



Deglacial hydroclimate of midcontinental North America



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ABSTRACT

During the last deglaciation temperatures over midcontinental North America warmed dramatically through the Bølling-Allerød, underwent a cool period associated with the Younger-Dryas and then reverted to warmer, near modern temperatures during the early Holocene. However, paleo proxy records of the hydroclimate of this period have presented divergent evidence. We reconstruct summer relative humidity (RH) across the last deglacial period using a mechanistic model of cellulose and leaf water $\delta^{18}\text{O}$ and δD combined with a pollen-based temperature proxy to interpret stable isotopes of sub-fossil wood. Midcontinental RH was similar to modern conditions during the Last Glacial Maximum, progressively increased during the Bølling-Allerød, peaked during the Younger-Dryas, and declined sharply during the early Holocene. This RH record suggests deglacial summers were cooler and characterized by greater advection of moisture-laden air-masses from the Gulf of Mexico and subsequent entrainment over the mid-continent by a high-pressure system over the Laurentide ice sheet. These patterns help explain the formation of dark-colored cumulic horizons in many Great Plains paleosol sequences and the development of no-analog vegetation types common to the Midwest during the last deglacial period. Likewise, reduced early Holocene RH and precipitation correspond with a diminished glacial high-pressure system during the latter stages of ice-sheet collapse.

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Introduction

During the transition from the Last Glacial Maximum to the early Holocene, the Laurentide ice sheet retreated northward by up to 1200 km in midcontinental and eastern North America, causing drastic changes to ocean circulation in the North Atlantic through meltwater additions. These deglacial events had both direct and indirect effects across North America as climates and associated vegetation types underwent a dynamic period of reorganization (Gill et al., 2009; Grimm and Jacobson, 2004; Shane and Anderson, 1993; Shuman et al., 2002a; Williams et al., 2004; Yu and Wright, 2001). Many lines of evidence from the midcontinent indicate the last deglacial period was characterized by temperatures increasing from 3 to 10°C or more depending on the location and seasonal resolution and paleo proxy employed (Gonzales et al., 2009; Grimley et al., 2009; Nordt et al., 2008; Shane and Anderson, 1993; Shuman et al., 2009; Viau et al.,

2006; Voelker et al., 2012; Webb and Bryson, 1972; Yu and Eicher, 1998). In contrast, the deglacial hydroclimate is poorly understood. For example, geomorphic evidence and records from buried soils during the Younger-Dryas (YD) have been interpreted to suggest the midcontinent was drier for at least portions of the deglacial period (Campbell et al., 2011; Cordova et al., 2011; Dorale et al., 2010; Haynes, 1991; Holliday, 2000; Wang et al., 2012), while other evidence, based largely on inferences from pollen, has been interpreted to suggest this period was characterized by relatively greater moisture availability (Buhay et al., 2012; Curry and Filippelli, 2010; Curry et al., 2013; Gonzales and Grimm, 2009; Gonzales et al., 2009; Grimm and Jacobson, 2004; Haynes, 2008; Mullins, 1998; Shuman et al., 2009; Webb and Bryson, 1972).

Over much of the midcontinent and the eastern United States, many late Quaternary records indicate the deglacial period was characterized by communities of plants and animals with no modern analogs. In the Midwest and eastern United States modern forest associates often include *Picea/Alnus/Betula* or *Fagus/Tsuga* and *Pinus* is abundant. During the deglacial *Pinus* was not as abundant while *Ostrya/Carpinus*

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communities were widespread and *Picea/Fraxinus* communities were common although these species are generally allopatric under modern climatic conditions (Williams et al., 2004). There are many possible reasons for these unique combinations of plants, including individualistic species responses to relatively low atmospheric $[CO_2]$, increased temperature seasonality, changes in ecosystem water balance and ecological effects following the demise of the Pleistocene mega-fauna (Gill et al., 2009, 2012; Shane and Anderson, 1993; Williams and Jackson, 2007). Although quantitative reconstructions of variables relevant for the deglacial hydroclimate may be poorly constrained due to no analog conditions, there are many qualitative signs pointing to increases in effective moisture. These include the prevalence of plant taxa that thrive in poorly drained or seasonally flooded environments, increases in fire-intolerant tree species and increases in species dependent on large, intense disturbances such as fires (Amundson and Wright, 1979; Curry et al., 2007; Gill et al., 2012; Gonzales and Grimm, 2009; Grimm and Jacobson, 2004; Williams et al., 2004). Due to prevalent no-analog conditions across the midcontinent during the deglacial period, other independent sources of data need to be developed to better characterize the hydroclimate.

In this paper, we use available data to provide new insight on the hydroclimate of midcontinental North America by employing a regional, multi-proxy approach. For our purposes we define the midcontinent of North America as the region encompassing the transition between the modern distributions of short grass prairies of the Great Plains and the Eastern Deciduous forest. Not all of the data we use or review here fall directly within this zone because long and well-dated sediment records that are sensitive to hydroclimate are relatively rare and sub-fossil wood has seen few systematic collections. Therefore, we also include

some data that are located downwind of the dominant meridional and/or zonal flows of moisture from this region. We reconstruct relative humidity (RH) using mechanistic models to interpret patterns of ^{18}O and 2H in wood cellulose from log cross-sections ^{14}C -dated to the last glacial and deglacial period in conjunction with a high-resolution pollen record of temperatures from this region. Although this approach cannot be used to discern higher-resolution, centennial-scale variation, uncertainties in other paleo records in regard to dating as well as ecological and physiological filters that influence many paleo records should be minimized. As a result we provide new insights on first-order variation in RH and hydroclimate for the Last Glacial Maximum, late deglacial and early Holocene.

