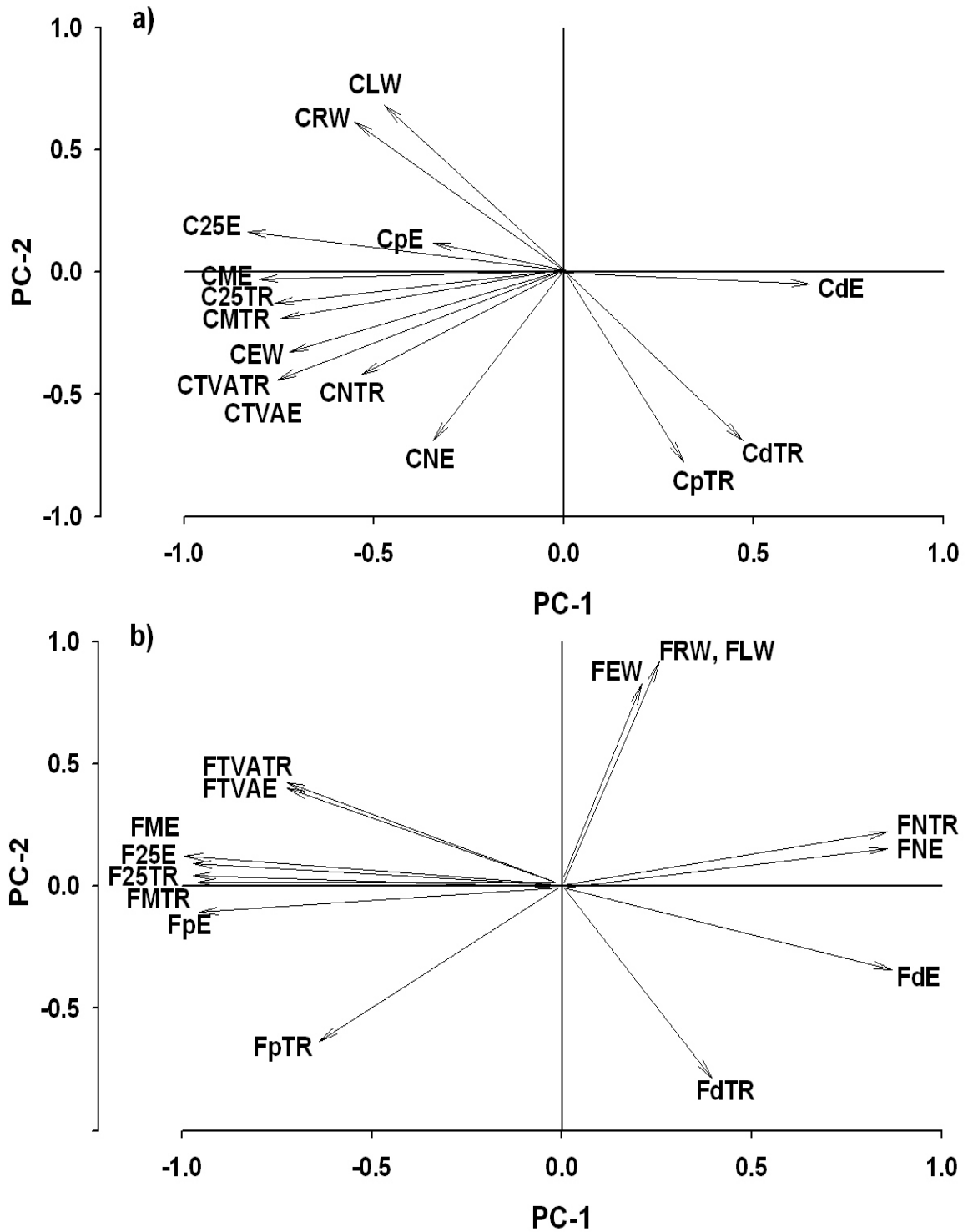


Figure 3.4. Principal components analysis of the 15 tree-ring chronologies for the a) control site and b) floodplain sites. The first two principal components axes are shown. The reference period is 1915-2005. The capital letter preceding each chronology abbreviation indicates their origin from the control site (C) or from the floodplain sites (F). Chronologies are abbreviated as in Table 3.1.

through the closer proximity of the vectors CNE and CNTR to CTVAE, CTVATR, CEW as opposed to vectors pertaining to the mean vessel area (CME, CMTR, C25E, C25TR) (Figure 3.4a). These results indicate that rings with abundant vessels (CNE, CNTR) also contain a higher total vessel area but not necessarily larger sized vessels as also shown by the correlation among these chronologies (Appendix A). Earlywood width was weakly positively associated with the mean cross-sectional vessel area chronologies (CME, CMTR, 25E, 25TR) (Appendix A) but the common variance among these chronologies was high as can be inferred from the proximity of the respective vectors (Figure 3.4a). Earlywood vessel density was negatively related to CEW, CME and CTVAE but not significantly correlated to CNE (Appendix A). Therefore rings showing high earlywood vessel density tended to have thinner CEW with earlywood vessels occupying smaller mean and total cross-sectional area. Latewood width and CRW shared a high amount of variance as indicated by the proximity of the respective vectors (Figure 3.4a). Both, CLW and CRW were strongly and inversely associated with CdTR and CpTR as indicated by the approximately 180° angle between the respective vectors (Figure 3.4a). Therefore, rings with thick latewood tended to have lower vessel density and porosity.

On the floodplain, the first and second PC of the PCA (Figure 3.4b) conducted with the 15 floodplain chronologies explained 15% more variance (59.0% and 27.1%, respectively) than for the control. As with the control, PC-1 was mainly reflective of earlywood vessel chronologies while those related to widths (FEW, FLW, FRW and to lesser extends FpTR and FdTR) had high loadings on PC-2. The distribution of floodplain chronologies in the ordination space showed, however, some differences with

that of the control chronologies (Figure 3.4). Unlike the control, the vectors of FNE and FNTR showed a near 180° angle with those of FME, FMTR, F25E, and F25TR (Figure 3.4b). Rings with a high number of earlywood vessels were characterized by having smaller cross-sectional area resulting in small FME, FMTR, F25E, F25TR values. Such rings were also associated with low porosity (FpE, FpTR) and high vessel density (FdE, FdTR) (Figure 3.4b, Appendix B). On the floodplain dE is more associated with NE than EW whereas in the control dE is more strongly related to EW than NE (Appendices A and B). Further differences between control and floodplain chronologies were found for the associations between EW and earlywood vessel chronologies. Compared to CEW, which was mostly associated with PC-1 (Figure 3.4a), FEW had a higher loading on PC-2 (Figure 3.4b). The FEW shared less variance with FME, FTVAE and FdE than the corresponding control chronologies as indicated by the loadings of floodplain earlywood vessels on PC-1 and FEW on PC-2 while the corresponding control chronologies loaded more commonly on PC-1 (Figure 3.4b). Unlike CEW, FEW was not significantly correlated to the mean cross-sectional vessel area chronologies (FME, FMTR, F25E, F25TR) (Appendices A and B). However, the FEW showed much stronger relationships with FRW and FLW than the corresponding chronologies on the control (Figure 3.4; Appendices A and B). As with the control, rings with thick LW or RW were related to lower vessel density (FdTR) and porosity (FpTR). The inverse associations of FLW and FRW with FdTR and FpTR were however less strong than with the control site (Fig. 3.4, Appendices A and B).

The respective PC-1 calculated from the 15 control and the 15 floodplain chronologies (Figure 3.5) were found to be non-significantly associated (Spearman $r=0.10$, $p=0.342$, $n=91$) despite mostly representing variance contained in their respective earlywood vessel chronologies. A significant correlation was not observed between control PC-1 and floodplain PC-2 (Spearman $r=0.15$, $p=0.142$, $n=91$) nor between control PC-2 and floodplain PC-1 (Spearman $r=0.06$, $p=0.601$, $n=91$). However, the years scores of control PC-2 and floodplain PC-2, which accounted largely for variance in latewood associated variables, were significantly cross-correlated (Spearman $r=0.30$, $p=0.004$, $n=91$). A PCA obtained from both, control and floodplain chronologies ($n=30$) showed that control chronologies loaded more strongly on PC-2 while floodplain chronologies loaded more strongly on PC-1 (Appendix C). Control and floodplain vessel chronologies therefore contained some dissimilar variance. The latewood related variables shared residual variance not common to earlywood related variables as indicated by the common loading of these vectors on PC-3 (Appendix C).

3.4.3 Associations between Tree-ring Chronologies and Climate Data

3.4.3.1 Control Site

Ring-width (EW, LW, RW) and many vessel chronologies showed the most consistent pattern with climate in being significantly associated with April temperature of the year prior to ring formation ($t-1$) and December precipitation ($t-1$) (Figure 3.6abc). In the current year (t), EW and total vessel area (TVAE, TVATR) and number of vessel

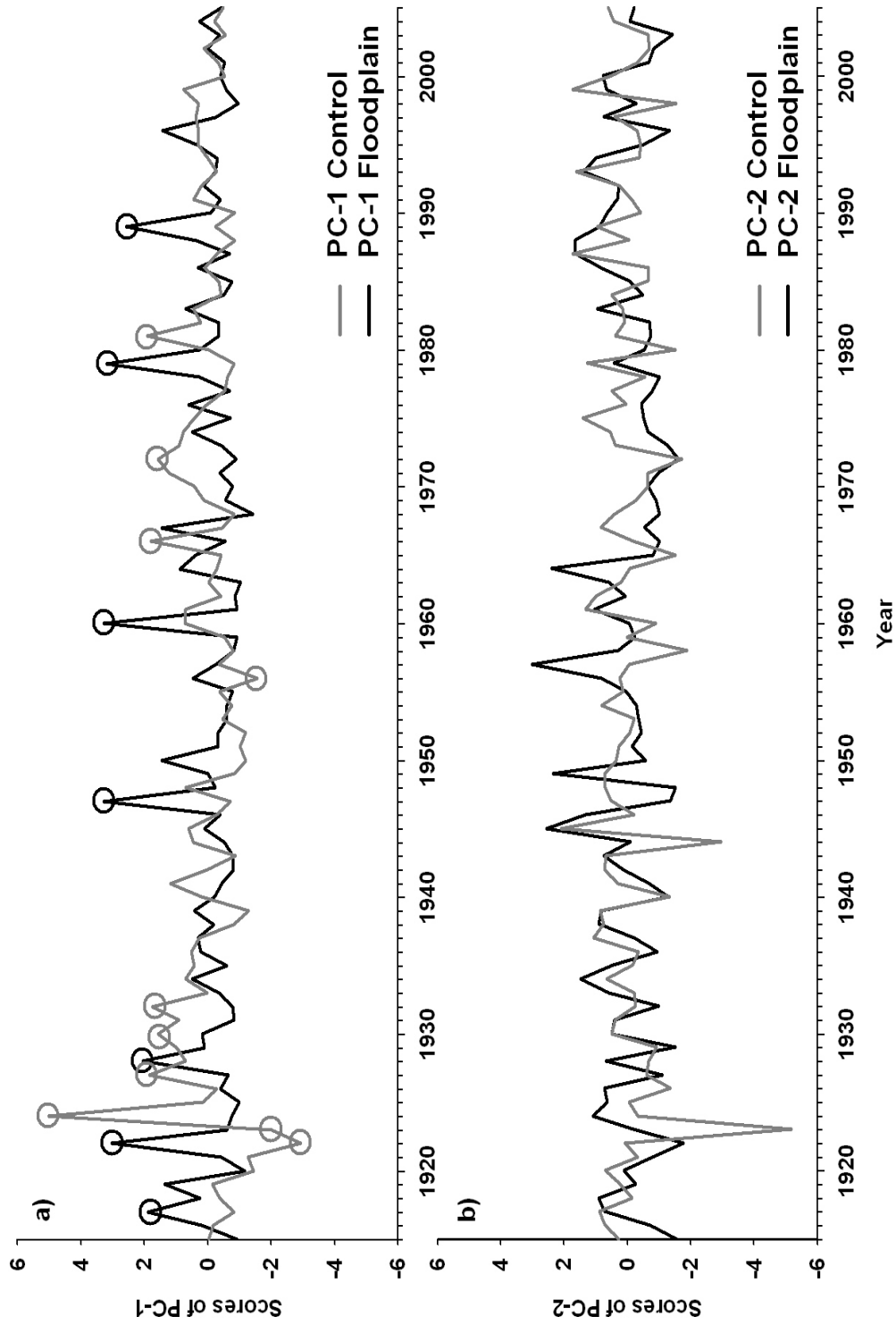


Figure 3.5. Year's scores of control (grey) and floodplain (black) principal component 1 (a) and principal component 2 (b). Year's scores of the two first principal components that deviate by ± 1.5 standard deviations are indicated by an open circle (a).

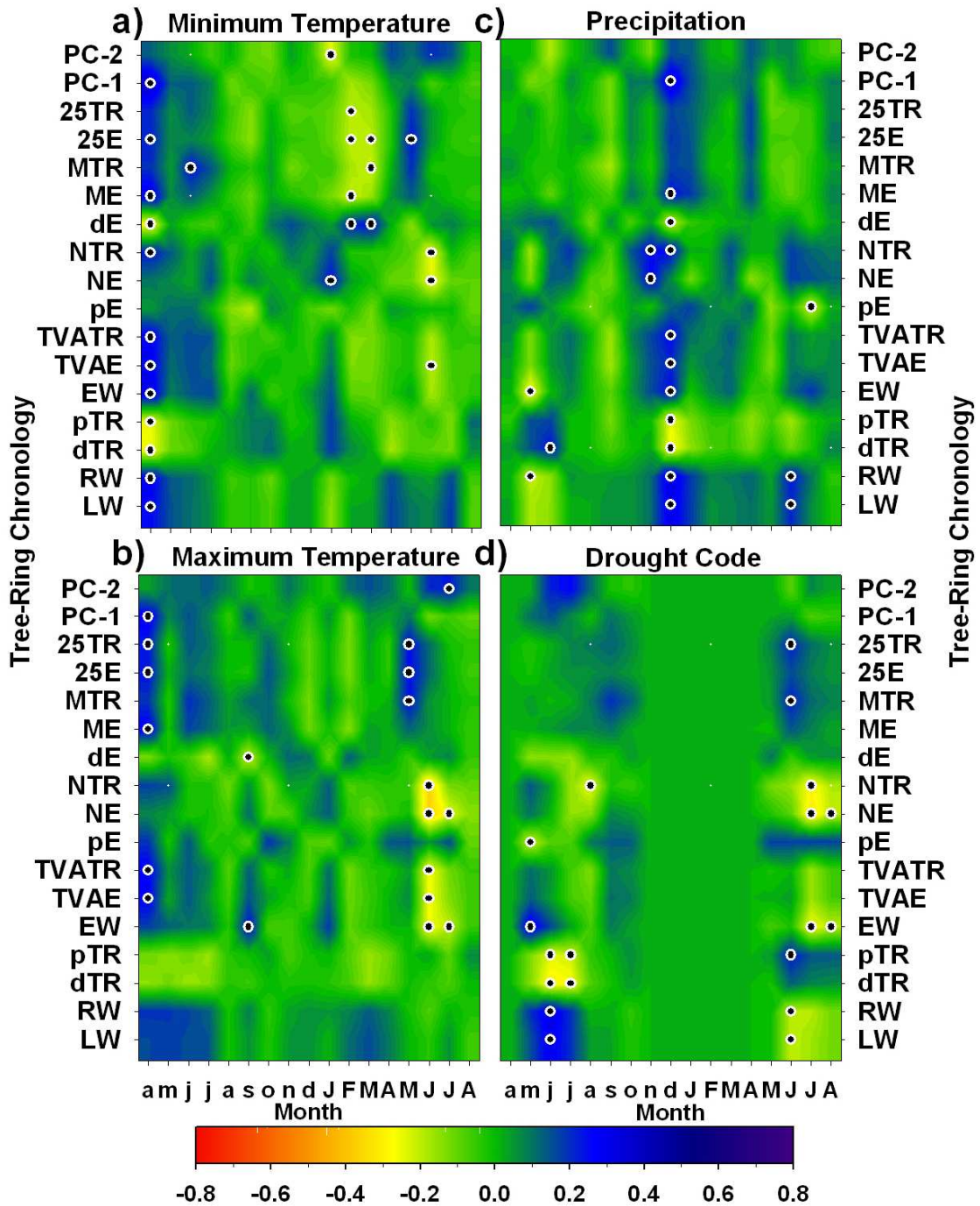


Figure 3.6. Spearman rank correlation coefficients between the 15 *Fraxinus nigra* chronologies from the control site and mean monthly minimum temperature (a), mean monthly maximum temperature (b), mean monthly drought code (c) and total monthly precipitation (d) from April of the year prior to ring formation to August of the year of ring formation 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 3.1.

chronologies (NE, NTR) were also commonly associated with maximum June temperature (Figure 3.6b).

