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RESEARCH ARTICLE

Response of vegetation and fire to Little Ice Age climate change: regional continuity and landscape heterogeneity

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Abstract Late-Holocene climatic conditions in the upper Great Lakes region have changed sufficiently to produce significant changes in vegetation and fire regimes. The objective of this study was to determine how the vegetation mosaic and fire regimes on an oak (*Quercus* spp.)- and pine (*Pinus* spp.)-dominated sand plain in northwestern Wisconsin responded to climatic changes of the past 1,200 years. We used pollen and charcoal records from a network of sites to investigate the range of natural variability of vegetation on a 1,500-km^2 landscape on the southern part of the sand plain. A major vegetation shift from jack pine (*Pinus banksiana*) and red pine (*P. resinosa*) to increased abundance of white pine (*P. strobus*) occurred between 700 and 600 calendar years before present (cal yr BP), apparently corresponding to more mesic conditions regionally. A decrease in charcoal accumulation rate also occurred at most sites but was not synchronous with the vegetation change. At some sites there were further changes in vegetation and fire regimes occurring ~500–300 cal yr BP, but these changes were not as strong or unidirectional as those that occurred 700–600 cal yr BP. Our results suggest that both the composition and the distribution of vegetation of the southern part of the sand plain have been sensitive to relatively small climatic changes, and that the vegetation at the time of European settlement was a transitory phenomenon, rather than a long-term stable condition.

Keywords Charcoal analysis · Fire history · Landscape history · Little Ice Age · Climatic change · Pollen analysis · Sand plain · Vegetation history · Wisconsin

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Introduction

Forest management and conservation goals are dependent on what managers perceive as the "natural" vegetation of a site (Svenning 2002), and in many cases the best sources of information in eastern North America are the records of the Public Land Survey (PLS) (Whitney 1986; He et al. 2000; Schulte and Mladenoff 2001, 2005). In much of the United States the PLS records can provide details of the landscape distribution of forest types and major disturbances such as wind throw and fire just before the period of Euro-American settlement (Canham and

Loucks 1984; Whitney 1986; He et al. 2000; Schulte and Mladenoff 2001, 2005), but it is not known how representative the landscape recorded in the PLS was of the species composition, distribution of patches, and disturbance regimes of the last several hundred to 1,000 years. Establishing realistic management goals requires understanding the "range of natural variability" of vegetation (Swetnam et al. 1999), as well as climate and disturbance regimes. Because the lifespan of most forest trees is measured in centuries, predicting the response of forests to future climate change and management practices depends upon understanding their response to past climate, and the interaction of climate change with fire and vegetation feedbacks and human land use.

The climate of the pre-European settlement period may not be representative of late-Holocene conditions generally. Climate is seldom constant, and the last 1,200 years have experienced widespread climatic fluctuations such as the "Medieval Warm Period" [MWP; 950–700 calendar years before present (cal yr BP); BP = A.D. 1950] and "Little Ice Age" (LIA; ~650–100 cal yr BP). The MWP and LIA were not uniformly warm or cold, but many Northern Hemisphere sites experienced warmer or colder conditions more frequently during these periods (Bradbury and Dieterich-Rurup 1993; Matthews and Briffa 2005). These climatic changes affected vegetation over a wide area, including the western Great Lakes region. The development of the Big Woods in southeastern Minnesota has become a classic example of a major vegetation change caused by relatively minor climatic change and its interaction with fire breaks and vegetation feedbacks (Grimm 1983, 1984); approximately 40,000 km^2 of oak (*Quercus* spp) woodland filled in with elm (*Ulmus*), sugar maple (*Acer saccharum*), and basswood (*Tilia americana*) after about 700–500 cal yr BP, apparently in response to more mesic conditions of the LIA (Waddington 1969; Grimm 1983, 1984; Umbanhowar 2004).

