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ARTICLE

# Ancient boreal forests under the environmental instability of the glacial to postglacial transition in the Great Lakes region (14 000 – 11 000 years BP)

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**Abstract:** Retreat of the Laurentide Ice Sheet 20 000 years ago tremendously altered environmental conditions and opened territory to the boreal spruce forest expansion. However, the details of forest colonization during the rapid climate warming and the adaptation of the newly developed stands to short cooling episodes during the warming and degradation of the ice sheet are not known. Preservation of wood from the glacial to postglacial transition offers the opportunity for examination of high-frequency growth variability in response to hemispheric and local forcings on temperature and hydrology. Here we consider growth of spruce at three sites from the interior of Northern America developed at ca. 13 700, 12 100, and 11 300 calibrated years before present (cal years BP), with well-replicated tree-ring chronologies spanning from 116 to 310 years. The data show at least two generations of trees established at each of the sites promoted by short, warm intervals. The tree mortality was variously affected by both cold conditions and the influence of rising water table and sediment burial. The history of these stands indicates breaks in forest colonization following a century (or two) of successful migrations. Interestingly, the thinning of the spruce forest did not seem to open pioneering opportunities for other tree species at those times.

**Résumé :** Le retrait de l'inlandsis laurentidien il y a 20 000 ans a considérablement modifié les conditions environnementales et créé de l'espace pour l'expansion de la forêt boréale d'épicéa. Cependant, on ne connaît pas les détails de la colonisation par la forêt durant le réchauffement rapide du climat ni comment les peuplements nouvellement établis se sont adaptés à de cours épisodes de refroidissement durant ce réchauffement et la dégradation de la nappe glaciaire. La préservation de pièces de bois datant de la période de transition entre les périodes glaciaire et postglaciaire fournit l'occasion d'étudier les variations de croissance très fréquentes en réaction aux forçages hémisphériques et locaux de la température et de l'hydrologie. Dans cet article, nous examinons la croissance de l'épicéa qui se développait à trois endroits sur le continent nord américain il y a approximativement 13 700, 12 100 et 11 300 ans à l'aide de séries dendrochronologiques répétées plusieurs fois et s'étendant sur 116 à 310 ans. Les données montrent qu'au moins deux générations d'arbres, profitant de brefs intervalles de chaleur, se sont établies à chacun des endroits. La mortalité des arbres était influencée de façon variable tant par le froid que par l'influence de la remontée de la nappe phréatique et l'ensevelissement par les sédiments. L'histoire de ces peuplements indique que la colonisation par la forêt a connu des pauses après un (ou deux) siècle de migrations réussies. Il est intéressant de constater que l'éclaircie de la forêt d'épicéa ne semble pas avoir créé de nouvelles opportunités pour d'autres espèces d'arbre à ces moments-là. [Traduit par la Rédaction]

## Introduction

During deglaciation, ca. 15 000 to 11 000 years ago, oxygen isotopes in Greenland ice cores chronicled large temperature variations prior to entering the more climatically stable Holocene period (Fig. 1), the impacts of which may have been hemisphere-wide, including the influence on vegetation and ancient boreal forests. The Bølling–Allerød warm period and the Younger Dryas cold event (Mayewski et al. 1993) are perhaps the best-known excursions in this time frame. In addition to the possible hemispheric temperature variability implicated in ice-core $\delta^{18}O$, the existence and movement of a continental-scale ice sheet in North America had profound effects on vegetation, including the boreal forest dominated by black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) and white spruce (*Picea glauca* (Moench) Voss). Evidence indicates that the southward expansion of the Laurentide Ice Sheet severely compressed the remnant boreal zone, with boreal tree species likely surviving in refugia (Williams et al. 2001; Shuman et al. 2002; Jackson and Booth 2007). When the ice sheet finally retreated, the boreal forest was able to migrate from the midlatitudes to its current tree-line position. The specifics of this massive tree colonization, however, have yet to be fully understood.

The presence of wood among macrofossil deposits of that age allows for dendrochronological analysis to examine changes in the trees and their environment at fine temporal scale. Year-to-year variability of tree-ring widths carries both an environmental signal related to climate and a stand disturbance signal related to stand and forest dynamics (Fritts 1976). A disturbance event in shade-tolerant spruce can be identified in a tree-ring subseries using methods of removing long-term trends (detrending) and converting ring-width measurement into unitless indices (standardization), as described by the "linear aggregate model" (Cook and Peters 1997). Tree-ring indices (climate signal) and original tree-ring width mean properties related to the age trend and disturbance can be analyzed to gain insights into both the environmental changes and the history of spruce forest.