The width chronologies (EW, LW, RW) were positively related to minimum but not to maximum April (t-1) temperature (Figure 3.6ab). Earlywood width was also negatively related to May (t-1) precipitation, and positively related to May (t-1) drought code (Figure 3.6cd). Contrarily, LW and RW were positively related to June (t-1) drought code (Figure 3.6d). All ring-width variables (EW, LW and RW) were also positively related to December (t-1) precipitation (Figure 3.6c). In the year of ring formation, EW was negatively related to June-July maximum temperature and to July-August drought code (Figure 3.6bd). Contrarily, LW and RW were positively to June (t) precipitation and negatively related to June (t) drought code (Figure 3.6cd). As for the ring-width chronologies (EW, LW, RW), the vessel chronologies TVAE, TVATR, NTR, ME, 25E and PC-1 were positively associated with minimum April (t-1) temperature (Figure 3.6a). In addition, TVAE, TVATR, ME, 25E, 25TR and PC-1 were positively related to maximum April (t-1) temperature (Figure 3.6b). The positive association of ring-width chronologies (EW, LW, RW) with December (t-1) precipitation was also observed for TVAE, TVATR, NTR, ME, and PC-1 while dTR, pTR and dE showed the inverse relationship (Figure 3.6c). Climate associations of TVAE, TVATR, NE and NTR further resembled those of EW in that they were all negatively correlated to maximum June (t) temperature (Figure 3.6b). Similarities between EW, NE and NTR also exist in the common negative association with July (t) drought code (Figure 3.6d). As with EW, NE was further negatively related to August (t) drought code.

Vessel chronologies also showed unique associations with climate, as ME, 25E and 25TR were negatively related to minimum February (t) temperature while dE showed the inverse association (Figure 3.6a). The dE was also positively related to minimum March (t) temperature while MTR and 25E showed a negative association. In contrast, MTR, 25E and 25TR were positively related to maximum May (t) temperature and 25E was further positively related to minimum May (t) temperature (Figure 3.6.ab).

3.4.3.2 Floodplain Site

As with the control site, the width chronologies (EW, LW and RW) showed few, if any, common correlation with climate variables (Figure 3.7). In contrast to the control, no floodplain chronologies were associated with April (t-1) minimum or maximum temperature (Figure 3.7ab). Unlike the control, LW was negatively related to June (t-1) precipitation whereas EW was positively related to June (t-1) drought code (Figures 3.6cd and 3.7cd). As with the control, the EW was positively related to December (t-1) precipitation, however, unlike control LW and RW floodplain LW and RW were not related to December (t-1) precipitation (Figures 3.6c and 3.7c).

Comparisons of climate associations of floodplain EW and vessel chronologies showed that contrary to the EW and the corresponding control vessel chronologies, TVAE, TVATR, pE, ME, MTR, 25E, 25TR were negatively related to minimum and maximum July (t-1) temperatures (Figures 3.6ab and 3.7ab). Unlike the vessel area related chronologies, the dE and PC-1 were positively related to minimum July (t-1) temperature

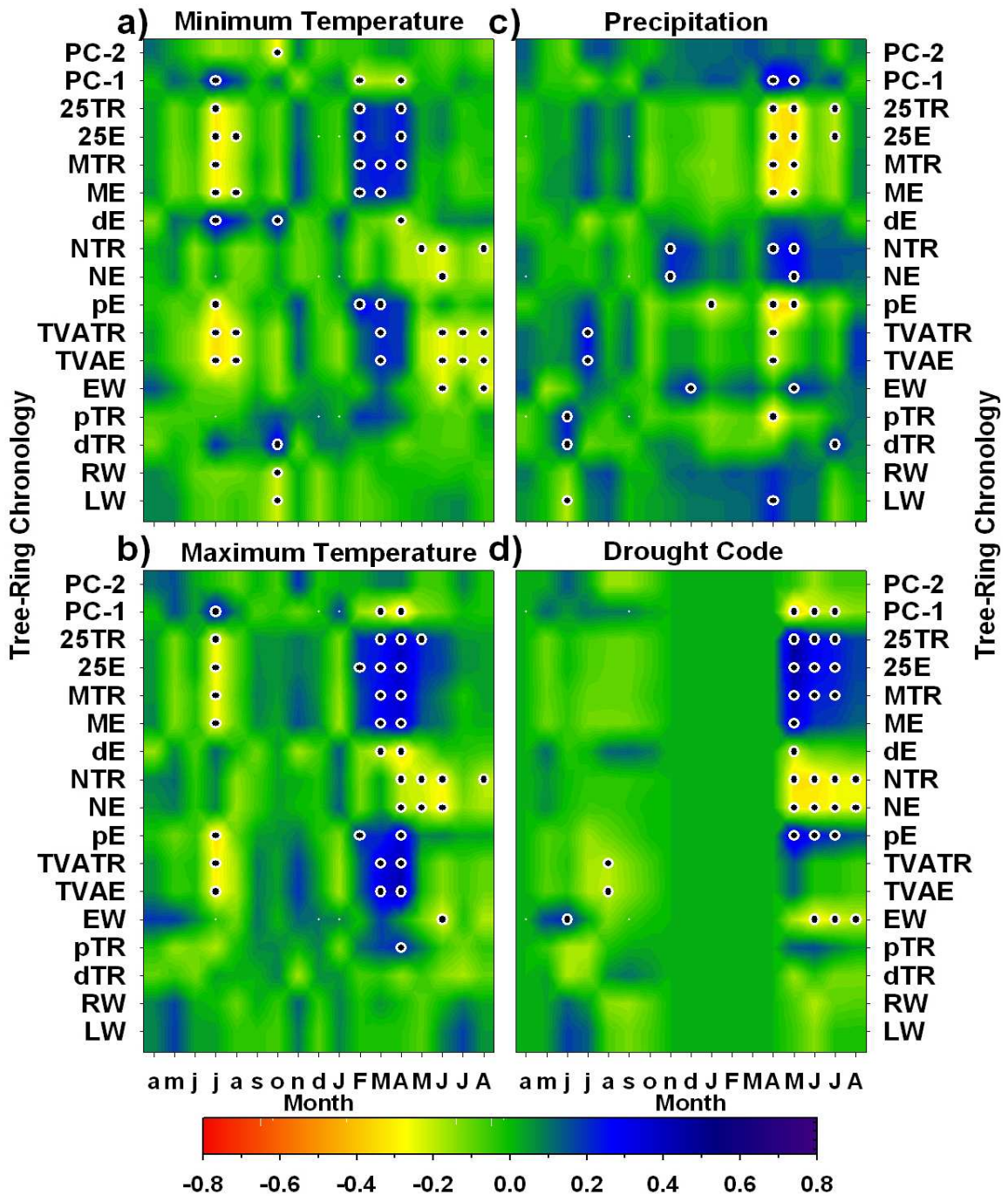


Figure 3.7. Spearman rank correlation coefficients between the 15 *Fraxinus nigra* chronologies from the floodplain site and mean monthly minimum temperature (a), mean monthly maximum temperature (b), mean monthly drought code (c) and total monthly precipitation (d) from April of the year prior to ring formation to August of the year of ring formation 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 3.1.

and PC-1 was further positively correlated to maximum July (t-1) temperature (Figure 3.7a). In addition, TVAE, TVATR, ME and 25E were negatively related to August (t-1) minimum temperature (Figure 3.7a). Many vessel area chronologies were positively related to minimum Feb-March-April (t) temperature and maximum March-April (t) temperature (Figure 3.7ab). These relationships differ from the negative associations of control mean vessel area related variables with minimum February (t) or March (t) temperature (Figure 3.6a, b). In contrast to the floodplain vessel area related variables, dE was negatively related to minimum and maximum April (t) temperature and maximum March (t) temperature (Figure 3.7a, b). The chronologies NE and NTR were negatively related to maximum April (t) temperature (Figure 3.7b).

Common associations of EW and many vessel chronologies were observed with climate variables during May-July (t) (Figure 3.7). The EW, PC-1 and the number of vessels (NE, NTR) were positively related to May (t) precipitation whereas vessel area related variables (pE, ME, MTR, 25E, 25TR) showed the inverse association (Figure 3.7c). In addition, TVAE, TVATR, pE, ME, MTR, 25E, 25TR were negatively related to April (t) precipitation whereas NTR and PC-1 showed a positive association. The EW, TVAE, TVATR, NE, NTR were also negatively related to minimum June (t) temperature whereas EW, NE and NTR were also negatively related to maximum June (t) temperature (Figure 3.7ab). Furthermore, EW, NE, NTR and PC-1 were negatively correlated to June-July (t) drought code while pE, MTR, 25E, 25TR showed the inverse association (Figure 3.7d). Unlike the EW, pE, ME, MTR, 25E, 25TR were positively correlated to May (t)

drought code while NE, NTR, dE and PC-1 were negatively related to this climate variable.

3.4.4 Associations between Tree-ring Chronologies and Hydrologic Data

As observed with the correlations with climate variables, the control and floodplain chronologies also greatly differed in their associations with discharge data (Figure 3.8). Similar to the correlations with April (t-1) minimum temperature, on the control site all ring-width variables (EW, LW, RW), TVAE, TVATR, NTR, ME, MTR, 25E, 25TR and PC-1 were positively related to April (t-1) discharge (Figures 3.6a and 3.8a). Contrarily, density (dE, dTR) and porosity (pTR) were negatively correlated with April (t-1) discharge (Figure 3.8a). In addition, LW, RW and PC-2 were negatively related to July (t-1) discharge whereas dTR and pTR showed the inverse association. Contrarily, ME, 25E, 25TR and PC-1 were negatively related to August (t-1) discharge. The chronologies ME, MTR, 25E, 25TR and PC-1 were further negatively related to September (t-1) discharge. As with April (t-1) discharge, LW and RW were positively related to April (t) discharge whereas dTR and pTR showed the inverse relationship (Figure 3.8a).

No significant correlations were observed between the floodplain chronologies and discharge data from the year prior to ring formation except for the positive correlation between pTR and July (t-1) discharge (Figure 3.8b). For hydrologic correlations of the current year, all ring-width chronologies (EW, LW, RW) were positively related to June (t) discharge and EW was further positively related to July (t) discharge (Figure 3.8b).

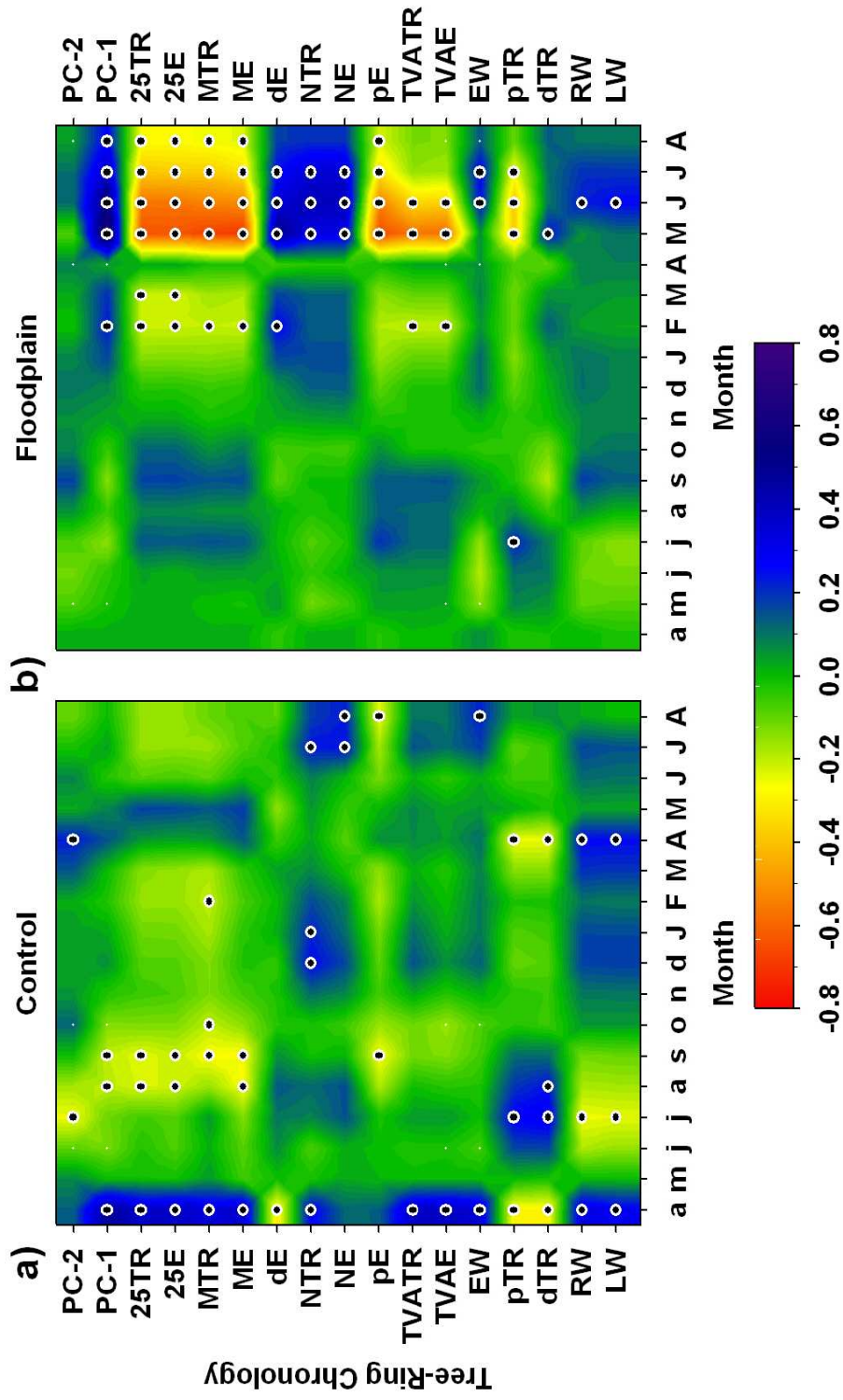


Figure 3.8. Spearman rank correlation coefficients between mean monthly *Fraxinus nigra* River discharge and control site *Fraxinus nigra* chronologies (a) and floodplain site *Fraxinus nigra* chronologies (b) from April of the year prior to ring formation to August of the year of ring formation for 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 3.1.

The floodplain vessel area chronologies (TVAE, TVATR, ME, MTR, 25E, 25TR) were negatively associated with February (t) discharge while dE and PC-1 showed the inverse relationship (Figure 3.8). In addition, 25E and 25TR were negatively related to March (t) discharge (Figure 3.8b). Of all correlation analyses (climate and hydrologic variables), the strongest associations were observed between floodplain vessel chronologies and May-June (t) discharge (Figure 3.8b). The chronologies TVAЕ, TVATR, ME, MTR, 25E, 25TR, pE and pTR were strongly negatively correlated to May (t) and June (t) discharge with Spearman rank correlations ranging in May from -0.40 to -0.72 ($p < 0.0001$, $n = 91$) and in June from -0.37 to -0.59 ($p < 0.001$, $n = 91$) (Figure 3.8b). Among those correlations, the strongest association was found for ME and May (t) discharge (Spearman $r = -0.72$, $p = 0.000001$, $n = 91$). Contrary to the negative associations of vessel area related chronologies and May-June (t) discharge, the number of vessels (NE, NTR), vessel density (dE, dTR) and PC-1 were positively related to these hydrologic variables (Figure 3.8b). Among the correlations of NE, NTR, dE, dTR and PC-1 with May discharge, Spearman rank correlation coefficients ranged from 0.23 to 0.68 ($p < 0.05$, $n = 91$) with PC-1 showing the strongest association (Spearman $r = 0.68$, $p = 0.000001$, $n = 91$). The NE, NTR, dE and PC-1 were also positively correlated with June discharge (Spearman rank correlation coefficients ranged from 0.35 to 0.56, $p < 0.001$, $n = 91$) with PC-1 showing again the strongest relationship (Spearman $r = 0.56$, $p = 0.000001$, $n = 91$). In contrast to the strong correlations of vessel chronologies with May (t) and June (t) discharge, correlations with July (t) and August (t) discharge were much weaker.

