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Asymmetric vegetation responses to mid-Holocene aridity at the prairie–forest ecotone in south-central Minnesota

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Abstract

The mid-Holocene (ca. 8000–4000 cal yr BP) was a time of marked aridity throughout much of Minnesota, and the changes due to mid-Holocene aridity are seen as an analog for future responses to global warming. In this study, we compare the transition into (ca. 9000–7000 yr ago) and out of (ca. 5000–2500 yr ago) the mid-Holocene (MH) period at Kimble Pond and Sharkey Lake, located along the prairie forest ecotone in south-central Minnesota, using high resolution (~5–36yr) sampling of pollen, charcoal, sediment magnetic and loss-on-ignition properties. Changes in vegetation were asymmetrical with increasing aridity being marked by a pronounced shift from woodland/forest-dominated landscape to a more open mix of grassland and woodland/savanna. In contrast, at the end of the MH, grassland remained an important component of the landscape despite increasing effective moisture, and high charcoal influxes (median 2.7–4.0 vs. 0.6–1.7 mm² cm⁻² yr⁻¹ at start of MH) suggest the role of fire in limiting woodland expansion. Asymmetric vegetation responses, variation among and within proxies, and the near-absence of fire today suggest caution in using changes associated with mid-Holocene aridity at the prairie forest boundary as an analog for future responses to global warming.

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Keywords: Climate; Ecotone; Fire; Mid-Holocene aridity; Prairie forest border; Big Woods

Introduction

The arid middle Holocene (MH, ~8000–4000 cal yr BP) is increasingly viewed as an analog for future changes associated with climate warming (Nelson et al., 2004), and a wide variety of studies have focused on describing the climate changes and associated vegetation, fire, and lake responses to the MH (Wright et al., 1963; Digerfeldt et al., 1992; Wright, 1992; Webb et al., 1993; Smith et al., 2002; Camill et al., 2003; Nelson et al., 2004). Given a predicted expansion of grasslands under several different climate-warming scenarios, continued interest in grassland–woodland boundaries during the MH is not surprising, and many ecological studies have focused on grassland–

woodland ecotones because they are assumed to be particularly sensitive to climatic changes, being located at sharp climatic boundaries and/or species range boundaries (Clark, 1993; Clark et al., 2001).

Whereas MH may be a useful analog for the future climate warming, an equally relevant set of questions focuses on the transient dynamics into and out of the MH warming, which is perhaps a better analog to the kinds of ecosystem changes that will be observed in modern systems over the next few centuries. How fast do vegetation and fire respond to these climatic changes? Is the response of plant communities and fire symmetrical across the climatic transitions, or do vegetation and fire change in a way that impose a legacy of constraint on how the system can change in the future? For example, might an increase in prairie vegetation and fire during the MH create conditions that

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make it difficult to transition back to mesic forests between 5000 and 2500 cal yr BP? During transient climatic change, how well are climate, vegetation, and fire proxies correlated, and do they show reliable patterns of leading or lagging one another? Unfortunately, almost no work to date has focused on the dynamics occurring at the transitions at the boundaries of the MH.

Here we contrast the response of vegetation and fire to the onset (decreasing effective moisture) and termination (increasing effective moisture) of the MH at two sites in the Big Woods region of Minnesota (Camill et al., 2003; Geiss et al., 2003). We focus on the periods of climatic transition (9000–7000 vs. 5000–2500 cal yr BP), using pollen analysis (vegetation), charcoal analysis (fire), and sediment loss-on-ignition and sediment magnetics (paleoclimate and local environment) as our proxies, recognizing that these proxies—especially pollen and charcoal—integrate over different spatial

and temporal scales. Using high resolution (~5–36yr) sampling, we establish records with adequate temporal resolution to address stand-level successional questions during these periods of large climatic change. We examine the questions outlined above through a combination of trend analysis and change-point analysis, and we investigate the extent to which changes are regional (coherent at both sites) or local (idiosyncratic for each site) and dependent upon the initial state of the vegetation.

Study region and study sites

The Big Woods region is a complex mix of woodland and grassland (Daubenmire, 1936; Mc Andrews, 1968; Grimm, 1983, 1984) located along the prairie forest border in south central Minnesota (Fig. 1a). In response to climate change, the region has undergone several major changes in vegetation over

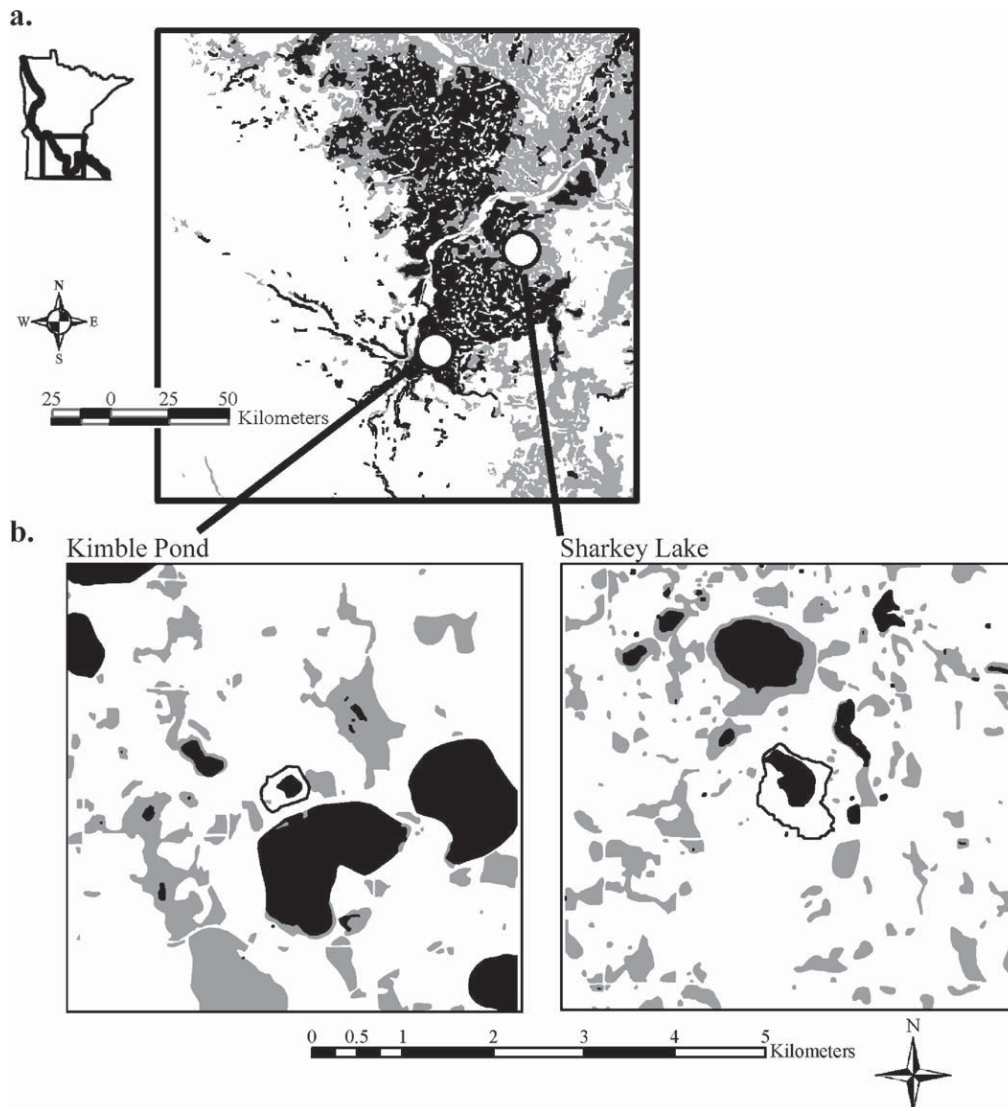


Figure 1. Location of Sharkey Lake and Kimble Pond sites in the Big Woods region (black, forest; gray, oak woodland; white, grassland) of Minnesota (a) and outline of watershed (thin black line) surrounding lakes (b). Locations and relative sizes of permanent (black) and semipermanent (gray) bodies of water within ~2.5 km of each site are shown (Minnesota.DNR., 2003). Semi-permanent bodies of water defined as usually not being covered with standing water over the course of an entire year.

the past 12,500 yr (Fig. 2), shifting from spruce-dominated forest to elm (*Ulmus*) and oak (*Quercus*)-dominated forest ~11,000 cal yr BP and then to a more open mosaic of grassland and woodland 8–9000 cal yr BP. Oak woodland expanded ~4000–4500 cal yr BP and then only about 600–700 cal yr BP did the mesic ‘bigwoods’ forest (*Ulmus–Acer–Tilia*) expand regionally (Camill et al., 2003; Umbanhowar, 2004). The flora of the region has remained constant over the past 11,000 yr, with regional responses to climate being characterized by changes in relative abundance of taxa (Camill et al., 2003). Site-to-site differences in the degree, direction, and timing of change are common, likely reflecting local edaphic and vegetation controls (Almendinger, 1992; Umbanhowar, 2004) rather than systematic errors in dating.