Studies of modern tree-line forests in interior Alaska and Canada provide strong evidence that density of stands (i.e., number of individuals) highly correlates with the warming trends of summer

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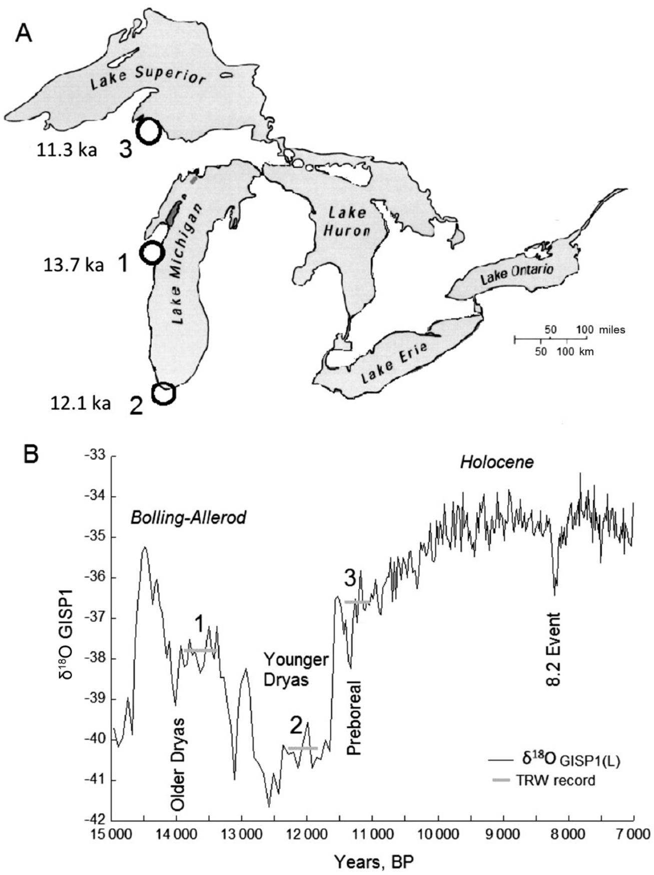
**Fig. 1.** (A) Map of location of three primary spruce sites (open circles): 1, Two Creeks type locality; 2, Liverpool East site; and 3, Gribben Basin site. (B) The δ18O record between 15 000 and 7000 years ago from the GISP1 Greenland ice core showing climate events and the calendar intervals of the three floating tree-ring records dated by radiocarbon wiggle-matching of crossdated tree rings (Leavitt et al. 2007).




temperature (Bunn et al. 2005), although the timing of tree-line advance greatly differs between regions (Lloyd and Fastie 2002). Expected positive response of tree growth to temperature may imprint on growth in other ways such as the interseasonal changes of soil moisture availability (Barber et al. 2000). The melting upper layers of permafrost develop oversaturated soil conditions in early spring and dry conditions in the late growing season as the melting layer deepens (Chapin et al. 2000). Various responses of black spruce and white spruce to the soil moisture variations, in addition to other hydrological effects on tree growth related to proximity to the continental ice sheet (e.g., rapid change in the local water table), may also be documented in the tree rings.

We have been systematically identifying wood deposits from the time of deglaciation in the Great Lakes region of North America and assembling a large collection of wood (Panyushkina and Leavitt 2010) for which we gain age control with radiocarbon dating, including "wiggle matching" of radiocarbon values measured in consecutive 5- to 10-year tree-ring sequences with a high-resolution master radiocarbon calibration chronology to more precisely place the sites into an absolute time context. With multiple tree samples frequently available from these sites, dendrochronological analysis can be conducted to learn about the environments to which the trees were exposed (Panyushkina et al. 2008). The collective set of tree-ring sites now also allows us to evaluate the forest establishment pattern during the temperature-driven shifts of boreal forest at high resolution. In this study, we focus on three spruce stands of different ages from ca. 14 000 to 11 000 years ago and at various positions southward of the ice margin, providing an opportunity for inferring stand dynamics and spruce growth variability both in space and time (Fig. 1A). Perhaps most remarkably, radiocarbon dating of the stands (Leavitt et al. 2007) appears to place each of them into various periods present in the Greenland ice records within which tree growth was subjected to abrupt temperature changes (brief warming or cooling excursions; Fig. 1B).

This study investigates the dendrochronology of these boreal forest sites during the abrupt hemisphere-wide temperature shifts to (*i*) identify possible imprints of hemispheric temperature and local moisture influences related to the spruce growth, (*ii*) determine spruce stand dynamics among the sites, and (*iii*) evaluate past progression of tree colonization under environmental change. The results are considered in light of the growth condition and northward movement of the boreal forest at that time period, which is important to improving paleoclimate understanding, as well as providing high-resolution records that could be useful to testing paleovegetation models. Indeed, temperature seems important to both tree growth and recruitment pulses, but changing local hydrology is tied to the death of the trees.

## Methods

### Sites

Three boreal forest sites spaced over ca. 500 km along longitude 75°W, each having more than 50 wood samples with complete diameter preserved, were selected from the Great Lakes network of remnant wood (Fig. 1) (Panyushkina and Leavitt 2010). The sites are also widely spread in time, but each represents spruce stands establishing near the ice sheet margin at the tundra–forest ecotone. The Two Creeks spruce forest type locality along the western shoreline of Lake Michigan near the town of Two Creeks, Wisconsin (ca. 44°20′N, 87°32′W), falls in the Bølling–Allerød period. The site is believed to mark the final advance of the ice sheet into the continental United States ca. 11 800 $^{14}$C years before present (BP) (Goldthwait 1907; Thwaites and Bertrand 1957; Broecker and Farrand 1963; Leavitt and Kalin 1992; Kaiser 1994). In fact, log and stump preservation at the type locality and other contemporary sites nearby was facilitated by the glacier advance overrunning the stands and burying the trees in glacial till. Radiocarbon wiggle-matching of tree rings from the site suggests that the trees grew at ca. 13 760 – 13 530 calibrated years BP (cal years BP) (Leavitt et al. 2007). Wilson (1932, 1936) found floral evidence (pollen, cones) for both black spruce and white spruce at the site, but Kaiser (1994) believed that his chronology contained wood from only black spruce. Because of the difficulty in distinguishing species of spruce from wood anatomy, our Two Creeks 296-year chronology from 26 selected tree samples may be a mix of the species.