As previously identified (section 3.4.1.2), the outlier years 1922, 1928, 1947, 1950, 1960, 1967, 1979 and 1989 all corresponded to years with high May and/or June discharge, except for 1950 (Figure 3.9). In the years 1890, 1909, 1917, 1922, 1928, 1947, 1950, 1960, 1967, 1979, 1989 and 1996 the floodplain ME deviated by more than the mean + 1.5 standard deviations (Figure 3.9). Except for 1950 and 1996 all years during which the ME deviated by more than 1.5 standard deviations also correspond to years in which May and/or June (t) discharge deviated by more than 1.5 standard deviations for the time span 1915-2005 (in May of 1922, 1928, 1947, 1960, 1967 and 1979 and in June of 1917, 1928, 1947, 1960 and 1989) (Figure 3.9). No discharge data are available for the time period prior to 1915 but the results indicate that 1890 and 1909 may correspond to years of major spring floods. Despite the low sample depths in 1890 (3 trees) and 1910 (10 trees) the EPS reached 0.85 for 3 trees and 0.97 for 10 trees, indicating strong signal strengths for both sample depths. The signal obtained for the ME chronology in 1890 is related to a strong decrease in the mean vessel area of all three trees, which showed a reduction in raw data values of 46% to 76% below the average mean vessel area. Since the youngest of these 3 trees originated in 1864, the small vessel areas observed in 1890 are not related to an age effect. In all years in which the ME deviated by more than 1.5 standard deviations, many floodplain 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 (Figure 3.10ab). Tree rings showing such vessel characteristics were not observed for control site trees in any given year (Figure 3.10cd).

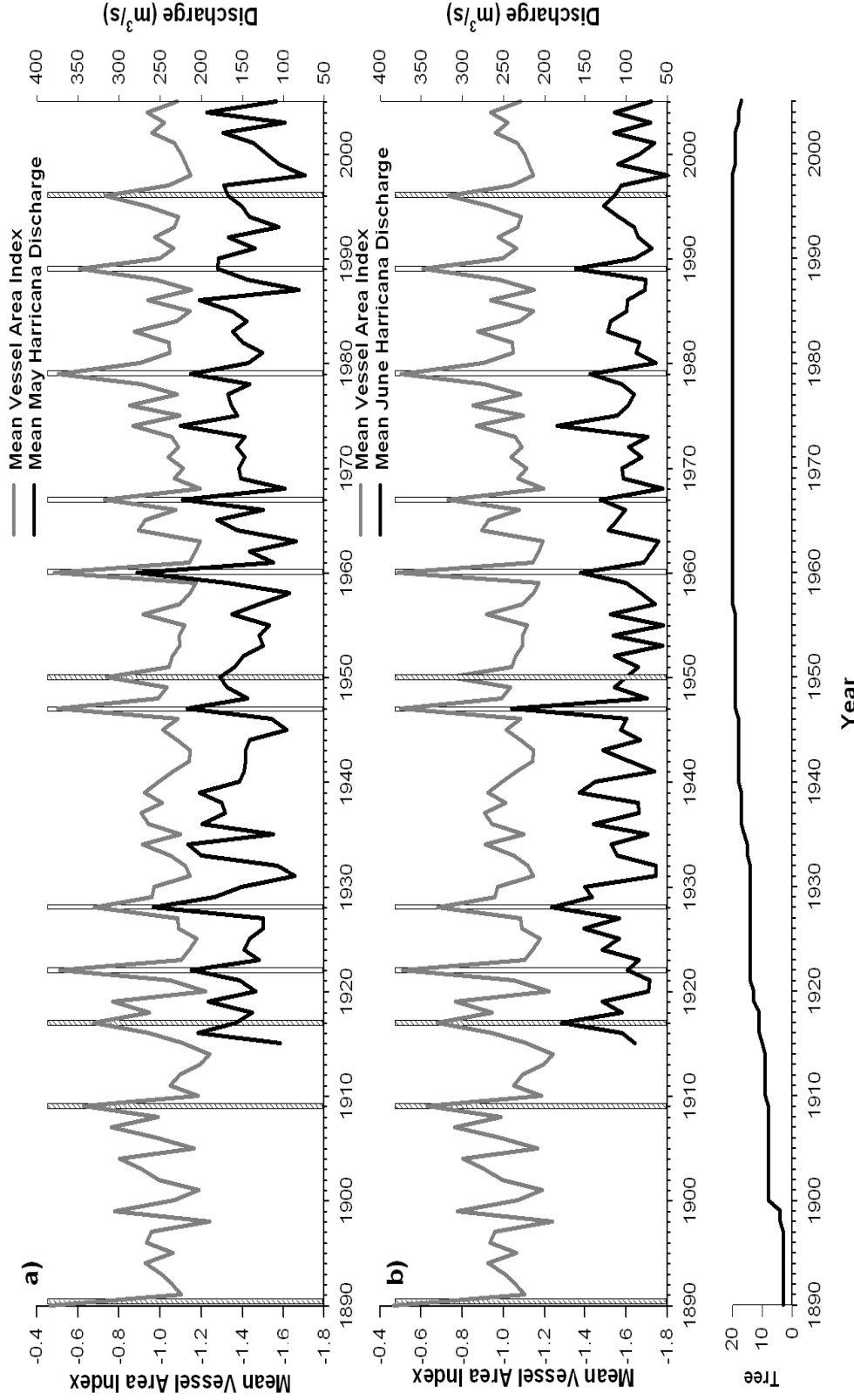


Figure 3.9. Floodplain mean earlywood vessel area index (grey line) and Harricana River Discharge (black line) for the month of May (a) and June (b) for the time periods 1890-2005 (mean earlywood vessel area index) and 1915-2005 (discharge). Years in which the mean earlywood vessel area index and discharge deviate by more than 1.5 standard deviations are highlighted by empty bars, those in which the mean earlywood vessel area index deviates by more than 1.5 standard deviations are highlighted by hatched bars.

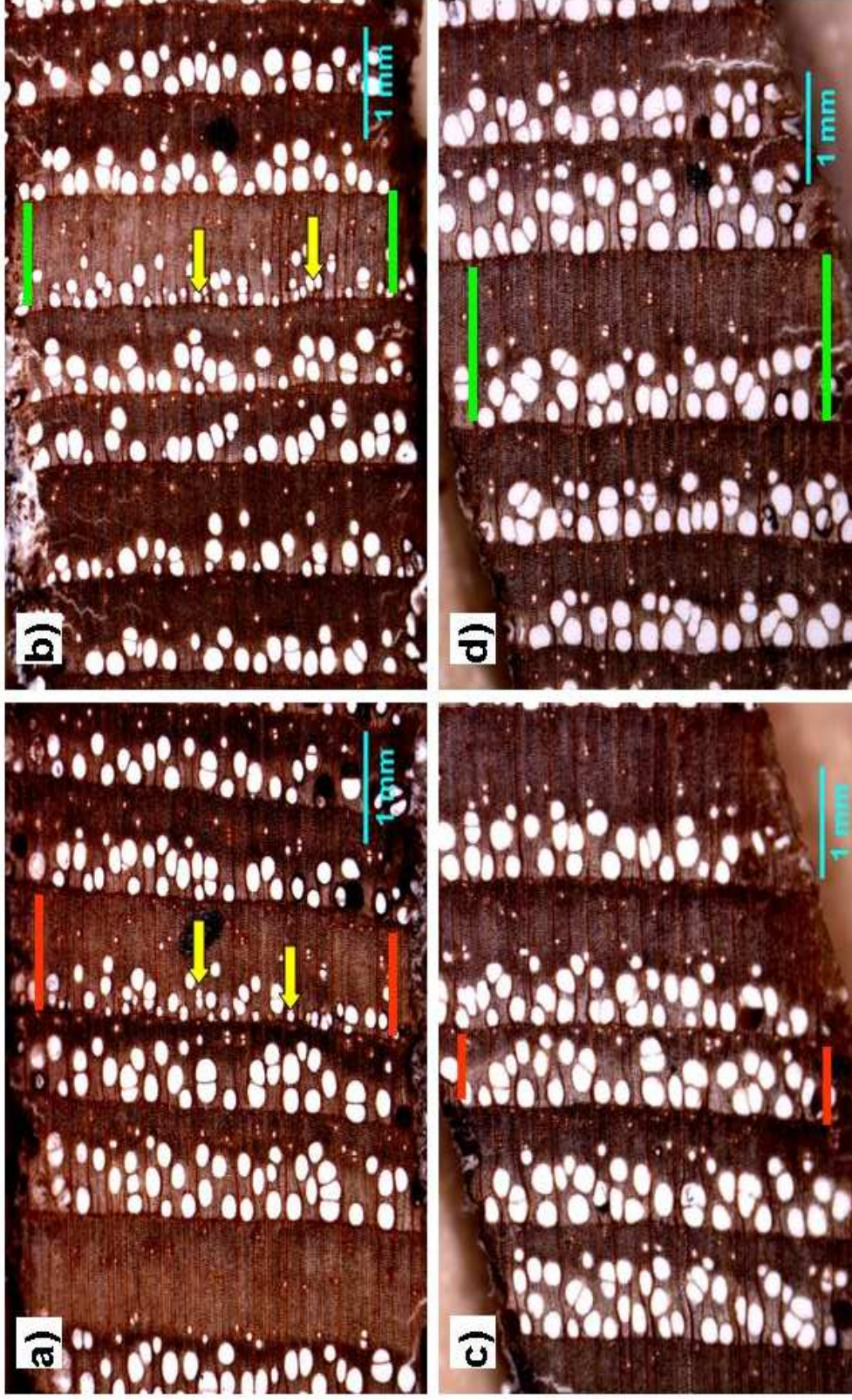


Figure 3.10. *Fraxinus nigra* tree rings magnified 20x of floodplain (a, b) and control (c, d) site trees showing rings of the years 1960 and 1979 delineated in red and green, respectively. Yellow arrows point to examples of vessels with largely reduced area.

Among first, second and third order polynomial models, the relationship between May river discharge and floodplain chronologies (PC-1, pE, dE, 25E, ME, TVAE and NE) was best modeled with the first order polynomial model indicating a linear relationship between variables (Figure 3.11a-g, Appendix M). The ME was the best predictor for May river discharge while a non-significant model was found for May river discharge and floodplain EW (Figure 3.11h, Appendix M).

3.4.5 Effects of Outliers on Statistical Analysis

The effect of outlier values (identified in section 3.4.1.2) did not change the correlation among the control chronologies and among the floodplain chronologies (Appendices A and D for control site chronologies, and appendices B and E for floodplain chronologies). Outlier values also did not affect the variance of the chronologies since the year's scores of the PCA from which outliers had been removed prior to the PCA were highly correlated with those from which outliers had been removed only following the PCA (Appendix F). The correlations of control and floodplain chronologies with climate variables containing or missing outliers largely resembled each other indicating that associations of chronologies with climate were not influenced by extreme years (Appendices G, H for control site chronologies and I, J for floodplain chronologies). Outlier values also did not induce important changes in the correlation of control and floodplain chronologies with discharge (Appendices K and L for control and floodplain chronologies, respectively). As the correlation coefficients between floodplain earlywood variables and spring river discharge decreased only slightly and remained highly significant, these results indicate that flooding had a continuous effect on floodplain

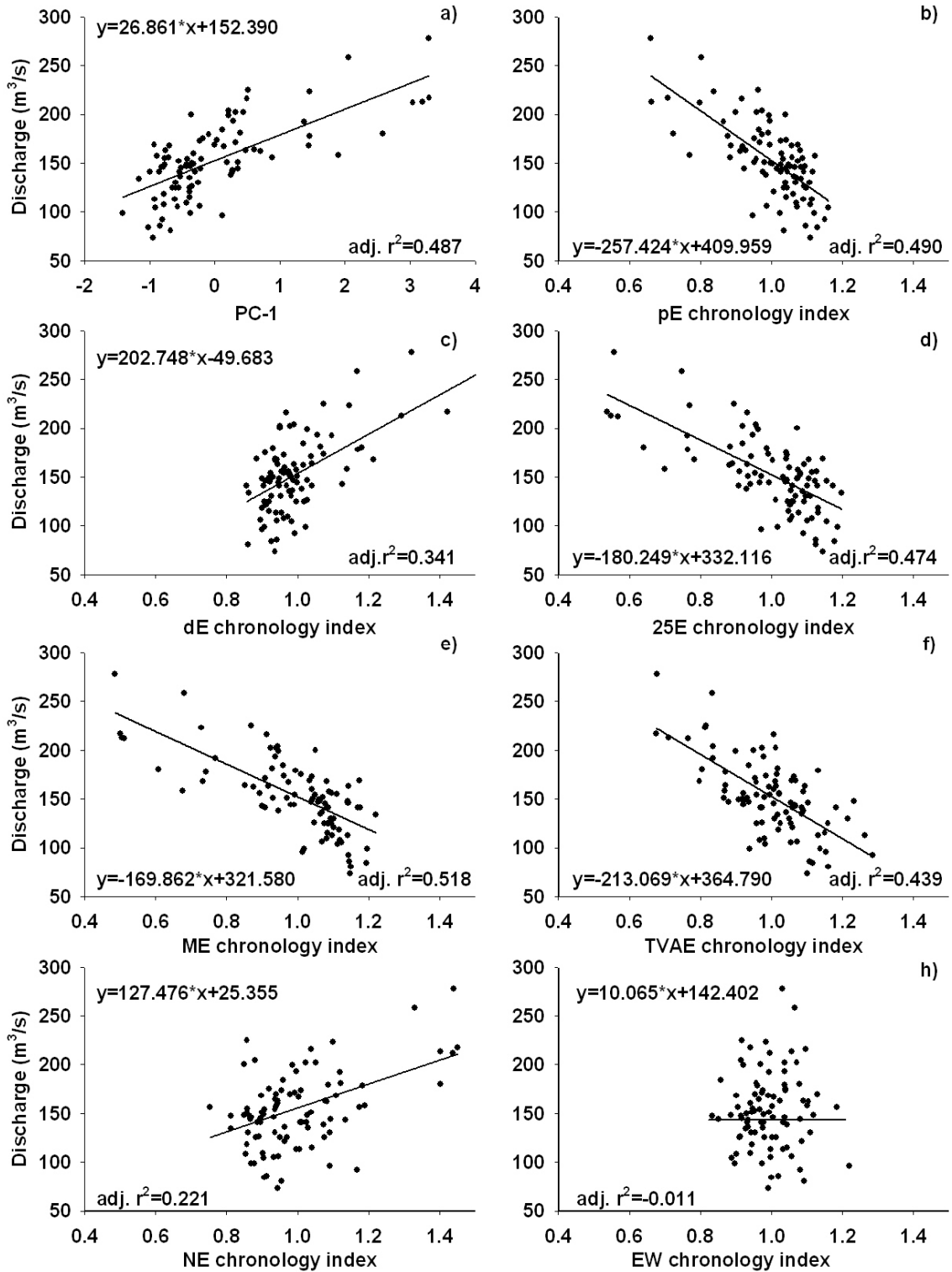


Figure 3.11. Relationships between mean May discharge (m³/sec) and PC-1 (a), the chronology indices porosity (pE) (b), density (dE) (c), 25% largest earlywood vessel area (25E) (d), mean vessel area (ME) (e), total vessel area (TVAE) (f), number of vessels (NE) (g) and earlywood width (EW) (h) for 1915-2005. Included are the regression model and the r^2 values adjusted for degrees of freedom.

vessel size and number (Appendices K and L for control and floodplain chronologies, respectively).

3.5 Discussion

3.5.1 Chronology Statistics

The lower interannual variability of EW compared to LW and RW as observed on both the control and floodplain sites are in accordance with a previous *F. nigra* study (Tardif 1996). These results were also reported for ring-porous post oak (*Quercus stellata* Wangenh.) (Phipps 1982), *C. sativa* (Fonti and García-González 2004), Portuguese oak (*Quercus faginea* Lam.) (Corcuera et al. 2004a), *Q. alba* and *Q. rubra* (Tardif and Conciatori 2006), *Q. petraea*, and pubescent oak (*Quercus pubescens* Willd.) (Fonti and García-González 2008). The low interannual variability of the earlywood thus appears to be a characteristic inherent to many ring-porous species. In ring-porous species, water transport relies primarily on earlywood vessels built in the current growing season (Sperry and Sullivan 1992; Tyree et al. 1994; Hacke and Sperry 2001). It is therefore crucial for ring-porous species to produce earlywood every year. The low variability in earlywood width from year to year compared to that of latewood width, for example, may reflect stronger developmental controls. For example, Chalk (1930) and Zasada and Zahner (1969) reported that earlywood ceased to be produced one to two weeks after shoot extension and full leaf expansion.