The Big Woods is on the prairie-forest border, perhaps making it unusually susceptible to changes in moisture balance and fire frequency. How unusual was the development of the Big Woods? Did other forests of the region also change significantly in the last millennium? If so, was the timing of vegetation change synchronous at both regional and local scales? And how did vegetation and fire interact through this period of climatic change? These questions can be answered by applying locally calibrated paleoecological methods to reconstruct landscape-scale changes in vegetation. Fossil pollen and charcoal from small sedimentary basins reflect local vegetation (Jacobson and Bradshaw 1981; Sugita 1994; Calcote 1995, 1998; Parshall and Foster 2002; Gavin et al. 2003) and fire regimes (Gardner and Whitlock 2001; Gavin et al. 2003), and a network of sites can be used to reconstruct vegetation patterns and fire regimes across a landscape (Brubaker 1975; Davis et al. 1991, 1998; Lynch 1996, 1998; Fuller et al. 1998; Parshall et al. 2003; Sugita 2007a, b; Brostrom et al. 2004, 2005).

In this paper we use paleoecological methods to examine the vegetation and fire histories from five sites less than 40 km apart in the southern portion of the northwestern Wisconsin sand plain (Fig. 1). We use sediment cores from five small, deep lakes and 31 pre-European pollen assemblages calibrated with PLS vegetation data to reconstruct changes in vegetation at relatively fine spatial scales (5–10 km). The vegetation history is complemented by charcoal

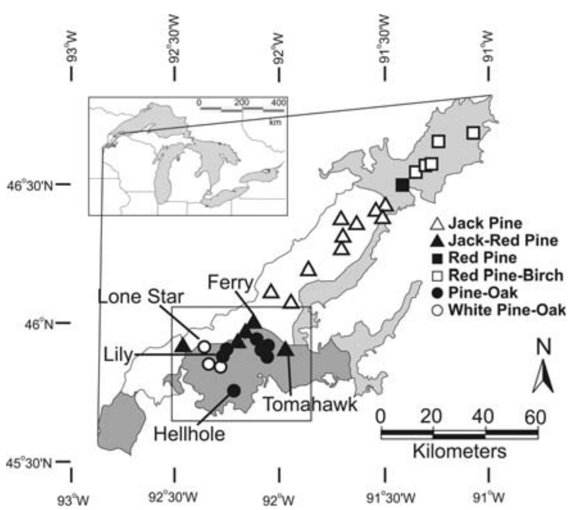

Fig. 1 Location of northwestern Wisconsin sand plain in the western Great Lakes region (inset). *Shading* indicates three major vegetation regions outlined in Radeloff et al. (1998); *White* indicates open jack pine vegetation and jack pine barrens in the central region, *medium gray* indicates closed-canopy pine forests in the north, and *dark gray* indicates open oak and pine savannas in the southern region. *Symbols* indicate vegetation types classified from PLS vegetation proportions within 5 km of 33 lakes. *Box* outlines study region. *Labels* indicate lakes from which pollen and charcoal data are presented

analysis from each site, allowing us to reconstruct changes in fire regimes and their relationships to vegetation changes. Our objective is to determine whether the distribution of vegetation types and the resulting landscape mosaic changed in response to the climatic changes of the last 1,200 years.

Description of study area

The northwestern Wisconsin sand plain is a large (~450 km^2) area of well-drained to excessively well-drained glacial outwash deposits with many kettle lakes, located between longitude 45°40′N and 47°N and latitude 91°W and 93°W (Fig. 1). Many native sand plain habitats and species are threatened due to fire suppression and land use changes, so there is strong interest in understanding and restoring the ecosystem (Vora 1993; Eckstein and Moss 1995; Neimuth and Boyce 1998; Radeloff et al. 2000). The modern climate is continental, with mean annual precipitation of 770 mm and daily January mean temperature of -13 and 20°C in July (Midwest Regional Climate Center 2005). Our study area is in the southern region of the sand plain, which at the time of the PLS (~A.D. 1850–1860 in this region) contained red, jack, and white pine (*Pinus resinosa, P. banksiana, P. strobus*), and oak (*Quercus* spp.), in contrast to the central region of the sand plain which was dominated by jack pine, scrub oak (*Quercus ellipsoidalis*), and barrens (Radeloff et al. 1998) (Fig. 1). The average distance from survey points to sampled trees in PLS data was often greater than 50 m in the southern region of the sand plain, suggesting oak and pine savannas maintained by frequent surface fires and rare crown fires (Radeloff et al. 1998).