The Liverpool East site is located ca. 15 km south of the southern tip of Lake Michigan near Hobart, Indiana (ca. 41°33′N, 87°17′W). The site geology was originally studied by Schneider and Hansel (1990), with reported radiocarbon ages mostly older than 10 000 $^{14}$C years BP. Subsequently, more than 70 stumps preserved in apparent estuarine sands with a cover of dune sands were collected by Panyushkina et al. (2008) for tree-ring analysis and development of a highly replicated 116-year chronology. The glacial front at this time was more than 500 km north of the site. Radiocarbon wiggle-matching of tree rings indicates that the trees grew at ca. 12 100 – 12 020 cal years BP, i.e., in the mid-Younger Dryas interval (Leavitt et al. 2007). Only cones of black spruce were found (Panyushkina et al. 2008), so the trees are believed to be exclusively black spruce.

The Gribben Basin site is located ca. 15 km south of Marquette, Michigan (ca. 46°21′N, 87°24′W), where trees were buried by sediments from ponding and outwash from the Marquette glacial

**Table 1.** Main statistics of floating tree ring width (TRW) chronologies of ancient spruce from the Great Lakes sites used in the study.

| Site | Length of record (years) | No. of trees | Missing rings (%) | Mean TRW (mm) | Mean sensitivity | Auto-correlation lag 1 |
|---|---|---|---|---|---|---|
| Two Creeks | 296 | 29 | 0.05 | 0.47 | 0.22 | 0.33 |
| Liverpool East | 116 | 73 | 0 | 0.79 | 0.32 | 0.11 |
| Gribben Basin | 176 | 47 | 0.17 | 0.51 | 0.21 | 0.25 |



re-advance in Lake Superior (Lowell et al. 1999). The site was not overrun by the re-advance, but the lobe may have approached within kilometres of the site. Spruce trees in growth position were discovered at two different sites and employed in several investigations (Traver 1980; Lowell et al. 1999; Pregitzer et al. 2000). A tree-ring investigation by Pregitzer et al. (2000) developed a ring-width chronology of 125 years, and radiocarbon ages generally fall around 10 000 $^{14}$C years BP, near the end of the Younger Dryas interval. Based on age class and spatial distributions of the trees, as well as their size and radial growth rates, Pregitzer et al. (2000) concluded that the Gribben Basin forest was similar to modern spruce forests. They thought that the trees were the first colonizers of terrain exposed from a previous glacial retreat and representative of forest stands associated with advancing tree lines. Radiocarbon wiggle-matching of tree rings indicates that the trees grew at ca. 11 300 – 11 170 cal years BP (early Holocene) (Leavitt et al. 2007). Based on cones, Pregitzer et al. (2000) believed that the stand that they studied was pure white spruce, although Lowell et al. (1999) reported spruce and some larch (*Larix*) for the first Gribben Basin site.

### Tree rings

Tree rings were obtained as cross-sectional slices from buried logs and stumps excavated from alluvial, lacustrine, and glacial deposits at various positions southward of the Late Pleistocene ice sheet site. The outermost ring present in the samples is not necessarily the final growth ring that had been deposited by the tree prior to its death, although the occurrence of bark in some samples indicates the presence of the final growth ring, and the presence of sapwood in many others implies that the ring sequence is nearly complete. In addition to the tree rings from the Two Creeks type locality, wood specimens from four contemporaneous Two Creeks age locations in east–central Wisconsin (processed the same as the three primary sites) were included to compare spatial distribution of stand growth and termination patterns during the re-advance of the Green Bay lobe of the Laurentide Ice Sheet. These include (*i*) New Denmark (ND) and Amerihost (AH) in the Green Bay area, Brown County, (*ii*) Lake Butte des Morts (LB) in Winnebago County, and (*iii*) the W. Ferguson collection (WF) from Manitowoc County (near the Two Creeks type locality).

Dry wood samples were sanded with progressively finer sandpaper to bring out ring boundaries and wood microanatomy. For wet wood, sharp and frequently replaced razor blades were used to produce highly defined surfaces. Tree-ring widths were measured with a Henson measurement system (0.01 mm precision) and cross-dated within each site using the TSAP program (Rinn 2003).