Methods and materials

Data from wood samples considered here were collected at sites across midcontinental North America, with most collected in northern Missouri, USA (Fig. 1, Table S1). For Missouri samples, a chainsaw was used to cut cross-sections from sub-fossil oak logs recovered from stream channels and banks (Guyette et al., 2008; Stambaugh et al., 2011; Voelker et al., 2012). Stream channels and banks in northern Missouri are composed of alluvial sediments and conducive to the frequent burial and excavation of wood (Guyette et al., 2008). Sub-fossil oaks were distinguished from other taxa by their ring-porous vessel arrangement, the extensive radial cracks that form along their thick ray parenchyma, and the gray to black color of the heartwood, which occurs after hundreds of years of burial. Based on the current distribution of habitats along these streams most of these oaks are probably bur oak (*Quercus macrocarpa* Michx.), but swamp white oak (*Quercus bicolor* Willd.)



Figure 1. Locations of data collection sites for data used in RH and paleotemperature reconstructions. For sub-fossil wood collections, each symbol type gives the collector and/or curator of the wood and the symbol sizes were scaled to the number of sample trees collected at a site (see Table S1 for details). Crosses mark the locations of sediment/pollen collection sites used for the paleoclimate reconstructions at Crystal Lake (Gonzales et al., 2009), and Brewster Creek (Curry et al., 2007) sites in northeast Illinois as well as Blood Pond (Marsicek et al., 2013) in Massachusetts and Sutherland Pond (J. Marsicek, unpublished data) in New York.

also occurs in the region and the two species cannot be differentiated by wood anatomy. Slight differences in the isotopic signals of source water uptake could have contributed to among-tree variation.

In this analysis we include stable isotope data from other sub-fossil wood collections, most of which are spruce (*Picea* spp.) wood that date from the last glacial maximum through the early Holocene (Fig. 1, Table S1). These include data from collections described by Leavitt et al. (2006) and Feng et al. (2007). Finally, Dr. David Grimley contributed radiocarbon-dated wood samples of the last glaciation and stratigraphically dated samples from the penultimate glaciation (Table S1). These were prepared and analyzed using the same methods described below for sub-fossil oak wood.

Radiocarbon dating

For sub-fossil oak log cross-sections, small blocks were removed from the outer edge and given an acid–alkali–acid treatment before radiometric measurements of ^{14}C content. The procedures used for sub-fossil oaks, analytical laboratory, raw data, and associated uncertainty are available in the appendix of Voelker et al. (2012). Dating for other samples used here is described in Table S1 and elsewhere (Feng et al., 2007; Leavitt et al., 2006; Panyushkina and Leavitt, 2013). For the analyses presented here, all radiocarbon data were either recalibrated with the INTCAL13 calibration data set (Reimer et al., 2013) using CALIB Version 6.0 software (Stuiver and Reimer, 1993) or the dates from “wigggle-matching” were used in a few cases (Panyushkina and Leavitt, 2013). Details regarding dates, locations and taxa of each sample are available in Table S1.

Stable isotope analyses

For the samples not reported on previously (from Guyette, Stambaugh and Grimley, Fig. 1, Table S1) wood was cleaned to remove any sediment, ground to a powder, heat-sealed within a polyester filter bag (mesh size 25 μm , ANKOM Technology, Macedon, NY), extracted to α -cellulose (Leavitt and Danzer, 1993; Sternberg, 1989), a fraction of which was converted to cellulose nitrate (Sternberg, 1989). Oxygen isotope ratios were determined by pyrolyzing α -cellulose in an elemental analyzer (TC/EA, Isoprime Elementar varioPyrocube, Isoprime Ltd., Manchester, UK) and analyzing the resulting gas with an isotope ratio mass spectrometer (Isoprime100, Isoprime Ltd.) at Southern Oregon University. D/H isotope ratios were determined on cellulose nitrate at two labs. At the UC Davis Stable Isotope Facility, D/H ratios were determined using a Hekatech HT Oxygen Analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). At the Purdue University isotope laboratory, samples were pyrolyzed in a ThermoFinnigan TC/EA and the resulting gas analyzed with a ThermoDelta V mass spectrometer fitted with a hydrogen spur (Thermo Fisher Scientific Inc., Waltham, MA, USA). Mean δD of each sample from the two labs were used. Results are reported using the conventional δ notation relative to the VSMOW standard for δD (replicate analysis SD = 6.72‰) and $\delta^{18}\text{O}$ (replicate analysis SD = 0.358‰).

Stable isotope data and paleoclimate proxies

Oxygen and hydrogen isotope ratios of precipitation were estimated using empirical relationships with surface air temperature (T_{air}) derived from GNIP data (Global Network of Isotopes in Precipitation, http://www.naweb.iaea.org/napc/ih/IHS_resources_isohis.html) as follows:

$$\delta^{18}\text{O} = 0.48T_{\text{air}} - 15.45, \quad (1)$$

$$\delta\text{D} = 3.60T_{\text{air}} - 109.83. \quad (2)$$

The relationships given in Eqs. (1) and (2) derive from precipitation collected for individual days spanning one or more events, across

seasons in Mead, Nebraska, North Platte, Nebraska, Kalamazoo, Michigan, and Atitokan, Ontario ($R^2 > 0.72$, $P < 0.0001$) and the slopes are comparable to the average temperature effects on $\delta^{18}\text{O}$ calculated from stations across the United States for summer of 0.47‰/°C and somewhat less than that for winter of 0.64‰/°C (Liu et al., 2010). Equations (1) and (2) were then used to reconstruct source water (δ_s) values across the deglacial period by applying them to summer and winter temperatures inferred using a high-resolution pollen record from Crystal Lake, Illinois (Gonzales et al., 2009). The mean summer and winter isotopic values were then multiplied by a scaling factor of 0.75 (SD = 0.026 among sites in the Midwest) to reflect precipitation amount-weighted isotopic means for this region being nearer to summer than to winter precipitation signals. This empirical representation of source water dynamics does not explicitly consider global ice volumes and their impact on ocean isotopic values as well as the potential for differences in the rates of Rayleigh fractionation due to colder glacial conditions. However, for these two processes are opposite one another in sign and magnitude (see Discussion). With the resulting estimates of δ_s , we then used a mechanistic model of cellulose isotope ratios (δ_c , see Roden et al., 2000; Barbour et al., 2004), to reconstruct the leaf lamina water (δ_l). This approach was fully described by Voelker et al. (2014), but the $\delta^{18}\text{O}$ and δD relationships can be simplified as:

$$\delta_l = \frac{\delta_c - f(\delta_s + \varepsilon_H)}{1 - f} + \varepsilon_A, \quad (3)$$

where f is the proportion of atoms that exchange with source water during post-photosynthetic metabolism leading to cellulose synthesis, ε_A is the autotrophic fraction factor and ε_H is the heterotrophic fractionation factor. Although f can vary in certain situations, for the cambium of most trees f has been established as 0.42 and 0.35 for ^{18}O and D, respectively (Roden et al., 2000). For ^{18}O , ε_A and ε_H were both set to 27‰ and for δD they were set to -171‰ and $+158\text{‰}$, respectively (Luo and Sternberg, 1992).

In combination with independent estimates of δ_s , cellulose stable isotope values can be inserted into Eq. (3) to calculate δ_l , and thereafter be used to reconstruct enrichment above source water, Δ_l . By using Δ_l from both isotopes, the deuterium deviations from the global meteoric water line, Δd_l , can be calculated after Voelker et al. (2014) as:

$$\Delta d_l = \delta\text{D} - (8\delta^{18}\text{O} + 10). \quad (4)$$

As shown by Voelker et al. (2014), for standard conditions Δd_l is linearly related to relative humidity (RH) as:

$$\text{RH} = 0.58\Delta d_l + 102.54. \quad (5)$$

However, large changes in air temperature and/or source water can induce significant bias on reconstructed RH values (Voelker et al., 2014). Because the deglacial period would have been characterized by large shifts in temperature and δ_s , a means to account for these shifts is necessary to accurately reconstruct RH. Here we use a variant of the steady state Craig–Gordon model (Barbour et al., 2004; Craig and Gordon, 1965; Farquhar and Lloyd, 1993) to adjust Δd_l for past variation in temperature and δ_s .

According to the Craig–Gordon model, steady state isotopic variation, relative to source water, at the site of evaporation within a leaf [Δ_e for either of $\Delta^{18}\text{O}_e$ or ΔD_e] can be described as follows:

$$\Delta_e = \varepsilon^+ + \varepsilon_k + (\Delta_v - \varepsilon_k) \frac{e_a}{e_i} \quad (6)$$

where ε^+ is the temperature-dependent equilibrium fractionation factor between liquid and vapor water (Cappa et al., 2003), ε_k is the kinetic fractionation factor for water–vapor diffusion determined by stomatal and boundary layer conductances to water vapor, Δ_v is the isotope

ratio of atmospheric water vapor relative to source water, e_a is the ambient vapor pressure and e_i is the saturation vapor pressure at leaf temperature. To determine Δ_v , water vapor isotopes were assumed to be in equilibrium with summer precipitation $\delta^{18}\text{O}$ and δD .

Eq. (4) predicts the enrichment above source water at the site of evaporation. However, the δ_i isotopic signal recorded in photosynthates is a mixture that balances the advection of [unenriched] δ_s into the leaf lamina being opposed by the back-diffusion of water enriched at the sites of evaporation within sub-stomatal cavities (Farquhar and Lloyd, 1993) and can be described by a leaf's Péclet number (ρ):

$$\rho = \frac{LE}{CD} \quad (7)$$

where E is the transpiration flux from the leaf ($\text{mmol m}^{-2} \text{s}^{-1}$), L is the effective pathlength for water through the leaf (m), C is the molar concentration of water ($55,500 \text{ mol m}^{-3}$) and D is the diffusivity of heavy molecules in water (2.66 and $2.34 \times 10^{-9} \text{ m}^2 \text{ s}^{-1}$ for molecules containing ^{18}O and D , respectively). E was determined as the product of stomatal conductance and the ratio of the leaf-to-atmosphere vapor pressure difference ($e_a - e_i$) divided by the barometric pressure. For the oaks and conifers investigated here, stomatal conductances were set to 0.2 and $0.1 \text{ mol m}^{-2} \text{ s}^{-1}$, respectively. L was set to scale with the transpiration rate after Song et al. (2013):

$$L = 0.094E^{-1.20} \quad (8)$$

Following Farquhar and Lloyd (1993), the Péclet number can be applied to Δ_e to estimate the isotopic enrichment of leaf lamina water above δ_s (Δ_l):

$$\Delta_l = \frac{\Delta_e(1 - e^{-\rho})}{\rho} \quad (9)$$

By subtracting δ_s from Δ_l , predicted values of leaf lamina water, δ_p , can be obtained for each isotope using different T_{air} and source water inputs and by assuming leaf temperature tracked T_{air} . To address glacial conditions we parameterized the model initially using standard conditions with RH, δ_s , and temperatures set to modern means for midcontinental locations and calculated a predicted leaf lamina water (δ_{p1}). We then established a second parameterization (δ_{p2}) for each wood sample with temperatures set to the record from Gonzales et al. (2009) and δ_s from Eqs. (1) and (2) set to vary with the same paleotemperature record. For samples older than 16 ka, we set the paleo summer temperatures to 10.5°C , the earliest paleotemperature record of Gonzales et al. (2009). This should approximate average growing season temperatures approaching the modern latitudinal treeline in Canada. Using this approach we calculated values of leaf lamina water by using the initial reconstructed δ_i (from Eq. (3)) and subtracting values of ($\delta_{p1} - \delta_{p2}$) for each isotope and then converting to Δd_i using Eq. (4). Voelker et al. (2014) also showed that for a given RH, Δd_i of conifers is more enriched by about 30‰. These differences derive largely from non-steady state (i.e., sub-daily) leaf water dynamics combined with lower transpiration rates of conifers. It is not appropriate to incorporate non-steady state dynamics into mechanistic models for paleo wood that integrate isotopic signals across time scales of years. To account for this difference between hardwoods and conifers we instituted a correction. Before RH was calculated using Eq. (4), conifers Δd_i was increased by adding $40(\Delta d_i / -177.41)$, causing the conifer correction to Δd_i to be nearly 40‰ under extremely low RH conditions and progressively smaller for as RH approaches 100%, the point where leaf water enrichment of any leaf type necessarily converges towards zero. For the conifer samples reported on here, this correction caused reconstructed RH values to increase by an average of 8%.