The vegetation in the southern sand plain was heterogeneous before European-American settlement (hereafter referred to as 'pre-European'). The northern, eastern, and western parts of the study area had more jack pine and red pine, while the east-central region had more oak, and a patch in the west-central portion of the study area was characterized by mixed white pine and oak (Fig. 1). We selected five lakes that sampled the three major PLS vegetation types (jack-red pine, pine-oak, and white pine-oak, defined in S.C. Hotchkiss et al., in review) that were present in the southern sand plain study area (Fig. 1).

Methods

Sediment coring and chronology

We collected sediment cores from five small (<10 ha), deep (>10 m) lakes in the southern region of the sand plain. Cores from each lake were collected in a single drive using a 2- to 3-m polycarbonate tube fitted with a tennis-ball piston. The top of the tube was cut off in the field to remove the piston, and a surface sample was removed from the top of the core with a large bulb syringe. The top of the tube was then stuffed with floral foam to absorb excess water and pack the unconsolidated surface sediments to preserve the stratigraphy as cores were cut into <1.5 m sections and transported horizontally. Cores were split longitudinally at the Limnological Research Center, University of Minnesota, and subsampled for pollen, charcoal and Accelerator Mass Spectrometer (AMS) radiocarbon dating. Cores are archived at the National Lacustrine Core Repository, University of Minnesota.

Accelerator Mass Spectrometer radiocarbon dates were obtained on pollen concentrated from 5–6 ml of wet sediment (Brown et al. 1989; Regnell 1992; Richardson and Hall 1994) and converted to cal yr BP, where "present" is A.D. 1950, using OxCal version 3.9 (Ramsey 2003). Chronologies are based on linear interpolation between calibrated ^{14}C dates. The rise in *Ambrosia* (ragweed) pollen commonly associated with European settlement (Jacobson Jr and Grimm 1986) was also used as a chronological marker in all cores and assigned an age of 80 cal yr BP.

Pollen analysis and vegetation reconstruction

Fossil pollen from the lake-sediment cores was analyzed in 1-ml subsamples prepared with standard methods (Faegri and Iverson 1989). An average of 480 upland pollen grains (range 200–827) were identified and counted in each sample. Pine grains were counted in three categories; (1) white pine type (*Pinus* subgenus *Strobus*), (2) red-jack pine type (*Pinus* subgenus *Pinus*), and (3) undifferentiable pine type. Unfortunately, red and jack pine cannot be distinguished by their pollen. Undifferentiable pine pollen counts were divided between white and red-jack types in proportion to grains identified by type. Pollen samples were analyzed with 50–100 year resolution and plotted as percentages (% upland pollen) with TGView 2.02 (Grimm 2002). Pollen zones were determined by stratigraphically constrained cluster analysis (CONISS; Grimm 1987). Pollen zones are numbered from the most recent to the oldest so that deeper sediments can be added to the stratigraphy without changing zone numbers.

Interpretation of pollen assemblages as vegetation types is based on squared chord distance (SCD) analog analysis (Overpeck et al. 1985) and a decision tree developed with pre-European pollen assemblages from 31 small deep lakes spread across the northwestern Wisconsin sand plain (Fig. 2). Vegetation types were defined from the PLS vegetation data using cluster analysis of relative abundance of tree species within a 5-km radius around each reference lake (Fig. 1) as well as 50 random points spread across the landscape to place the lakes in an unbiased context (S.C. Hotchkiss et al., in review). Pollen assemblages from the pre-European sediment level of the 31 lakes (identified by the rise in *Ambrosia* pollen associated with European settlement) were taken to represent pollen assemblages produced by the PLS vegetation types and the range of ratios of pollen types found within a vegetation type was used to construct a pollen-based key to differentiating vegetation types (S.C. Hotchkiss et al., in review). The decision tree uses SCD analogs (Overpeck et al. 1985) to determine whether there are pollen assemblages in our 31 pre-European samples that are similar enough to the fossil assemblage to be interpreted from our PLS vegetation classification. Fossil samples with fewer than three pre-European analogs (SCD < 0.07) are considered to be outside the range of our calibration data set and are not classified by the decision tree. Fossil samples with at least three analogs continue through the decision tree, comparing ratios of major pollen types in the fossil sample to ratios typical of pre-European vegetation types. After ratio comparisons the fossil sample is classified as one of the pre-European vegetation types or, in rare cases, not assigned to a vegetation type because the pollen ratios fall outside of the ranges defined by the calibration set. (Fig. 2; additional details in S.C. Hotchkiss et al., in review).

