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Late-Holocene vegetation and fire history from Ferry Lake, northwestern Wisconsin, USA

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Abstract: We used charcoal and fossil pollen to investigate how fire, vegetation and climate have interacted over the past 2300 years at Ferry Lake, located on a sand plain in northwestern Wisconsin. Pollen analysis shows a rapid transition from oak (*Quercus* spp.)-dominated woodland to a relatively open pine (*Pinus* spp.) forest at 1450 cal. yr BP, and a more closed-canopy pine forest beginning about 700 cal. yr BP. We calculated accumulation rates of 125–250 μm charcoal fragments (CHAR) in contiguous 0.5 cm thick sediment samples, each representing 7–10 years. Graminoid charcoal fragments were tallied separately to track the relative abundance of grass charcoal. During the oak period charcoal peaks have relatively weak periodicity and relatively high accumulation rates of grass charcoal. Charcoal peaks are less frequent (with a periodicity of 130–200 years), and larger during the open-canopy pine period, with lower grass CHAR. CHAR of both charcoal types decreases further between 1000 and 850 cal. yr BP and remains low until the period of European settlement. Several hundred years later (700 cal. yr BP) white pine pollen increases and pollen from herbaceous taxa decreases, suggesting a more mesic, closed-canopy forest. Our results demonstrate that the vegetation and fire regime at this sandplain site changed substantially, but apparently not synchronously, during the last 2300 years, a period when millennial-scale regional climate was relatively similar to modern.

Key words: Charcoal analysis, climate change, fire history, pollen, palaeoecology, pine barrens, late Holocene, Wisconsin.

Introduction

Restoration and conservation of fire-prone ecosystems depend on understanding the interactions between vegetation and fire and their sensitivity to climate. Theoretical and empirical studies suggest that feedbacks between vegetation and fire can either stabilize vegetation or lead to sudden, dramatic changes in an ecosystem in response to relatively minor changes in climate (Brubaker, 1975; Wilson and Agnew, 1992; Lynch, 1998; Davis *et al.*, 1998; Scheffer and Carpenter, 2003; Beisner *et al.*, 2003; Lytle, 2005). The possibility of multiple stable states and sudden state changes makes predicting the response of fire-prone ecosystems to climate change challenging without long-term observations. Palaeoecological methods offer a way to examine the dynamics of vegetation and fire regimes over several thousand years of natural climatic variability.

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Our study focused on the last 2300 years, when the long-term average climate and tree species ranges have been relatively stable in the western Great Lakes region (Webb, 1974; Webb *et al.*, 1983; Bartlein *et al.*, 1984; Davis, 1987; Davis *et al.*, 2000; Calcote, 2003). This period of relative stability offers an opportunity to study how small decadal- to century-scale climate changes and human activities have affected vegetation and disturbance regimes. The archaeological record from northwestern Wisconsin is sparse; consequently little is known about changes in human population densities and ecosystem management practices until historical times.

Within the past 2300 years there was a widespread climatic change from generally warmer conditions during the 'Mediaeval Climatic Anomaly' (MCA: AD 900–1250; 1050–700 cal. yr BP) to cooler and/or moister conditions of the 'Little Ice Age' (LIA: AD 1250–1850; 700–100 cal. yr BP). Although these changes are relatively small compared with early- and middle-Holocene climatic changes, tree ring studies document severe droughts during the period roughly corresponding to the MCA

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in the American Midwest (Cook *et al.*, 2004), and fossil pollen and charcoal records from western Wisconsin and eastern Minnesota suggest increasingly mesic conditions in the past several centuries corresponding to the period of the LIA. Pollen studies in northern Wisconsin show an increase in mesic tree species beginning 600–900 cal. yr BP (Swain, 1978; Gajewski *et al.*, 1985; Parshall, 2002). In southeastern Minnesota mesic tree expansion began by 400–300 cal. yr BP ago (Waddington, 1969; Grimm, 1983), although recent work suggests that a gradual expansion of mesic species in the Big Woods region may have begun somewhat earlier, *c.* 950 cal. yr BP (Umbanhowar, 2004). Charcoal records from laminated lake sediments suggest a decrease in fire frequency 400–100 cal. yr BP in northern Wisconsin (Swain, 1978) and north-central Minnesota (Clark, 1988, 1990), beginning long before effective fire suppression efforts. The responses of vegetation and fire regimes to decadal or century-scale climatic changes such as these are not likely to have been uniform across the upper Midwest because soils differ among regions, and fire breaks are unevenly distributed across the landscape (Grimm, 1984; Camill *et al.*, 2003; Umbanhowar, 2004). Changes in human land use practices during the past 2000 years may also have differed among regions.

The vegetation on sandplains in Minnesota, Wisconsin and Michigan is controlled largely by fire and edaphic conditions (Murphy, 1931; Curtis, 1959; Vogl, 1970; Pregitzer and Saunders, 1999) and may have responded differently to changes in climate than did vegetation on other soil types in the region. On one hand, the importance of fire and edaphic conditions might be expected to overwhelm minor climatic fluctuations. For example, Brubaker (1975) found that jack pine (*Pinus banksiana*) was dominant on a sandplain in the Upper Peninsula of Michigan for the past 9000 years, suggesting that sandplain vegetation was stabilized by feedbacks among soils, vegetation and fire, and changed very little in response to the climatic changes that occurred during the Holocene. However, results from other studies in the Upper Peninsula of Michigan (Lytle, 2005) and in north-central Minnesota (Almendinger, 1990, 1992) suggest that vegetation and fire regimes have changed significantly on sandplains during the Holocene.

