TREE-RING RESEARCH, *Vol. 58(1/2), 2002, pp. 3–10*

TRENDS IN *QUERCUS MACROCARPA* VESSEL AREAS AND THEIR IMPLICATIONS FOR TREE-RING PALEOFLOOD STUDIES

SCOTT ST. GEORGE

Geological Survey of Canada
360-1395 Ellice Avenue
Winnipeg, Manitoba, Canada, R3G 3P2

ERIK NIELSEN

Manitoba Geological Survey
360-1395 Ellice Avenue
Winnipeg, Manitoba, Canada R3G 3P2

FRANCE CONCIATORI and **JACQUES TARDIF**

Centre for Forest Interdisciplinary Research (C-FIR)
University of Winnipeg
515 Portage Avenue
Winnipeg, Manitoba, Canada R3B 2E9

ABSTRACT

Changes in mean earlywood vessel areas in mature *Quercus macrocarpa* were analyzed to determine possible sources of bias in paleoflood records derived from anatomical tree-ring signatures. Tree-ring cores were collected at intervals along the vertical axis of four *Q. macrocarpa* in a flood-prone stand near the Red River in Manitoba. The WinCELL PRO image analysis system was used to measure mean vessel areas in each annual ring. Most cores displayed a pronounced juvenile increase in mean vessel area before stabilizing between 40 and 60 years. The lowest samples from several trees contain rings with anomalously small mean vessel areas that are coincident with high-magnitude Red River floods in 1950 and 1997. The anatomical response of *Q. macrocarpa* appears to be conditional on the relative timing of earlywood development and flooding. Flood signatures are most strongly developed near the tree base and become less evident up the trunk. Most signatures disappear between one and three meters in height. Differences in flood response between trees are likely caused by internal differences rather than hydrological or topographic factors. Paleoflood studies based on samples obtained exclusively at breast height may miss some anatomical flood signatures and underestimate flood frequency relative to earlier intervals.

Keywords: Flood rings, Manitoba, paleoflood, *Quercus macrocarpa,* Red River, vessel area, WinCELL PRO.

INTRODUCTION

Under normal growing conditions, ring-porous trees develop single or multiple rows of large conductive vessels in the spring and form smaller vessels during the rest of the growing season (Panshin and de Zeeuw 1970). However, inundation of the roots and stem during the growing season can disrupt the physiological processes that control cambial growth, and lead to anomalous tissue development within the annual ring. Anatomical abnormalities caused by flooding may include irregularities in the size and distribution of earlywood and latewood vessels, narrow rings, and thin-walled fibers within the latewood (Yanosky 1983; St. George and Nielsen 2000; Yanosky and Jarrett 2002). In *Quercus* species, abnormalities associated with spring flooding most often take the form of anomalously small vessels in the earlywood (Astrade and Bégin 1997; St. George and Nielsen

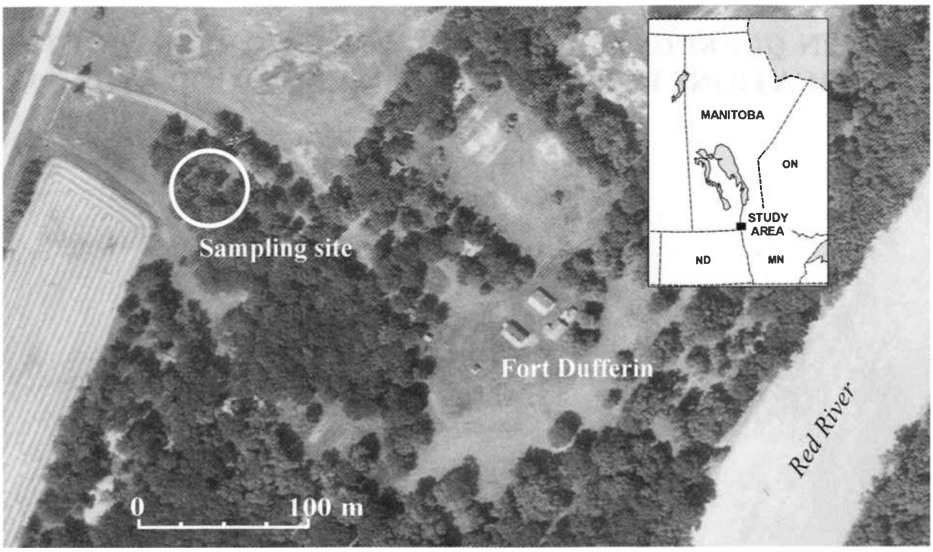

Figure 1. Aerial photograph of sampling site.