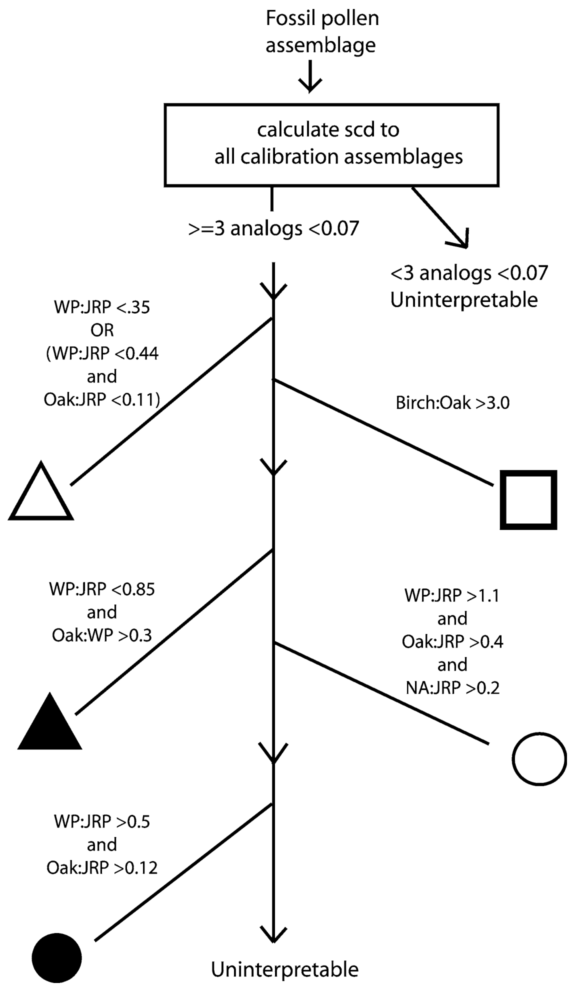

Fig. 2 Decision tree used for interpretation of vegetation types from pollen assemblages. *SCD* squared chord distance used to calculate similarity between each pollen assemblage to be interpreted and 31 pre-European pollen assemblages from the sand plain. Pollen types are abbreviated as follows: *WP* white pine, *JRP* jack-red pine, *PF* Prairie forbs (sum of Chenopodiaceae, *Artemisia*, and unidentified Asteraceae), *NA* non-arboreal (sum of PF, Poaceae, *Corylus*, *Salix* and *Myrica/Comptonia-type*)

Charcoal analysis

The influx rates of charcoal fragments sieved from contiguous sediment samples are routinely used as a record of prehistoric fire occurrence (methods reviewed in Whitlock and Larsen 2002). Theoretical and empirical studies demonstrate that charcoal >125 µm in length is generally not transported long distances from fires, so it provides a good indicator of local fire events (Clark and Royall 1995; Gardner and Whitlock 2001; Gavin et al. 2003; Lynch et al. 2004). The charcoal source area of small lakes on the sand plain has not been empirically tested, but observations from lakes of similar sizes in the western US and Canada suggest that fires occurring beyond about 500 m from the lake will not be detected (Gardner and Whitlock 2001; Gavin et al. 2003).

We identified and counted charcoal >125 μm in length in contiguous 0.5-cm intervals below the *Ambrosia* rise in each core, calculated accumulation rates, and separated the accumulation curve into background and peak components, producing a pre-European charcoal record with a resolution of ca. 10–20 years from 80 to 1,200 cal yr BP. 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 gently wet-sieved. All charcoal particles >125 μm in length were counted to determine the concentration (number of particles/cm^3 sediment). Charcoal identified as graminoid cuticle type (hereafter referred to as 'grass charcoal') is included in the total CHAR category, but is also reported separately in order to give some indication of the fuel burned (Palmer 1976; Jensen et al. 2007). Charcoal concentration values were converted to charcoal accumulation rates (CHAR; number of particles/cm^2/year) by dividing concentration by the number of years/cm.