Results

Across the midcontinent (Fig. 1), stable isotope patterns of $\delta^{18}\text{O}$ and δD indicate that summer RH was at a minimum of about 59% during the last glacial period (Fig. 2A), whereas the summer RH of 70% during the early Holocene was near the modern summer value of about 68% for this region. Although datum density is low, a gradual rise in RH can be inferred provisionally for the late glacial, reaching an average of 77% during the Bølling-Allerød, peaking near 80% during the late YD and followed by drying during the early Holocene (Fig. 2A). By grouping the data within these time periods, the Bølling-Allerød and YD had significantly greater RH conditions than the other time periods (Table 1). Three additional wood samples from St. Clair County, Illinois that date

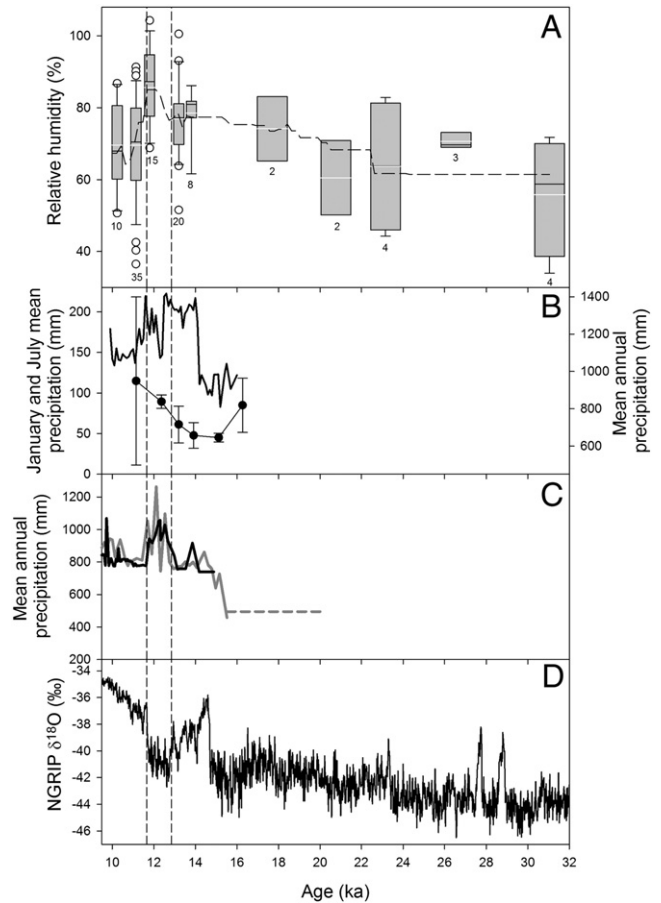


Figure 2. (A) Summer relative humidity values reconstructed from wood $\delta^{18}\text{O}$ and δD using a mechanistic model of cellulose and leaf water stable isotopes parameterized with paleotemperatures reconstructed by Gonzales et al. (2009). From 9.5 to 14.5 ka the data were binned at 1000 yr intervals (narrow boxplots) and data from earlier were binned at 4000 yr intervals, with boxplots being centered on the mean age within each bin. The central black and/or white lines in boxplots are the median and mean values, respectively. The boxplot boundaries and whiskers represent the 25th and 75th and 10th and 90th percentiles, respectively. Data points outside of the whiskers are outliers and values below each boxplot represent the number of radiocarbon dated sub-fossil wood cross-sections sampled (calibrated with IntCal13). Additionally, the dashed line shows a 15-point moving average of RH estimates from individual trees. (B) The black line represents summer and winter precipitation reconstructed from the pollen record at Crystal Lake, Illinois, after Gonzales et al. (2009), the data points represent mean annual precipitation ($\pm\text{SD}$) reconstructed from six biozone ostracode assemblages identified at Brewster Creek, Illinois (after Curry et al., 2007). (C) The thick black and gray lines represents mean annual precipitation reconstructed from the pollen record at Blood Pond, Massachusetts (after Marsicek et al., 2013) and Sutherland Pond, New York (J. Marsicek, unpublished data), respectively. The gray dashed line represents the mean precipitation level inferred from Sutherland Pond for which the region was ice free but uncertainty in the age model precludes assignment to specific ages. (D) The North Greenland Ice Core Project (NGRIP) $\delta^{18}\text{O}$ record. In each panel the dashed vertical lines indicate boundaries of the Younger-Dryas cold period.

Table 1

Probability values comparing relative humidity (RH) inferred from sub-fossil wood among major time periods associated with the North Atlantic event stratigraphy. The first column lists the mean RH estimated for each period and the next three columns list the P-values from t-tests comparing RH among periods (significant differences at $P < 0.05$ and $P < 0.01$ are indicated by * and **, respectively). "Glacial" refers to the period between 14.7 and 32.0 ka.