2000). These anatomical signatures ('flood rings', after Yanosky 1983) may serve as excellent proxy indicators of past flood events and may be used to identify and date floods prior to instrumental and historical records, with annual resolution.

The objectives of this study were to use vessel area data obtained using an image analysis system to characterize anatomical flood signatures in mature *Quercus macrocarpa* Michx. (bur oak). The variability of mean vessel size is described within individual tree rings and over time. The study also compares a composite vessel series spanning the last 115 years to nearby discharge gauge station data to estimate the sensitivity of vessel area signatures to floods of known magnitude and duration. Lastly, we determine how anatomical signatures related to flooding vary along the tree stem and discuss possible implications for sampling strategies for paleoflood studies.

STUDY AREA

Tree cores were collected from a stand of *Q. macrocarpa* growing near Fort Dufferin, Manitoba (49°01′50″N, 97°12′10″W; Figure 1). *Q. macrocarpa* is the only oak native to Manitoba and is often found at the prairie-forest boundary near local rivers and streams.

The stand is approximately 350 meters west of the western bank of the Red River, which flows northward into Manitoba from the United States and can produce extensive spring flooding. During its most recent severe flood in 1997, the Red River flooded nearly 2000 km^2 in Manitoba and caused substantial social and economic disruption (direct damages of CAN $500 million in Manitoba and US $4.5 billion in North Dakota and Minnesota; Manitoba Water Commission 1998; International Joint Commission 2000). A high water level marked in 1997 on a nearby tree (not sampled) indicated that the Red River flooded the Fort Dufferin stand to a depth of roughly 1.5 meters. In addition to the flood of 1997, other recent major floods occurred in 1996, 1979 and 1950 (Water Survey of Canada 2001). Fort Dufferin itself is a heritage site that includes several 19th century buildings constructed by the British North American Boundary Commission in 1872–1873. The buildings served subsequently as a North-West Mounted Police supply base and a Canadian immigration station prior to their abandonment in the early 1880s (P. Badertscher, personal communication 2001).

METHODS

Increment borers were used to collect several single-radius cores along the vertical axes of four oaks (sample designations F0001–F0004) between ground level and six meters up the stem. Samples above 1.5 meters were collected with the assistance of a mobile elevated work platform. Cores were air-dried, mounted and sanded following Stokes and Smiley (1968). A high-power air hose was used to remove sawdust and other foreign material trapped inside the earlywood vessels. Chalk was rubbed into the vessels to increase contrast with the surrounding wood fiber.

The surface of each core was scanned using a Polaroid digital microscope camera coupled with a Nikon dissecting microscope. Color pictures were captured and transferred as TIFF images with a resolution of 1,600 × 1,200 pixels. Working at a magnification of 30× usually captured rings in groups of three or four. Each ring was then separated into individual images. WinCELL PRO Version 5.6c (Régent Instruments 2001) was used to identify earlywood vessels and to measure their transverse areas in each annual ring. Previous studies have shown that this parameter in *Q. macrocarpa* and *Fraxinus pennsylvanica* Marsh. growing under normal (*i.e.* non-flood) conditions to be influenced by drought stress (Woodcock 1989; Shumway *et al.* 1991). The threshold for vessel detection was set to exclude objects with areas below 1,200 μm^2 to prevent non-vessel elements and latewood vessels from being detected. Some vessels needed to be highlighted manually to correct errors in the automatic detection process. Vessels whose boundaries were obscured by cracks in the cores were not measured. When cracking disrupted most of the vessels in an individual ring, the ring was omitted from further analysis.