In order 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), CHAR values were interpolated to 10-year intervals, then smoothed using LOWESS (Cleveland 1979) with a window width of 300 years. Interpolation of the CHAR record to even age intervals and smoothing of the interpolated record were done in the CHARSTER program (Gavin 2006; version 0.8.3).

To identify the charcoal peaks most likely to be associated with local fire events we used CHARSTER to create a Gaussian mixture model that fit two overlapping Gaussian distributions to the peak frequency distribution for each site (Gavin et al. 2006). We looked for a threshold value that fell between the means of the two distributions described by the Gaussian mixture model and that was within a range of values to which the number of peaks detected was insensitive. Each CHAR peak exceeding the threshold for that site is interpreted as a fire event that represents one or more fires occurring within the charcoal source area of the lake.

Results

Chronology

The sediments from all five lakes were homogeneous brown diatomaceous sappropel, with occasional very fine light laminae suggesting meromixis and preservation of fine temporal resolution. All five sites had relatively constant sedimentation rates over the past 1,200 years (Fig. 3). Lily, Lone Star, and Tomahawk Lakes had brief age plateaus around 1,200 cal yr BP. For purposes of our focus on long-term changes in vegetation, we estimated age by linear interpolation to the average of the two plateau dates. Additional dates will be needed to determine whether the apparent plateaus are real, perhaps due to a period of rapid sediment deposition. Dates assigned to lower sections of the cores, especially before 800 cal yr BP, may be off by 100–200 years.

Sediment accumulation rates calculated from AMS dates provide a temporal resolution of 5–12 years/charcoal sample, although Ferry Lake has 14–28 years/sample and Lonestar Lake has 23 years/sample during the period 80–557 cal yr BP, compromising our ability to detect fire frequencies smaller than about 50 years.

Lily Lake

The most abundant pollen types in the earliest pollen zone (Lil-3, 1,200–690 cal yr BP) are red-jack pine (30–40%) and oak (~20%) (Fig. 4a). Lil-3b is characterized by increasing abundance of oak pollen, which reverses sharply at the beginning of Lil-3a (840 cal yr BP). There are few analogs to this zone in our pre-European library due to higher oak pollen abundance than in any of our 31 pre-European pollen assemblages. Weak analogs to jack-red pine, pine-oak, and white pine-oak, and ratio interpretations of jack-red pine vegetation begin just before 800 cal yr BP, switching to pine-oak at the end of Lil-3a. In Lil-2 (690–80 cal yr BP) white pine increases to ~30% and remains fairly constant until the post-settlement zone. Toward the end of this zone (Lil-2a; 250 cal yr BP) jack-red pine and ironwood (*Ostrya–Carpinus*) pollen percentages decrease further and alder (*Alnus*) increases. Lil-2 has strong analogs in the pine-oak and white pine-oak types throughout, with