	Relative humidity	Younger Dryas	Bølling-Allerød	Glacial
Holocene	70.1%	0.008**	0.021*	0.141
Younger Dryas	80.3%	–	0.407	0.002**
Bølling-Allerød	77.3%	–	–	0.001**
Glacial	63.9%	–	–	–

stratigraphically to the Illinoian glaciation (135–160 ka, Curry et al., 2011) had an isotopic composition and mean RH of 57% that is comparable to that from the last glacial maximum (Table S1).

For much of the deglacial period, from 15 to 11 ka, most of our data were centered more than 500 km south and west of the nearest glacial ice boundary, which at that time was near Lake Superior and northern Lake Michigan. Trees sampled near the shores of modern Green Bay, WI ca. 13.5 ka (i.e., Two Creeks and nearby sites) or those trees sampled near the shores of modern lake Superior ca. 11.4 ka (i.e., Gribben Basin and White Pine Mine sites) had average RH values that were very near, or slightly lower than the values of trees from Missouri that grew during the same time period. This suggests the mean RH record (Fig. 2A) is representative of broad regional patterns since trees growing in Missouri were too distant from the glacier for cold air subsidence or orographic effects to have determined local patterns in precipitation or RH.

A period of relative scarcity of sub-fossil oak deposition occurred during the early YD (only three ^{14}C -dated trees between 12.9 and 11.9 ka), preventing inferences about the timing of any abrupt changes to the climate during the YD. However, it is clear that RH peaked above 80% near the YD to Holocene boundary. Thereafter, the early Holocene hydroclimate was characterized by rapid drying, reaching RH conditions that are near the modern value of 68% for the period from 11 to 10 ka (Fig. 2A, Table 1). These results of progressively greater RH during the deglacial period also coincide with peaks in precipitation reconstructed from two sites in northeastern Illinois (Fig. 2B) and at downwind sites in Massachusetts and New York (Fig. 2C). Despite some variability among individual records, particularly the during the Bølling-Allerød (Fig. 2A–C), overall the various data sets show a strong synchronization with North Atlantic conditions, as indicated by the $\delta^{18}\text{O}$ ice-core record from Greenland (Fig. 2D). Therefore, the last deglacial period marked the wettest known hydroclimate for this region, starting during the Bølling-Allerød in the Midwest and peaking during the YD across the midcontinent and to the east coast of North America before a period of drying conditions started abruptly near the boundary to the Holocene.

Discussion

Atmospheric relative humidity (RH) is a central component in determining evaporation rates and thus water balance for most aquatic and terrestrial ecosystems. Therefore, the RH values reconstructed here should provide valuable insight on midcontinental hydroclimate variability during the last deglaciation. These insights on paleo-RH make it clear that a concerted effort is needed to determine cellulose $\delta^{18}\text{O}$ and δD from additional plant macrofossils for periods where sample representation is low (Fig. 2). Additional data could help address climate dynamics during the Holocene, the YD, and the so-called "mystery interval" that immediately precedes the Bølling-Allerød (Broecker and Putnam, 2012). Bur oaks could be used for the Holocene as more than 280 additional oak cross-sections from northern Missouri have been radiocarbon-dated (Guyette and Stambaugh, unpublished data) and additional samples dated absolutely across the late Holocene using

dendrochronology (Stambaugh et al., 2011). Extending the approach used here could provide a unique opportunity to compare to other dual-isotope records from lake sediment or groundwater records of hydroclimate from the Holocene (Castro et al., 2012; Henderson et al., 2010). Bur oak has a wide ecological amplitude, helping explain the consistent presence of this species in Missouri across the wide-ranging climate conditions of the deglacial and Holocene. This is reflected by a modern species range that spans >2000 km in both latitude and longitude (Burns and Honkala, 1990).

Previous investigations employing $\delta^{18}\text{O}$ or δD of sub-fossil wood cellulose from the last deglacial were characterized by relatively small sample sizes (Edwards and Fritz, 1986; Leavitt et al., 2006) or were from widespread locations across the continent (Feng et al., 2007; Yapp and Epstein, 1977). As such, even if a dual-isotope approach would have been utilized, the resolution necessary for determining regional trends in RH would not have been possible. Edwards and Fritz (1986) used an early dual-isotope approach that preceded the mechanistic models of cellulose isotopes employed here (e.g. Roden et al., 2000; Barbour et al., 2004). We did not include these data in our analyses because the samples consisted of fine twigs, which can undergo evaporative enrichment of xylem water via cuticular transpiration (Dawson and Ehleringer, 1993), and would thereby have been biased towards reconstructed RH values below those that the trees encountered.

Inferences regarding hydroclimate responses to deglacial changes in atmospheric circulation

Our evidence suggests a scenario in which the northward movement of the thermal equator from a latitudinal low near 16.1 ka (Broecker and Putnam, 2012) and the high-pressure system over the Laurentide ice sheet (Bartlein et al., 1998; Bromwich et al., 2005; Krist and Schaeztl, 2001), allowed low-pressure systems to prevail at greater frequencies over the northern Great Plains. Similar to modern conditions, these low-pressure systems would have increased northward penetration of moist air masses from the Gulf of Mexico after being entrained by the Rocky Mountain Front (Liu et al., 2010). Analogous to the entrainment by the Rocky Mountains, the ice sheet itself would have prevented moist air masses from reaching the higher latitudes of present day Canada and resulted in increased precipitation and humidity across the midcontinent (*sensu* Grimm and Jacobson, 2004). During the early Holocene this high-pressure system must have been greatly diminished, as driven by the collapse of the Laurentide ice sheet, resulting in a dramatic decline in RH (Fig. 2A) and precipitation (Fig. 2B, C) being associated with a reorganization of atmospheric circulation towards patterns recognizable during the modern era. These events would agree with evidence that lake levels in the upper Midwest started to decrease in the early Holocene (Shuman et al., 2002b; Winkler et al., 1986). A regional summer RH regime, as proposed above, would not preclude locally heavy precipitation events in summer or winter being induced by the ice sheet or adjacent glacial lakes (*sensu* Curry and Filippelli, 2010) or for anticyclonic winds induced from the high-pressure system over the ice sheet to have exerted some influence on precipitation regimes (Bartlein et al., 1998; Krist and Schaeztl, 2001).