The pre-European 'pine barrens' vegetation of sandplains contrasted sharply with the surrounding northern hardwood forests. Pine barrens were dominated by grasses, low shrubs, small trees and scattered large pine (*Pinus* spp.) and oak (*Quercus* spp.) trees (Vogl, 1970; Addis *et al.*, 1995). Early descriptions suggest that the vegetation was patchy, with mature forests and wetlands included within the larger barrens landscape mosaic. These landscapes were dynamic because of the prevalence of fires, resulting from both lightning and intentional burning for berry production and hunting (Murphy, 1931). Over the last 150 years the sandplain vegetation has been greatly altered by logging, slash fires, agriculture, tree plantations, fire suppression and development around lakes. At the time of European settlement in the late nineteenth century approximately 20 000 km^2 of pine barrens vegetation existed on sandplains in northern Wisconsin, Michigan and Minnesota (Vora, 1993). Today only scattered fragments too small to ensure long-term viability of populations of characteristic plants and animals remain (Addis *et al.*, 1995). Federal, state and county land managers are working to restore vegetation structure and fire regimes in former barrens landscapes (Addis *et al.*, 1995; Borgerding *et al.*, 1995); however, restoration efforts are limited by a lack of information about the pre-European settlement vegetation structure and fire regimes, and about the stability and dynamics of these patterns over multiple generations of trees.

The objective of this study was to describe the late-Holocene vegetation and fire history of a site on the sandplain in northwestern Wisconsin (Figure 1) and to examine patterns of interaction among vegetation, fire and climate over the past 2300 years. In particular, we consider whether vegetation and fire regimes on this sandplain site were sensitive to relatively small changes in climate during this period. The record from this site provides a useful perspective for understanding the responses of sandplain vegetation and fire to recent climatic variability.

Study area

The northwestern Wisconsin sandplain is an extensive area of glacial outwash occupying approximately 450 km^2 in Douglas, Bayfield, Burnett and Washburn Counties (Figure 1). Sandy soils make the vegetation prone to drought and frequent forest fires. The vegetation of the northwestern Wisconsin sandplain at the time of European settlement was reconstructed from historical documents and General Land Office Survey (GLO) notes from the 1850s by Radeloff *et al.* (1998, 1999). The vegetation in the central region was dominated by jack pine stands and open areas with no trees. The northern region was characterized by mixed red pine (*Pinus resinosa*), white pine (*P. strobus*) and oak forests with few openings. Trees tended to be more widely spaced in the south, suggesting that savannas with oak and red and white pines were the dominant community type (Radeloff *et al.*, 1998).

Frequent fires and modern logging have eliminated ancient forests on the sandplain, limiting the usefulness of dendrochronological methods to reconstruct the range of prehistoric fire frequencies. Instead, fire frequencies prior to European settlement have been inferred from the composition of the vegetation in GLO records and from published studies of fire regimes in similar vegetation types in the upper Midwest (Radeloff *et al.*, 1998, 1999). In the south, pine and oak savannas suggest the prevalence of low-intensity frequent surface fires returning at 3–20 yr intervals; in the central sandplain, dominance by jack pine forests and barrens implies

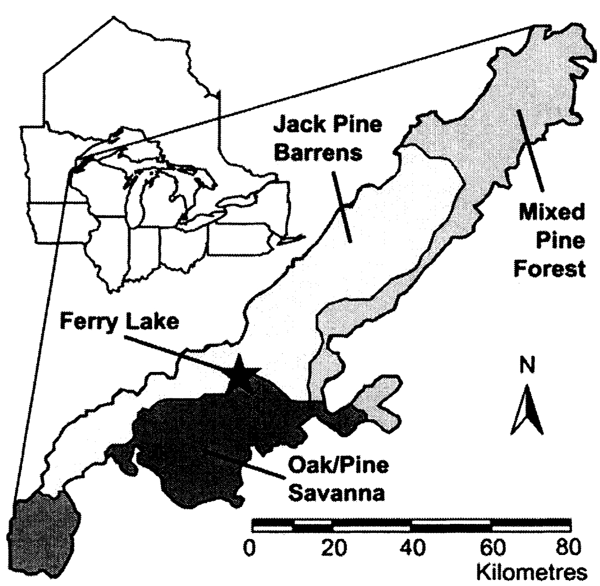

Figure 1 Location of the northwest Wisconsin sandplain (inset) and pre-European vegetation regions of the sandplain (Radeloff *et al.*, 1998). Location of Ferry Lake is indicated by a star

stand-replacing crown fires every 20–70 yr, and in the north, relatively dense mixed red, white and jack pine forests suggest crown fires every 100–300 yr. Thus, the sandplain appears to have maintained a range of vegetation and fire regimes over a relatively homogeneous substrate before European settlement (Radeloff *et al.*, 1998, 1999).

Ferry Lake is a small (6.5 ha), deep (12 m) lake in Burnett County, Wisconsin (46° 1′N, 92° 8′W) with no outlet or inlet streams. The climate is continental, with daily mean temperatures of −13°C in January and 20°C in July (1971–2000 average from Danbury WI, 18 km west of Ferry Lake; Midwest Regional Climate Center, 2005). Mean annual precipitation is approximately 770 mm, approximately two-thirds of which falls during the growing season. Ferry Lake is located just north of the tension zone, a floristic boundary separating northern forests and prairie (Curtis, 1959), and within the sandplain it is located at the transition between the central jack pine barrens and southern oak/pine savanna (Radeloff *et al.*, 1998; Figure 1). GLO notes collected in *c.* AD 1850 show a mix of jack and red pines around the lake just prior to European settlement. Within 5 km of Ferry Lake 51% of the witness and bearing trees were jack pine, 19% red pine, 7% white pine, 3% tamarack (*Larix laricina*), 4% oak, 1% yellow birch (*Betula alleghaniensis*), 1% paper birch (*B. papyrifera*) and 1% aspen (*Populus* spp.) (Forest Landscape Ecology Laboratory, 2001). Eight percent of the points were in water and 4% had no tree listed. Based on interpretation of LANDSAT images (Wolter *et al.*, 1995) the modern vegetation within 5 km of Ferry Lake is 19% unforested, 17% oak, 12% jack pine, 8% red pine, 9% other conifers, 6% aspen, 14% mixed deciduous and 16% mixed deciduous/coniferous forest. The modern vegetation, therefore, has approximately one-third as much pine and three times as much oak as the vegetation before European settlement.