Climatic change in the region most directly reflects a shift in insolation over the past 10,000 yr (Wright, 1992; Dean et al., 1996; Baker et al., 2002; Webb et al., 2004) and resulting changes in the strength of the summer monsoon over the American Southwest (Harrison et al., 2003). The final collapse of the Laurentide ice sheet (~8200 cal yr BP) is a singular event (Shuman et al., 2002a) marking the onset of the mid-Holocene arid period and may explain more rapid decreases in annual

precipitation and increases in annual temperature at the onset versus the termination of the MH. The mid-Holocene arid period probably ended as a result of a weakening of the summer monsoon (Harrison et al., 2003) and the return of moist Gulf air at ~3000–4000 cal yr BP that is marked by changes in speleothem $\delta^{18}\text{O}$ and the rapid return of trees in northeastern Iowa (Baker et al., 2002).

Pollen, lake-level reconstructions, and a host of other magnetic or geochemical proxies indicate that the mid-Holocene period was more arid than today but punctuated by brief wet periods from 6750 to 6250 cal yr BP and again from 5400 to 4800 cal yr BP (Wright et al., 1963; Digerfeldt et al., 1992; Wright, 1992; Webb et al., 1993; Smith et al., 2002). Pollen-based reconstructions suggest that in annual precipitation of ~50–100 mm and an increase of ~2°C in July air temperatures (Bartlein and Whitlock, 1993; Webb et al., 1993). Speleothem-based reconstructions of climate from NE Iowa indicate a 3–4°C temperature increase associated with the mid-Holocene (Dorale et al., 1992), although this estimate may be too high (Denniston et al., 1999). Based on speleothem $\delta^{18}\text{O}$, macrofossil, and pollen data, Denniston et al. (1999) and Baker et al. (2002) suggested that a shift to

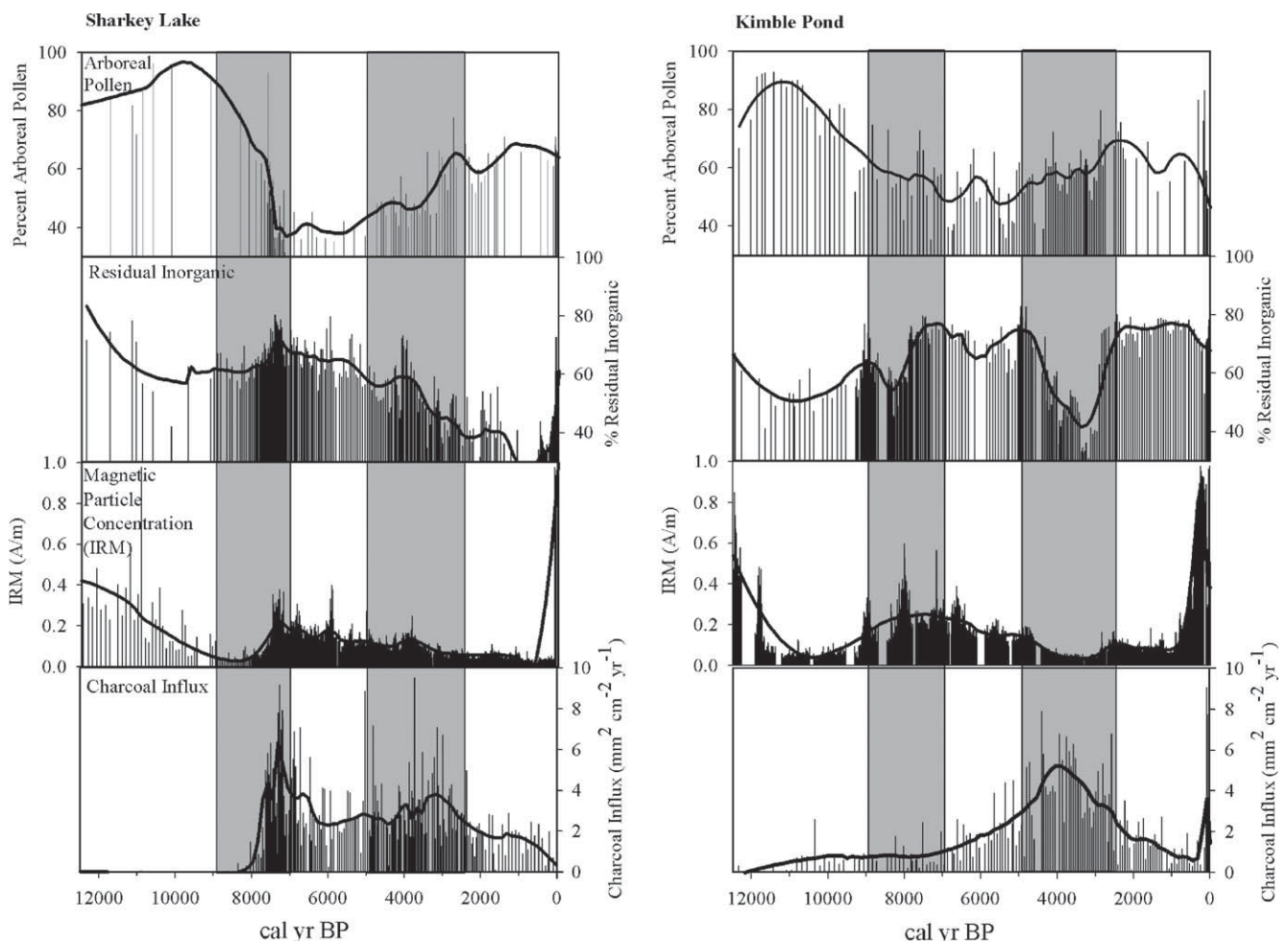


Figure 2. Summary of changes for Sharkey Lake and Kimble Pond over the past 12,000 yr based on data presented in Camill et al. (2003). Loess (as implemented in Sigmaplot 8.0) was used to smooth series (2nd degree polynomial, 20% of points, outliers rejected).