Error analysis: During analysis of the first two cores (F0002a and 2b), every earlywood vessel was measured in each ring, with the number of vessels ranging between 9 and 70 per ring. Some rings, particularly those near the pith, had relatively few vessels. To determine the minimum number of vessels necessary to obtain a good estimate of mean vessel size within a given ring, we plotted the standard error of the mean as a function of number of vessels measured. For example, standard errors were calculated from the first pair of vessels measured in each ring. These values were then averaged over all rings to estimate the standard error of the mean obtained by measuring only two vessels. Subsequent vessel measurements were added in sequence to determine the improvement in the precision of the mean with increasing sample depth. As the number of measurements increased from 2 to 10 vessels per ring, the standard error of the mean improved from 23 percent (of the mean) to 13.5 percent (Figure 2). Doubling the number of measurements from 10 to 20 caused the standard error to drop to 11.4. Increasing the number of measurements per ring to 50 provided essentially no improvement. Based on these results, we limited the number of measurements made for subsequent samples to the first 20 earlywood vessels in each ring, starting from the top of the image. Any remaining earlywood vessels were manually eliminated. However, the results from the entire dataset (Figure 2) suggest that roughly 10 vessel measurements would provide similar quality information.

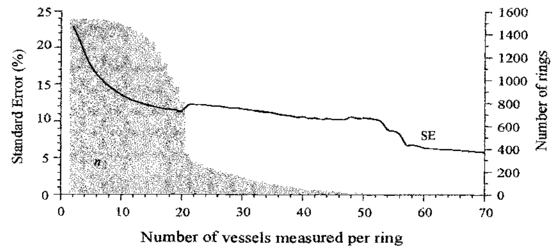

Figure 2. Changes in the standard error of mean vessel area (as a percentage of the mean) as the number of vessels measured per ring increases. The gray bars illustrate the number of rings containing a given number of vessel measurements.

Data analysis: To emphasize interannual changes in mean vessel size and rings containing locally unusual vessels, we developed a filtered series that combined vessel areas from the bottom cores of all four trees. Vessel area series were converted to differences as:

$$DIFF_i = \frac{(\bar{A}_i - \bar{A}_{i+1}) + (\bar{A}_i - \bar{A}_{i-1})}{2}$$

where $DIFF_i$ is the difference value (μm^2) for ring i, $\bar{A}_i$ is the mean vessel area for ring i, and $\bar{A}_{i-1}$ and $\bar{A}_{i+1}$ are the mean vessel areas for the preceding and following rings, respectively. This function is equivalent to a first-difference filter applied in both directions and reduces the magnitude of spurious positive anomalies for rings that immediately precede those containing flood signatures.

RESULTS

Temporal Trends for Individual Cores

Most cores displayed a pronounced juvenile trend in mean vessel area, as vessels increased with distance away from the pith, stabilizing between 40 and 60 years (Figure 3). Phelps and Workman (1994) observed similar, but more rapid, juvenile increases in percentage earlywood vessel area within the innermost 10 rings of *Quercus alba*. Since 1950, vessel sizes have rarely shown any departures from the long-term average lasting more than two to three years. Vessel areas within each ring are quite variable, especially when compared to the total variance along each core.

Vessel Composite Record

The samples taken from the lowest portion of the stem contained rings with anomalously small mean vessel areas, most prominently for rings formed in 1950 and 1997. However, the relative strength of individual flood signatures does vary from tree-to-tree. For example, tree F0002 contains a basal flood signature for 1997 but not 1950, while the opposite is true for tree F0004.