Methods

Ferry Lake core

A sediment core 2 m long was collected through the ice in a single drive with a piston in a polycarbonate tube. This core was split lengthwise, the fresh sediment surface was described at a macroscopic scale, and smear slides of whole sediment were sealed in Norland optical adhesive to confirm microscopic sediment composition. Split core sections are archived in the National Lacustrine Core Repository, University of Minnesota – Twin Cities. A shorter core through the sediment–water interface was collected nearby and extruded vertically in the field in 1 cm increments. The chronology is based on four AMS radiocarbon dates and a ^{210}Pb profile of recent sediments from the short core. AMS radiocarbon dates were obtained on pollen concentrated from 5 ml of wet sediment (Brown *et al.*, 1989; Regnell, 1992; Richardson and Hall, 1994). AMS dates were converted to calendar years BP using OxCal version 3.9 (Bronk Ramsey, 2001). Dates are reported in cal. yr BP, where 'present' is AD 1950. A polynomial function derived from the converted ^{14}C dates was used to establish the sediment chronology (Figure 2). A polynomial function describing the ^{210}Pb profile of the top 1 m of sediment from the extruded core was used to estimate dates for the last 140 years.

Pollen

Fossil pollen from lake-sediment cores was analysed in 1-ml subsamples prepared with standard methods (Faegri and Iversen, 1989). In the Ferry Lake core, the most recent 100 years were analysed at 20-cm intervals, or approximately every 20 years. Below this, in more compacted sediments, subsamples were analysed at 2–3 cm intervals, about every 35–55 years. An average of 560 upland pollen grains were identified and counted in each sample (range 364–826). Pine grains were counted in three categories; (1) white pine type (*Pinus* subgenus *strobus*), (2) red/jack pine type (*Pinus* subgenus *pinus*), (3) undifferentiable pine type. Undifferentiable pine pollen counts were divided proportionately between white and red/jack types for analysis. Pollen percentages (% upland pollen) were plotted with TILIA 2.2 (Grimm, 1992), and pollen zones were determined by stratigraphically constrained cluster analysis (CONISS; Grimm, 1987).

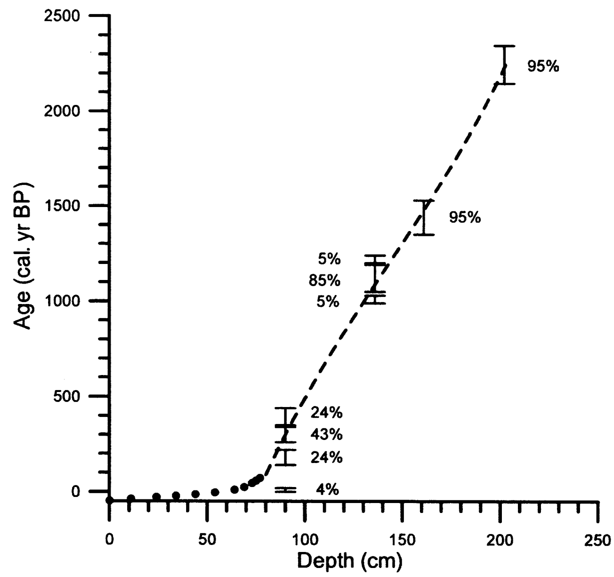

Figure 2 Age–depth relationship based on ^{210}Pb profile (dotted line) and four AMS radiocarbon dates (Table 1). Dashed line represents third degree polynomial fit to calibrated ^{14}C dates. Error bars represent 95% probabilities for the calibrated ^{14}C dates; where multiple potential calibrated dates occur for one sample the probabilities for each range are indicated

Marker grains were added to pollen samples in order to calculate pollen deposition rate. However, we suspect that the calculated concentrations of marker grains added were inaccurate, and calculations of pollen deposition rates for Ferry Lake are problematic. We do not present a pollen influx diagram because of these uncertainties.

Pollen assemblages from the entire record were compared with one another using non-metric multidimensional scaling ordination (NMS) (Kruskal, 1964a, b; Mather, 1976) with Sørenson's distance measure, $1 - 2w/(A+B)$, where A and B are the areas under two species curves and w is the overlap of the two areas. We performed an initial series of 500 runs using random starting configurations and an instability criterion of 0.0005. An increase in number of axes was considered only if the additional axis contributed significant reduction in final stress (Monte Carlo p-value ≤ 0.05). Starting coordinates for the final NMS run were produced from 50 runs on real and randomized data for the two-axis solution. A Monte Carlo test with 50 randomized runs was used to determine the statistical significance of the final ordination configuration. Correlations between pollen taxa and each axis in the final configuration were calculated using Sørenson's distance and a Monte Carlo procedure. NMS was performed using PC-ORD®4 software (McCune and Mefford, 1999).

Charcoal

Fluctuations in the amount of charcoal in sediments provide a basis for comparing fire regimes over centuries and millennia.

Empirical and theoretical studies (reviewed in Whitlock and Larsen, 2001) demonstrate that charcoal >125 μm is deposited close to the fire, thus supporting the use of sedimentary charcoal peaks to identify fires burning within the watersheds of small lakes. We identified and counted charcoal in contiguous 1-cm thick samples from the sediment surface to the *Ambrosia* rise, and in 0.5-cm intervals below the *Ambrosia* rise, producing a charcoal record with a resolution of *c.* 7–10 yr through most of the core. Sediment samples of 1–2 ml were treated with 6% H_2O_2 (50°C) for 24 h to bleach non-charred organic material, then sieved through 125 μm and 250 μm nested sieves. Fragments >125 μm were identified as either 'charcoal' or 'charred graminoid cuticle' (hereafter referred to as grass charcoal) based on comparison with reference samples. The charcoal category may include charcoal produced by burned plant material derived from any taxon, including grass. The grass charcoal category was used only for charred plant material with visible structure matching that of burned graminoid (Poaceae and *Carex*) cuticles (Palmer, 1976, Lynch *et al.*, 2005).