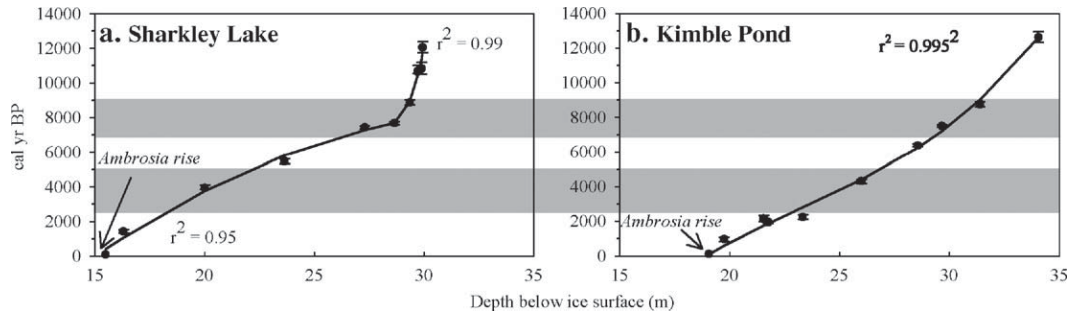


Figure 3. Age–depth models for (a) Sharkey Lake and (b) Kimble Pond with transitional regions highlighted by gray backgrounds. The figure is taken from Camill et al. (2003) and complete information on dates and depths is provided in Table 1 of Camill et al. (2003).

relatively more cool season precipitation accompanied increased aridity during the mid-Holocene dry period. Grimm (2001) and Filby et al. (2002), however, suggested the reverse with moist summers and dry winters resulting in lower lake levels and increased abundance of *Ambrosia* during the MH. Beginning at ~4500 cal yr BP, there was an increase in annual precipitation and winter temperatures (Bartlein and Whitlock, 1993; Webb et al., 1993; Baker et al., 2002) and woodland expanded again along the prairie forest border.

Our two study sites (Fig. 1b) are Kimble Pond (44°13'15' N, 93°50'24' W) and Sharkey Lake (44°35'39' N, 93°24'49' W). Both are kettle lakes formed in the Altamont stagnation moraine of the Des Moines lobe during the last phase of the Wisconsin glaciation (Hobbs and Goebel, 1982), and detailed descriptions of the lakes are provided by Geiss et al. (2003) and Camill et al. (2003). Kimble Pond has a surface area of 4.9 ha with a maximum depth of 16 m, and it is surrounded by a mosaic of oak woodland (*Quercus macrocarpa*) and bigwoods taxa (*Tilia americana*, *Ulmus americana*, *Acer saccharum*, and *Fraxinus pennsylvanica*) within an agricultural landscape (*Zea mays* and *Glycine max*). Kimble Pond has a watershed area of 17.8 ha (including the area of the lake itself). Sharkey Lake has a surface area of 28 ha and consists of two basins with a maximum depth of 15 m in the southeast basin (Geiss et al., 2004) and a maximum depth of ~1–2 m in the northern basin. The watershed for Sharkey is 59 ha and currently lies within an agricultural landscape, but oak woodland is more prominent relative to bigwoods forest at this site.

Methods

Age control and core sampling

Field work and core storage are described by Camill et al. (2003). Age control for the two cores is based on (a) identification of the post-Euro-American settlement rise in *Ambrosia* pollen set to ~90 cal yr BP (AD 1860) and (b) a total of nine Accelerator Mass Spectrometry (AMS) ¹⁴C dates for each lake obtained from wood macrofossils, seeds, leaves, and charcoal. The radiocarbon dates were calibrated using CALIB v. 4.3 (Stuiver et al., 1998), and all dates reported in this paper are expressed in calendar years BP; we used the same age–depth curves (Fig. 3) reported by Camill et al. (2003).

To achieve a new high resolution record of changes during the two transitions (9000–7000 and 5000–2500 cal yr BP), cores were sampled at intervals of 2–5 cm. Median time between samples among series ranged from 5 to 36 yr (Table 1). Small gaps in sampling were present in each series and in a few cases represented missing samples but most typically were associated with small (physical) gaps between the individual drives making up each core. The largest of these gaps was a 15-cm gap in the Kimble early to mid-Holocene transition (Fig. 4), which combined with low sediment accumulation rates represents approximately 200 yr from ~8500 to 8700 cal yr BP.

Pollen analysis

To describe local and regional changes in vegetation, we used pollen analysis on 0.5-cm³ samples using standard palynological methods (Fægri et al., 1989; Shane, 1992) modified to include an additional sieving step with 8-μm Nitex to remove detritus. For this paper, we report pollen percentages of *Ulmus*, *Quercus*, and *Ostrya* (woodland taxa), Poaceae (grass), and two forb taxa (*Ambrosia* and *Artemisia*). *Ambrosia* and *Artemisia* were included because they may respond differently to winter and summer precipitation (Grimm, 2001). These taxa represent on average more than 60% of the pollen grains enumerated, are sensitive to shifts in climate and/or fire regimes, and provide a direct basis for comparison with previously published works (Aaby, 1986; Clark et al., 2001; Nelson et al., 2004). More complete pollen diagrams for Kimble Pond and Sharkey Lake can be found in

Table 1
Sampling resolution of proxies for 9000–7000 and 5000–2500 cal yr BP transitions

Period	Lake	Charcoal	Pollen	LOI	Magnetics
9–7ka	Sharkey	19 (11.0; 86)	16 (5.7; 87)	15 (11.4; 86)	5 (2.1; 163)
	Kimble	21 (1.5; 73)	21 (1.5; 71)	25 (13.0; 67)	10 (1.0; 156)
5–2.5 ka	Sharkey	34 (5.0; 88)	36 (2.5; 62)	36 (6.0; 73)	20 (5.0; 152)
	Kimble	24 (7.5; 104)	24 (7.0; 101)	36 (18.0; 75)	8 (11.0; 155)

Numbers are median time step between adjacent pairs of samples (in parentheses, semiquartile range; sample size). Variation around the medians is given as the semiquartile range which is equal to one half the distance between the 25th and 75th quartiles.

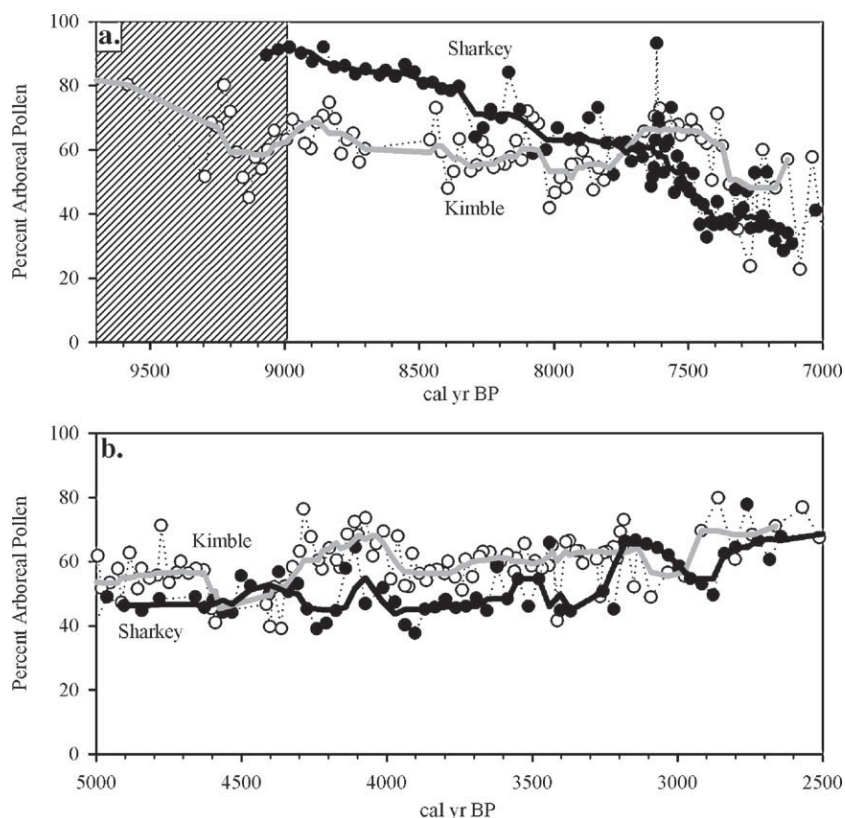


Figure 4. Changes in percent arboreal pollen during the (a) onset (9000–7000 cal yr BP) and (b) termination (5000–2500 cal yr BP) of the mid-Holocene arid period. Thick lines based on smoothing of data with a 200-yr median smoother.

Camill et al. (2003), and pollen data are available from the North American Pollen Database.