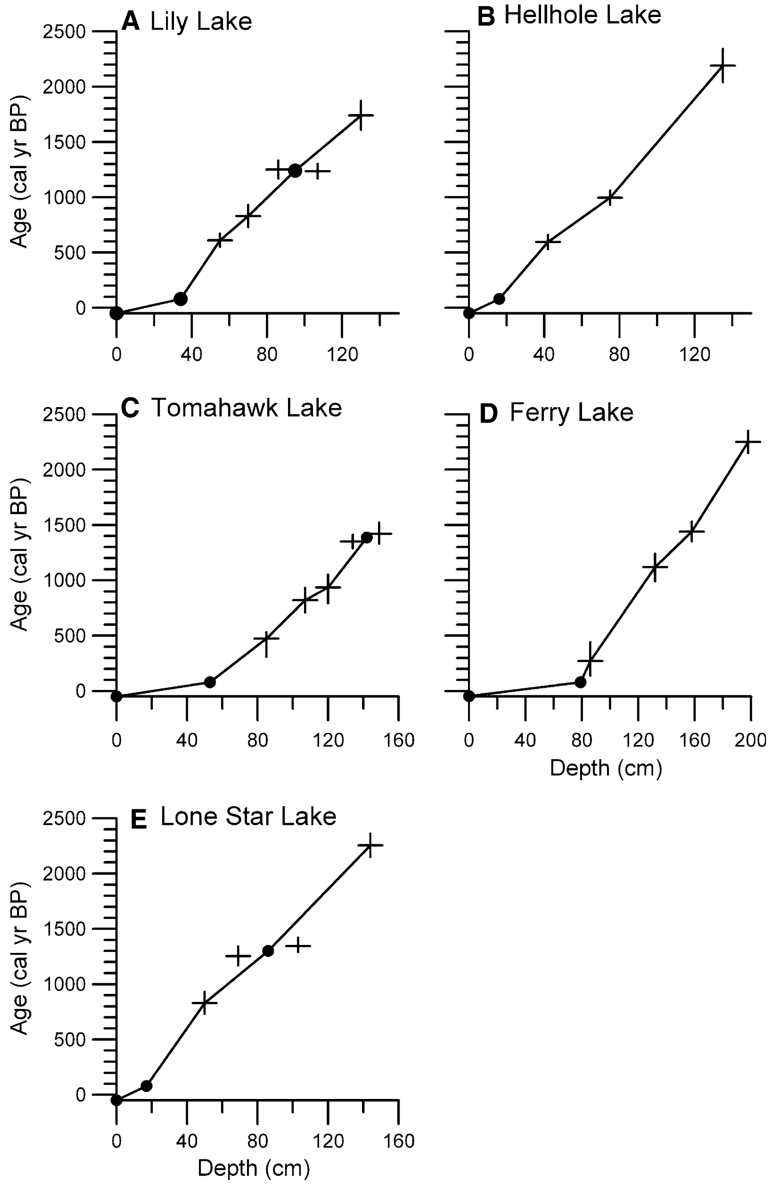

Fig. 3 Age–depth relationships for chronological interpretation of sediments from five lakes. *Crosses* indicate AMS radiocarbon dates. *Horizontal line* indicates age estimate used in chronologies for Figs. 4 and 5, *vertical line* indicates 95% confidence interval of calibrated radiocarbon age (OxCal v 3.9). *Black circles* indicate surface (defined as −50 cal yr BP), pre-European sample (defined as 80 cal yr BP) and ages interpolated between problematic AMS radiocarbon dates. *Lines* show linear interpolations between radiocarbon dates or other age estimates used to establish the chronology

ratio interpretations consistently indicating white pine-oak vegetation type after 400 cal yr BP. Lil-1 represents the period of European settlement, with a sudden drop in white pine and an increase in ragweed pollen. Ratio interpretations shift to jack-red pine and pine-oak vegetation during Lil-1. Oak increases dramatically in the surface sample and there are no pre-European analogs to the surface pollen assemblage.

Total CHAR in Lily Lake was higher than at the other sites (median = 6.04; range 0.59–28.8 fragments/cm^2/year) (Fig. 4a). Prior to ca. 575 cal yr BP charcoal influx rates were relatively high (ca. 10 fragments/cm^2/year), and peaks of CHAR occurred one to two times per century. After 575 cal yr BP both total CHAR and the frequency of charcoal peaks decreased, although influx rates at this site remained higher than at the others. Although there is a large CHAR peak 700 cal yr BP when oak and jack-red pine pollen decreases and white pine increases (pollen zone boundary between Lil-3a and Lil-2b), the decrease in CHAR occurs about 100 years after the pollen zone boundary. The influx of grass charcoal was high at Lily Lake throughout