Tree-ring chronologies were calculated with the ARSTAN program (Cook and Krusic 2011) as required by dendroclimatic studies. To estimate and remove tree-age growth trend, the "Friedman Super Smoother" (Friedman 1984) or, optionally, a cubic smoothing spline two-thirds the length of the series was applied to the tree-ring width series. Because the growth rings formed in trees likely growing in very dynamic environments and therefore carrying disturbances from various sources, the variance of the tree-ring width series was stabilized with adaptive power transformation prior to the detrending (Cook and Peters 1997). Tree-ring indices were calculated with a robust biweight mean (Cook and Krusic 2011). Common variance caused by climatic factors and directly associated with quality of the tree-ring chronologies was checked with the expressed population signal statistic (Cook and Krusic 2011).

Periodicity of climatically induced tree-ring width variance was studied with wavelet methods (http://paos.colorado.edu/research/wavelets/). Wavelet analysis isolates periodic signals in a time series and follows their frequency changes in time (Torrence and Compo 1998). This transformation detects an evolution of nonstationary signals. With respect to our tree-ring chronologies, Morlet wavelet function estimates significance of magnitude for various periodicities (bands and modes) approximated from the tree-ring width indices attributed to climatic forcings.

The disturbance signal of the tree rings related to forest history was analyzed from tree-age growth curves, tree-ring chronology segment length, tree-ring sample depth, and residuals between the tree-ring width index chronologies and tree-ring width mean chronologies (Cook and Krusic 2011). The sample depth of a tree-ring chronology (the number of trees contributing to each year in the chronology) was used as a proxy for spruce population size, as an indication of relative abundance–presence (Fritts 1976). The mean tree-ring chronology averages raw tree-ring width measurements at the site and represents cumulative variations of tree growth at the stand. Additionally, where possible, the tree-ring specimens were screened visually for disturbance patterns or years associated with flooding (abundance of resin ducts), freezing events during the growing season (frost rings), and reaction wood (tilting of trees frequently associated with saturated soils).

## Results

More than 40 trees contributed to the final Liverpool East and Gribben Basin chronologies over the total length of each of their records (116 and 176 years, respectively), and 26 trees contributed over a portion of the Two Creeks chronology (296 years) (Table 1; Fig. 2). Both the Gribben Basin and Two Creeks chronologies are longer and have more trees than previously published chronologies of 125 years (Pregitzer et al. 2000) and 252 years (Kaiser 1994), respectively. Mean tree-ring widths are in the order Liverpool East > Gribben Basin > Two Creeks, although the latter two are almost identical. Mean sensitivity (a measure of year-to-year variability in ring size) of the standardized tree-ring chronologies is above 0.2 at Two Creeks and Gribben Basin sites and above 0.3 at Liverpool site.

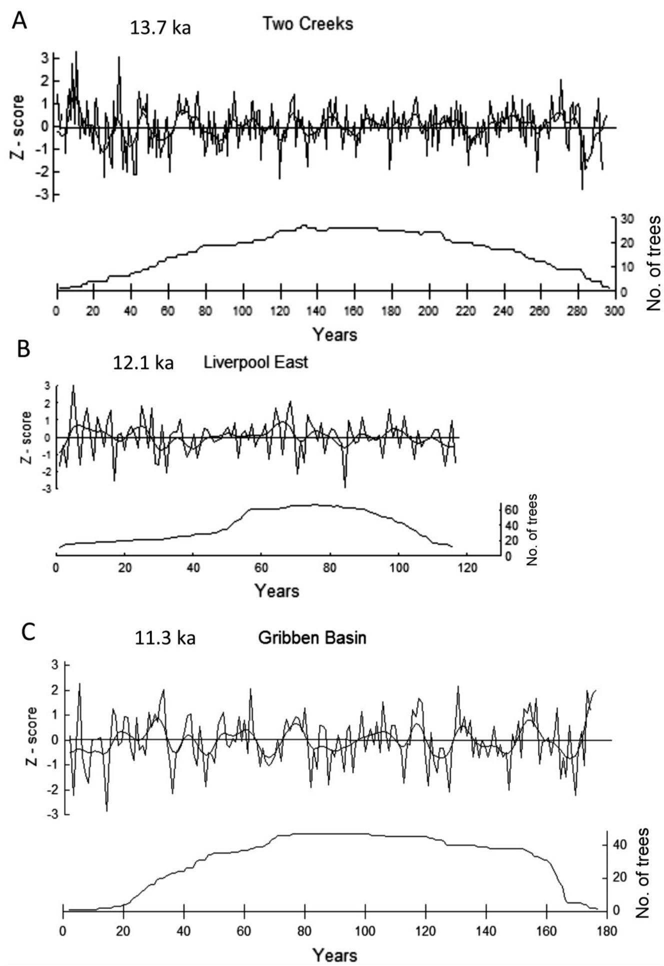
The standardized ring-width index series for these sites along with the "sample depth" (number of trees contributing to the mean index for each ring) are plotted in Fig. 2. Wavelet power spectra show the strongest periodicity in the data over the length of the chronologies (Fig. 3). Individual ring-width chronologies of approximate Two Creeks age from northeastern Wisconsin are presented in Fig. 4. These results are interpreted in the next section.