Charcoal concentrations (number of particles/cm^3 sediment) were converted to charcoal accumulation rates (CHAR; number of particles/cm^2 per yr) by dividing concentration by the number of years per centimetre. In the unconsolidated sediments from the upper portion of the core, charcoal counts from adjacent 1-cm thick samples were combined to give a temporal resolution comparable with 0.5-cm thick samples in the lower portion of the core. Consequently, the charcoal influx rates for each decade after 1930 were derived from 4–10 combined samples to represent 5–10 years.

The series of total CHAR (including grass charcoal) values was subjected to iterative spectral analysis using Arand time series analysis software (Howell, 2001). After linear interpolation to 10-yr intervals, the most recent 100 years were removed, linear detrending was applied to the total CHAR series and spectral density was calculated within a 400-yr window that was advanced at 40-yr intervals. Spectral density is reported in arbitrary units proportional to the square of the amplitudes of the CHAR peaks.

To aid in the identification of charcoal peaks associated with local fires, the total CHAR and grass CHAR records were smoothed to separate the gradually varying, low-frequency background component from the high-frequency peaks that represent the charcoal contributed by local fires (Long *et al.*, 1998). Using LOWESS smoothing (Cleveland, 1979) with a window width of *c.* 330 yr, we calculated the centre-weighted moving average using SYSTAT 10.2 (SYSTAT, 2002) to approximate background rates of charcoal accumulation. This window width was selected because wider windows obscured long-term variations in CHAR, while narrower windows closely tracked the peaks in CHAR. Conspicuous CHAR peaks were interpreted as evidence for local forest fires within the time period represented by each sample. Similar charcoal studies from small lakes in pine forests in north-central Minnesota (Clark, 1990) and western coniferous forests (Long *et al.*, 1998; Brunelle and Whitlock, 2003; Hallett *et al.*, 2003) used known fire histories reconstructed with dendrochronological methods or historical records to establish thresholds to identify peaks large enough to identify local fires. We do not use a threshold in this study because the forests in the study area are too young to provide fire-scar records.

Large peaks in CHAR represent a useful characterization of fire frequency, but we do not interpret them as a direct measure of the frequency of past forest fires at a site. First, the temporal resolution of our interpretation is limited. If the actual fire frequency around the lake was less than *at best* 20 years, we would not be able to resolve individual fires in samples that contain sediment that accumulated over 7–10 years. A second reason that it is difficult to interpret peaks as individual fires is that peaks may be sustained over several contiguous samples. Separate fires on different sides of the lake, frequent fires or delayed deposition of charcoal after a fire (Whitlock and Millspaugh, 1996) could create such a signal. For these reasons we discuss changes in charcoal influx and patterns of charcoal peak frequency rather than changes in fire frequency.

Results

Core description and chronology

The sediment of Ferry Lake above 150 cm is dark, homogeneous diatomaceous sapropel (Schnurrenberger *et al.*, 2003) with no visible structure. Below 150 cm the sediment is a sapropelic diatomite with frequent light-coloured bands 1–10 mm thick. Examination of smear slides of raw sediment from the light bands showed that they are composed of large numbers of diatoms. The most recent pair of prominent bands occur at 157 and 155 cm depth, corresponding to *c.* 1450 cal. yr BP.

AMS radiocarbon dates were obtained on pollen concentrated from 85–86, 131–132, 157–158, and 197–198 cm in the 2-m core (Table 1). Figure 2 shows calibrated ages and ranges, with the 3rd degree polynomial functions used to estimate sediment age in the ^{210}Pb-dated short core and the radiocarbon-dated long core. Pollen and charcoal data from the surface core were grafted to data from the long core at the *Ambrosia* rise (the point where *Ambrosia*-type pollen increased in response to land clearing by Europeans, 80 cm depth in the extruded core). The ^{210}Pb profile estimates the age of the *Ambrosia* rise to be ~AD1860, consistent with the beginning of large-scale logging of white pine in this region.

Ferry Lake pollen

The fossil-pollen diagram from Ferry Lake (Figure 3) is divided into three pollen zones determined using stratigraphically constrained cluster analysis (CONISS; Grimm, 1987).

FL-1: oak period (2300–1450 cal. yr BP)

This zone contains moderately abundant pine, with oak pollen percentages increasing by 1800 cal. BP. The ratio of oak:pine is consistently higher during FL-1 than in more recent sediments. Oak:pine is ≤0.4 before 1800 cal. yr BP, then increases over the next 400 yr to 1.0 by 1450 cal. yr BP. The end of FL-1 is characterized by oak pollen percentages and ratios of oak:pine higher than at any other time in the past 2300 years. Birch (9–21%) ironwood (*Ostrya*: 0.2–2.1%) and elm (*Ulmus*: 0.9–2.4%) pollen are consistently present in moderate to low abundances during the oak period.

Non-arboreal pollen percentages are relatively high during the oak period, suggesting that the arboreal canopy was somewhat open. *Alnus* makes up ~5% of the pollen sum and was probably *Alnus rugosa* growing along the shore of the lake. Prairie forbs (sum of Chenopodiaceae/Amaranthaceae, *Artemisia*, and Asteraceae subfamily Tubuliflorae-type pollen, excluding *Ambrosia*-type) account for 2–4%, and Poaceae for 0.5–3% of upland pollen.