Loess deposits over many localities in the midcontinent indicate that during the last glacial maximum, dry conditions conducive to eolian activity were characterized by predominately west and northwesterly winds (Bettis et al., 2003; Forman et al., 2001; Mason, 2001; Muhs and Bettis, 2000; Schaeztl et al., 2014). Midwestern rivers that drained glaciers were the source of most loess deposited during this period and were likely to be full of meltwater from late spring to early fall, so that exposure of glacially-derived sediments and thereby most loess deposition must have occurred during dry conditions from late fall through early spring. Although it is uncertain how episodic these dry conditions were, this evidence qualitatively suggests model predictions of anticyclonic winds associated with the ice sheet extending far into the

midcontinent (Bartlein et al., 1998; Bromwich et al., 2005) may be somewhat exaggerated. Although the ice sheet-centered high-pressure system may not have had strong effects on winds and all aspects of synoptic climate conditions of the midcontinent, it almost certainly would still have influenced patterns of atmospheric circulation.

Comparison to other paleoclimate records

Patterns of precipitation are likely to have been more regionally variable than temperatures or RH during the last deglacial, thus accounting for some variation in apparent lake levels or ecosystem water availability. In addition, many tree species become insensitive to changes in extra water availability after a certain threshold, with the average being near 1000 mm of annual precipitation whereas temperature dependence is quasi-linear across the range of paleo-temperatures relevant to the midcontinent (Voelker, 2011). This suggests that palynology-based precipitation reconstructions from wet and humid ecosystems would have been highly dependent on few species and thereby less robust than temperature reconstructions. Nonetheless, below we review pollen and other paleo studies relevant to the hydroclimate of the midcontinent. Webb et al. (1998) used pollen studies from across the Eastern U.S. to infer greater-than-modern annual precipitation during the deglacial period. In Northern Illinois, Gonzales et al. (2009) reconstructed substantially greater precipitation compared to glacial or modern conditions from 14.2 to 11.6 ka (Fig. 2B), with most of this increase resulting from winter precipitation. Another reconstruction from the same vicinity that used ostracode assemblages determined there to have been greater mean annual precipitation during the YD compared to the Bølling-Allerød, with the greatest and most variable precipitation occurring in the biozone that spanned the YD to early Holocene (Fig. 2B, Curry et al., 2007). This large variability agrees with the records of a peak in wetness during the late YD transitioning to a dry early Holocene as indicated by the trend in RH (Fig. 2A). Evidence of wetness from the YD to Holocene boundary also includes a peak in oak deposition in streams of northern Missouri that has not been exceeded at any other time from 13.5 to .5 ka (Guyette et al., 2008). This anomalously high deposition rate likely represents greater flooding frequency, which eroded stream banks and deposited trees in sediments where they were preserved after burial. Compared to oaks that grew across the late deglacial period, those dating near the YD to Holocene boundary were characterized by the highest variability in growth rates among trees as well as decadal- to multi-decadal variability in growth within each tree (S. Voelker, unpublished manuscript). Presumably these patterns reflect a highly variable, or “flickering” hydroclimate as atmospheric circulation reorganized. Sediment core records from the upper Midwest have found vegetation responses lagged the NGRIP ice-core record by about 300 yr (Gill et al., 2012; Gonzales and Grimm, 2009). By occurring at multiple sites, it is unlikely to be a problem with age-depth models. Therefore either vegetation composition or Midwestern climate variability may be lagging North Atlantic events. The record from oaks including RH inferred from stable isotopes (this study), variability in oak wood anatomy and oak deposition (Voelker et al., 2012), as well as oak growth and growth variability (S. Voelker, unpublished data) indicate an average inflection point of 12.86 ka in northern Missouri, presumably representing effects of rapid climate change at the onset of the YD. These data point toward a lag in vegetation responses rather than Midwestern climate variability compared to the dating of events in the North Atlantic since the collection area for the sub-fossil oak wood was directly upwind from the other Midwestern sites and these data used would have been much less affected by community-level interactions that could be perceived as lags in climate variability.

A dual isotope record from paleo groundwater samples in a southern Michigan aquifer exhibited deuterium excess values that were lower by about 1.5‰ during the YD and near 15 ka, with peaks during the LGM and on either side of the YD and near 5 ka (Castro et al., 2012). The

authors suggested this represented rapid transitions to an arid YD and a humid early Holocene. These patterns could be plausible if evaporation occurred as rains consistently fell through an extremely dry air mass, or if evaporated soil water near the surface infiltrated down into the soil profile during periodic rainfall events. Although the data support rapid transitions in climate and/or atmospheric circulation on either side of the YD, neither of these mechanisms are likely to impart strong differences in soil water for an ecosystem that was not known to be arid, particularly where evaporation from soils would have been buffered by a dense forest canopy, ground layer vegetation and associated litter layer during the deglacial period. Alternatively, we suggest the deuterium excess data presented by Castro et al. (2012) are more consistent with the relative contribution of winter precipitation recycled after evaporating from the surrounding Great Lakes as shown in waters sampled in shallow groundwater of Michigan by Bowen et al. (2012). Therefore, the paleo groundwater record (Castro et al., 2012) and our inferred RH patterns would be consistent with midcontinent being cooler during the YD which promoted less evapotranspiration and greater percolation of summer precipitation into aquifers. Likewise, during relatively dry summer periods Michigan aquifers would have recorded a relatively stronger winter precipitation signal with higher deuterium excess values such as the short drought period just prior to the YD, the early Holocene and the mid-Holocene climatic optimum.