The higher autocorrelation in EW versus LW and RW chronologies has also been reported for floodplain *F. nigra* (Tardif 1996). In accordance with other studies of ring-

porous species, LW and RW chronologies from both sites contained a stronger common signal than the EW chronology (Tardif 1996; Fonti and García-González 2004, 2008; Lebourgeois et al. 2004; Tardif and Conciatori 2006). A lower common signal strength and mean sensitivity of earlywood vessel characteristics versus ring-widths as observed on the control were also found for *Q. rubra*, *Q. alba*, *C. sativa* and *Q. macrocarpa* (Woodcock 1989a; Fonti and García-González 2004; Tardif and Conciatori 2006). Contrary to the control vessel chronologies, most of the floodplain earlywood vessel chronologies showed greater common signal strength. The strength of this signal was also reflected in a higher mean sensitivity and a more synchronized/common response to environmental forcing.

Another difference between radial growth of the control and floodplain trees was the thicker EW zone observed in floodplain trees and its greater contribution to the total ring width. This specificity may relate to annual spring floods and altered concentrations of growth regulators. During flooding, the concentration of ethylene was observed to greatly increase in submerged portions of plants, including *Fraxinus* species (Newsome et al. 1982; Tang and Kozlowski 1984 and references therein; Yamamoto and Kozlowski 1987; Jackson 1990; Yamamoto et al. 1995; Jackson and Colmer 2005 and references therein). Ethylene is known to block basipetal and lateral indole-3-acetic acid (IAA) transport (Burg and Burg 1967; Suttle 1988) and tissues with high concentrations of ethylene have been associated with elevated concentrations of IAA (Junghans et al. 2004). Digby and Wareing (1966) observed that the transition from earlywood to latewood production in ring-porous black locust (*Robinia pseudoaccacia* L.) followed decreasing exogenously

applied concentrations of IAA and after cessation of primary growth. In flood years, leaf development in *F. nigra* trees is slower than in non-flood years (Tardif, personal communication 2009) and earlywood production may last longer than on the control site. Alternatively, the larger earlywood zone may also relate to the subjective delineation of the EW zone. Ring-porous species were reported to have a clear bimodal distribution of vessel diameter characterizing the transition from earlywood to latewood (Panshin and de Zeeuw 1980; Woodcock 1989b). Many studies however have reported that the ring-porous nature of stem wood was plastic and that it changed to a more diffuse-porous structure upon stem burial with sediments (Sigafos 1964, Cournoyer and Bégin 1992). Juvenile tree rings of ring-porous species also display a rather diffuse-porous vessel arrangement (Fig. 3.2 right panel; Helinska-Raczkowska 1994; Helinska-Raczkowska and Fabisiak 1999). As will be discussed later, earlywood vessels in this study's floodplain trees had decreased mean cross-sectional area which may impose difficulties to clearly distinguishing the earlywood and latewood zones.

3.5.2 Differences among Control and Floodplain Chronologies

On the control site, the strength of the correlation between EW and LW as well as between EW and RW lied within the range of values reported by others (Woodcock 1989c; Nola 1996; García-González 2004; Tardif and Conciatori 2006). Contrarily, correlations between the corresponding floodplain chronologies were much higher and apparently relate to the larger EW as previously mentioned. The strong correlations between LW and RW were on both sites similar to those found elsewhere (Tardif 1996; Corcuera et al. 2004a; Lebourgeois et al. 2004; Fonti and García-González 2004, 2008;

Tardif and Conciatori 2006). The inverse association of LW and RW with dTR and pTR as observed on both sites has also been reported by Tardif and Conciatori (2006). These findings suggest that latewood vessels contribute little to density of vessels and porosity of the entire ring.

The floodplain and control EW chronologies differed in their correlation structure with their respective earlywood vessels characteristics. Only in the control site were the cross-correlations among EW and vessel chronologies fairly similar to those observed for *C. sativa*, *Q. rubra* and *Q. alba* (Fonti and García-González 2004; Tardif and Conciatori 2006). The strong positive associations of EW with TVAE and NE have been previously reported (Fonti and García-González 2004; Tardif and Conciatori 2006). As in Tardif and Conciatori (2006), EW was negatively related to dE but in the present study the EW was also weakly positively related to ME. Thus, environmental forcings that favored large EW on the control may also promote the production of less dense but more and somewhat larger sized vessels, resulting in a higher total vessel area.

In contrast, environmental forcings on the floodplain influenced EW and earlywood vessel formation differently. On the floodplain, the formation of large EW was strongly associated with an increase in NE but much less related to vessel size (ME, TVAE) and dE. Contrary to the control, floodplain dE was strongly positively related to the number of vessels and more negatively related to vessel area (ME, TVAE). Thus, on the floodplain, rings with high vessel density and high number of vessels tend to contain very small sized vessels with low total vessel area (Figure 3.9). These rather “diffuse-porous”

earlywood vessel patterns were most pronounced in years of high magnitude spring flood and not observed with the control. This result confirms the hypothesis that only floodplain trees produce a higher number of vessels of smaller area in years of high spring floods.

3.5.3 Ring-Width Chronologies and Hydro-Climatic Factors

3.5.3.1 Earlywood Width

In ring-porous species, the earlywood is mostly produced from carbohydrates accumulated during the year prior to ring formation (Barbaroux and Bréda 2002; Barbaroux et al. 2003). The positive association of the control EW with April (t-1) temperature may relate to conditions favoring breakage of dormancy and to a longer growing season which could allow for a higher amount of storage carbohydrates to be produced for the following year's earlywood production. The control EW was also positively related to April (t-1) discharge which could be an indirect effect of warm April temperatures leading to faster snow and ice melt. However, floodplain EW showed no significant association with April (t-1) temperature or discharge, which was also observed by Tardif (1996) for the EW of *F. nigra* trees growing in another floodplain location of the Lake Duparquet (Fig. 3.1, site 5). These results indicate that on the floodplain other factors such as spring floods may be more limiting than early dormancy breakage.

On the control dry conditions in May (t-1) favour a larger EW whereas on the floodplain dry June (t-1) conditions promote EW increment. This positive association with the drought code could relate to the negative impact of excess water availability during this

time period on both sites. On the floodplain, excess water stress is likely related to spring floods whose drainage may be slowed down in years of high June precipitation and low June drought code. The positive association of control EW with dry May (t-1) conditions was unexpected. However, Sims et al. (1990) reported that *F. nigra* growing in north-western Ontario is typically found on moist to wet soils which were poorly drained. Trees sampled on the control site also grew in a depression characterized by poor drainage where snow melt water in April and May may lead to an elevated soil water table. A comparison of dates for the onset of cambial activity in yellow birch (*Betula lutea* Michx.) grown under three different moisture regimes in Ontario showed that the initiation of wood formation was delayed by one to two weeks on sites with supraoptimal moisture conditions (Fraser 1956). On control and floodplain sites, a delayed resumption of growth could have shortened the growing season resulting in a decreased storage carbohydrate pool needed for next year's earlywood production. *Fraxinus nigra* trees also exhibit determinate growth (Lechowicz 1984) therefore winter buds contain all leaf primordia that develop in the next growing season (Pallardy 2008). A reduced amount of photosynthates in the previous season could therefore relate to a lesser amount of foliage developing in the current season. Due to the lower amount of foliage a lesser amount of water could have been transported to the developing EW via the transpirational stream which could have negatively affected EW.

While the control EW was not expected to show a relationship with spring discharge, the absence of a significant association between the floodplain EW and May (t) discharge was unexpected. Tardif (1996) found a weak but significant negative relationship

between the EW of floodplain *F. nigra* growing on the floodplain of Lake Duparquet. It is possible that the author captured a more site specific signal as the trees analyzed on the floodplain of Lake Duparquet pertained to another location than those studied here (Fig. 3.1, site 5 versus sites 2 and 3, respectively). Trees analyzed by Tardif (1996) were growing at a very low elevation. These trees were suggested by Tardif and Bergeron (1992, 1999) to be more exposed to flooding than trees analyzed in the present study which also led to a different vegetation composition (Tardif and Bergeron 1992). In addition, the different results could be related to the identification of earlywood but the relatively low correlation between the standard ring-width chronologies of Tardif (1996) and the present study (Spearman $r=0.56$, $p=0.000001$, $n=74$) suggests site differences.

On the floodplain as well as on the control, water availability during the earlywood development seems to have a positive effect on earlywood width. This interpretation is directly indicated on the floodplain by the EW's positive association with December (t-1) and May (t) precipitation, June (t) discharge and its inverse association with June (t) drought code. The associations of EW with May (t) precipitation and June (t) discharge are only significant if extreme flood years are not removed from the hydro-climatic correlation analysis. The increase in floodplain EW could therefore be related to hormonal changes induced by flooding as discussed in section 3.5.1. The control EW was only positively related to December (t-1) precipitation. This result may indicate that a sufficient amount of water is supplied by snow melt during the EW production period.

The results further indicated that warm June (t) daytime temperatures negatively affected both the control and floodplain EW. This association was also observed by Tardif (1996). The negative association may be related to accelerated leaf development and an earlier transition from earlywood to latewood production in years with warm June. According to Digby and Wareing (1966) the transition from earlywood to latewood production is related to decreasing auxin concentrations in the stem tissue. Since young leaves contain higher amounts of auxin than older leaves (Savidge 1988; Aloni 1989; Taiz and Zeiger 2002) warm June temperatures could indirectly reduce the amount of auxin transported to the cambial tissue through leaf development. In *F. nigra* trees growing in northeastern Minnesota the first leaves in recognizable form were observed between the third week of May and the first week of June over a period of five years (Ahlgren 1957). Tardif (personal communication 2009) also observed that leaf expansion in Lake Duparquet regions could take place from mid-May to June but that it also varied from year to year.

3.5.3.2 Latewood Width

In the previous year, control LW and RW were mostly related to April (t-1) minimum temperature and discharge. Conditions leading to a longer growing season in the year prior to ring formation may have allowed for the formation of winter buds with more leaf primordia thus to larger photosynthate and latewood production during the current growing season. Tardif and Bergeron (1993) also reported a positive relationship between the RW chronology of floodplain *F. nigra* trees and mean April (t-1) temperature. These trees were sampled along transects perpendicular to the lake. It is therefore possible that many trees sampled by Tardif and Bergeron (1993) grew at a larger distance from the

lake than floodplain tree sampled in the present study, the latter of which showed no relationship to April (t-1) minimum temperature and discharge. In the case of Tardif and Bergeron (1993), the effects of spring flooding may have been reduced which could have increased the importance of early dormancy breakage.

On both sites dry June (t-1) conditions promoted LW production whereas in the current growing season moist June (t) conditions were related to an increase in LW. A negative relationship between the RW chronology of an unflooded *F. nigra* population growing 10 km north of the Lake Duparquet and June (t) drought code was also observed by Tardif and Bergeron (1997b). Similar to the present study, Tardif and Bergeron (1993, 1997b) found inverse relationships of floodplain *F. nigra* RW chronologies with previous and current year's June moisture related variables. These relationships therefore seem not to be a site-specific signal. It is possible that elevated soil water tables in June may negatively affect winter bud production and therefore the amount of foliage developing in the next year. On the other hand, during the year of bud development, high June water tables may promote leaf development, thus relating to a larger LW.

Since floodplain LW was not related to May (t) discharge, the hypothesis that spring flooding does not affect latewood production was confirmed. The very weak association of floodplain LW with June (t) discharge was only significant when extreme years were retained in the correlation analysis which indicates that LW is not a suitable chronology to reconstruct June discharge (Appendix L).

3.5.4 Vessel Chronologies and Hydro-Climatic Factors

3.5.4.1 Similarities in Hydro-Climatic Associations of Earlywood and Latewood

Vessels

On the control and floodplain sites, the association of earlywood vessel chronologies with hydro-climatic variables was very similar to that of the total ring vessel chronologies, indicating that the latewood vessels as measured in this study contributed little to the climatic signal stored in the chronologies. Woodcock (1989c) from the analysis of a 20-year sequence from two trees (one core per tree) reported that latewood vessel chronologies contained a distinct climate signal than earlywood vessel chronologies. In this study of *F. nigra*, the use of a threshold value of $800 \mu\text{m}^2$ for vessel recognition by the image analysis software did not allow for a real assessment of latewood vessels. The low amount of analyzed latewood vessels did also not permit to confirm the hypothesis that latewood vessels do not contain signals related to spring flooding. Further work on climatic and hydrologic signals of latewood vessels may be needed since most studies mainly focused on vessels in the earlywood (e.g. García-González and Eckstein 2003; Fonti and García-González 2004, 2008; Fonti et al. 2007) or the total ring (Tardif and Conciatori 2006). As indicated previously by Tardif and Conciatori (2006) the use of different threshold for vessel recognition by the image analysis software [$800 \mu\text{m}^2$ in this study, $450 \mu\text{m}^2$ in Tardif and Conciatori (2006) and $10,000 \mu\text{m}^2$ in Fonti et al. (2007)] may account for some of the variability observed among studies. It also makes it difficult to fully assess the usefulness of developing latewood vessel chronologies for climate analysis.

3.5.4.2 Current Year Hydro-Climatic Conditions during Quiescence and Onset of Cambial Activity

The most important factor influencing vessel number, vessel density and especially mean and total vessel area of floodplain trees was flooding which presumably occurred during the onset of cambial activity. The lack of any correlation between the control earlywood vessel chronologies and spring river discharge provided further evidences of an undisputable control of flooding over earlywood vessel formation. The large decrease in earlywood mean vessel area observed in this study was also consistent with observations made for *F. americana*, *F. pennsylvanica* (Yanosky 1983), *Q. macrocarpa* (St.George and Nielson 2000, 2003) and *Q. robur* (Astrade and Bégin 1997; Sass-Klaassen 2008, 2009).

A unique feature in *F. nigra*'s response to flooding was the production of more numerous earlywood vessels when compared to dendrohydrologic studies investigating *Quercus* species. It is possible that the response of floodplain *F. nigra* trees may be associated to their strong tolerance to flooding (Sims et al. 1990). Results from studies conducted with *Q. macrocarpa* (St.George and Nielson 2000, 2003) and *Q. robur* (Sass-Klaassen 2008, 2009) suggest that in these species the reduction in vessel area is not accompanied by an increase in vessel number. Comparisons with *F. nigra* is further complicated by the fact that Yanosky (1983) did not develop continuous vessel chronologies and Astrade and Bégin (1997) developed only short time series in which flood rings were only produced during a single year and the number of vessels were not assessed.

In the present study, the mean and total vessel area (vessel number) chronologies of floodplain trees showed a strong decrease in size (increase in number) in response to high May (t) and to lesser extent high June (t) discharge. These results support the hypothesis of smaller and more abundant vessel production in response to increasing flood magnitude. The hypothesis that floodplain earlywood vessel chronologies would better reflect the flooding signal than the EW was also confirmed since vessel chronologies were more strongly associated with May (t) and June (t) discharge. Contrary to the strong associations of vessel chronologies with May (t) and June (t) discharge, the relationships with July (t) and August (t) discharge were much weaker and related to significant autocorrelation in the river discharge data (for correlations of July discharge with May and June discharge Spearman $r = 0.39$ and Spearman $r = 0.69$, respectively, for $p < 0.001$, $n = 91$; for correlations of August discharge with May and June discharge, Spearman $r = 0.23$ and Spearman $r = 0.43$, respectively, for $p < 0.05$, $n = 91$). Warm February (t), March (t) and April (t) temperatures were associated with floodplain trees having larger mean and total vessel area. These results are in line with May (t) river discharge being negatively correlated to minimum February (t) and March (t) temperature (Spearman $r = -0.22$ and Spearman $r = -0.23$, respectively for $p < 0.05$, $n = 91$) and maximum February (t), March (t) and April (t) temperatures (Spearman $r = -0.22$, Spearman $r = -0.31$ and Spearman $r = -0.38$, respectively for $p < 0.05$, $n = 91$). 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. Tardif and Bergeron (1997a) did stress the

importance of spring precipitation on the Lake Duparquet water level. All these results converge towards revealing the major role played by flood magnitude and/or duration on ring development on the floodplain. These results clearly contrast with those obtained for the control site.