FL-2: pine period (1450–700 cal. yr BP)

The transition to FL-2 is marked by a sharp increase in pine pollen and a decrease in oak pollen from 33% to less than 15% within 50 years. Oak pollen percentages remain less than 15% until the very surface of the core. The oak:pine ratio decreases from 0.96 to <0.2 within 50 years after the zone boundary. A

Table 1 AMS radiocarbon dates from the 2-m core

Depth in core (cm)	Adjusted depth (cm)	^{14}C age (yr BP)	+/− s.d.	Calibrated age (cal. yr BP)	Lab ID #
85–86	90	250	40	300	Beta 206427
131–132	136	1198	33	1120	AA 59151
157–158	162	1554	34	1465	AA 59152
197–198	202	2237	39	2225	AA 44476

Depths were adjusted to match the bottom of the extruded surface core. Probability distributions of calibrated dates are shown in Figure 2.

single-sample peak in aspen and *Ambrosia*-type pollen follows the decline in oak pollen, followed by a brief peak of birch pollen. Birch pollen percentages then decline to about 10% and

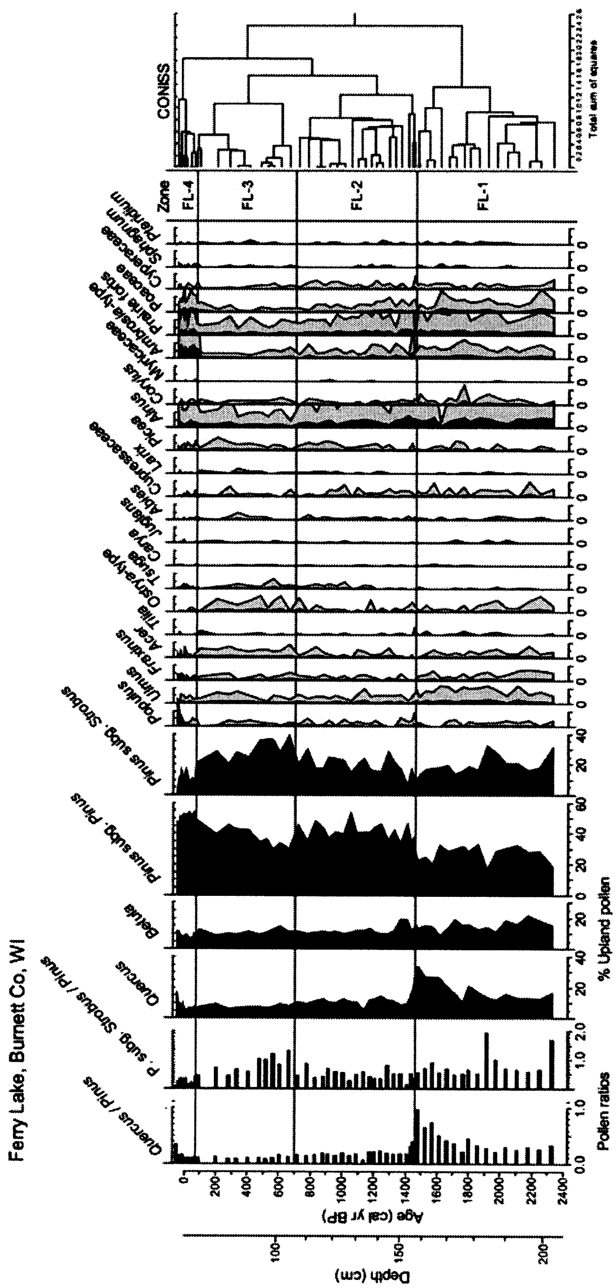

Figure 3 Pollen percentage diagram for Ferry Lake. Pollen percentages are plotted as continuous curves; light shading shows 5 × exaggeration. Ratios of pollen types are plotted as bars. Results of stratigraphically constrained cluster analysis of pollen are shown to the right of the pollen data

remain low throughout the pine period. Oak percentages decline to < 10% by *c.* 700 BP, the beginning of FL-3. Grass pollen percentages, which had been 1–3% in the oak zone (FL-1), decrease to 0.5–1.5% in the pine period.

FL-3: white pine period (700–90 cal. BP)

White pine pollen percentages increase to 30% at the beginning of FL-3, gradually decreasing to 20% by the end of the zone. Percentages of pollen from mesic taxa such as maple (*Acer*), ironwood, ash (*Fraxinus*), elm and hemlock (*Tsuga canadensis*) increase slightly. The ratio of white pine:jack/red pine pollen types reaches its highest levels (> 1.0) from 700 to 450 cal. yr BP. The sum of grass and prairie forb pollen percentages decreases to about 2% through most of this zone.

FL-4: post-European settlement (90 cal. yr BP-present)

Pine pollen percentages decrease and non-arboreal pollen percentages (primarily *Ambrosia*-type and Poaceae) increase because of land clearance. White pine pollen percentages decline to < 20%, while jack/red pine percentages increase to ~ 50%. The ratio of white pine:jack/red pine pollen decreases to < 0.4 after logging. Pollen percentages of several herbaceous species increase after European settlement, and oak and aspen increase in the last few decades.

Ordination of pollen assemblages

The final NMS ordination of Ferry Lake fossil pollen assemblage data had two axes that explained 42% and 54% of the total variance, with a final stress of 8.7 after 65 iterations. A Monte Carlo test of the final configuration with 50 randomized runs produced a p-value of 0.196, where $p =$ the proportion of randomized runs with stress $\leq$ the observed stress. The two-axis ordination separated the four pollen zones identified by stratigraphically constrained cluster analysis (Figures 3 and 4). Birch, white pine, jack/red pine and oak had $r^2 > 0.4$ with at least one of the two axes; relative r^2 values are shown as vectors in a joint plot with the samples (Figure 4).