Charcoal analyses

To reconstruct local fire histories, macroscopic charcoal analysis was conducted on 1.0-cm³ samples following the methods of Clark and Hussey (1996). Sediment samples were soaked in a 10% KOH for minimum of 24h and sieved with a 180- μ m screen. Sieved material was spread over the bottom of a gridded petri plate, and charred particles were identified at $\times 20$ magnification using a stereoscope. Digital images of the charcoal were made, and charcoal area and shape (L:W ratio) were measured from these images using SCION image analysis software. Area measurements are reported as concentrations (mm² cm⁻³) based on the volume of sediment analyzed. Charcoal influx rate (mm² cm⁻² yr⁻¹) was calculated by multiplying concentration and sedimentation rate (cm yr⁻¹). Throughout this paper, we use charcoal concentration and influx as measures of landscape-level fire severity, a proxy for biomass consumed that integrates area burned, fire intensity, and fire frequency.

Sediment loss on ignition and magnetics analysis

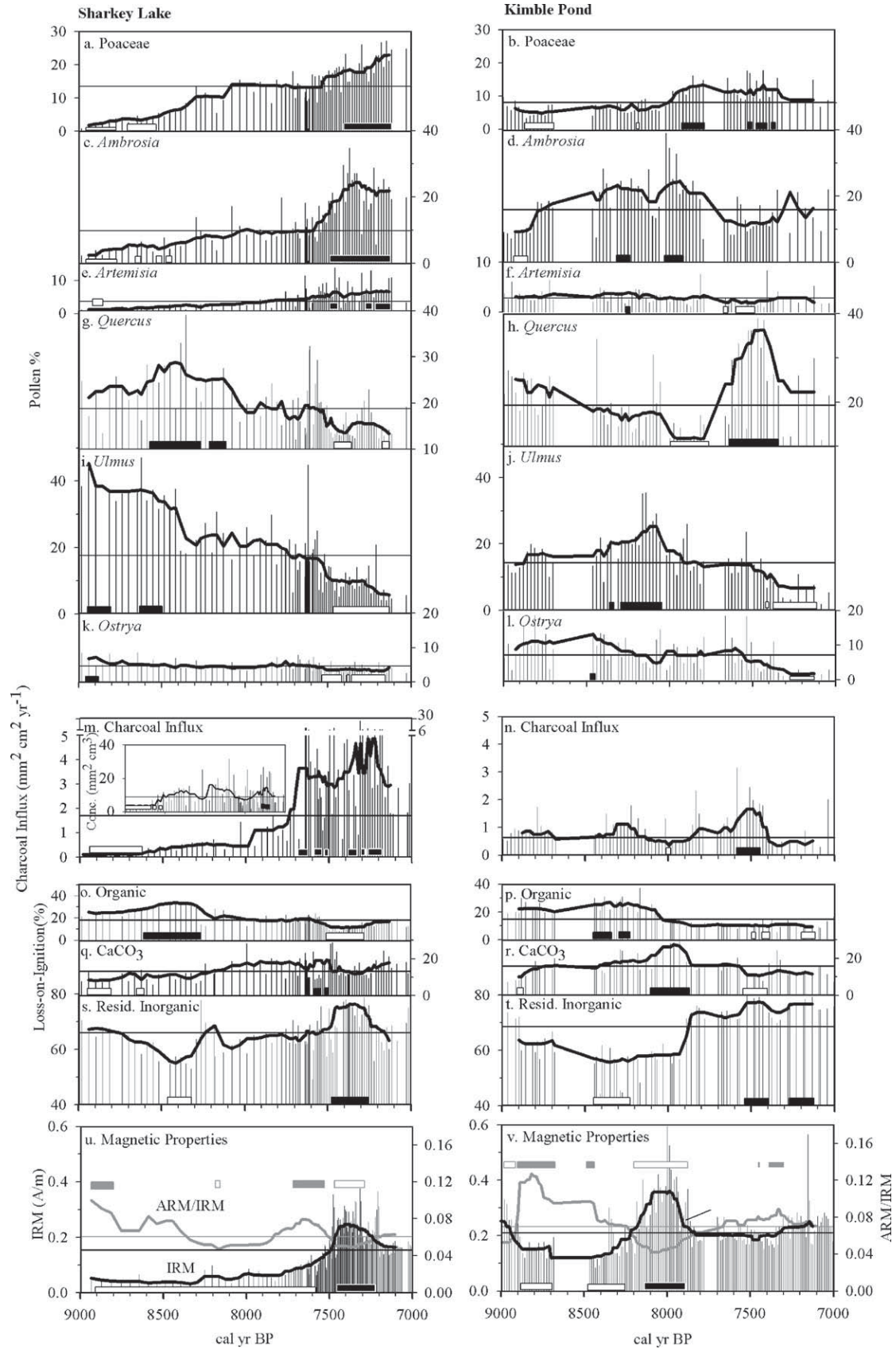
To describe changes in sedimentation (both allochthonous and autochthonous), we measured loss-on-ignition (LOI) and sediment magnetics. We used LOI to measure organic and inorganic sediment fractions (Dean, 1974). The organic fraction

was determined by the fraction of dry mass loss at 550°C, CaCO₃ was determined based on mass loss at 1000°C corrected to account for residual Ca, and the residual inorganic fraction was estimated as the fraction of dry mass remaining following combustion.

A range of sediment magnetics analyses have been performed on both lakes (Geiss et al., 2003, 2004), but in this paper we restrict ourselves to two analyses, isothermal remanent magnetization (IRM) and anhysteretic magnetic remanence (ARM). IRM was acquired in a static magnetic field of 100mT and is used as a measure of the concentration of ferromagnetic minerals. Anhysteretic magnetic remanence (ARM) was acquired in a peak alternating field of 100mT and a bias field of 50 μ T. Both remanence parameters were measured with a model 760-R cryogenic magnetometer (2G Enterprises, Mountain View, CA, USA). The concentration-independent ratio of ARM/IRM was used to characterize the relative abundance of fine-grained (SD) magnetic particles with respect to coarser (PSD and MD) magnetic grains. Low ratios of ARM/IRM indicate a significant fraction of coarse-grained particles, and high ratios indicate a significant fraction of fine-grained particles (Almquist-Jacobson et al., 1992; Geiss et al., 2003, 2004).

Statistical analyses

Both long-term gradual changes and abrupt sudden changes have been previously documented for the prairie forest border



(Williams et al., 2002; Shuman et al., 2002a,b), so in describing the dynamics associated with the beginning and end of the MH, we were interested in describing overall trends, local abrupt change points, and cross correlations among selected proxies. Exploratory data analyses revealed highly skewed or leptokurtic distributions, so statistical techniques based on medians were employed as a way of avoiding assumptions of sample normality as well as the multiple different data transformations that would be necessary to meet assumptions of normality. All statistical analyses were done using S-Plus (Insightful Corporation, 2001).

We evaluated trends in the different proxies using a median-based 200-yr smoothing window that was centered on each sampled time point in a series. The statistical significance of the difference between local medians and the overall global median for each transitional series was assessed with bootstrapped confidence intervals (95%) generated by resampling (with replacement, 5000 replicates) each series and running the window through each bootstrapped replicate series. The windowed medians were bootstrapped instead of the overall median to account for a variable number of sampling points in the sliding window resulting from missing samples and/or uneven sampling with respect to time. Changing the width of the smoothing window had only a minor effect on the shape of the smoothed series, but increasing window widths shrank the confidence intervals as the number of data points increased in the windows resulting in more time points being identified as statistically significantly different from the overall median.

Change-point analysis was used to identify locally abrupt changes in series using a technique initially described by Webster (1973) and then by Legendre and Legendre (1998) that involves sliding a 400-yr-wide window (divided into equal 200-yr halves) through each series from time point to time point. At each point, the difference between the medians of the two respective window halves was calculated and significance assessed based on 5000 bootstrapped (with replacement) replications of the series data to construct a 95% confidence interval.