On the control site, the absence of significant correlations between vessel chronologies and spring discharge or precipitation indicates that number and vessel area are related to other limiting factors. Interestingly and in contrast to floodplain trees February (t) – March (t) temperatures were negatively correlated with ME and 25E of control trees. A correlation with February (t) temperature was also observed in *Q. robur* trees from northwestern Spain (García-González and Eckstein 2003) and in *C. sativa* growing in the Swiss Alps (Fonti et al. 2007). García-González and Eckstein (2003) attributed this signal to climatic influences in the early growing season conditions as wood formation has been reported to commence in February in northwestern Spain. Fonti et al. (2007) suggested that warm February and March temperatures could re-activate IAA carriers in quiescent overwintering cambial derivatives leading to smaller earlywood vessel area. In fact, cells with re-activated IAA efflux carriers would be more sensitive to IAA and would differentiate faster, leading to smaller sized vessels.

However, the reactivation of existing IAA carriers (in overwintering cambial derivatives during February and March) has yet to be confirmed. It is further questionable whether auxin carriers re-activated by warm February and March temperatures greatly enhance IAA transport rates and are able to re-establish the cellular sensitivity to auxin. Results by

Schrader et al. (2003) showed that following bud break, IAA transport rates increased more than 10 fold which was highly correlated with expression of genes encoding IAA transport carriers. These results strongly point to a positive feed-back mechanism of IAA on IAA transport rates on a transcriptional level (Schrader et al. 2003). The amount of auxin transported by re-activated carriers could therefore be negligible in contrast to transport rates by newly produced carriers. In a more recent study, Fonti and García-González (2008) contrastingly observed a positive relationship between February temperature and the mean vessel area of *Q. petraea* and *Q. pubescens* trees growing respectively at 20 km and 120 km distance from the *C. sativa* stand analyzed by Fonti et al. (2007). This inverse association was however not discussed and more specific studies are required to fully understand the mechanisms occurring at the onset of cambial activity and that promote or decrease mean vessel area.

As in Fonti et al. (2007) who found first annual vessels to appear between the third week of April and the last week of May, wood formation of *F. nigra* in the Lake Duparquet region is not likely to start prior to the end of April. In fact, Ahlgren (1957) reported that *F. nigra* trees over a 5-year period started radial growth between the first to the third week of May in northeastern Minnesota. In southeastern Ontario wood formation was also initiated in *F. nigra* at the beginning of May (Fraser 1958). Bud swelling either occurred concurrently or shortly followed the initiation of wood production and required at least 5 consecutive days of nonfreezing temperature followed by an increase of maximum temperature to 20°C (Ahlgren 1957).

In the Lake Duparquet region, warm temperatures during the onset of cambial activity favored the production of large sized vessels on both sites (control and floodplain). These results concur with those for *Q. rubra* and *Q. alba* trees growing in Quebec (Tardif and Conciatori 2006). In regions where winter precipitation and snow melt water contribute little to replenish soil moisture during spring the mean vessel area tends to decrease under conditions of warm spring temperature and low precipitation (e.g. Woodcock 1989a; García-González and Eckstein 2003; Schume et al. 2004). Thus, a sufficient amount of water during the earlywood vessel production period could play an important role in the formation of large sized vessels.

Several studies with ring-porous species have indicated that only very few, if any, newly formed earlywood vessels have reached their final size upon bud burst (Zasada and Zahner 1969; Atkinson and Denne 1988; Suzuki et al. 1996; Fonti et al. 2007). Many earlywood vessels are thus still in the cellular expansion period during which the increase in vessel area depends on the cellular uptake of water (Ray and Green 1972; Samuels et al. 2006). Warm spring temperatures promote leaf development (Ahlgren 1957) which could re-initiate the transpirational stream which may account for water transported to developing vessel elements providing a sufficient amount of soil moisture.

3.5.4.3 Reserve Storage Periods in the Year Prior to Ring-Formation

Interestingly, the mean vessel area of trees growing in both habitats was not only related to water availability and temperature during the onset of cambial activity but also presumably to the carbohydrate storage reserves laid down in the year prior to ring

formation. As discussed previously, associations of vessel chronologies with April (t-1) temperature and/or discharge may relate to an early initiation of the growing season. The increase in the number and to lesser extent total vessel area are probably related to the concurrent increase in EW. The associations between control chronologies and April (t-1) conditions possibly stresses the importance of the length of the previous growing season, a variable not fully investigated in most dendroclimatological studies using vessels chronologies (e.g. Eckstein and Frisse 1982; Woodcock 1987, 1989*a*; Sass and Eckstein 1995; Villar-Salvador et al. 1997; Pumijumnong and Park 1999; García-González and Eckstein 2003; Corcuera et al. 2004*a, b*; Verheyden et al. 2005; Fonti and García-González 2004, 2008; Eilmann et al. 2006; Tardif and Conciatori 2006).

Similar to results obtained by Tardif and Conciatori (2006) and Fonti and García-González (2008), the floodplain vessel area chronologies (total and mean vessel area) were negatively related to July (t-1) and August (t-1) temperatures. Surprisingly, control mean vessel area chronologies were uniquely and negatively related to previous year's late summer discharge. The relationships of floodplain vessel chronologies with July (t-1) and August (t-1) temperatures and those of control vessel chronologies with late summer discharge may be related to a lesser amount of carbohydrate accumulation. However, further studies are necessary to validate these hypotheses and clarify why floodplain and control vessel chronologies did not show a synchronized response to these hydro-climatic variables.

3.5.4.4 Possible Physiological Pathways by which Flooding may alter Vessel Development

The large decrease in mean vessel area and the increase in the number of vessels in response to spring flooding may be related to changes in hormonal balances such as ethylene and auxin which act on xylem development (Doley and Leyton 1968; Aloni 1991; Uggla et al. 1998; Han 2001). An interplay of both, auxin and ethylene on vessel size is supported through studies with hybrid poplars (*Populus tremula* L. x *Populus tremuloides* Michx. and *Populus tremula* L. x *Populus alba* L.), white poplar (*Populus alba* L.), and tomato (*Lycopersicon esculentum* Mill.) as in these plants large increases in the concentrations of auxin and ethylene led to reductions in vessel area (Tuominen et al. 1995; Aloni et al. 1998; Junghans et al. 2004). A decreased vessel area was also observed following the application of the ethylene releasing compound ethrel in American elm (*Ulmus americana* L.) (Yamamoto et al. 1987) and in Norway maple (*Acer platanoides* L.) (Yamamoto and Kozlowski 1987). In *U. americana*, ethrel application also caused an increase in the number of vessels (Yamamoto et al. 1987). The authors suggested that the changes in vessel number and size in *U. americana* were related to both, auxin and ethylene. In addition, largely decreased concentrations of biologically active IAA in tobacco (*Nicotianum tabacum* L. cv. Samsun) plants were associated with decreased production of vessel elements that showed a larger cross-sectional area (Romano et al. 1991). Further, ethylene was reported to decrease the vessel diameter in Manitoba maple (*Acer negundo* L.) (Savidge 1988).

In addition, cross-talk between signaling pathways of auxin with other hormones than ethylene are likely and in addition, many other factors such as cytokinin, brassinosteroids, xylogen, CLE peptides and HD-Zip genes have been suggested to be involved in tracheary element formation (Little and Savidge 1987; Aloni 1991, 2007; Moritz and Sundberg 1996; Woodward and Bartel 2005; Turner et al. 2007; Nilsson et al. 2008). The production of more abundant and smaller vessels in floodplain *F. nigra* during years of high discharge may therefore be related to a complex interplay of growth regulators.

Furthermore, the decreased earlywood vessel area observed in years of high spring lake water levels may be related to the cellular energy metabolism which may be altered due to the lowered availability of oxygen (Perata and Alpi 1993; Angelov et al. 1996; Drew 1997; Kozłowski 1997, 2002). The cellular differentiation of vessel elements requires a high amount of energy since a large number of genes are expressed during the differentiation process which are engaged in metabolism and protein synthesis (Hertzberg et al. 2001; Schrader et al. 2004; Vanholme et al. 2008 and references therein). Shifts from aerobic respiration to fermentative processes result in a highly decreased formation of ATP, as a result cells of submerged plant tissues commonly experience severe energy crises (Kreuzwieser et al. 2002; Geigenberger 2003; Gibbs and Greenway 2003 and references therein). Insufficient oxygenation of the vascular cambium during the time of vessel ontogeny could therefore negatively act on vessel size.

Another explanation for decreased vessel area may be related to the change in cambial temperature of the submerged stem and root induced by cold spring flood water. The plastic changes of tracheary element size and number observed in other studies indicate that not only excess water stress but also temperature and light may be important factors influencing vessel size and number. In *F. pennsylvanica* the vessel arrangement of the ring-porous stem wood changed to a more diffuse-porous vessel patterns upon burial of the stem wood, hence resembling root wood (Sigafos 1964; Cournoyer and Bégin 1992). In contrast, erosion and exposure of diffuse-porous European ash (*Fraxinus excelsior* L.) roots to the atmosphere caused a change to a more ring-porous anatomy (Hitz et al. 2008). In the earlywood of European larch (*Larix decidua* Mill.) and Norway spruce (*Picea abies* [L.] Karst.), exposure of the root wood caused a reduction in tracheid size (Gärtner et al. 2001; Hitz et al. 2008). In *L. decidua* an increased production of tracheids in the earlywood was also observed. Cournoyer and Bégin (1992) and Gärtner et al. (2001) suggested the observed changes in wood anatomy to be related to changes in temperature and/or light availability. However, Gärtner et al. (2001) pointed out that the exact mechanisms by which light and temperature could induce changes in tracheid size and number have not been elucidated.

3.5.5 Utility of Continuous Vessel Chronologies in Hydrologic Reconstructions

In the present study, the linear relationships between vessel chronologies (pE, dE, NE, 25E, ME and TVAE) with May river discharge suggest that changes in vessel size and number are proportional to flood magnitude. 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 2000, 2002, 2003; St. George et al. 2002; Sass-Klaassen 2008, 2009) but they could also serve as a continuous proxy for hydrological records. Among all earlywood vessel chronologies, ME best predicted May discharge and the development of continuous ME chronologies may best be able to reconstruct lake water levels or river discharge. Even though the number of earlywood vessels is easier to measure less accurate hydrologic reconstruction could occur due to its weaker association. More work is, however, needed to assess if the development of continuous vessel chronologies for lake or river water reconstructions is only valid for trees growing in close proximity to such water bodies where trees are exposed to annual flood events. In tree species rarely flooded, it may be that developing continuous vessel chronology may be of little utility.

One of the advantages that vessel chronologies have over dendrohydrological methods that use ring-widths and forest stand dynamics, species composition and distribution, to date floods lies in the unequivocal flood signal. The correlations between ME and discharge observed in this study are extremely high if compared to vessel or RW associations with climate obtained from trees growing in the same or similar climatic regions (Tardif 1996; Tardif and Bergeron 1997*b*; Tardif and Conciatori 2006). While the incorporation of other factors such as species composition and ring-widths may aid in identifying major floods, these methods may still be not accurate to the year. For example, ring-widths may only decrease in size after two years of consecutive floods (Bégin 2000) whereas vessel chronologies offer an annual resolution. In boreal regions,

ice scar height and/or frequency chronologies have been used frequently to reconstruct spring floods (e.g. Bégin and Payette 1991; Lepage and Bégin 1996; Tardif and Bergeron 1997a; Bégin 2001). In years of *in situ* ice melting and little wind, however, fewer floating ice blocks are present to induce scar formation which may induce an underestimation of spring water levels (Tardif and Bergeron 1997a). Also, in years in which the flood magnitude is greatly increased due to abundant spring precipitation occurring after ice break-up, the ice scar chronologies may underestimate spring flood magnitude (Tardif and Bergeron 1997a). In other years, abundant ice accumulation on the shore could cause the formation of more and higher ice scars that could overestimate spring flood magnitudes (Tardif and Bergeron 1997a). In addition, the development of ice scar chronologies may require a high amount of trees to be sampled since many trees may not be hit by floating ice blocks that induce scar formation. Also, scar tissues may not be externally visible and thus require more extensive field work since the detection of scars might require felling of trees and subsequent sectioning of the stem.

Vessel chronologies may be best used in conjunction with ice-scar chronologies for more complete hydrologic reconstructions. For the period 1890-1990, Tardif et al. (in press) observed a significant negative correlation between the floodplain ME chronology (presented here) and both chronologies developed from the frequency and maximum height of ice scars of northern white-cedar (*Thuja occidentalis* L.) trees growing on the lake shore of Lake Duparquet (Spearman $r=-0.573$, $p<0.001$ and -0.329 , $p=0.001$, respectively). These negative correlations indicate that in years of major ice-floods spring flood events are high and long enough to cause a decrease in the cross-sectional

earlywood vessel area of floodplain *F. nigra* trees. As opposed to ice-scar height and frequency chronologies, the ME chronology also identified major floods events in 1928, 1960 and 1989. Contrarily, in the year 1934 May discharge exceeded the mean + 1.5 standard deviations but was only identified by ice-scar frequency and height chronologies (Tardif and Bergeron 1997a) as a year of major spring flood. In addition, only the ice-scar frequency chronology identified 1939 as a major flood year (Tardif and Bergeron 1997a), during which May discharge was larger than the mean + 1 standard deviation and June (t) discharge deviated by more than 1.5 standard deviations.

Even though no obvious relationship to minimum or maximum temperature were discovered for 1934 and 1939 that differed obviously from those of other main flood years, it is possible that in the years 1934 and 1939 earlywood production was initiated very early. In addition, the length of the earlywood production period may vary from year to year due to differing amounts of storage carbohydrates and/or different rises in spring temperatures. Thus, potential limitations to the use of ME chronologies for hydrologic reconstructions may relate to annual variations in the initiation and duration of earlywood vessel formation which should be further investigated. Such studies may also help to assess why the ME chronologies may identify medium flood events as high magnitude flood events. In the present study over the time span 1915-2005 only two years (1950, 1996) were misidentified as a major flood year whereas ice-scar chronologies for the time period 1910-1990 indicated 1950 to be a year of average flood magnitude (Tardif and Bergeron 1997a). The misidentifications of the years 1950 and 1996 as a high magnitude flood event may possibly relate to extremely cold March and April minimum and

maximum temperatures. Low March and April temperatures could have delayed vessel production so that the entire vessel expansion period may have co-occurred with the main flood interval.

3.5.6 Potential Biases in Vessel Chronologies

Some biases in the present study may have resulted from the technical approach used in delineating earlywood and latewood vessels. The separation of earlywood from latewood vessels was based on two dots whose x-coordinates allowed for a subsequent separation of earlywood and latewood vessels. However, using this approach, some latewood vessels may have been falsely recognized as earlywood vessels and vice versa. This problem could be circumvented in analyzing each tree ring twice, once for earlywood and once for latewood vessels. This bias may not have been very important, however, as the threshold used identified, on average, five latewood vessels. The great correspondence between earlywood vessel and total vessel chronologies indicated that latewood vessels contributed little to hydro-climatic correlations as the threshold used was fairly high.

Due to the low number of captured latewood vessels per ring, it is suggested that a threshold smaller than $800 \mu\text{m}^2$ be used for the analysis of latewood vessels in *F. nigra*. More latewood vessels might have been analyzed in *Q. alba* and *Q. rubra* by Tardif and Conciatori (2006) whose threshold for vessel recognition was set to $450 \mu\text{m}^2$. Since latewood vessels contain thicker cell walls than earlywood vessels (Butterfield 2003), the former may be best analyzed using microtome slides which would allow to see cell wall thickness. It may also be useful to quantify cell wall thickness since Yamamoto et al.

(1995) observed an increase in the number and size of wood fibers and a reduction in the cell wall thickness of wood fibers following a flood treatment of Manchurian ash (*Fraxinus mandshurica* Rupr. var. *japonica* Maxim.) seedlings. Using anatomical slides would tremendously increase the amount of time spent per ring. Such detailed analyses aimed at specific flood rings may, however, contribute to a better understanding of alterations in vessel or fibre development induced by flooding.

Future studies using vessel chronologies for hydrologic reconstructions may have to limit the extraction of cores to positions close to the tree base. St. George et al. (2002) found that vessel flood signatures in *Q. macrocarpa* were mostly present in stem wood close to the ground whereas the flood signatures were lost if cores were taken at a larger distance from the ground. Aloni (1991) also stated that in flooded stems numerous narrow vessels form below the water surface while those formed above the water surface were wider. For accurate flood reconstructions, it may be important to investigate whether the longitudinal changes in vessel flood signatures also occur in other species. For example, such studies could be done on Lake Duparquet by studying trees located at different elevations on the floodplain and controlling for core height.

3.6 Conclusion

The descriptive statistics of vessel chronologies of control and floodplain trees were very similar. However, the floodplain earlywood vessel chronologies showed greater common signal strength, a higher mean sensitivity and a synchronized response to spring flooding.