Ferry Lake charcoal record

The charcoal record shows clear changes in total charcoal and grass charcoal influx rates over time (Figure 5). Charcoal influx is relatively high from 2300 to 800 cal. yr BP, and then drops to its lowest values 800–100 cal. yr BP. Grass influx is highest 1900–800 cal. yr BP and decreases to near 0 after 800 cal. yr BP. Where grass charcoal influx is high the peaks tend to coincide with peaks in total CHAR. Spectral analysis and visible trends in total charcoal influx show that the frequency and magnitude of CHAR peaks also vary over time. Between 1800 and 1500 cal. yr BP the frequent small CHAR peaks are weakly periodic, with some spectral density in the 50–65 yr range and some in the 90–140 yr range. Less frequent but larger peaks during the period 1300–800 cal. yr BP show strong 130–200 year periodicity (Figure 5). Charcoal influx is very low 800–100 cal. yr BP.

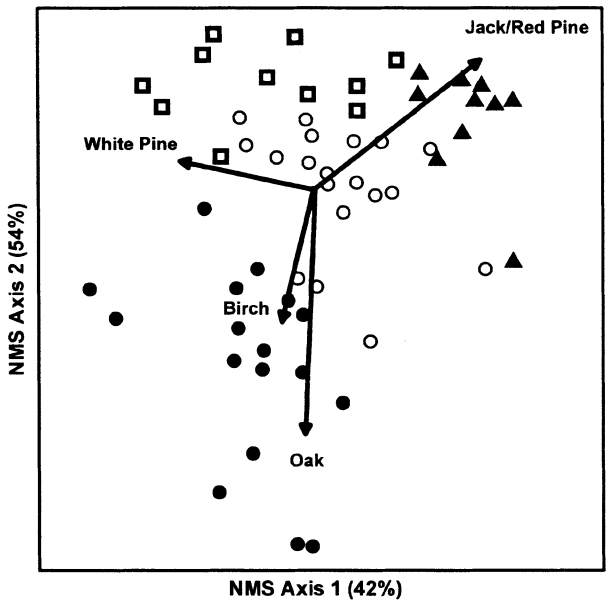

Figure 4 Non-metric multidimensional scaling (NMS) ordination of Ferry Lake fossil pollen assemblages. Solid circles represent samples from FL-1, open circles from FL-2, open squares from FL-3 and solid triangles from FL-4. Axes 1 and 2 represent 42 and 54% of total variance, respectively. Vectors represent linear correlations of pollen taxa with axes 1 and 2 on a relative scale, for all taxa with $r^2 > 0.4$

Vegetation and fire history

Prior to 1450 cal. yr BP, relatively high oak pollen percentages and oak:pine pollen ratios suggest oak-dominated vegetation occurred around Ferry Lake. Pollen percentages of mesic tree taxa, especially elm, were also relatively high during this time. The relatively high percentages of herb pollen during this period suggest an open canopy, perhaps even oak savanna. Oak pollen increased in abundance beginning at about 1800 cal. yr BP, and reached peak values just before 1450 cal. yr BP. During this time oak pollen percentages were higher than in any of the 33 presettlement samples we have collected from the sandplain, reaching pollen percentages similar to our most oak-dominated modern surface sample assemblages (Hotchkiss *et al.*, 2005). This period of increasing oak pollen percentages roughly coincides with weak < 150-yr periodicity in the CHAR series.

During the oak period (FL-1) the background charcoal and grass charcoal components were higher and charcoal peaks were more frequent than in the pine period (FL-2), suggesting a greater incidence of fire in the early part of the record. Higher grass CHAR values mirror the higher grass pollen percentages during the oak period, supporting the interpretation of a more open canopy with abundant grass in the vegetation and a greater importance of surface fires. It is likely that the fire regime during the oak period consisted of frequent surface fires with relatively rare crown fires in an open-canopied savanna or woodland.

Oak pollen percentages decreased rapidly at 1450 cal. yr BP and were replaced by higher percentages of pine pollen, suggesting a rapid switch from oak to pine dominance in the surrounding vegetation. Percentages of pollen types from mesic tree taxa were at their lowest during the pine period (FL-2), and jack/red pine pollen was at its most abundant, suggesting dry conditions and vegetation dominated by jack pine. Despite uncertainties with pollen influx calculations, the influx data are consistent with a sudden decrease in oak at 1450 cal. BP without a correspondingly sudden increase in pine pollen influx. After the switch to open pine forest, the grass charcoal influx dropped and charcoal peaks became less frequent, though larger (Figure 5). The most striking change in charcoal influx occurred about 150 years after the pollen assemblage changed from oak to pine dominated, with a shift to a strong 130–200 yr periodicity in large charcoal peaks. The decrease in both grass CHAR and the frequency of total CHAR peaks suggests that surface fires became less common. The accumulation of fuels over longer periods may have led to larger, more sporadic crown fires, consistent with the interpretation that the slight decrease in herb pollen represents a more closed canopy.

The increase of white pine and decrease of jack/red pine pollen types indicates more mesic conditions by 700 cal. yr BP. Other mesic taxa including ironwood and maple also increased slightly, and percentages of non-arboreal pollen types were low, suggesting a more closed forest canopy, perhaps related to the

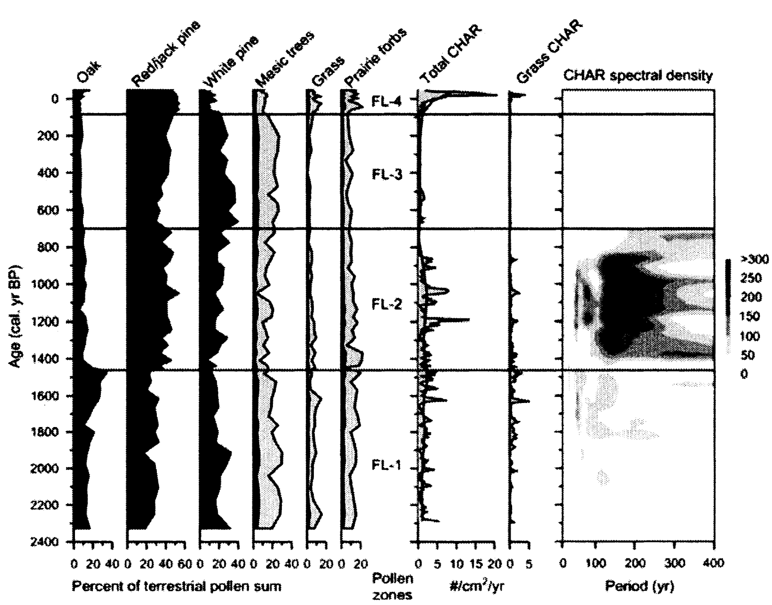

Figure 5 Summary of major changes in pollen percentages and total CHAR and grass CHAR profiles. The line shows changes in background charcoal inputs derived from locally weighted regression smoothing of total CHAR values. Iterative spectral analysis of total CHAR is shown at the right