Proxy data for the charcoal, Poaceae, and ARM/IRM series were cross correlated using a binned geostatistical approximation of cross correlation because the data were neither (a) sampled equally with respect to time, or among series (b) sampled at the same time points (Kirchner and Weil, 2000; Williams et al., 2002). Each series was first detrended using a local regression technique (Locfit, $\alpha=0.2$; Loader, 1999). Bin sizes were set to 30 yr (the approximate median sampling interval for the pollen and charcoal data series) and lags were calculated out to +150 yr. Statistical significance was assessed based on 2000 bootstrapped (with replacement) replications of the series data to construct a 95% confidence interval.

Results

Pollen and vegetation history

As indicated by the high resolution pollen data, vegetation at both Kimble and Sharkey sites was continually shifting, and this shifting is a product of both gradual directional and more abrupt changes in the balance of woodland/forest and grassland (Fig. 4). The abrupt changes are often reversible and lake specific (Fig. 4). For example, at Kimble arboreal pollen shows a peak at ~7500 cal yr BP whereas at Sharkey arboreal pollen is declining rapidly (Fig. 4a). Long-term changes in the balance of woodland and grassland are most evident at Sharkey with a nearly linear 67% decline in arboreal pollen from 90% to 30% during the 9000- to 7000-yr transition into the MH (Fig. 4a). A much less dramatic (29%) decrease from 68% to 48% in arboreal pollen is observed at Kimble during the same period. This smaller decline reflects both the greater continued presence of arboreal pollen at Kimble; it also is the result of an earlier shift towards grassland (~9700 cal yr BP) which if included in the calculation of percent change, results in an overall drop of 40% for arboreal pollen. Percentage increases in woodland associated with the termination of the MH arid period are less pronounced over the 2500 yr from 5000 to 2500 cal yr BP (Fig. 4b). At Sharkey, arboreal pollen increases by 41% from 46% to 65% arboreal, whereas at Kimble arboreal pollen rises by 29% from 53% to 69% of total pollen.

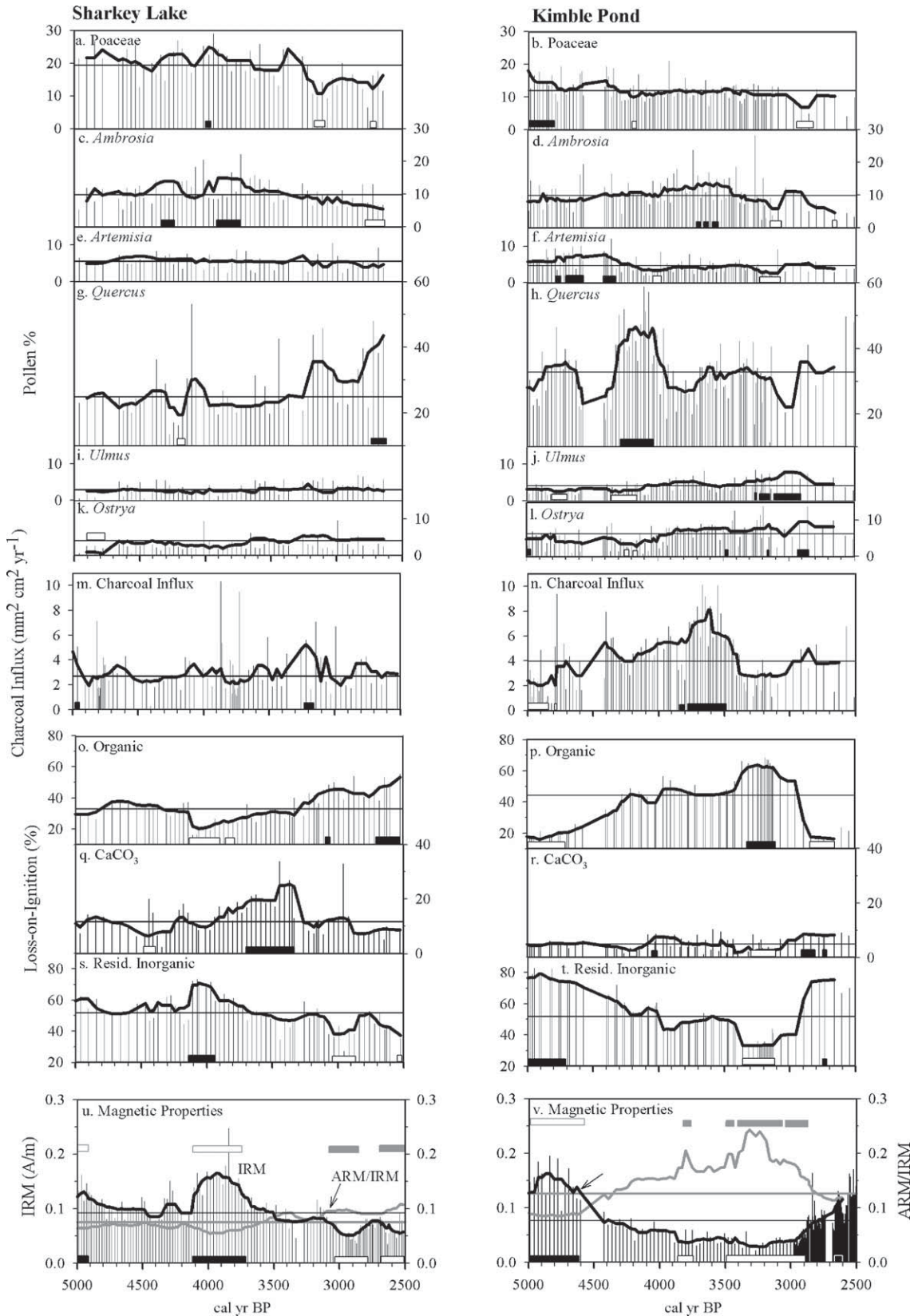
At 9000 cal yr BP, Sharkey Lake is surrounded by a dense, forest of *Ulmus* and *Quercus* with no modern analog, and then around 8700 cal yr BP a 1000-yr-long gradual change from forest to grassland is evidenced by nearly linear declines in the median percentages of *Ulmus* (40% to <5%) (Fig. 5i) and *Quercus* (20–25% to ~15%) (Fig. 5g) and a nearly linear twenty-fold increase in Poaceae (<1% to >20%) (Fig. 5a), which are paralleled by increases in the grassland forbs *Ambrosia* and *Artemisia* (Figs. 5c and e). At Sharkey, the increase in Poaceae and the grassland forbs is accelerated at ~7500 cal yr BP, following an increase in charcoal influx (below) by ~200 yr (Fig. 5m).

Kimble is more open than Sharkey (Figs. 5b, d, f) at 9000 cal yr BP and remains a variable mix of *Quercus* woodland and grassland throughout the entire 9000–7000 cal yr BP period despite an initial and gradual decline in *Quercus* that extends from 9000 to 7800 cal yr BP (Fig. 4d). At Kimble, *Quercus* pollen is particularly abundant (40%) from 7700 to 7300 cal yr BP, coincident with a peak in charcoal influx (Fig. 5n), and *Ulmus* peaks briefly at ~8200 cal yr BP and then declines from 20% to <5% of pollen over the next 1000 yr (Fig. 5j). Poaceae pollen increases rapidly from ~5% to 15% at 8000 cal yr BP,

Figure 5. Profiles for pollen, charcoal, sediment properties, and sediment magnetic properties for the early to mid-Holocene transition (9000–7000 cal yr BP) at Sharkey Lake and Kimble Pond. Pollen data (a–l) are presented as a percent of total pollen sum. Charcoal (m, n) as a measure of fire severity is provided as an influx ($\text{mm}^2 \text{cm}^{-2} \text{yr}^{-1}$). Sediment properties include percent organic (o, p), CaCO_3 (q, r), and residual inorganic (s, t). Sediment magnetic properties (u, v) include isothermal remnant magnetization (IRM) as a measure of the concentration of ferromagnetic minerals and ARM/IRM ratio as a measure of magnetic particle size (decreases as ARM/IRM goes up). Data are smoothed with a 200-yr fixed-width median smoothing window. The horizontal line represents the median for the series and boxes at bottom (and top for ARM/IRM series) of profiles indicate where the local median is statistically significantly greater (filled) or less (open) than the series median (based on a 95% confidence interval generated with 5000 bootstrap samples).

preceding a peak in charcoal (Fig. 5n) by ~400yr. The rise in Poaceae is followed by a decrease in *Ambrosia* and a still-later drop in *Artemisia* (Figs. 5d and f).