The associations of control site vessel and width chronologies also fairly resembled those of other studies, whereas those of floodplain trees were distinct and may be characteristic among ring-porous floodplain species.

Vessel and ring-width chronologies of trees growing on the control were more related to conditions potentially influencing the length of the previous growing season than those of floodplain trees. The respective ring-width variables of trees growing on both sites resembled each other in their associations with climate variables during the year of ring formation. On both sites, EW, NE and TVAE were commonly related to current summer conditions. However, only floodplain and no control vessel chronologies were related to current year's climate that influenced spring river discharge. In contrast to ring-widths, control and floodplain vessels were related to current year's February and March temperature, control vessels were associated with previous year's late summer discharge while floodplain vessels were related to previous year's summer temperature. Since these correlations were weak, vessel chronologies may not be useful for dendroclimatic reconstructions of these variables. Nevertheless, studies investigating the relationships between vessels and climate may aid in understanding how the environment may influence vessel formation.

The strong and linear relationships of the floodplain vessel chronologies with spring discharge clearly indicate the potential of developing continuous vessel chronologies for dendrohydrologic reconstructions. Floodplain *F. nigra* trees may be particularly useful as they are annually exposed to spring flood events and thus do not only record high

magnitude flood events. Further studies are required that investigate the relationships of vessels of other ring-porous floodplain species with flooding. Species specific differences may not only be related to different size decreases of the mean vessel area but may also relate to the amount of vessels produced during flooding. Vessel chronologies developed from diffuse-porous species have also not been investigated sufficiently for their potential in dendrohydrologic reconstructions. Based on the results of the present study, it is proposed for the southern boreal forest to use ME chronologies in conjunction with ice-scar chronologies to obtain more accurate hydrologic records. However, further studies are suggested to investigate more fully why the ME chronology over-or underestimated flood magnitude in specific years, perhaps as a result of the timing of flooding and vessel formation.

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Appendix A. Spearman rank correlation coefficients between all tree-ring chronologies developed from trees growing on the control site for the time span 1915-2005. Significant correlations ($p \leq 0.05$) are shown in bold. Chronologies are abbreviated as in Table 3.1.

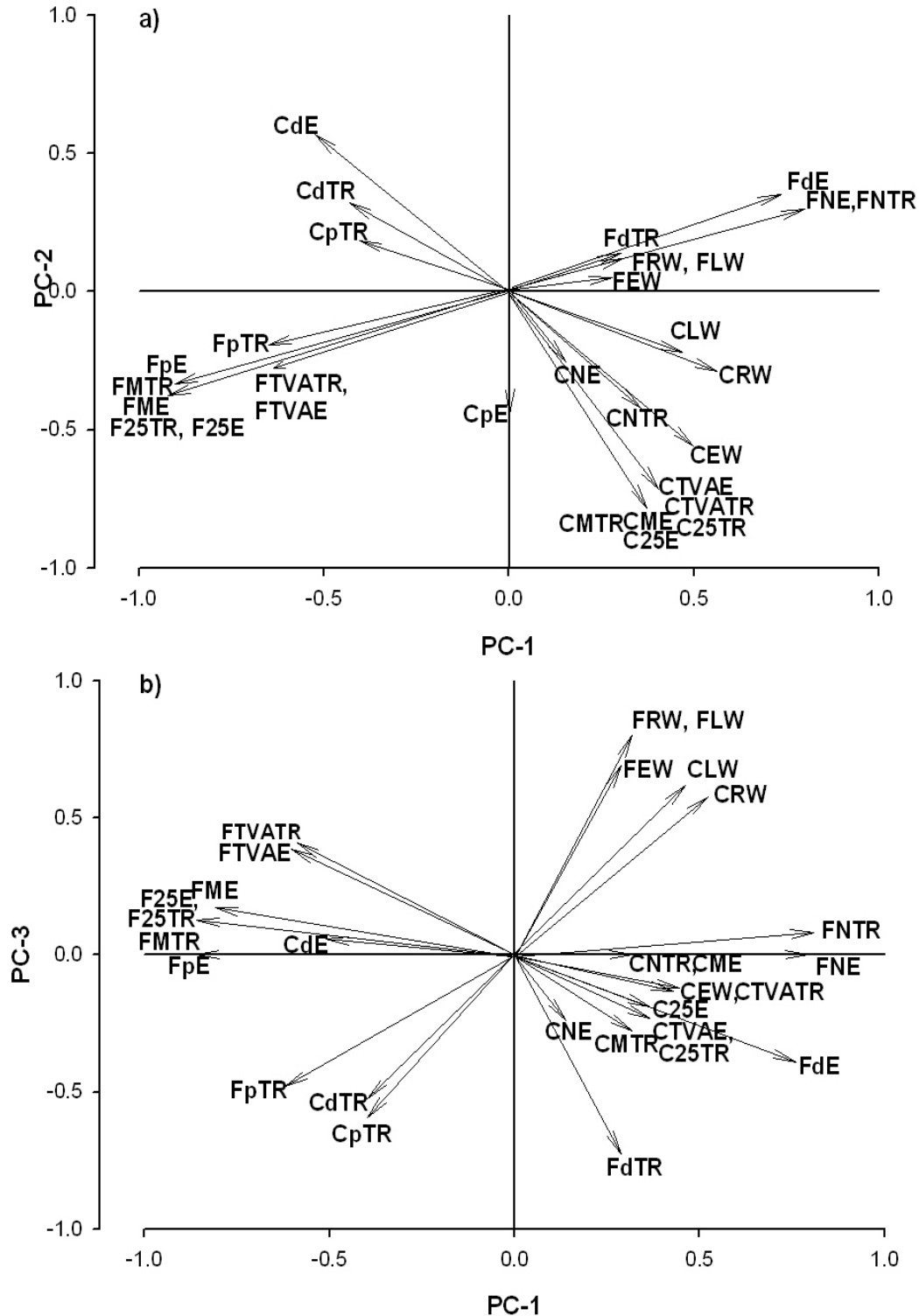
	EW	LW	RW	NE	NTR	TVAE	TVATR	ME	MTR	25E	25TR	dE	dTR	pE	pTR
EW	1.00														
LW	0.23	1.00													
RW	0.33	0.98	1.00												
NE	0.69	-0.09	-0.01	1.00											
NTR	0.76	0.30	0.38	0.82	1.00										
TVAE	0.85	0.16	0.26	0.68	0.76	1.00									
TVATR	0.82	0.27	0.35	0.61	0.81	0.95	1.00								
ME	0.33	0.35	0.36	-0.19	0.10	0.51	0.54	1.00							
MTR	0.32	0.07	0.09	-0.05	0.09	0.56	0.55	0.86	1.00						
25E	0.33	0.21	0.22	-0.08	0.14	0.54	0.53	0.90	0.87	1.00					
25TR	0.33	0.18	0.19	-0.06	0.13	0.56	0.54	0.90	0.89	0.98	1.00				
dE	-0.58	-0.28	-0.32	0.02	-0.18	-0.47	-0.47	-0.69	-0.60	-0.62	-0.60	1.00			
dTr	-0.19	-0.92	-0.92	0.26	-0.11	-0.12	-0.19	-0.46	-0.17	-0.30	-0.28	0.43	1.00		
pE	-0.13	0.15	0.11	-0.14	0.03	0.26	0.29	0.53	0.51	0.53	0.55	0.07	-0.12	1.00	
pTR	-0.19	-0.95	-0.92	0.15	-0.22	-0.09	-0.19	-0.33	-0.05	-0.19	-0.16	0.31	0.93	-0.05	1.00

If $r \geq 0.34$, $p \leq 0.001$, if $r \geq 0.27$, $p \leq 0.01$, if $r \geq 0.21$, $p \leq 0.05$.

Appendix B. Spearman rank correlation coefficients between all tree-ring chronologies of trees growing on floodplains of the year of ring formation for the time span 1915-2005. Significant correlations ($p \leq 0.05$) are shown in bold. Chronologies are abbreviated as in Table 3.1

	EW	LW	RW	NE	NTR	TVAE	TVATR	ME	MTR	25E	25TR	dE	dTR	pE	pTR
EW	1.00														
LW	0.66	1.00													
RW	0.76	0.96	1.00												
NE	0.60	0.35	0.46	1.00											
NTR	0.64	0.44	0.54	0.98	1.00										
TVAE	0.44	0.13	0.26	0.04	0.05	1.00									
TVATR	0.46	0.15	0.27	0.05	0.06	1.00	1.00								
ME	-0.06	-0.16	-0.11	-0.54	-0.52	0.69	0.67	1.00							
MTR	-0.15	-0.29	-0.24	-0.57	-0.58	0.65	0.63	0.97	1.00						
25E	-0.11	-0.17	-0.14	-0.59	-0.57	0.62	0.60	0.96	0.94	1.00					
25TR	-0.14	-0.20	-0.17	-0.60	-0.58	0.61	0.59	0.97	0.96	1.00	1.00				
dE	-0.21	-0.16	-0.20	0.44	0.38	-0.62	-0.61	-0.75	-0.68	-0.72	-0.71	1.00			
dTr	-0.44	-0.75	-0.71	0.19	0.09	-0.39	-0.40	-0.32	-0.19	-0.31	-0.29	0.63	1.00		
pE	-0.26	-0.35	-0.32	-0.53	-0.55	0.59	0.57	0.87	0.90	0.87	0.88	-0.42	-0.06	1.00	
pTR	-0.51	-0.86	-0.79	-0.41	-0.49	0.26	0.24	0.51	0.62	0.50	0.52	-0.13	0.53	0.67	1.00

If $r \geq 0.34$, $p \leq 0.001$, if $r \geq 0.27$, $p \leq 0.01$, if $r \geq 0.21$, $p \leq 0.05$.



Appendix C. Principal components analysis of all 30 tree-ring chronologies from the control (15) and floodplain (15). Upper figure (a) shows PC-1 and PC-2 and lower figure (b) shows PC-1 and PC-3. The reference period is 1915-2005. The capital letter preceding each chronology abbreviation indicates the origin of the trees from the control (C), and floodplain (F). Chronologies are abbreviated as in Table 3.1.

Appendix D. Spearman rank correlation coefficients between all 15 tree-ring chronologies originating from the control site of for the time period 1915-2005. Note that outlier years were excluded (N=81; see section 3.4.1.2). Significant correlations ($p \leq 0.05$) are shown in bold. Chronologies are abbreviated as in Table 3.1

	EW	LW	RW	NE	NTR	TVAE	TVATR	ME	MTR	25E	25TR	dE	dTR	pE	pTR
EW	1.00														
LW	0.17	1.00													
RW	0.29	0.98	1.00												
NE	0.72	-0.12	-0.02	1.00											
NTR	0.77	0.23	0.31	0.85	1.00										
TVAE	0.89	0.08	0.18	0.73	0.76	1.00									
TVATR	0.84	0.18	0.27	0.67	0.81	0.95	1.00								
ME	0.33	0.28	0.28	-0.16	0.07	0.48	0.50	1.00							
MTR	0.32	-0.02	-0.01	-0.04	0.05	0.53	0.52	0.85	1.00						
25E	0.33	0.12	0.11	-0.04	0.11	0.51	0.49	0.88	0.86	1.00					
25TR	0.33	0.09	0.08	-0.02	0.10	0.53	0.51	0.88	0.88	0.98	1.00				
dE	-0.55	-0.20	-0.25	0.02	-0.14	-0.47	-0.46	-0.70	-0.61	-0.61	-0.59	1.00			
dTr	-0.14	-0.92	-0.92	0.27	-0.03	-0.03	-0.08	-0.37	-0.06	-0.18	-0.15	0.37	1.00		
pE	-0.09	0.18	0.13	-0.09	0.05	0.24	0.29	0.53	0.50	0.54	0.56	0.05	-0.10	1.00	
pTR	-0.14	-0.94	-0.92	0.18	-0.15	-0.02	-0.10	-0.25	0.05	-0.09	-0.05	0.24	0.93	-0.06	1.00

If $r \geq 0.36$, $p \leq 0.001$, if $r \geq 0.29$, $p \leq 0.01$, if $r \geq 0.22$, $p \leq 0.05$.

Appendix E. Spearman rank correlation coefficients between all tree-ring chronologies originating from the floodplains of the for the time period 1915-2005. Note that outlier years were excluded (N=81; see section 3.4.1.2). Significant correlations ($p \leq 0.05$) are shown in bold. Chronologies are abbreviated as in Table 3.1

	EW	LW	RW	NE	NTR	TVAE	TVATR	ME	MTR	25E	25TR	dE	dTR	pE	pTR
EW	1.00														
LW	0.66	1.00													
RW	0.70	0.96	1.00												
NE	0.67	0.37	0.36	1.00											
NTR	0.74	0.49	0.48	0.97	1.00										
TVAE	0.57	0.27	0.27	0.27	0.32	1.00									
TVATR	0.59	0.29	0.29	0.28	0.33	0.99	1.00								
ME	-0.03	-0.11	-0.10	-0.47	-0.43	0.58	0.55	1.00							
MTR	-0.14	-0.27	-0.25	-0.52	-0.51	0.52	0.49	0.97	1.00						
25E	-0.08	-0.12	-0.10	-0.51	-0.47	0.49	0.47	0.96	0.93	1.00					
25TR	-0.11	-0.16	-0.14	-0.53	-0.49	0.49	0.46	0.96	0.94	1.00	1.00				
dE	-0.30	-0.26	-0.28	0.30	0.22	-0.51	-0.50	-0.67	-0.59	-0.63	-0.62	1.00			
dTr	-0.53	-0.88	-0.87	-0.03	-0.15	-0.31	-0.32	-0.18	-0.03	-0.17	-0.14	0.55	1.00		
pE	-0.26	-0.32	-0.31	-0.45	-0.47	0.45	0.43	0.84	0.88	0.84	0.85	-0.25	0.12	1.00	
pTR	-0.53	-0.90	-0.88	-0.35	-0.44	0.05	0.02	0.39	0.53	0.38	0.41	0.07	0.78	0.58	1.00

If $r \geq 0.36$, $p \leq 0.001$, if $r \geq 0.29$, $p \leq 0.01$, if $r \geq 0.22$, $p \leq 0.05$.

Appendix F. Spearman rank correlation coefficients of the years scores of the first two principal components axes obtained from control site and floodplain chronologies. In PCA (A) outlier years (see section 3.4.1.2) were excluded from the time span 1915-2005 prior to conducting the PCA. In PCA (B) these years were removed from the years scores after the PCA for the entire time span 1915-2005 had been conducted. The capital letter preceding the abbreviation PC indicates the origin of the chronologies from control (c) or floodplain trees (F). Significant correlations ($p \leq 0.05$) are shown in bold. Chronologies are abbreviated as in Table 3.1.

	CPC-1 a	CPC-2 a	FPC-1 a	FPC-2 a	CPC-1 b	CPC-2 b	FPC-1 b	FPC-2 b
CPC-1 a	1.00							
CPC-2 a	-0.20	1.00						
FPC-1 a	-0.02	0.05	1.00					
FPC-2 a	-0.18	0.36	0.01	1.00				
CPC-1 b	-0.95	0.42	0.02	0.29	1.00			
CPC-2 b	0.18	0.89	0.03	0.27	0.05	1.00		
FPC-1 b	0.00	0.00	0.99	-0.13	-0.01	-0.01	1.00	
FPC-2 b	-0.14	0.43	0.27	0.94	0.26	0.35	0.14	1.00

If $r \geq 0.36$, $p \leq 0.001$, if $r \geq 0.29$, $p \leq 0.01$, if $r \geq 0.22$, $p \leq 0.05$.

Appendix G. Spearman rank correlation coefficients between selected control chronologies and mean monthly minimum temperature from April of the year prior to ring formation (t-1) to August of the year of ring formation for the period 1915-2005 (N=91) and for the period 1915-2005 from which outlier years were excluded (N=81; see section 3.4.1.2). Significant correlations ($p \leq 0.05$) are shown in bold. Chronologies are abbreviated as in Table 3.1.