Downwind of the study region, in the northeastern U.S., the pollen record suggests a pulse of greater precipitation during the YD followed by drying across the early Holocene (Fig. 2C; Shuman et al., 2009; Marsicek et al., 2013). The timing of this pulse of precipitation closely coincides with North Atlantic events (Fig. 2C, D). These sites are much closer to the North Atlantic and may have been influenced by the Labrador Current and Atlantic Ocean conditions as well climate variability in the midcontinent that influenced the northeastern United States via zonal transport. Nonetheless, the data agree well with our RH record, suggesting both Gulf of Mexico and Atlantic-derived air masses tracking progressively further northward across the midcontinent as the thermal equator and glacial front moved northward, but then was blocked from further advection northward by the ice sheet and associated high-pressure system in present day Canada. Thereafter, for the northeastern U.S. the early Holocene was the driest hydroclimate of the late deglacial and Holocene despite being somewhat cooler than modern conditions (Marsicek et al., 2013; Shuman et al., 2004).

Although megafaunal extinctions may have interacted to modify species-climate responses across the Great Lakes region, more abundant pollen from taxa that thrive in wet environments between 14 and 11.5 ka are indicative of greater ecosystem water balance during the deglacial period (Curry et al., 2007; Gill et al., 2012; Gonzales and Grimm, 2009). Early Holocene forest dynamics were characterized by mesophytic and fire-dependent tree species quickly replacing formerly no-analog vegetation types. Similar patterns occurred in Minnesota and North Dakota, but prairie-dominated vegetation types also became more common at sites near the modern Great Plains (Clark et al., 2001; Grimm et al., 2011; Hu et al., 1997; Williams et al., 2009; Wright et al., 2004). Further East, in the “Prairie Peninsula” of Illinois, fire and aridity increased starting at about 10.0 ka (Nelson et al., 2006). Sediment records from the deglacial period for northern Illinois suggest generally high lake levels, punctuated by regular storm deposits from 14.5 to 11.9 ka and less frequent storm events from 9.6 to 7.4 ka (Curry and Filippelli, 2010). Lithostratigraphic evidence from Illinois was interpreted to reflect drier hydroclimatic conditions during the YD, as a result of proximity to the Laurentide ice sheet (Wang et al., 2012). However, because of uncertainties in dating dune activity, the evidence of Wang et al. (2012) could not be absolutely attributed to the YD (Wang et al., 2013) and may have resulted from a shorter drought interval or a discrete fluvial event (Curry et al., 2013).

In contrast to our records that indicate drying occurred from about 11.6 to 10 ka, a sediment record of carbonate and stable isotopes from

northwestern Minnesota lead Buhay et al. (2012) to conclude there was increased moisture from Gulf of Mexico air masses transported northward from 12.0 to 9.5 ka. Atmospheric circulation may have been characterized by increased Gulf moisture delivery to the midcontinent. However, if this occurred, we suggest it must have started earlier, closer to the peak in RH and in line with a 1000-yr pulse of black spruce pollen and increased precipitation starting near 12.5 ka in Northern Illinois (Fig. 2A, B; Gonzales and Grimm, 2009). The stable isotope records of Buhay et al. (2012) may also have been influenced by greater temperatures during the early Holocene that could have increased enrichment of lake water $\delta^{18}\text{O}$ without greater Gulf of Mexico moisture. This scenario would agree better with our results as well as the switch in deposition from calcite to aragonite near 10.7 ka in Kettle Lake, located in the northern Great Plains, that is thought to represent a wetter deglacial climate being replaced by increasing aridity and regular drought cycles starting in the early Holocene (Grimm et al., 2011).

Across the Great Plains, patterns of soil organic matter (SOM) $\delta^{13}\text{C}$ reflect the relative productivity of C_4 grasses versus C_3 vegetation, which in turn has been related primarily to temperature, but is also influenced by water availability (Cordova et al., 2011; Dorale et al., 2010; Leavitt et al., 2007; Nordt et al., 2008). At a paleosol sequence in Missouri, situated near the boundary between the Great Plains and eastern forests, increased SOM $\delta^{13}\text{C}$ centered on the YD was ostensibly interpreted as a response to increased aridity (Dorale et al., 2010). However, about two thirds of the $\delta^{13}\text{C}$ amplitude documented by Dorale et al. (2010) occurred before the start of YD, during the Bølling-Allerød period that is thought to have been relatively warm and wet compared to the last glacial maximum. Moreover, SOM $\delta^{13}\text{C}$ patterns are highly variable among locations in the Great Plains, likely reflecting the geomorphology of the site and a number of other factors that influence species compositions at the grassland to woodland transition zone (Cordova et al., 2011). In agreement with our record of RH and patterns in precipitation (Fig. 2), other studies from the Great Plains have found declining SOM $\delta^{13}\text{C}$ during the Bølling-Allerød and extending through the YD (indicative of a cooler/wetter hydroclimate) followed by an abrupt change to higher SOM $\delta^{13}\text{C}$ and a warmer/drier hydroclimate (Bement et al., 2007, 2014; Nordt et al., 2008). Our record of RH has a temporal resolution that is too low to ascribe wet or dry conditions to the early YD, but it is clear that high RH conditions persisted over Missouri during the late YD. This leaves open the possibility that a severe drought did occur during the early YD (*sensu* Haynes, 1991; Holliday, 2000), helping account for some of the increase in SOM $\delta^{13}\text{C}$ demonstrated by Dorale et al. (2010). A major drought would also help explain the lower frequency of sample deposition of sub-fossil oak logs in streams of northern Missouri during this period since more trees would be deposited during wet conditions that promoted flooding. In agreement with our record of RH, widespread lithostratigraphic evidence from the Great Plains suggests that moisture availability increased across the late deglacial period (Haynes, 2008; Holliday et al., 2011; Mason et al., 2008), likely contributing to the development of cumulic horizons in paleosol sequences (Mandel, 2008; Cordova et al., 2011). Altogether, these records and the evidence provided here point toward widespread wet conditions during most of the Bølling-Allerød and YD, and drier conditions during the early Holocene.