## Discussion

### Environments of the glacial–postglacial transition

The high interannual variability of the chronologies suggests that the common variance of chronologies was limited by climate variations (Table 1). The climatic signal in the tree-ring indices is

**Fig. 2.** Tree-ring width indices for (A) Two Creeks, (B) Liverpool East, and (C) Gribben Basin spruce sites showing interannual (thin lines) and decadal (thick lines = 10-year Hamming window smoothing curve) variability. The variability of these floating tree-ring chronologies indicates summer temperature fluctuations during the post-Older Dryas period, late Younger Dryas, and Preboreal, respectively. *Z* scores represent normalization of the indices to their respective standard deviations about a mean of zero, which allows the index series to be directly compared. The high number of tree-ring samples throughout the full length of the records, as shown on the lower panel of each pair, indicates unbiased variance of the developed records.




very likely to be dominated by summer temperature (Fig. 2) because of the location of sites at the ancient tree lines. Up to 40% of Liverpool East specimens show some frost-damaged cells in the first half of the record. The two other records show partially formed tree rings present in the juvenile part of cambial growth, which occur in extremely cold summers.

Long-term temperature changes as tracked by tree growth are shown in Fig. 1B. Although the Two Creeks type forest (13.7 ka) was established during a millennium-scale cooling event, the stand dynamics were driven by a warm century in the second half of the chronology. The Liverpool forest (12.1 ka, Younger Dryas) existed in a much colder environment but again had a few decades of rapidly rising temperature in the middle of the chronology. The Gribben Basin (11.3 ka) forest occurred in times much warmer than the Two Creeks forest, but the trees had started growth during a very abrupt temperature change from cold to warm (Fig. 1B).

Mean widths of tree rings of Two Creeks and Gribben Basin spruce are similar but much lower (almost 40%) than mean tree-ring width of the Liverpool black spruce that grew in the coldest conditions of the Younger Dryas. This difference in the tree growth rate is anomalous and cannot be simply explained by the difference in spruce species, as there is evidence for faster growth of modern white spruce than black spruce in the same region (e.g., Winslow 2008). This is evidence for much younger age of trees at that time, which will be discussed further. The two-decade warm excursion in the middle of the Liverpool record (Figs. 1B, 2) and generally younger age of black spruce trees at Liverpool are possibly responsible for the observed contrast in growth rates.

Overall, the decadal variability of the tree-ring chronologies from all sites is comparable in amplitude (Fig. 2), but the Gribben Basin and the Two Creeks chronologies have longer warm decades as expected. The tree-ring growth limited by temperature provides evidence that the environments ca. 11.3 and 13.7 ka were more or less similar and much warmer than the late Younger Dryas time (12.1 ka), even though the Liverpool site is much farther south and more distant from the ice margin than two other sites.

Moreover, deteriorating (cold) climate conditions appear to have strongly impacted the frequency of tree-ring variability as well. Spruce variance seems to have been strongly reduced by temperature during cold anomalies, whereas the variance of tree rings experienced fewer changes during the warmer episodes. A wavelet analysis of Two Creeks tree-ring indices shows that the low-growth departures in the record were characterized by enhanced power within the 3- to 7-year band (Fig. 3). This high-frequency cycle is attributed to El Niño – Southern Oscillation (ENSO). The ENSO state is defined by the difference in sea-level pressure across the tropical Pacific Ocean and is known to influence precipitation patterns in parts of North America. In our case, the ENSO-like frequency is consistent with the temperature regime of the post-Older Dryas boreal environment during the final advance of the ice sheet.