onset of more mesic conditions. This is consistent with the decrease in charcoal influx and lack of charcoal peaks after about 800 cal. yr BP.

Discussion

Vegetation change at 1450 cal. yr BP

The largest vegetation change in the last 2300 years around Ferry Lake occurred rapidly at *c.* 1450 cal. yr BP, and does not correspond to climatic change documented in other studies from northern Wisconsin (Swain, 1978; Gajewski *et al.*, 1985; Parshall, 2002). The severity, timing and extent of relatively short-term (decadal- to century-scale) climatic changes in the western Great Lakes region within the past 2000 years, however, are poorly understood (Fritz *et al.*, 2000; Booth and Jackson, 2003; Laird *et al.*, 2003). A recent palaeohydrological record based on testate amoebae in the Upper Peninsula of Michigan shows a relatively wet period at 1800–1400 cal. yr BP (Booth *et al.*, 2004), coincident with the rising oak pollen percentages at Ferry Lake just prior to the switch to pine. The wet period ends at about 1400 cal. yr BP and is followed by 600 years of average to dry conditions. Syntheses of multiple climate records indicate that droughts were especially common between 670 and 1040 cal. yr BP in the Great Plains (Daniels and Knox, 2005) and other parts of the western USA (Cook *et al.*, 2004). Daniels and Knox (2005) show an increase in the incidence of droughts at multiple sites in the Great Plains beginning *c.* 1300 cal. yr BP, corresponding to the timing of the change from oak to pine at Ferry Lake.

The abrupt change from oak to pine dominance occurred in a much shorter time than the lifespan of individual trees, suggesting that it was caused by a discrete event. Surprisingly, there is no large charcoal peak at the time, so it is not likely that a large crown fire led to the decline of the oaks. It is possible that some other disturbance, such as a windstorm, a period of frequent surface fires, insect outbreak, pathogen or severe drought may have led to the replacement of oaks by pines. Changes in the sediment composition at Ferry Lake suggest that the vegetation change at 1450 cal. yr BP corresponds to a climate change. Diatom-rich layers ceased to be preserved in the sediment at the depth where oak pollen percentages declined (FL-2). The diatom-rich layers may have been the result of higher productivity or better preservation during the oak period (FL-1), which could have been linked to climate either directly or indirectly through changes in groundwater–lake interactions, aeolian inputs or wind exposure.

An especially severe drought (perhaps accompanied by a disturbance event) may have created conditions favourable for a switch to a more pine-dominated ecosystem (Givnish 2002). A severe recent drought in the AD 1980s resulted in 20% oak mortality over five years on a sandplain in central Minnesota (Faber-Langendoen and Tester, 1993). It is also possible that relatively small incremental changes in environmental factors can trigger a major shift in vegetation if a critical threshold is passed (Wilson and Agnew, 1992; Lynch, 1998; Scheffer and Carpenter, 2003; Lytle, 2005).

Response of vegetation and fire to regional climate change 800–100 cal. yr BP

There is evidence at Ferry Lake for a dramatic decline in fire after 800 cal. yr BP, when background CHAR values dropped to their lowest levels and stayed low until European settlement. The decrease in background charcoal influx roughly corresponds to a slightly more mesic pollen assemblage at Ferry Lake as well as to regional vegetation changes occurring off the sandplain (Laird *et al.*, 1996; Knox, 2000), including the expansion of mesic tree species in the Big Woods of Minnesota (Waddington, 1969; Grimm, 1983; Umbanhowar, 2004) and increases in mesic taxa in northern hardwood forests of Wisconsin (Swain, 1978; Gajewski *et al.*, 1985; Parshall, 2002). Although the gradual change in pollen assemblages at Ferry Lake is small and must to some degree reflect regional vegetation in addition to vegetation changes on the sandplain, the corresponding change in fire regime supports the interpretation that local vegetation and fire regimes responded to the regional climatic change.

The long-term perspective gained from this study raises the possibility that the mid-nineteenth century GLO surveys recorded a closed-canopy forest that developed over several centuries with less regular and possibly smaller or less intense fires than in previous centuries. The vegetation near Ferry Lake observed at the time of the GLO survey had developed during what was probably the most mesic period of the past 2300 years. The pollen assemblages from 700–100 cal. yr BP suggest a forest community with a more closed canopy than during any earlier period. The fire regime was also different 800–100 cal. yr BP, with much lower background CHAR than in previous centuries, and with no large charcoal peaks indicating local fires after 300 cal. yr BP. Our results suggest that the vegetation and fire regimes on the sandplain before and after 800 years ago may represent alternative management scenarios for the future, depending on the relative strengths of precipitation and evaporation in future climate regimes.