The differenced vessel area series from the basal cores were converted to deviates and then averaged together to produce the composite series (Figure 4). Four years have negative vessel area deviates greater than one SD: 1901, 1950, 1972, and 1997. Years that show as large positive anomalies usually precede or follow strong negative departures (*e.g.*, 1949, 1951, and 1998), and do not themselves contain abnormally large vessels. The two largest deviates, 1950 and 1997, coincide with high-magnitude Red River floods (Figure 4). The Red River did not flood significantly in 1972 or 1901, which implies that smaller decreases in annual vessel size are caused by factors other than flooding. However, the 1979 flood, which had a peak discharge roughly equal to 1950, did not produce any reduction in mean vessel sizes. Flood hydrographs indicate that the Fort Dufferin stand was under water for 24 days in 1979 (from April 23 to May 16). These trees were flooded for a longer period in 1997 and 1950, with flooding occurring between April 21 and May 20 in 1997 (30 days) and between April 24 and June 2 in 1950 (40 days). Vessels formed in 1950 were smaller than those of 1997 despite the greater flow of the later flood, suggesting that the duration of flooding has a greater influence on earlywood vessel size than does peak flood stage.

Floods in 1979 and 1997 have very similar timing, with inundation caused by the 1997 flood lasting only six more days. Daily temperature data from Emerson indicate that the timing of floods relative to the beginning of spring growth may be a critical factor determining *Q. macrocarpa*'s anatomical response. Spring thaw occurred in early April during 1979, with minimum temperatures above freezing for nearly three weeks prior to the onset of flooding. In contrast, the Fort Dufferin stand was already under water for seventeen days in 1950 before minimum temperatures rose above 0° Celsius[1]. The spring warmth in 1979 may have stimulated early bud break in *Q. macrocarpa* and allowed earlywood vessels to form completely before trees were affected by flooding. The differences in anatomical development during these major floods suggest that the response of *Q. macrocarpa* to prolonged flooding is conditional on the relative timing of earlywood development and flooding. Severe floods that occur several weeks after the spring thaw will not likely create discernible anatomical signatures in riparian oaks.

Vertical Trends in Vessel Area

In general, trees did not exhibit substantial vertical changes in mean earlywood vessel areas from core-to-core along the sampled intervals. However, vessel areas for rings formed in 1950 and 1997 are unusually small near the tree base and generally become larger as they progress up the tree trunk (Figure 5). Above three meters, most signatures disappear and some that are strongly developed near the tree base are absent at breast height. The 1950 signature in tree F0001 is visible at 0.45 meters but vessel areas at 1.1 meters are close to average. Trees F0003 and

[1] Daily climate data is not available at Emerson during the period of the 1997 flood.