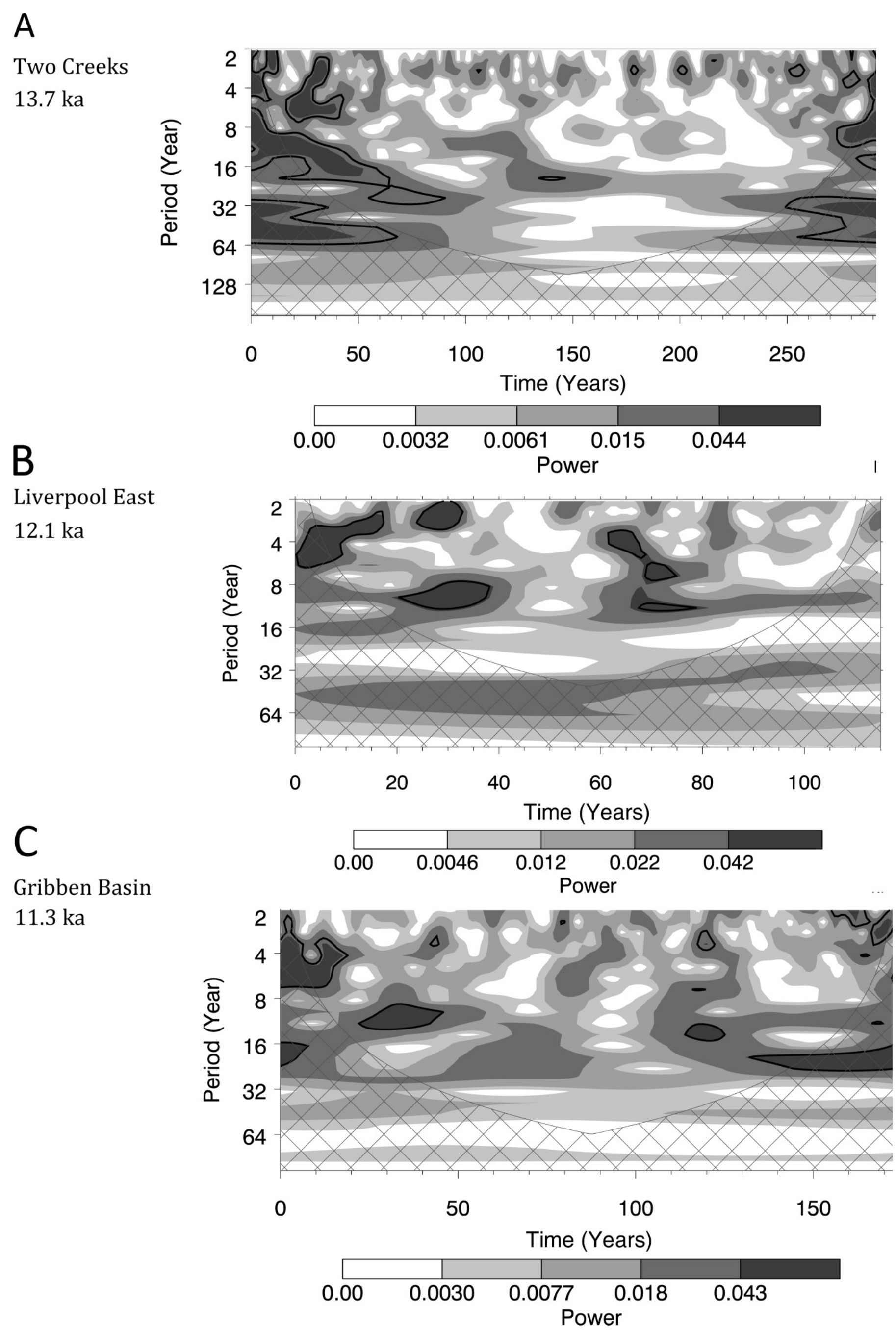
The wavelet of the Liverpool (late Younger Dryas) tree-ring chronology reveals very different periodicities. Warmer conditions (higher tree-ring indices) correspond with significant power bands. The Liverpool wavelet has a shorter 2- to 5-year power band, but an 8- to 12-year periodicity is more pronounced throughout the record. The Gribben Basin record returns to dominance of a 3- to 7-year band but with much weaker power than the Two Creeks record and often below its significance. Generally, temporal behavior of this record is more irregular and its power spectrum is weaker than the others.

## Population dynamics and environmental forcing

Despite limitations imposed by the assembled data set, the results provide evidence for interaction between both long- and short-term temperature fluctuations and forest dynamics at the ancient tree lines. Tree colonization of postglacial ecotones was a complex process. Overall, periods of long-term warming, as seen in the Greenland GISP1 ice core $\delta^{18}O$ record (Fig. 1B), seem to favor colonization by new spruce stands during deglaciation. However, changes in vegetation density within respective stand life-spans occur during short-term temperature fluctuations (Figs. 2, 4B). Segment length of the tree-ring records (not shown) and age of trees (Fig. 4B) identify at least two generations of trees at each site promoted by short, warm intervals within generally cool or cold periods compared with the Holocene. Average length of individual tree-ring series of the chronologies varies from 69 years for the shorter chronology of the Liverpool site to 164 years for the longer Two Creeks chronology.