At 5000 cal yr BP, a similar mix of woodland and grassland surrounds both lakes, but the Sharkey site is probably more open as indicated by a slightly greater percentages of Poaceae (~20%



vs. 12%) (Figs. 6a and b; Table 2) and slightly lower percentages of *Quercus* (~25% vs. 30%) (Figs. 6g and h). Observed at both sites are (i) a distinct peak in *Quercus* at 4200 cal yr BP (Figs. 6g and h) and (ii) a broad peak of *Ambrosia* from 4500 to 3500 cal yr BP (Figs. 6c and d) despite an overall decline.

At Sharkey, *Quercus* pollen increases from 20% to nearly 40% at 3300 cal yr BP (Fig. 6o; Table 2), coincident with a slight peak in charcoal (Fig. 6m). When combined with a 50% drop in Poaceae at the same time, the increase in *Quercus* pollen strongly suggests an expansion of *Quercus* woodland. *Ulmus* at Sharkey changes little, rarely exceeding 5% of total pollen (Fig. 6i) and *Ostrya* (Fig. 6k) increase rapidly to pre-MH levels at ~4800 cal yr BP.

Kimble has more *Quercus* than Sharkey (Figs. 6g and h; Table 2), and with the exception of the peak at ~4200 cal yr BP *Quercus* remains at ~30% through this period for Kimble. The peak in *Quercus* is accompanied by significant drops of about 30% for *Artemisia* (Fig. 5h) and Poaceae (Fig. 5b) which, unlike *Quercus*, do not rise again. *Ulmus* and *Ostrya* (Figs. 6j and l) both increase slightly during the transition at ~3000 cal yr BP, but only the latter approaches levels observed prior to the onset of the MH (Figs. 5j and l).

Charcoal and fire history

Charcoal influx shows considerable variation during both transitional periods but displays the greatest range during the transition into the MH (Figs. 5m and n; Table 2). This is particularly true for Sharkey with charcoal ranging from a low of 0.04 mm² cm⁻² yr⁻¹ to a high of 26.06 mm² cm⁻² yr⁻¹ (Fig. 5m). Charcoal influx to Sharkey rises slightly at 8500 cal yr BP and then again at both sites at 8000 cal yr BP (Figs. 5m and n). Influx increases to its highest 7600–7700 cal yr BP for both sites (Figs. 5m and n) and remains high until 7400–7200 cal yr BP. Charcoal concentration (not shown) and charcoal influx are nearly identical with the exception of the Sharkey transition into the MH (Fig. 5m). The disjunct between charcoal concentration and influx is largely a product of a modeled ten-fold increase in the sedimentation rate (Fig. 3b) at ~7660 cal yr BP. At 7600 cal yr BP, sediment accumulation rises from an average of 0.044 to 0.385 cm yr⁻¹. As with influx, charcoal concentration for Sharkey increases beginning at 8500 cal yr BP, reflecting higher peaks and a higher minimum baseline (Fig. 5m).

Charcoal influx rates do not decline with the end of the MH, and median influx to the two lakes during the transition out of the MH is almost twice as high as that observed for the beginning of the MH (Table 2; Figs. 6m and n). Influx is less variable at the end of the MH, and the higher medians and lower variability are

largely a product of higher minimum influx values (minimum 0.08 vs. 0.62 mm² cm⁻² yr⁻¹, Kimble; minimum 0.04 vs. 0.30 mm² cm⁻² yr⁻¹, Sharkey) rather than greater peak values. At Kimble, charcoal influx increases gradually from 5000 to 3500 cal yr BP before dropping by nearly half, whereas at Sharkey charcoal values remain largely constant, although there is a peak in charcoal between 3 and 3.5 cal yr BP that is offset by ~500 yr from an even larger peak observed at Kimble (Figs. 6m and n).

Charcoal median length–width ratios exceed 3.5 at both Kimble and Sharkey (Table 3), indicating that the principle fuels at both sites were grasses or more generally graminoids which have typically have a L:W ratio of 3.5 or greater (Umbanhowar and McGrath, 1998). The lower L:W ratios for the Sharkey 9–7 cal yr BP charcoal reflects L:W values that range between 2 and 3 at the start of the series that are indicative of deciduous leaf or wood charcoal. Individual pieces of charcoal are nearly twice as large at Sharkey vs. Kimble possibly indicating a more local origin.

Loss-on-ignition and magnetics

For both lakes, the start of the MH is marked by significant, rapid (100–300-yr) decreases in organic matter (Figs. 5o and p, Figs. 6o and p) and increases in the concentration and size of magnetic particles (greater IRM and lower ARM/IRM) (Figs. 5u and v). At Kimble the concentration of ferromagnetic particles (IRM) begins to rise at 8300 cal yr BP, coincident with an increase in carbonates (Fig. 5r), whereas inorganic matter rises 400 yr later at 7900 cal yr BP (Fig. 5t). At Sharkey, inorganic content of the sediment begins to rise, and organics fall, at about 8300 cal yr BP (Figs. 5o and s) but the change is more gradual than observed at Kimble and is in part masked by an abrupt drop at 8400 cal yr BP in the biogenic silica (not shown, and included in the inorganic-LOI as presented) from 30% to 15–20% of total sediment. Such marked changes in the biogenic silica content of sediment are not observed in the other three series. The rise in inorganic content at Sharkey is accompanied by a gradual drop in the size of magnetic particles (Fig. 5u) but only a slight increase in their concentration (Fig. 5v), and the shifts in LOI and magnetics are accelerated between 7200 and 7600 cal yr BP.

The end of the MH is accompanied by significant, rapid decreases in the sediment inorganic fraction (Figs. 6s and t) and the concentration and size of magnetic particles (Figs. 6u and v), which generally mirror the changes observed at the onset of the MH. At Kimble, inorganic matter content decreases by half from 5000 to 4200 cal yr BP (Fig. 6t) and is paralleled by a decrease in concentration and size of magnetic particles (Fig. 6v). These trends continue until 2900

Figure 6. Profiles for pollen, charcoal, sediment properties, and sediment magnetic properties for the early to mid-Holocene transition (5000–2500 cal yr BP) at Sharkey Lake and Kimble Pond. Pollen data (a–l) are presented as a percent of total pollen sum. Charcoal (m, n) as a measure of fire severity is provided as an influx (mm² cm⁻² yr⁻¹). Sediment properties include percent organic (o, p), CaCO₃ (q, r), and residual inorganic (s, t). Sediment magnetic properties (u, v) include isothermal remnant magnetization (IRM) as a measure of the concentration of ferromagnetic minerals and ARM/IRM ratio as a measure of magnetic particle size (decreases as ARM/IRM goes up). Data are smoothed with a 200-yr fixed-width median smoothing window. The horizontal line represents the median for the series and boxes at bottom (and top for ARM/IRM series) of profiles indicate where the local median is statistically significantly greater (filled) or less (open) than the series median (based on a 95% confidence interval generated with 5000 bootstrap samples).