	EW	LW	RW	NE	TVAE	ME	25E	dE	pE
Full time (N=91)									
April (t-1)	0.31	0.26	0.28	0.09	0.29	0.30	0.22	-0.29	0.04
May (t-1)	0.08	0.15	0.13	0.06	0.10	0.06	0.06	0.02	0.11
June (t-1)	0.14	0.10	0.11	0.02	0.15	0.13	0.08	-0.06	0.11
July (t-1)	0.16	0.06	0.05	0.15	0.12	0.05	0.03	-0.08	0.00
August (t-1)	-0.06	-0.05	-0.07	-0.04	-0.11	-0.05	-0.09	0.01	-0.15
September (t-1)	0.11	-0.04	-0.04	0.08	-0.05	-0.12	-0.16	-0.08	-0.20
October (t-1)	-0.06	-0.08	-0.11	0.02	0.00	0.02	0.02	0.09	0.07
November (t-1)	-0.02	0.04	0.02	-0.01	-0.04	-0.03	-0.05	0.15	0.01
December (t-1)	0.05	0.03	0.02	0.09	-0.04	-0.06	-0.06	0.09	-0.09
January	0.15	-0.16	-0.13	0.23	0.11	-0.14	-0.11	0.03	-0.13
February	-0.10	0.02	-0.01	0.03	-0.14	-0.22	-0.22	0.21	-0.03
March	-0.11	0.02	0.01	-0.02	-0.13	-0.17	-0.21	0.24	-0.12
April	-0.04	0.17	0.16	-0.11	-0.05	0.04	-0.04	0.01	0.04
May	0.02	0.09	0.05	-0.12	-0.03	0.13	0.23	-0.15	0.01
June	-0.19	0.07	0.03	-0.27	-0.21	0.02	0.04	0.04	-0.01
July	-0.08	0.18	0.16	-0.11	-0.07	-0.02	-0.04	0.08	-0.01
August	-0.06	-0.10	-0.07	-0.10	-0.06	-0.05	-0.06	0.01	-0.11
Extreme values removed (N=81)									
April (t-1)	0.27	0.20	0.22	0.10	0.23	0.24	0.14	-0.22	0.03
May (t-1)	0.03	0.09	0.06	0.04	0.05	-0.02	-0.01	0.09	0.08
June (t-1)	0.08	0.11	0.11	-0.02	0.08	0.07	0.00	-0.01	0.08
July (t-1)	0.08	0.04	0.01	0.08	0.06	0.05	0.01	0.00	0.05
August (t-1)	-0.11	-0.09	-0.10	-0.10	-0.14	-0.06	-0.11	0.04	-0.15
September (t-1)	0.10	-0.02	-0.01	0.02	-0.06	-0.08	-0.14	-0.08	-0.17
October (t-1)	-0.08	-0.13	-0.17	-0.01	-0.04	0.00	0.01	0.09	0.08
November (t-1)	0.03	0.07	0.04	0.05	-0.02	-0.02	-0.04	0.14	-0.05
December (t-1)	0.08	0.08	0.08	0.09	-0.03	-0.04	-0.04	0.06	-0.07
January	0.13	-0.18	-0.15	0.22	0.14	-0.12	-0.08	0.04	-0.11
February	-0.05	0.12	0.11	-0.01	-0.11	-0.15	-0.16	0.15	-0.02
March	-0.06	0.03	0.03	-0.06	-0.14	-0.16	-0.20	0.15	-0.14
April	-0.02	0.20	0.20	-0.14	-0.06	0.06	-0.04	-0.05	0.04
May	-0.06	0.08	0.03	-0.20	-0.06	0.17	0.29	-0.11	0.07
June	-0.23	0.05	0.00	-0.31	-0.25	0.01	0.03	0.06	-0.01
July	-0.10	0.17	0.14	-0.17	-0.12	-0.02	-0.04	0.05	0.02
August	-0.03	-0.07	-0.06	-0.13	-0.09	-0.02	-0.03	-0.06	-0.15

For N=91: If $r \geq 0.34$, $p \leq 0.001$, if $r \geq 0.27$, $p \leq 0.01$, if $r \geq 0.21$, $p \leq 0.05$.

For N=81: If $r \geq 0.36$, $p \leq 0.001$, if $r \geq 0.29$, $p \leq 0.01$, if $r \geq 0.22$, $p \leq 0.05$.

Appendix H. Spearman rank correlation coefficients between selected control chronologies and total monthly precipitation from April of the year prior to ring formation (t-1) to August of the year of ring formation for the period 1915-2005 (N=91) and for the period 1915-2005 from which outlier years were excluded (N=81; see section 3.4.1.2). Significant correlations ($p \leq 0.05$) are shown in bold. Chronologies are abbreviated as in Table 3.1.

	EW	LW	RW	NE	TVAE	ME	25E	dE	pE
Full time period (N=91)									
April (t-1)	0.01	0.03	0.00	0.06	0.03	-0.02	0.00	0.07	0.10
May (t-1)	-0.29	-0.19	-0.22	-0.14	-0.14	0.00	0.01	0.12	0.17
June (t-1)	-0.01	-0.16	-0.16	0.13	0.04	-0.11	-0.05	0.15	0.05
July (t-1)	0.07	0.01	0.05	0.11	0.10	0.01	0.01	0.03	-0.04
August (t-1)	-0.02	0.02	0.02	-0.08	-0.03	-0.04	0.03	-0.13	-0.13
September (t-1)	-0.10	0.06	0.04	-0.12	-0.19	-0.09	-0.11	0.05	-0.05
October (t-1)	0.04	0.04	0.05	0.07	0.03	0.10	0.07	-0.08	0.02
November (t-1)	0.15	0.10	0.10	0.25	0.15	0.01	-0.01	0.03	-0.02
December (t-1)	0.25	0.31	0.33	0.07	0.21	0.23	0.18	-0.22	0.12
January	-0.03	0.18	0.18	-0.13	0.04	0.18	0.14	-0.05	0.17
February	0.07	0.05	0.08	0.01	0.10	0.06	0.01	-0.03	0.07
March	0.12	0.07	0.08	0.12	0.10	-0.01	-0.01	0.00	0.05
April	-0.05	0.10	0.12	-0.15	0.00	0.16	0.17	0.02	0.11
May	-0.06	0.04	0.03	-0.08	-0.14	-0.05	-0.07	0.00	-0.16
June	0.11	0.21	0.23	0.17	0.09	-0.11	-0.08	0.04	-0.03
July	0.19	0.06	0.10	0.15	0.04	-0.04	-0.07	-0.06	-0.23
August	0.08	-0.02	-0.05	0.12	0.06	0.07	0.09	0.04	0.02
Extreme values removed (N=81)									
April (t-1)	0.05	0.06	0.05	0.07	0.09	0.03	0.05	0.06	0.16
May (t-1)	-0.33	-0.26	-0.31	-0.12	-0.18	-0.05	-0.03	0.15	0.09
June (t-1)	-0.03	-0.19	-0.20	0.15	0.05	-0.13	-0.05	0.15	0.02
July (t-1)	0.11	-0.01	0.04	0.16	0.11	0.00	0.02	-0.05	-0.12
August (t-1)	-0.06	0.02	0.01	-0.08	-0.01	0.00	0.08	-0.10	-0.08
September (t-1)	-0.17	0.03	0.00	-0.13	-0.24	-0.15	-0.18	0.13	-0.09
October (t-1)	0.00	0.01	0.02	0.10	0.04	0.08	0.05	-0.03	0.04
November (t-1)	0.12	0.09	0.10	0.22	0.19	0.07	0.05	0.06	0.08
December (t-1)	0.25	0.25	0.27	0.06	0.19	0.22	0.17	-0.21	0.19
January	-0.02	0.17	0.17	-0.09	0.06	0.19	0.15	-0.05	0.22
February	0.09	0.13	0.15	0.01	0.08	0.08	0.00	-0.02	0.02
March	0.18	0.04	0.05	0.20	0.12	-0.05	-0.03	-0.01	-0.06
April	-0.13	0.01	0.01	-0.17	-0.07	0.08	0.09	0.14	0.14
May	-0.09	0.02	0.01	-0.12	-0.13	-0.01	-0.04	0.03	-0.11
June	0.08	0.20	0.23	0.18	0.13	-0.12	-0.07	0.10	0.02
July	0.15	0.02	0.06	0.13	0.06	-0.03	-0.07	0.00	-0.16
August	0.09	0.00	-0.02	0.10	0.14	0.17	0.20	-0.03	0.08

For N=91: If $r \geq 0.34$, $p \leq 0.001$, if $r \geq 0.27$, $p \leq 0.01$, if $r \geq 0.21$, $p \leq 0.05$.

For N=81: If $r \geq 0.36$, $p \leq 0.001$, if $r \geq 0.29$, $p \leq 0.01$, if $r \geq 0.22$, $p \leq 0.05$.

Appendix I. Spearman rank correlation coefficients between selected floodplain chronologies and mean monthly minimum temperature from April of the year prior to ring formation (t-1) to August of the year of ring formation for the period 1915-2005 (N=91) and for the period 1915-2005 from which outlier years were excluded (N=81; see section 3.4.1.2). Significant correlations ($p \leq 0.05$) are shown in bold. Chronologies are abbreviated as in Table 3.1.

	EW	LW	RW	NE	TVAE	ME	25E	dE	pE
Full time period (N=91)									
April (t-1)	0.15	0.08	0.07	-0.02	0.02	0.05	0.04	-0.14	-0.03
May (t-1)	0.05	0.06	0.02	0.07	-0.09	-0.13	-0.12	0.11	-0.09
June (t-1)	-0.09	-0.06	-0.10	-0.13	-0.17	-0.08	-0.03	0.06	-0.06
July (t-1)	-0.11	-0.10	-0.13	0.05	-0.36	-0.31	-0.33	0.32	-0.29
August (t-1)	-0.13	-0.05	-0.12	-0.12	-0.26	-0.21	-0.21	0.20	-0.13
September (t-1)	0.00	-0.10	-0.08	-0.10	-0.06	-0.01	-0.03	0.04	0.01
October (t-1)	-0.15	-0.24	-0.24	0.04	-0.18	-0.15	-0.11	0.26	-0.03
November (t-1)	0.01	0.02	0.02	-0.12	0.13	0.18	0.13	-0.10	0.17
December (t-1)	0.04	-0.16	-0.15	-0.08	-0.05	0.00	-0.02	-0.05	-0.09
January	0.01	-0.02	0.00	0.07	-0.15	-0.12	-0.07	0.17	-0.02
February	-0.04	-0.11	-0.10	-0.13	0.11	0.21	0.23	-0.09	0.29
March	0.13	-0.07	-0.01	0.01	0.21	0.22	0.17	-0.12	0.21
April	-0.03	-0.01	0.00	-0.18	0.19	0.19	0.24	-0.22	0.19
May	-0.10	0.01	-0.02	-0.20	-0.20	-0.04	0.02	-0.07	-0.11
June	-0.26	0.06	-0.04	-0.26	-0.27	0.02	0.08	0.07	0.05
July	-0.04	0.06	-0.02	-0.13	-0.22	-0.08	-0.03	0.08	-0.07
August	-0.26	-0.04	-0.07	-0.19	-0.23	-0.06	-0.02	0.09	0.00
Extreme values removed (N=81)									
April (t-1)	0.23	0.11	0.12	-0.01	0.11	0.13	0.10	-0.23	0.02
May (t-1)	0.07	0.05	0.01	0.13	-0.06	-0.14	-0.13	0.14	-0.09
June (t-1)	-0.03	0.00	-0.04	-0.09	-0.22	-0.13	-0.07	0.10	-0.11
July (t-1)	-0.13	-0.13	-0.15	0.03	-0.38	-0.32	-0.35	0.32	-0.31
August (t-1)	-0.15	-0.03	-0.11	-0.11	-0.33	-0.27	-0.27	0.24	-0.18
September (t-1)	-0.01	-0.10	-0.08	-0.11	-0.07	-0.01	-0.04	0.06	0.01
October (t-1)	-0.14	-0.22	-0.22	0.04	-0.20	-0.17	-0.12	0.29	-0.04
November (t-1)	0.02	-0.01	0.00	-0.01	0.06	0.10	0.04	0.02	0.11
December (t-1)	0.04	-0.12	-0.12	-0.07	-0.14	-0.06	-0.08	0.00	-0.16
January	-0.01	-0.04	-0.02	0.06	-0.16	-0.10	-0.05	0.16	0.00
February	-0.04	-0.06	-0.07	-0.08	0.00	0.14	0.17	-0.01	0.23
March	0.11	-0.01	0.04	0.03	0.16	0.19	0.14	-0.08	0.17
April	-0.04	0.02	0.04	-0.11	0.13	0.13	0.19	-0.15	0.14
May	-0.15	-0.04	-0.07	-0.28	-0.17	0.02	0.09	-0.14	-0.08
June	-0.27	0.08	-0.02	-0.29	-0.31	0.03	0.10	0.09	0.06
July	-0.04	0.12	0.03	-0.16	-0.30	-0.11	-0.05	0.10	-0.10
August	-0.29	-0.04	-0.08	-0.18	-0.33	-0.13	-0.08	0.19	-0.03

For N=91: If $r \geq 0.34$, $p \leq 0.001$, if $r \geq 0.27$, $p \leq 0.01$, if $r \geq 0.21$, $p \leq 0.05$.

For N=81: If $r \geq 0.36$, $p \leq 0.001$, if $r \geq 0.29$, $p \leq 0.01$, if $r \geq 0.22$, $p \leq 0.05$.

Appendix J. Spearman rank correlation coefficients between selected floodplain chronologies and total monthly precipitation from April of the year prior to ring formation (t-1) to August of the year of ring formation for the period 1915-2005 (N=91) and for the period 1915-2005 from which outlier years were excluded (N=81; see section 3.4.1.2). Significant correlations ($p \leq 0.05$) are shown in bold. Chronologies are abbreviated as in Table 3.1.

	EW	LW	RW	NE	TVAE	ME	2SE	dE	pE
Full time period (N=91)									
April (t-1)	0.16	0.04	0.10	0.10	0.10	-0.04	-0.04	-0.04	-0.07
May (t-1)	-0.18	-0.02	-0.02	-0.02	0.05	0.05	0.03	-0.05	0.03
June (t-1)	-0.09	-0.21	-0.15	-0.01	0.07	0.05	0.02	0.04	0.07
July (t-1)	0.11	0.07	0.12	-0.05	0.24	0.17	0.16	-0.18	0.17
August (t-1)	0.06	0.13	0.17	0.04	0.01	0.03	0.04	-0.04	-0.03
September (t-1)	-0.03	-0.01	0.00	-0.09	0.12	0.15	0.13	-0.14	0.09
October (t-1)	-0.06	0.03	0.00	0.00	-0.13	-0.13	-0.10	0.05	-0.16
November (t-1)	0.14	0.05	0.10	0.21	0.03	-0.05	-0.04	0.05	-0.07
December (t-1)	0.23	0.09	0.13	0.15	0.03	-0.06	-0.05	0.00	-0.10
January	0.05	0.10	0.10	0.07	-0.07	-0.13	-0.12	-0.07	-0.24
February	0.11	0.10	0.15	0.11	-0.02	-0.13	-0.12	0.01	-0.15
March	0.15	0.12	0.14	0.00	0.00	-0.05	0.01	0.01	-0.02
April	0.01	0.23	0.21	0.17	-0.26	-0.34	-0.32	0.13	-0.39
May	0.22	0.10	0.14	0.27	-0.08	-0.27	-0.37	0.13	-0.36
June	0.17	0.11	0.12	0.15	0.04	-0.08	-0.10	0.08	-0.06
July	0.07	-0.13	-0.07	0.15	-0.08	-0.18	-0.21	0.11	-0.18
August	0.11	-0.01	0.04	0.11	0.19	0.07	0.05	-0.08	0.02
Extreme values removed (N=81)									
April (t-1)	0.15	0.05	0.11	0.12	0.10	-0.07	-0.07	-0.04	-0.12
May (t-1)	-0.18	-0.07	-0.08	0.03	0.07	0.05	0.01	-0.04	0.02
June (t-1)	-0.10	-0.27	-0.19	-0.01	0.09	0.07	0.02	0.03	0.08
July (t-1)	0.16	0.09	0.16	0.02	0.26	0.17	0.15	-0.19	0.14
August (t-1)	0.00	0.04	0.09	-0.03	0.13	0.14	0.15	-0.13	0.09
September (t-1)	-0.02	-0.04	-0.01	-0.07	0.18	0.20	0.16	-0.18	0.12
October (t-1)	-0.06	0.02	0.00	0.01	-0.10	-0.12	-0.09	0.02	-0.16
November (t-1)	0.14	0.05	0.13	0.20	0.10	0.02	0.03	-0.05	-0.04
December (t-1)	0.22	0.06	0.10	0.09	0.16	0.04	0.05	-0.08	-0.01
January	0.03	0.08	0.10	0.09	-0.08	-0.17	-0.15	-0.06	-0.28
February	0.17	0.13	0.18	0.19	-0.04	-0.19	-0.19	0.06	-0.21
March	0.18	0.08	0.10	0.11	0.00	-0.10	-0.03	0.07	-0.05
April	0.04	0.26	0.24	0.14	-0.16	-0.28	-0.26	0.03	-0.36
May	0.17	0.05	0.07	0.22	0.00	-0.24	-0.35	0.07	-0.34
June	0.14	0.03	0.05	0.07	0.20	0.05	0.03	-0.07	0.06
July	0.04	-0.14	-0.07	0.07	0.00	-0.11	-0.15	0.02	-0.12
August	0.07	-0.03	0.03	0.13	0.21	0.07	0.05	-0.10	-0.01

For N=91: If $r \geq 0.34$, $p \leq 0.001$, if $r \geq 0.27$, $p \leq 0.01$, if $r \geq 0.21$, $p \leq 0.05$.