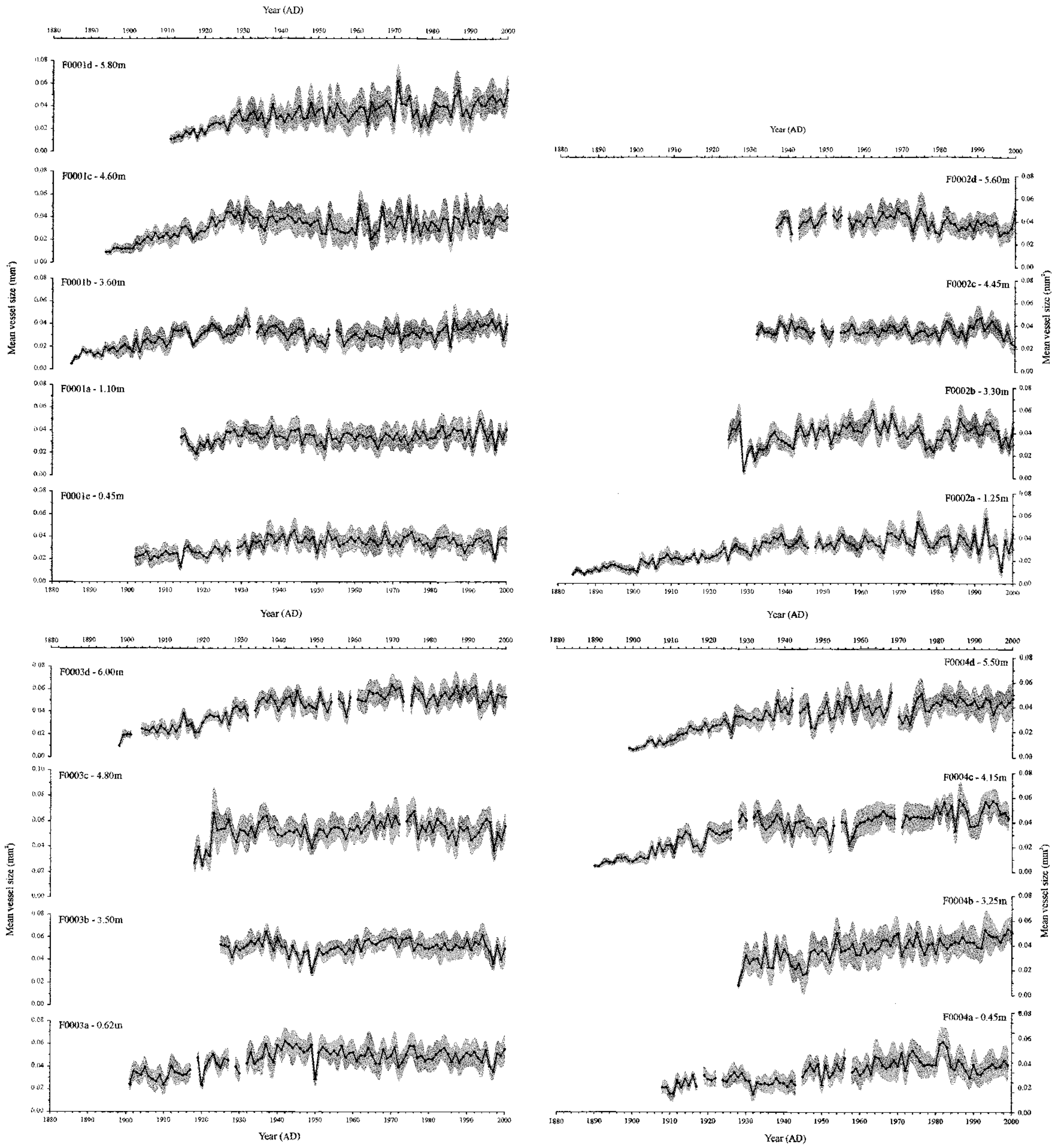

Figure 3. Mean vessel area series for *Q. macrocarpa* cores collected at Fort Dufferin, Manitoba. Elevations indicate coring height above the base of the tree, while the gray confidence limits represent twice the standard error of the mean. While tree age decreases with increasing height up the stem, the number of rings analyzed does not. This inconsistency is due to lower-height cores missing the pith or containing broken segments near the pith that are too short to determine ring dates with confidence.

F0004 were sampled in less detail near ground level but rings formed in 1950 contain similar overall patterns. At 3.5 meters, the 1950 vessel areas in tree F0003 are very close to normal; the 1949 ring actually has the smallest vessels at this height (Figure 3). Although some flood signatures persist several meters up the stem (particularly within the 1997 ring from tree F0003), the most detailed record of severe flooding is provided by cores extracted near the tree base.

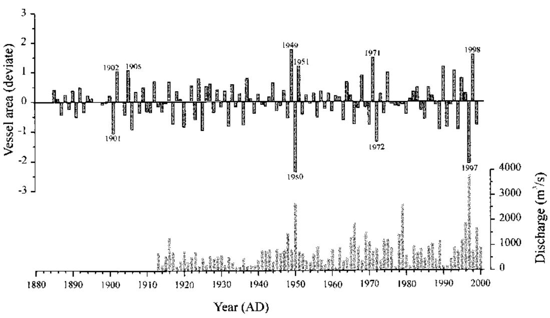

Figure 4. Vessel area composite for the Fort Dufferin stand compared to the Red River discharge record at Emerson, Manitoba (data from the Water Survey of Canada). The bottom vessel area series (shown in Figure 3) were filtered to emphasis annual departures from the mean and combined. Dates are shown for years with values greater than ± one standard deviation.

DISCUSSION

These results indicate that true 'flood signature' rings contain anatomical features that are clearly different from those of adjacent rings. Although rings with mean vessel areas roughly two SD or more below the mean for the entire tree are coincident with major spring floods, deviations on the order of one SD appear to be related to alternate causes. Since vessel areas appear to be relatively insensitive to the influence of less severe spring floods, this approach is probably most useful for paleoflood studies that are interested only in high-magnitude, low-frequency events.