Sources of uncertainty in relative humidity estimates

Our assumptions about source water isotopic signatures affect the inferred RH patterns. It is known that ocean isotopic values, the origin of most precipitation (some is recycled from evapotranspiration), were higher in $\delta^{18}\text{O}$ by about 1‰ (8‰ δD) because lighter isotopes were locked up in massive ice sheets across the globe (Schrug et al., 1996). Over the midcontinent, most precipitation derives from air-mass advection from the Gulf of Mexico (Shadbolt et al., 2006). If sea levels were up to 120 m lower during the Last Glacial Maximum, the expanded land surface of the continental shelf would have resulted in

air masses having to travel further across land by up to 100 km to reach the midcontinent. For this distance, according to Liu et al. (2010), North American rainout gradients would have decreased precipitation $\delta^{18}\text{O}$ by about 0.38‰ during summer and 0.73‰ during winter. Likewise, during the last glacial maximum, Pacific-sourced air masses making it to the midcontinent would have been characterized by isotopic signatures that were lower than modern Pacific air masses because Rayleigh fractionation becomes steeper with decreasing temperature, and these air masses would have passed over the glacier itself or the alpine glaciers of the Rocky Mountains, which were presumably also colder compared to modern conditions. These competing ocean vs. terrestrial influences on isotopic signals should have cancelled each other out, resulting in source water isotopic signals displaying little secular variation for midcontinental locations across the multi-millennial scales that concern these processes. At shorter time scales, differences in atmospheric circulation may have caused variation in source water not accounted for by the paleotemperature record such as those noted by Castro et al. (2012). Again this could be caused by more air masses deriving from the Gulf of Mexico bringing precipitation with a heavier isotopic composition and decreased deuterium-excess values compared to Pacific-sourced air masses (Liu et al., 2010; Simpkins, 1995). Finally, for sub-fossil wood collections in Nebraska, Missouri, Illinois, Ohio and Tennessee, it is highly unlikely that glacial meltwater could have affected source water signals. For collections in Iowa, North Dakota, Wisconsin and upper Michigan it is not possible to rule out glacial meltwater as an influence on source water isotopic signals. Indeed, some of these trees died as a result of flooding from glacial meltwater or being buried under glacial till during glacial re-advances (Panyushkina and Leavitt, 2013). However, spruces growing in hydric soils would have been shallow-rooted and would not normally have tapped groundwater, which could have had a meltwater signal. Therefore meltwater is likely to only have influenced the outer few rings of flooded trees just before tree death, which would not have affected the mean isotopic signals of the wood used in this study.

The reconstructed RH values for each sample of sub-fossil are given in Table S1. However, as noted in Voelker et al. (2014), the signal to noise ratio of dual isotope from individual tree-rings or individual trees does not allow for individual data points to yield robust information. This is why these data need to be time-averaged or binned (Fig. 2A). Even using a time-averaging approach, caution must be urged in interpreting climatic dynamics from the moving average previous to 15 ka, when datum density was low. The temperature reconstruction we employed here (Gonzales et al., 2009) comes from a region known to have exhibited no-analog vegetation types during the last deglacial. Although the YD was undoubtedly characterized by the highest RH of the deglaciation, time-averaged RH values exceeding 80% suggest that perhaps the pollen-based temperature reconstruction, in suffering from no-analog problems, may have underestimated temperatures during this period. One possibility for future research is to use other independent, but lower resolution evidence of temperatures from sub-fossil wood growth or wood anatomy to constrain high resolution pollen-based temperature reconstructions and thereby yield more accurate multi-proxy climate reconstructions employing stable isotopes.

Implications for the development of no-analog vegetation types

The deglacial period is well known for having produced vegetation types with no modern analogs. No-analog vegetation types resulted from no-analog environmental conditions, which during the deglacial period would have included relatively low atmospheric $[\text{CO}_2]$ and increased temperature seasonality interacting with the ecological cascades of the Pleistocene mega-faunal extinction (Gill et al., 2009, 2012; Shane and Anderson, 1993; Williams and Jackson, 2007). Changes in insolation patterns and mega-faunal extinctions should have affected many regions of North America. Yet, no-analog vegetation types have a

distinct spatial manifestation, being most prevalent over eastern and midcontinental North America and absent over much of the west (south of the ice sheet). If climatic controls had a strong impact on the spatial expression of no-analog vegetation types over the American midcontinent, it is likely that these would be most strongly linked to the hydroclimate, which would in turn have been controlled by atmospheric circulation patterns interacting with the Laurentide ice sheet during its recession. Our data indicate that for the deglacial period the midcontinental growing season would have been more humid. Due to reduced evaporative demand, increased effective moisture would help explain the prevalence of plant taxa that have competitive advantages in swamps, poorly drained soils or seasonally flooded environments such as the Cyperaceae, *Salix* spp., *Alnus* spp., *Fraxinus nigra* and *Picea mariana* as well as a high abundance of *Abies* that is highly susceptible to fires and favored by deep winter snows and the low abundances of more fire-dependent taxa such as *Pinus* and *Betula* in conjunction with *Picea* (Amundson and Wright, 1979; Curry et al., 2007; Gill et al., 2012; Gonzales and Grimm, 2009; Grimm and Jacobson, 2004; Williams et al., 2004). In turn, this increase in effective moisture surely contributed to the formation of those no-analog vegetation types that were located across the American midcontinent (Shuman et al., 2002a; Williams and Jackson, 2007).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.yqres.2015.01.001>.

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