Table 2
Median (semiquartile range in parentheses) values for proxies by transitional period and lake

Period	Lake	Charcoal (mm ² cm ⁻² yr ⁻¹)	Poaceae %	Prairie forbs %	<i>Quercus</i> %	<i>Ulmus</i> %	Organic %	Carbonate %	Inorganic %	IRM A/m	ARM/IRM
9–7ka	Sharkey	1.7 (1.5) <i>n</i> = 86	13.5 (4.1) <i>n</i> = 87	20.4 (9.6)	18.7 (4.1)	17.6 (8.4)	18.0 (4.6) <i>n</i> = 88	13.2 (3.8)	66.0 (3.8)	0.15 (0.06) <i>n</i> = 163	0.06 (0.01)
	Kimble	0.6 (0.4) <i>n</i> = 74	8.3 (2.9) <i>n</i> = 72	24.7 (6.4)	19.3 (5.5)	14.3 (4.3)	14.9 (6.3) <i>n</i> = 68	15.7 (3.4)	68.4 (8.1)	0.21 (0.09) <i>n</i> = 156	0.07 (0.13)
5–2.5ka	Sharkey	2.7 (0.9) <i>n</i> = 88	19.5 (3.7) <i>n</i> = 62	21.1 (3.7)	24.9 (5.3)	2.8 (0.6)	33.0 (6.1) <i>n</i> = 73	11.7 (3.8)	51.6 (5.6)	0.09 (0.02) <i>n</i> = 152	0.08 (0.01)
	Kimble	4.0 (1.5) <i>n</i> = 104	12.0 (1.7) <i>n</i> = 102	19.4 (2.7)	32.7 (5.8)	4.1 (1.1)	44.3 (15.2) <i>n</i> = 75	5.0 (1.6)	51.9 (13.8)	0.08 (0.04) <i>n</i> = 155	0.13 (0.03)

Sample sizes (*n*) for pollen, LOI, and magnetics given only for first proxy. Prairie forbs include both *Ambrosia* and *Artemisia*.

cal yr BP before abruptly inverting in the span of 60 yr (see also Fig. 2). At Sharkey the decrease in the sediment inorganic matter initiates later at 4000 cal yr BP (Fig. 6s) and is similar in magnitude (70% to 40%) to Kimble but the rise in the organic fraction is reduced (Fig. 6o) because of a similar rise in carbonates (Fig. 6q). Concentration and size of magnetics particles begin to decline at ~3800 cal yr BP, and the magnitude of this change is greater than the change observed for LOI. At Sharkey, neither LOI nor magnetics show the 4200 cal yr BP reversal observed for Kimble (Fig. 6u).

Change points and cross correlation

Change-point analysis highlights the existence of many significant, and often abrupt, shifts among the different proxies (Fig. 7). Significant change points are sometimes present at both sites, for example the abrupt increase in charcoal influx at ~7600 cal yr BP seen at both Kimble and Sharkey (Figs. 7a and b), but more commonly the change points are unique to one site, for example the abrupt increase in ARM/IRM at 4100 cal yr BP seen only at Sharkey (Figs. 7c and d). Comparison of the number and timing of local change points highlights greater variability associated with the beginning versus the end of the MH. Numbers of change points for LOI and magnetics do not differ much between sites, but both Sharkey and Kimble show nearly twice as many changes (9000–7000 cal yr BP, 11,000 and 14,000 cal yr BP, respectively, vs. 5000–2500 cal yr BP, and 6000 and 7000 cal yr BP) during the earlier transitional period. Kimble pollen types have greater number of significant change points overall (9000–7000 cal yr BP, 7; 5000–2500 cal yr BP, 9) than Sharkey (9000–7000 cal yr BP,

2; 5000–2500 cal yr BP, 2). At the beginning of the MH, significant change points are more clustered than observed at the end of the MH, being centered at ~7500 cal yr B.P. at Sharkey (Fig. 7a) vs. ~8000 cal yr BP at Kimble (Fig. 7b). There is not a clear ordering of change points at Sharkey (Figs. 7a and c), whereas at Kimble, significant change points for LOI and magnetics generally precede change points for pollen or charcoal at the onset of the MH (Fig. 7b), although at end of the MH significant vegetation change points precede changes in LOI and magnetics (Fig. 7d).

Cross correlation of detrended charcoal, Poaceae, and ARM/IRM series suggested only weak and varied relationships among the proxies at the scale of the 30yr (bin size) with *r* values typically ranging between 0.1 and 0.2. The degree or direction of correlation among proxies showed little consistency.

Discussion

Our results further document broad, asymmetric regional shifts in the mix of woodland and grassland associated with the onset and termination of the arid mid-Holocene (MH) period in the Big Woods region of Minnesota (Figs. 4–6). The outlines of the changes in the context of the Holocene (Fig. 2) have been described previously (Wright et al., 1963; Grimm, 1983; Wright, 1992; Camill et al., 2003), but higher resolution sampling reveals many abrupt changes and considerable within- and among-site variation in vegetation, fire, and/or local environmental responses to climate change. The recognition of intersite variability in the Big Woods and elsewhere along the prairie forest border is not new (Grimm, 1983; Almendinger, 1992) and likely reflects local landscape-controls on fire as well as strong feedbacks between fire and vegetation (Grimm, 1983; Almendinger, 1992; Umbanhowar, 2004). Such strong feedbacks can result in vegetation switches and alternate stable states/dynamic regimes (Wilson and Agnew, 1992; Scheffer and Carpenter, 2003; Mayer and Rietkerk, 2004). Variability within and among sites also likely reflects climatic variation on the scale of 100s of years that is overlaid on the longer term trends of increasing or decreasing aridity (Bartlein and Whitlock, 1993; Yu and Ito, 1999; Fritz et al., 2000).

At Sharkey, and to a lesser degree Kimble, the contraction of woodland at the onset of the mid-Holocene arid period is far greater than the expansion of woodland at the end of the mid-

Table 3
Summary of morphological characteristics of charcoal imaged for early→mid (9000–7000 cal yr BP) and mid→late (5000–2500 cal yr BP) transition periods

Period	Lake	<i>n</i>	Area (mm ²)	Length–width ratio
9–7ka	Sharkey	86	0.063 (0.009)	3.59 (0.59)
	Kimble	50	0.032 (0.006)	3.91 (0.36)
5–2.5ka	Sharkey	87	0.051 (0.007)	5.31 (0.73)
	Kimble	61	0.028 (0.005)	4.09 (0.31)

Values are medians (semiquartile range).