For N=81: If $r \geq 0.36$, $p \leq 0.001$, if $r \geq 0.29$, $p \leq 0.01$, if $r \geq 0.22$, $p \leq 0.05$.

Appendix K: Spearman rank correlation coefficients between selected control chronologies and mean monthly Harricana Amos discharge from April of the year prior to ring formation (t-1) to August of the year of ring formation for period 1915-2005 (N=90-91) and those from which outlier years were excluded (N=81; see section 3.4.1.2). Significant correlations ($p \leq 0.05$) are shown in bold. Chronologies are abbreviated as in Table 3.1.

	EW	LW	RW	NE	TVAE	ME	25E	dE	pE
Full time period (N=90-91)									
April (t-1)	0.35	0.28	0.33	0.11	0.40	0.38	0.40	-0.32	0.12
May (t-1)	-0.01	-0.01	-0.01	0.02	0.00	-0.08	-0.02	-0.02	0.00
June (t-1)	-0.07	-0.17	-0.20	0.01	-0.03	-0.10	-0.09	0.06	-0.01
July (t-1)	-0.01	-0.26	-0.27	0.15	0.04	-0.15	-0.10	0.09	-0.03
August (t-1)	-0.04	-0.18	-0.19	0.15	-0.05	-0.28	-0.23	0.14	-0.20
September (t-1)	-0.07	-0.12	-0.13	0.00	-0.15	-0.29	-0.22	0.05	-0.28
October (t-1)	-0.09	0.04	0.04	-0.06	-0.17	-0.16	-0.14	-0.04	-0.18
November (t-1)	0.01	0.09	0.09	0.07	-0.04	-0.08	-0.08	-0.03	-0.08
December (t-1)	0.13	0.18	0.17	0.16	0.05	-0.03	-0.09	-0.05	-0.10
January	0.09	0.16	0.16	0.10	0.01	-0.05	-0.13	0.01	-0.13
February	0.09	0.08	0.10	0.07	-0.01	-0.08	-0.17	-0.01	-0.19
March	0.07	0.19	0.20	-0.03	-0.04	-0.05	-0.17	0.03	-0.16
April	0.10	0.25	0.25	-0.10	0.04	0.14	0.03	-0.07	0.05
May	0.04	0.02	0.03	-0.06	0.03	0.18	0.16	-0.16	0.00
June	0.02	0.10	0.11	0.00	-0.05	-0.02	-0.08	-0.05	-0.14
July	0.17	0.15	0.16	0.24	0.10	-0.09	-0.16	-0.03	-0.18
August	0.21	-0.01	0.02	0.22	0.09	-0.08	-0.17	-0.10	-0.26
Extreme values removed (N=80-81)									
April (t-1)	0.34	0.24	0.29	0.15	0.36	0.34	0.35	-0.26	0.12
May (t-1)	-0.04	0.02	0.01	0.02	-0.04	-0.12	-0.07	0.02	-0.06
June (t-1)	-0.07	-0.17	-0.19	0.00	-0.02	-0.09	-0.07	0.02	-0.03
July (t-1)	0.01	-0.28	-0.28	0.15	0.06	-0.15	-0.08	0.02	-0.08
August (t-1)	-0.02	-0.22	-0.23	0.17	-0.02	-0.29	-0.22	0.11	-0.21
September (t-1)	-0.08	-0.12	-0.14	0.02	-0.13	-0.30	-0.23	0.08	-0.28
October (t-1)	-0.19	0.00	-0.02	-0.09	-0.22	-0.20	-0.18	0.03	-0.15
November (t-1)	-0.06	0.09	0.07	0.05	-0.05	-0.07	-0.08	0.02	-0.03
December (t-1)	0.08	0.17	0.16	0.14	0.06	-0.01	-0.09	-0.01	-0.04
January	0.04	0.14	0.13	0.09	0.01	-0.03	-0.12	0.05	-0.06
February	0.01	0.06	0.05	0.07	-0.02	-0.09	-0.18	0.07	-0.14
March	0.03	0.17	0.18	-0.04	-0.04	-0.05	-0.18	0.07	-0.12
April	0.07	0.25	0.25	-0.13	0.02	0.13	0.01	-0.05	0.10
May	-0.08	-0.08	-0.10	-0.09	-0.01	0.16	0.13	-0.02	0.13
June	-0.04	0.05	0.06	-0.01	-0.04	-0.01	-0.08	0.05	-0.05
July	0.13	0.12	0.14	0.23	0.12	-0.08	-0.18	0.07	-0.08
August	0.20	-0.02	0.02	0.19	0.13	-0.03	-0.13	-0.10	-0.21

For N=80 If $r \geq 0.36$, $p \leq 0.001$, if $r \geq 0.29$, $p \leq 0.01$, if $r \geq 0.22$, $p \leq 0.05$.

For N=81 If $r \geq 0.36$, $p \leq 0.001$, if $r \geq 0.28$, $p \leq 0.01$, if $r \geq 0.22$, $p \leq 0.05$.

For N=90 If $r \geq 0.34$, $p \leq 0.001$, if $r \geq 0.27$, $p \leq 0.01$, if $r \geq 0.21$, $p \leq 0.05$.

For N=91 If $r \geq 0.34$, $p \leq 0.001$, if $r \geq 0.27$, $p \leq 0.01$, if $r \geq 0.21$, $p \leq 0.05$.

Appendix L. Spearman rank correlation coefficients between selected floodplain chronologies and mean monthly Harricana Amos discharge from April of the year prior to ring formation (t-1) to August of the year of ring formation for the period 1915-2005 (N=90-91) and those from which outlier years were excluded (N=81; see section 3.4.1.2). Significant correlations ($p \leq 0.05$) are shown in bold. Chronologies are abbreviated as in Table 3.1.

	EW	LW	RW	NE	TVAE	ME	25E	dE	pE
Full time (N=90-91)									
April (t-1)	0.06	-0.03	0.00	0.02	-0.01	0.01	0.01	-0.05	-0.04
May (t-1)	-0.15	-0.10	-0.11	-0.07	0.02	-0.02	0.01	0.04	0.04
June (t-1)	-0.21	-0.14	-0.12	0.00	0.05	0.03	0.01	0.01	0.05
July (t-1)	-0.17	-0.16	-0.10	-0.04	0.11	0.14	0.13	0.00	0.19
August (t-1)	0.00	0.00	0.05	-0.01	0.11	0.05	0.07	0.01	0.12
September (t-1)	0.04	0.13	0.18	-0.01	0.14	0.15	0.17	-0.10	0.14
October (t-1)	-0.05	0.10	0.08	-0.08	-0.02	0.09	0.12	-0.08	0.05
November (t-1)	0.01	0.07	0.06	0.04	-0.03	-0.01	0.01	0.02	-0.04
December (t-1)	0.10	0.08	0.10	0.13	-0.03	-0.05	-0.04	0.05	-0.10
January	0.11	0.07	0.10	0.15	-0.11	-0.14	-0.15	0.16	-0.17
February	0.04	0.02	0.03	0.12	-0.22	-0.23	-0.23	0.26	-0.20
March	0.07	0.04	0.05	0.13	-0.11	-0.20	-0.24	0.17	-0.16
April	0.05	0.08	0.08	-0.05	0.03	-0.03	0.02	-0.07	-0.02
May	0.05	0.10	0.05	0.32	-0.60	-0.72	-0.66	0.50	-0.68
June	0.24	0.26	0.22	0.41	-0.38	-0.54	-0.58	0.35	-0.56
July	0.27	0.19	0.19	0.36	-0.18	-0.34	-0.39	0.25	-0.35
August	0.14	0.09	0.09	0.19	-0.15	-0.25	-0.29	0.17	-0.24
Extreme values removed (N=80-81)									
April (t-1)	0.14	-0.02	0.02	0.01	0.11	0.11	0.10	-0.15	0.04
May (t-1)	-0.13	-0.11	-0.11	-0.01	0.01	-0.06	-0.03	0.10	0.01
June (t-1)	-0.21	-0.13	-0.11	0.01	0.03	0.01	-0.01	0.01	0.01
July (t-1)	-0.15	-0.13	-0.07	0.00	0.06	0.10	0.10	0.03	0.15
August (t-1)	0.01	0.02	0.09	0.03	0.09	0.02	0.05	0.02	0.10
September (t-1)	0.04	0.13	0.19	-0.03	0.18	0.18	0.20	-0.12	0.18
October (t-1)	-0.07	0.08	0.06	-0.11	0.06	0.17	0.20	-0.15	0.13
November (t-1)	0.01	0.06	0.07	0.06	0.02	0.03	0.05	-0.02	-0.01
December (t-1)	0.13	0.10	0.15	0.14	0.02	0.00	0.00	-0.02	-0.09
January	0.13	0.08	0.12	0.13	-0.05	-0.09	-0.10	0.11	-0.14
February	0.05	-0.02	0.01	0.08	-0.13	-0.15	-0.16	0.20	-0.13
March	0.10	0.05	0.08	0.10	-0.04	-0.15	-0.20	0.10	-0.12
April	0.08	0.12	0.13	-0.05	0.08	0.00	0.06	-0.13	0.00
May	0.00	0.03	-0.02	0.15	-0.49	-0.65	-0.57	0.38	-0.59
June	0.18	0.21	0.16	0.29	-0.31	-0.50	-0.54	0.25	-0.50
July	0.23	0.15	0.15	0.24	-0.05	-0.25	-0.30	0.12	-0.25
August	0.06	0.03	0.03	0.11	-0.09	-0.22	-0.26	0.11	-0.20

For N=80 If $r \geq 0.36$, $p \leq 0.001$, if $r \geq 0.29$, $p \leq 0.01$, if $r \geq 0.22$, $p \leq 0.05$.

For N=81 If $r \geq 0.36$, $p \leq 0.001$, if $r \geq 0.28$, $p \leq 0.01$, if $r \geq 0.22$, $p \leq 0.05$.

For N=90 If $r \geq 0.34$, $p \leq 0.001$, if $r \geq 0.27$, $p \leq 0.01$, if $r \geq 0.21$, $p \leq 0.05$.

For N=91 If $r \geq 0.34$, $p \leq 0.001$, if $r \geq 0.27$, $p \leq 0.01$, if $r \geq 0.21$, $p \leq 0.05$.

Appendix M: Linear regression using chronologies as predictors and mean May Harricana river discharge as predictant for the period 1915-2005.

	Adjusted r²	Standard error of the estimate	F_{1,89}	Significance	Beta coefficient
Variable					
PC-1	0.487	27.56058	86.441	9.1x10 ⁻¹⁵	0.702
Earlywood porosity chronology index	0.490	27.47208	87.573	6.81x10 ⁻¹⁵	-0.704
Earlywood density chronology index	0.341	31.24567	47.499	7.60x10 ⁻¹⁰	0.590
25% largest earlywood vessel area chronology index	0.474	27.91896	81.966	2.91x10 ⁻¹⁴	-0.692
Mean earlywood vessel area chronology index	0.518	26.71895	97.668	5.59x10 ⁻¹⁶	-0.732
Total earlywood vessel area chronology index	0.439	28.8331	71.297	5.31x10 ⁻¹³	-0.667
Number of earlywood vessel chronology index	0.221	33.95715	26.562	1.52x10 ⁻⁶	0.479
Earlywood width chronology index	-0.011	38.68836	0.032	0.858	0.019

4.0 General Conclusions

The objectives of this thesis were to describe earlywood vessel anomalies in relation to post-fire tree-ring formation and to assess the impact of flooding on vessel and width characteristics in *F. nigra* growing in the Lake Duparquet region in boreal northwestern Quebec. The associations of climate with earlywood vessels and ring-widths in flooded and unflooded *F. nigra* trees were also investigated. The two trees that survived a severe fire in 1923 produced almost no latewood during the year of the fire but showed a strong decrease in the size of the largest earlywood vessels in 1924. This synchronized response was not observed in any other year on the control nor among floodplain trees in 1924.

The loss of branch and shoot material during the 1923 fire event could have led to lowered auxin concentrations throughout the year 1924, therefore suboptimal auxin concentrations might have triggered the formation of smaller sized vessels. In addition, the 1923 forest fire may have affected the timing of snow melt resulting in a larger amount of water available in the spring over a shorter period; excess water stress could have therefore also caused the formation of smaller sized vessels. For fire history reconstructions that rely on datable fire scars of surviving trees, decreases in vessel size of ring-porous species in the year following a forest fire may be useful to allow for a more precise delineation of the burned area. In addition, it is suggested to investigate the effect of forest fires on vessel area since the accuracy of dendroclimatological studies using vessel area chronologies relies on a proper identification of climatic signals.

The climatic response of vessel and ring-width chronologies were on both sites related to current and previous year conditions that influenced bud and leaf development hence

relating to photosynthetic processes. However, for control vessel and ring-width chronologies, the temperature at the beginning of the previous growing season played a more important role than for the according floodplain chronologies which is likely related to the interfering impact of spring flooding. On both sites vessel and width chronologies showed common associations with climate but vessel chronologies were also uniquely correlated with climatic conditions during tree quiescence. In addition, control vessel chronologies were related to previous year's late summer discharge while floodplain vessel chronologies were related to previous year's summer temperature. Since these relationships were weak, the development of continuous vessel chronologies may not be suitable for climate reconstructions. Despite being low, these relationships merit further investigations since they may contribute to a better understanding of how environmental factors act on vessel formation.

On the control site environmental forcings that favored large EW also tended to promote the production of less dense but more and somewhat larger sized vessels, resulting in a higher total vessel area. On floodplains the most important factor influencing vessel number, vessel density and especially mean and total vessel area were the spring flood events. Spring flooding promoted the formation of rings with numerous and dense vessels of small mean and total vessel area. These rather diffuse-porous vessel patterns in the earlywood were most pronounced in tree rings produced in years of high magnitude spring flood events (1922, 1928, 1947, 1960, 1967, 1979, 1989). In contrast to previous studies which mainly used vessel anomalies as indicators of high magnitude flood events, the present study showed that all earlywood vessel chronologies of floodplain *F. nigra*

were linearly related with spring river discharge. The strongest relationship was found for the mean earlywood vessel area chronology and spring river discharge which proposes its usefulness for dendrohydrologic reconstructions prior to instrumental data. For the southern boreal forest, it is suggested to employ both, vessel area chronologies and ice-scar chronologies for dendrohydrologic reconstructions when feasible. The use of both types of chronologies could help to identify years in which only one chronology over- or underestimates flood magnitudes which should be further validated with other ring-porous species.

Further studies are also suggested to better understand why the mean vessel area chronology over- or underestimated flood magnitude in specific years which may relate to the timing of flooding and vessel formation. It is therefore proposed to study annual xylem development of trees exposed to flooding for example through repeatedly taking micocores. Together with phenological observations such as bud and leaf development and knowledge about climatic conditions as well as the timing and length of the flood period and the temperature of the flood water such studies may contribute to a better understanding of how flooding influences vessel formation. It may also be useful to examine whether the flood signature is confined to regions below the water surface. Knowledge about the location of flood signatures will not only determine the height of wood samples to be extracted for dendrohydrologic analysis but may also provide further insights regarding processes that are altered by flooding during vessel formation. Reasons for the development of numerous and small vessels in *F. nigra* may be related to flood-

induced hormonal alterations and changes related to temperature or cellular energy metabolism which need to be further investigated.

While the present studies have shown that the environment exerts a strong effect on vessel variables, many questions remain as to how environmental factors translate into physiological and molecular mechanisms that directly control vessel formation. Answers to these questions may require a better collaboration of researchers investigating cell developmental and physiological processes acting on vessel formation and dendrochronologists using vessel chronologies for fire, climate and/or hydrologic reconstructions.

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