However, the mechanism causing the anatomical response of mature *Quercus* to spring flooding is not known, especially since flood tolerance experiments with this species have used seedlings exclusively (Tang and Kozlowski 1982). Aloni (1991) suggested that flooding disrupts normal vessel induction in trees, causing vessels formed below the water surface to be much smaller than normal. As flood signatures in the Fort Dufferin oaks are most strongly developed near the tree base, our results may indicate that the water surface acts as a physical barrier to auxin flow that impedes vessel differentiation in the submerged portion of the stem. However, other potential mechanisms that could also affect vessel development, such as prolonged root flooding, might alter the basipetal transport of auxin regardless of the total depth of inundation. It also seems likely that differences in inter-tree mean vessel size coincident with flooding are caused by internal differences rather than hydrological or topographic

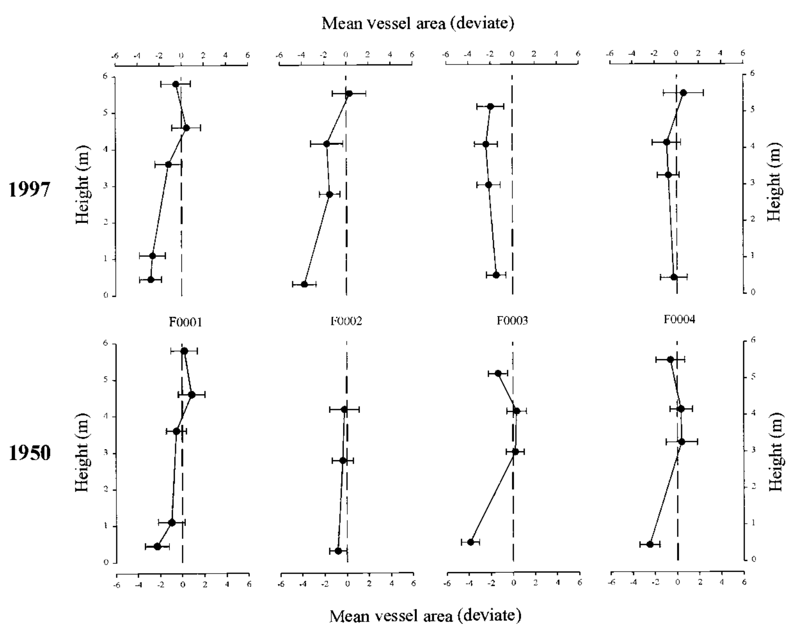

Figure 5. Vertical trends in vessel size for rings coincident with Red River floods in 1950 and 1997. Error bars represent twice the standard error of the mean.

factors. Because the Fort Dufferin trees are located on a flat prairie surface with little local relief, it is unlikely that their duration or depth of inundation would vary during extreme floods.

Changes in anatomical response to flooding along the tree stem have the potential to introduce biases into paleoflood records that are derived from flood rings, depending on the number and origin of tree-ring samples. Samples derived from logs entrained in river alluvium are often cut just above the root ball to maximize the number of rings in the cross-section. Therefore, most alluvial logs should contain the most complete flood signature record available in their parent tree. The original vertical position of cross-sections obtained from historical buildings is usually less obvious, as any indications of location on the trunk are removed on hewn timbers. Although samples derived from the middle or upper portion of the tree may not contain some flood signatures that are present near the base, the original height of samples from historical buildings should be essentially random and should not bias any derived paleoflood record, given large numbers of samples. In contrast, samples collected from live trees are usually obtained at breast height (~1.5 m), which may cause some flood signatures present in the lower portion of the stem to be missed. If living trees dominate the composite tree-ring record for an extended interval (such as the 20th century), more recent flood signatures may appear less often than during earlier intervals. Although other factors, particularly the development of regional flood protection structures, can also reduce the impact of extreme floods on riparian trees, samples derived from live trees could be taken too high to obtain a complete, recent flood record.