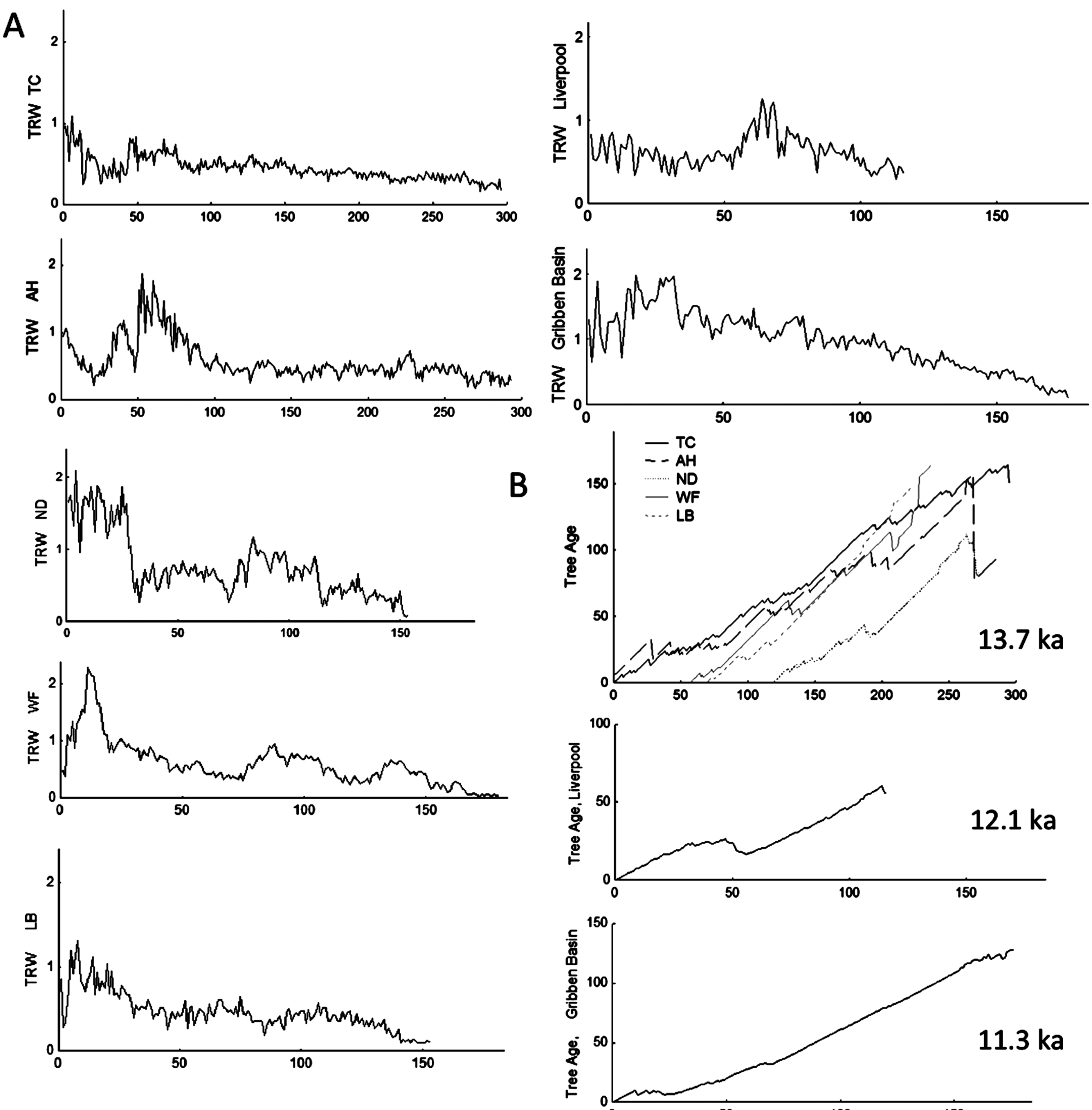
Spatially and temporally, the changes in spruce population dynamics exhibited in the tree rings may have followed the tree cover pattern in the region. A sharp increase in the chronology sample size (sample depth) at Liverpool and Gribben Basin sites, as

**Fig. 3.** Wavelet power spectrum (using the Morlet wavelet function) of tree-ring width chronologies for (A) Two Creeks, (B) Liverpool East, and (C) Gribben Basin sites. The *y* axis is the wavelet period in years (similar to Fourier frequencies). The black contours mark the 10% significance band using a red-noise background spectrum. The contour levels represent 75%, 50%, 25%, and 5% of the wavelet power. The wavelet power at each period is normalized by the global wavelet spectra. The darker areas indicate that tree-ring widths were strongly influenced by temperature, while the lighter areas show less climatic impact. The cross-hatched region corresponds to the cone of influence where zero-padding has reduced the variance (Torrence and Compo 1998), which is not meaningful.




the second tree generation established, demonstrates the turbulence of the Younger Dryas and Preboreal climates and the abrupt change in temperature (Figs. 2, 4). The final years' growth and tree mortality at the sites were variously affected not only by cold conditions, but also by the influence of rising water table and sediment burial. The declining pattern in the sample size at the end of the records suggests that rather than slow degradation of growth conditions as seen in the Two Creeks chronology, trees at the Liverpool and Gribben Basin locations rapidly perished in response to an external (nonstand dynamic) factor as the environment degraded rapidly. Rising water and sediment burial could be such factors driving mortality, with only a very few trees surviving the final decades. Tree cover would likely decline sharply in the region in response to decreased seed productivity and seed germination because of low tree vigor and fewer trees. A detailed analysis of establishment and mortality at the Liverpool site by Panyushkina et al. (2008) interpreted a surge in establishment between years 60 and 70 (Fig. 3, middle) as a

**Fig. 4.** Tree-ring raw data demonstrating disturbance signals in the tree growth and stand dynamics. (A) Site mean chronologies of tree-ring widths for Two Creeks, 13.7 ka interval (all have more than 11 trees per chronology), Liverpool East, 12.1 ka interval, and Gribben Basin, 11.3 ka interval. The Two Creeks sites include two southerly sites from Brown and Winnebago Counties (WF, LB), and 3 more northerly sites from Green Bay area, Brown and Manitowoc Counties (TC, AH, ND). (B) Changes in average age of trees from year to year plotted per site. The site plots are aligned according to overlap of the tree-ring records. The overlap suggests that the termination of these spruce stands occurred at different times. Steady increase in the tree age (*x* axis) shows increase in the stand density. Band of the lines indicates temporal decrease of stand density caused by tree mortality.






consequence of warming, further corroborated by the large tree rings at that time.