Patterns of change on the northwest Wisconsin sandplain

The record from Ferry Lake shows that at 1450 cal. yr BP an abrupt change in vegetation occurred in the apparent absence of strong regional climatic change or sudden change in fire regime. Similar state changes between barrens and forest vegetation during the early Holocene have been described on 30 km^2 sandplain in the Upper Peninsula of Michigan (Lytle, 2005). As at Ferry Lake, these rapid vegetation changes do not correspond with major regional climatic changes, although there is evidence that fire may be associated with the shifts. Rapid switches between contrasting vegetation types are anticipated by Scheffer and Carpenter (2003) in ecosystems with alternative stable states. The ability of sandplain vegetation to switch rapidly between different vegetation types and fire regimes suggests that future changes in vegetation and fire regimes may be unpredictable, making restoration efforts challenging in the face of climatic change (Suding *et al.*, 2004).

Our results also suggest that vegetation and fire regimes may change at different times and rates, even where vegetation–fire feedbacks may be strong. Studies of the response of vegetation and fire to middle-Holocene climatic change at the prairie–forest border in the upper Midwest show that changes in fire regimes lagged vegetation response to changing climate (Clark *et al.*, 2001; Camill *et al.*, 2003), although when examined at finer spatial and temporal scales in the Big Woods region of Minnesota the order of change in vegetation and fire regime appears to have varied among sites. In response to climatic change at *c.* 950 cal. yr BP, at some sites in the Big Woods region the vegetation change preceded changes in charcoal influx, while at some sites the reverse was true, and at others the changes in vegetation and fire regimes roughly coincided (Umbanhowar, 2004).

At Ferry Lake the vegetation change at *c.* 1450 cal. yr BP was preceded by a brief period with weakly periodic CHAR peaks tending to occur at 50–150 yr intervals. About 150 years after the vegetation change the first of several large charcoal peaks appears and the charcoal signal shifts to a pattern of large peaks every 130–200 years. This time lag in the response of fire to the change in vegetation may represent the time required for forests to mature and dead wood to accumulate. Alternatively a disease, disturbance or human activities may have caused the vegetation shift with only subtle climatic change, and then further climatic change (or vegetation change) in the next century may have altered the fire regime. In the more recent transition from the pine period (FL-2) to the white pine period (FL-3) at *c.* 700 BP, the charcoal influx dropped about 100 years before the pollen assemblage changed and the changes in the pollen percentages were relatively minor. This pattern suggests a slow successional change in vegetation following a decrease in fire frequency.

Interpreting feedbacks between vegetation and fire regimes from fossil records is intriguing, but may be misleading because it can be difficult to precisely pinpoint the timing and cause of a shift in vegetation or fire regime. Change may be continuous and gradual over a long period in response to an ongoing gradual climatic change, or fire regimes may respond gradually to relatively swift climatic change or to ecological succession and vegetation feedbacks that are independent of climatic change. Learning to differentiate among these possibilities remains an important future direction of palaeoecological research and will require better understanding of the spatial resolution of sedimentary records of vegetation and fire, as well as records from multiple sites. Local climate histories will have to be derived independently of the vegetation and fire histories using proxies such as testate amoebae (Booth and Jackson, 2003; Booth *et al.*, 2004), lake levels (Shuman *et al.*, 2001), diatom assemblages, and stable isotopes (Laird *et al.*, 1996; Valero-Garces *et al.*, 1997; Fritz *et al.*, 2000). Pre-historic human populations also had important effects on fire and vegetation dynamics (Curtis, 1959). Interviews with Ojibwa elders now living in this region support the importance of fire in managing blueberry crops on the sandplain in the past century (E. A. Lynch, personal observation, 1995). Unfortunately, little is currently known of cultural events at the times of vegetation change near Ferry Lake.

Conclusions

This is the first high-resolution study of the vegetation and fire history of the northwestern Wisconsin sandplain, an ecosystem distinctly different from the mesic forests that dominate the upper Great Lakes region. The record from Ferry Lake shows that there have been substantial changes in both vegetation and fire regimes during the last 2300 years, even though climatic changes during this period are generally assumed to be relatively minor. An abrupt vegetation change occurred at the site at 1450 cal. yr BP, when there is neither well-documented regional climate change nor evidence of a large fire. The onset of a fire regime with strong periodicity and relatively large CHAR peaks lagged the change in vegetation by nearly 150 years. The rapid switch from oak- to pine-dominated vegetation suggests that alternative states (Beisner *et al.*, 2003; Jasinski and Payette, 2005) exist for this sandplain as they do on a smaller sandplain 300 km east in the Upper Peninsula of Michigan (Lytle, 2005). The history of fire and vegetation near Ferry Lake suggests that future interactions among vegetation, climate and disturbance may result in sudden and unpredictable changes.

In the case of more mesic conditions 700–100 cal. yr BP, the Ferry Lake record shows that, as at other sites in the upper Midwest, vegetation and fire regimes on the sandplain responded to increased effective moisture. At Ferry Lake, there was a dramatic decrease in charcoal abundance *c.* 800 cal. yr BP, followed by gradual change to more mesic vegetation that occurred over several hundred years.

The feedbacks between vegetation and fire appear to have behaved differently at different time periods in the Ferry Lake record. At this point our ability to precisely document the causes of environmental changes and their spatial extent is limited, but we hope that with a network of strategically spaced sites across the sandplain we will be better able to resolve the late-Holocene dynamics of vegetation and fire on this landscape. In addition to increasing sampling density, our ability to understand the nature of feedbacks between vegetation and fire will improve when there are more independent climate records from this region and more information about prehistoric human land use patterns.

The late-Holocene dynamics in vegetation and fire provide an important perspective for land management goals on the sandplain. In many cases management goals reflect a desire to return the landscape to conditions at the time just prior to European settlement. However, the vegetation and disturbance regimes reconstructed from GLO vegetation data offer a snapshot in time and are not typical of the late-Holocene landscape. Prior to about 800 cal. yr BP, fire played a much larger role and the pollen assemblages suggest that the vegetation was open woodland or savanna. The dominance of pine and oak switched rapidly in the past, presenting the possibility of at least two alternative vegetation states. Restoration goals should take into account the range of pre-European settlement landscapes over the past 2300 years as well as future climate conditions.

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