CONCLUSION

Mean vessel area series derived from tree rings can provide a proxy record of high-magnitude floods that permits researchers to identify and date paleofloods with better temporal resolution than any other non-calendrical technique available. The duration and timing of inundation during large spring floods appears to be the critical factors controlling the formation of these signatures. However, vessel signatures produced by extreme floods appear to be highly variable within the same stand, which emphasizes the need to develop paleoflood records from multiple trees. Our results also demonstrate that the strength of vessel area signatures related to extreme flooding may vary considerably over relatively short distances along the tree stem. These changes, which can occur over less than one meter in height, have important implications for paleoflood studies based on anatomical tree-ring signatures and future attempts using anatomical signatures as proxy flood records should focus sampling at the base of flooded trees, if possible.

ACKNOWLEDGMENTS

We wish to thank Greg Keller and Gaywood Matile (Manitoba Geological Survey) for assistance in the field and David Sutherland for his skillful operation of the elevated work platform. Greg Keller also provided invaluable suggestions and support during analysis of the vessel area database. Earlier versions of this manuscript were greatly improved by comments by Henri Grissino-Mayer and two anonymous reviewers. The Water Survey of Canada provided discharge data for the Red River at Emerson. The Red River Valley Flood Protection program and an NSERC equipment grant to J. Tardif supported this work. This paper is GSC contribution number 2001184.

REFERENCES CITED

Aloni, R.
1991 Wood formation in deciduous hardwood trees. In *Physiology of Trees,* edited by A. S. Raghavendra, John Wiley & Sons, New York; pp. 175–197.

Astrade, L., and Y. Bégin
1997 Tree-ring response of *Populus tremula* L. and *Quercus robur* L. to recent spring floods of the Saône River, France. *Ecoscience* 4:232–239.

International Joint Commission
2000 Living with the Red. A report to the Governments of Canada and the United States on reducing flood impacts in the Red River basin. International Joint Commission, Ottawa-Washington.

Manitoba Water Commission
1998 An independent review of actions taken during the 1997 Red River flood: a report to the Honourable J. Glen Cummings, Minister of Natural Resources. Government of Manitoba, Winnipeg.

Panshin, A. J., and C. de Zeeuw
1970 *Textbook of Wood Technology,* 3rd ed. McGraw-Hill, New York.

Phelps, J. E., and E. C. Workman, Jr.
1994 Vessel area studies in white oak (*Quercus alba* L.). *Wood and Fiber Science* 26:315–322.

Régent Instruments
2001 WinCELL V5.6: Introduction. Québec. Québec.

St. George, S., and E. Nielsen
2000 Signatures of high-magnitude 19th century floods in *Quercus macrocarpa* tree rings along the Red River, Manitoba, Canada. *Geology* 28:899–902.

Stokes, M. A., and T. L. Smiley
1968 *An Introduction to Tree-Ring Dating.* University of Chicago Press, Chicago.

Shumway, D. L., K. C. Steiner, and M. D. Abrams
1991 Effects of drought stress on hydraulic architecture of seedlings from five populations of green ash. *Canadian Journal of Botany* 69:2158–2164.

Tang, Z. C., and T. T. Kozlowski
1982 Some physiological and morphological responses of *Quercus macrocarpa* seedlings to flooding. *Canadian Journal of Forest Research* 12:196–202.

Water Survey of Canada
2001 Unpublished stage data for Emerson, Manitoba. Environment Canada, Winnipeg.

Woodcock, D. W.
1989 Climate sensitivity of wood-anatomical features in a ring-porous oak (*Quercus macrocarpa*). *Canadian Journal of Forest Research* 19:639–644.

Yanosky, T. M.
1983 Evidence of floods on the Potomac River from anatomical abnormalities in the wood of flood-plain trees: U.S. Geological Survey Professional Paper, v. 1296, 42 p.

Yanosky, T. M., and R. D. Jarrett
2002 Dendrochronologic evidence for the frequency and magnitude of paleofloods. In *Paleoflood Hydrology,* edited by P. K. House, D. R. Levish, R. H. Webb, and V. R. Baker, American Geophysical Union Monograph, Washington, D.C. pp. 77–89.

Received 6 February 2002; accepted 18 June 2002.