In contrast, the Two Creeks record has a gradual increase in the sample size, possibly conforming to the slowly warming environments during the Bølling–Allerød period (Figs. 1B, 2). If the Two Creeks chronology is accurately placed on the GISP1 $\delta^{18}O$ curve, the middle part of the chronology would have been influenced by a cold excursion, resulting in the slow decline in sample size (after ca. year 160). The late period of the chronology would have been warmer with the exception of a final cooling excursion.

The tree mortality at the sites was variously affected not only by cold conditions, but also by the influence of rising water table and sediment burial. Proximate ice fronts, sediment deposition, and rising water (flooding of soil) may have variously influenced the outside rings of trees at the three sites and contributed to stand disturbances. The combined influence on tree growth of both climatic and stand disturbance related variance is shown in Fig. 4A. Notably, the open-canopy stands of the five Two Creeks type sites show no evidence of synchronized response of tree growth to stand disturbances. This suggests that the disturbances were caused by local events probably conveyed by local topography and permafrost patterns. This is no surprise because the spruce habitat in the postglacial environment was threatened by changes in the soil moisture availability caused by local hydrology.

However, although the spatial patterns of growth termination in Two Creeks type trees overrun by the advancing glacier front were variable, they generally match the described regional pattern of temperature impact on spruce growth dynamics (Figs. 2, 4A). The last decades of spruce growth are punctuated by a rapid growth decline followed by a pronounced growth increase (Fig. 2). The Two Creeks type specimens have a few event years at the end of their life-span, with a band of resin ducts throughout the entire ring circumference as the tree response to high-water levels. Additionally, most trees have reaction wood in the second half of their records attributed to soils saturated with water (Fig. 4A). As represented by tree age plots (Fig. 4B), tree-ring records from the more northern contemporaneous tree stands (Green Bay area) appear to have ended growth decades earlier than the southern set of chronologies of east–central Wisconsin (Two Creeks site). The distance between these two locations is only about 70 km. Several tree-ring records have a ring-size increase just prior to the end of the chronologies, suggesting favorable growth conditions just prior to their death. Growth of trees in topographic depressions may have been severely diminished by rising water from ponding in front of the advancing ice sheet, but trees at higher elevations may have escaped this ponding so growth could respond positively to warm years. A tree-ring study by Kaiser (1994) determined that in addition to the cold-air temperature effects from the advancing glacier, which he thought responsible for the very small 20–30 outer rings of many samples, rising lake level as the glacial lobe blocked a northern drainage outlet could have killed any survivors prior to finally being overrun by the glacial front.

### Overview of spruce colonization during the glacial–postglacial transition

Overall, the studied interaction between the environmental change and spruce forest dynamics suggests that the spruce colonization during the glacial–postglacial transition was controlled to a greater extent by long-term rather than short-term temperature variability. The history of the studied stands indicates reoccurring breaks in forest colonization following a century (or two) of successful migrations. Interestingly, even though other tree species were found at the sites (e.g., larch), the thinning of the spruce forest at these locations did not seem to open pioneering opportunities for the other tree species at those times.

Growth variability and local stand dynamics documented by the tree rings likely correspond more generally to changes in vegetation density on the landscape as represented in pollen records, i.e., germination of spruce (and other vegetation) on peatlands of the Great Lakes plains would be favored within warming episodes associated with lowering of the water tables. However, responses of ancient forests to the warming trends appeared to be both direct and inverse because of conflicting moisture availability and complex hydrology of the postglacial landscapes. As shown, centennial-scale adaptation of trees to the environmental change could be terminated in just a few decades by moisture stress. Obviously, this could cause extended contraction of spruce colonization and boreal forest distribution in the past.

These are three specific localities that by themselves do not produce a full regional picture for their three respective time periods. Discovery of contemporaneous tree stands, such as those of approximate Two Creeks age in Wisconsin can add a spatial perspective in addition to the temporal perspective from the tree rings. The changes in vegetation density shown in this study were most likely widespread over the full ancient tree lines, but additional evidence is needed to verify this contention.

## Conclusions

Tree rings from ancient wood at three sites provide an opportunity to explore environmental changes in the Great Lakes region at high resolution and, additionally, to understand vegetation dynamics during postglacial spruce colonization. The ancient wood deposits contribute exact locations and ages of forest occupation of land previously covered by the continental ice sheet, and the tree-ring chronologies from the sites spaced over ca. 2500 years help quantify environmental variability during the North American deglaciation and stand dynamics at the ancient tree lines.

The greater portion of each tree-ring chronology shows ring-width variability related to temperature variations. The wavelet spectra in the warm intervals seem to correspond to the 3- to 7-year periodicity of the ENSO climate modes, particularly strongly for the Two Creeks site but also for the Gribben Basin site during warming trends. The number of samples that contribute to various intervals of the chronology (sample depth), as well as ring-width variations and tree ages, provide evidence of at least two generations of tree establishment at each of the sites, corresponding to warm intervals. Some of these growth shifts seem to be tracking hemispheric long-term temperature changes as represented in the GISP $\delta^{18}O$ record. Reduced sample depth at the end of records may result from fewer trees surviving deteriorating environmental conditions related to rising water and sediment deposition, in addition to possible influence of low temperature.

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