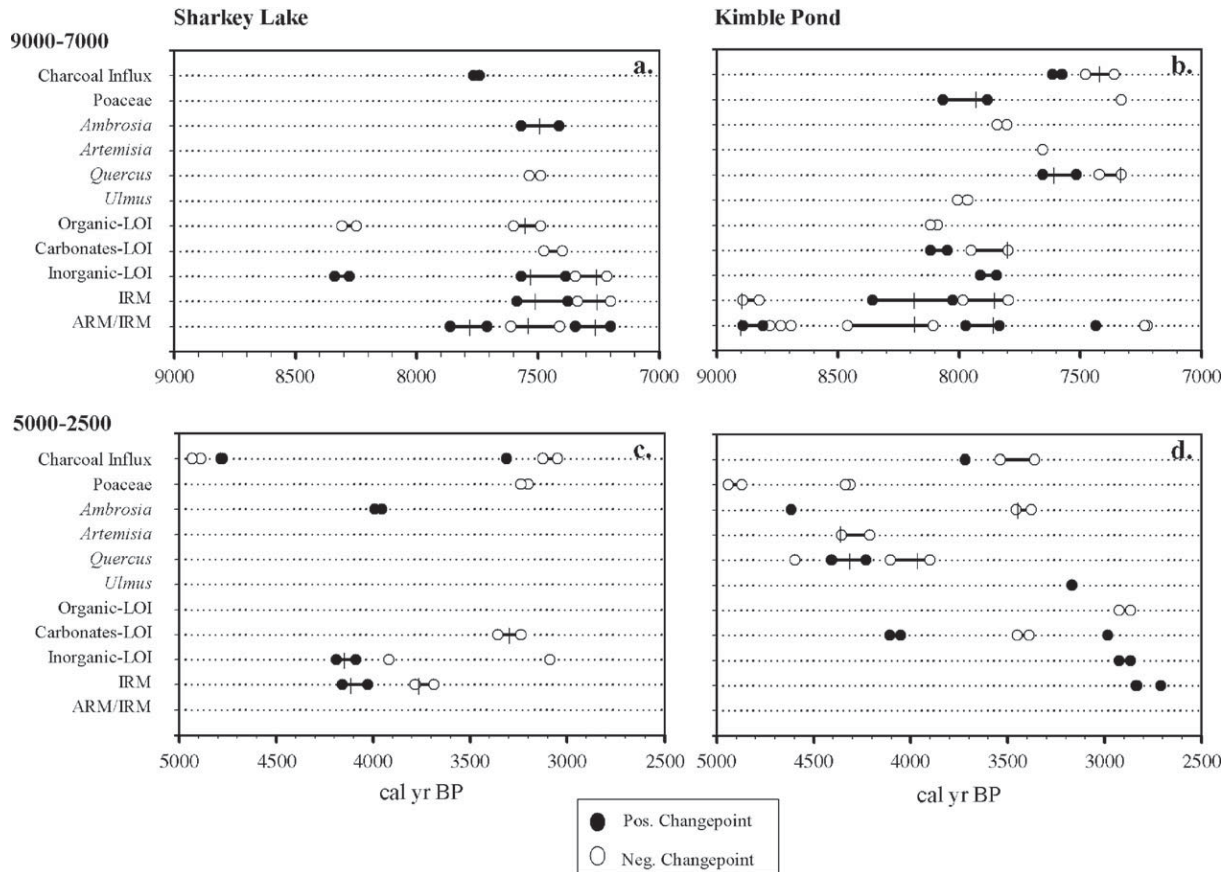


Figure 7. Summary of locations of significant local change points. Dark circles represent significant positive change points and open circles represent significant negative change points. Change points are calculated as a median difference within the halves of a 400-yr sliding window (Webster, 1973), and significance of change points is based on a 95% confidence interval generated by bootstrapping (with replacement, 5000 replicates) each series. Adjacent significant change points are connected with a horizontal line and a vertical line was added to indicate the location of the largest significant change point within each group of adjacent significant points.

Holocene (Fig. 4), perhaps the result of a more rapid shift to dry conditions at the onset of the MH and a more gradual return of moisture at the end of the MH (Laird et al., 1996; Dean et al., 2002; Shuman et al., 2002a). In part, the asymmetry reflects the disappearance of nonanalogous elm forests from the landscape, which Wright (1992) argued was due to a combination of declining insolation and a waning Laurentide ice sheet. Wright (1992) suggested that cool/moist conditions at the end of the MH kept elm populations from expanding, but this may not be a complete explanation because increased charcoal at the end of the MH (Camill et al., 2003, and references there within) suggests warm/humid conditions, and in fact elm did expand rapidly under the cool/humid conditions of the ‘Little Ice Age’ (Grimm, 1983; Umbanhowar, 2004). Baker et al. (2002) indicated a sharp climatic boundary located just to the south and east of the Big Woods that complicates climatic interpretations. Increasing aridity at the start of the MH probably caused reproductive failures of trees (including elm), especially on dry sites, impacting seedlings and sapling more than mature trees (Hanson and Weltzin, 2000; Weltzin et al., 2003). Stand-changing fires are possible in deciduous forests (Potter and Moir, 1961), but they are considered to be extremely rare (Frelich, 2002), and we saw no evidence of catastrophic woodland fires at our sites (Figs. 5 and 6; Table 3). This does not

mean that fire did not play a role, and burning of litter and invading grasses would further open the canopy and speed the transition from grassland to woodland until the point that increasing aridity might begin to limit fuel production (Clark et al., 2002; Nelson et al., 2004).

While increasing effective moisture, especially summer precipitation, at the end of the MH would enhance tree reproduction and growth, it would also promote grass productivity, resulting in higher fuel loads and more frequent/intense burns that would inhibit woodland expansion (Peterson and Reich, 2001). The asymmetric response of woodland to the MH is probably the product of increased burning and the restriction of woodland expansion to areas protected by rising water levels in wetlands and lakes (Almendinger, 1992; Digerfeldt et al., 1992). Consistent with the importance of fire throughout much of the landscape is the dominance of oak and limited/nonexpansion of elm following the MH. The impacts of fires in the understory of oak woodlands are well documented (Peterson and Reich, 2001). Oak-dominated woodland persisted for 3000–4000 yr until it was replaced by mesic forest (*Ulmus, Acer, Tilia*) at ~300 cal yr BP as a result of either even greater moisture and/or cooling (Grimm, 1983), or perhaps cultural/population changes that resulted in fewer ignitions (Mc Andrews, 1968).

Some of the variation in vegetation and fire recorded by the high resolution sampling may be the product of sudden climate shifts overlaid on top of the changes in insolation (Shuman et al., 2002a). One increasingly well-documented shift is the ‘8.2 ka event,’ which has been linked to the final collapse of the Laurentide ice sheet. At Deep Lake in northern Minnesota, this cooling is associated with increased aridity signaled by increases in residual inorganic matter and the relative abundance of herb pollen (Hu et al., 1999), whereas at Kirchner Marsh (~25 km NW of Sharkey) an increase in *Ambrosia* at 7920 cal yr BP has been linked to the 8.2 ka event by Shuman et al. (2002a). In contrast, at our sites there is an increase, albeit slight at Sharkey, in the concentration of *Ulmus* (Figs. 5i and j), indicating a re-expansion of mesic forest in the region. Residual inorganic matter does increase at Sharkey but not at Kimble, which shows a sustained rise in the concentration of magnetic particles (IRM) that is not evident at Sharkey. Differences in the responses among the four sites may reflect the presence of steep climatic gradients in the region and are consistent with Baker et al. (2002).

Variation among the proxy records for the two sites seems unlikely to be explained simply by differences in climate, landscape heterogeneity, or forest cover. This variation may instead be the product of differences between the lakes, including (a) the surface area and morphometry, (b) the balance of groundwater versus surface precipitation, (c) the processes involved in the transport and preservation of proxies, or (d) the error associated with the reconstructed chronologies for the two sites. For example, the reconstructions presented in this paper are based on single cores and large differences among cores within a lake have been recorded by Digerfeldt et al. (1992). The pollen data are not calibrated with modern data sets and so percent arboreal pollen (Fig. 4) may not accurately represent tree cover (Williams, 2002). Charcoal influx is relatively insensitive to lake area and the majority of charcoal comes from within 10 to 60 m of the lakes (Clark, 1988; Clark et al., 1998), but pollen influx is strongly dependent on surface area and the larger surface size of Sharkey means that its pollen record is more regional (Jackson, 1990; Sugita, 1994). Differences in source area have been previously used by Clark et al. (1996) to explain low correlations between charcoal and pollen, and it may explain very low r values ($r < 0.2$) for cross correlations (not presented) based on the proxies included in this paper. Connections to groundwater are particularly important in understanding lake response to climate change (Digerfeldt et al., 1992; Smith et al., 2002) but have not been formally described. Finally, unavoidable errors involved in the reconstruction of the chronology would result in differences in timing among the two sites and these might include polynomial fits of the age–depth curve and the necessity of splicing together two polynomials for Sharkey, errors in calibration and/or finally ^{14}C plateaus present during both transitions (Stuiver et al., 1998; Guilderson et al., 2005). Clearly, there is a need to combine multiple proxies with multiple cores from multiple sites when reconstructing regional patterns of change.

Conclusions

Although the changes in temperature and moisture associated with the MH are similar to those projected for future climate warming, our results indicate major site- and time-specific differences in the relations among proxies, suggesting that there will be no one single vegetation response to climate. The modern absence of fire in most grassland–woodland borders further suggests that neither the transition into or out of the MH provide a good model for vegetation responses to anticipated climatic warming. In landscapes where fires have been eliminated, the utility of the paleoecological record as a way to understand future changes may depend on locating sites that were historically “protected” from fire, based on modern understandings of fire behavior relative to topography, water bodies, and other landscape features.

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