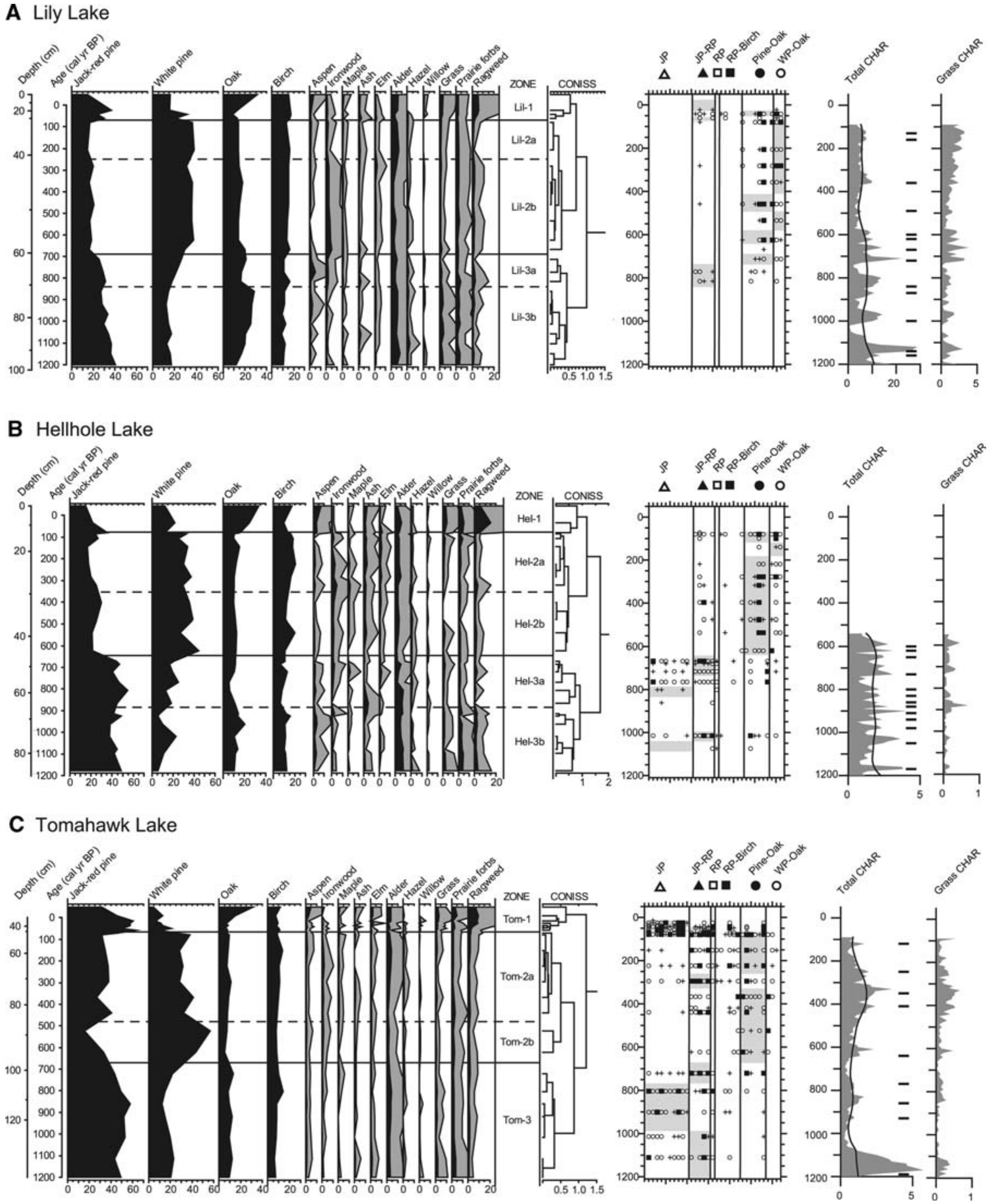

Fig. 4 Pollen percentage diagram of selected pollen types, pre-European pollen analog and ratio interpretations, and accumulation rate (CHAR) of total and grass-type charcoal for five sites. Pre-European vegetation analogs are shown as *black dots* for samples with squared chord distance (SCD) analogs < 0.4, *open dots* for analogs with SCD > 0.4 but <0.6, *plus symbols* for analogs with SCD > 0.6 but < 0.7, and *no mark* for samples without analogs with SCD < 0.7. *Shading* behind samples within a vegetation type indicates that our decision tree leads to the interpretation that the fossil sample represents that PLS vegetation type (S.C. Hotchkiss et al., in review). *No shading* indicates that our decision tree does not interpret the sample, either because too few analogs are present, or because the pollen assemblage does not fall within an interpretable range

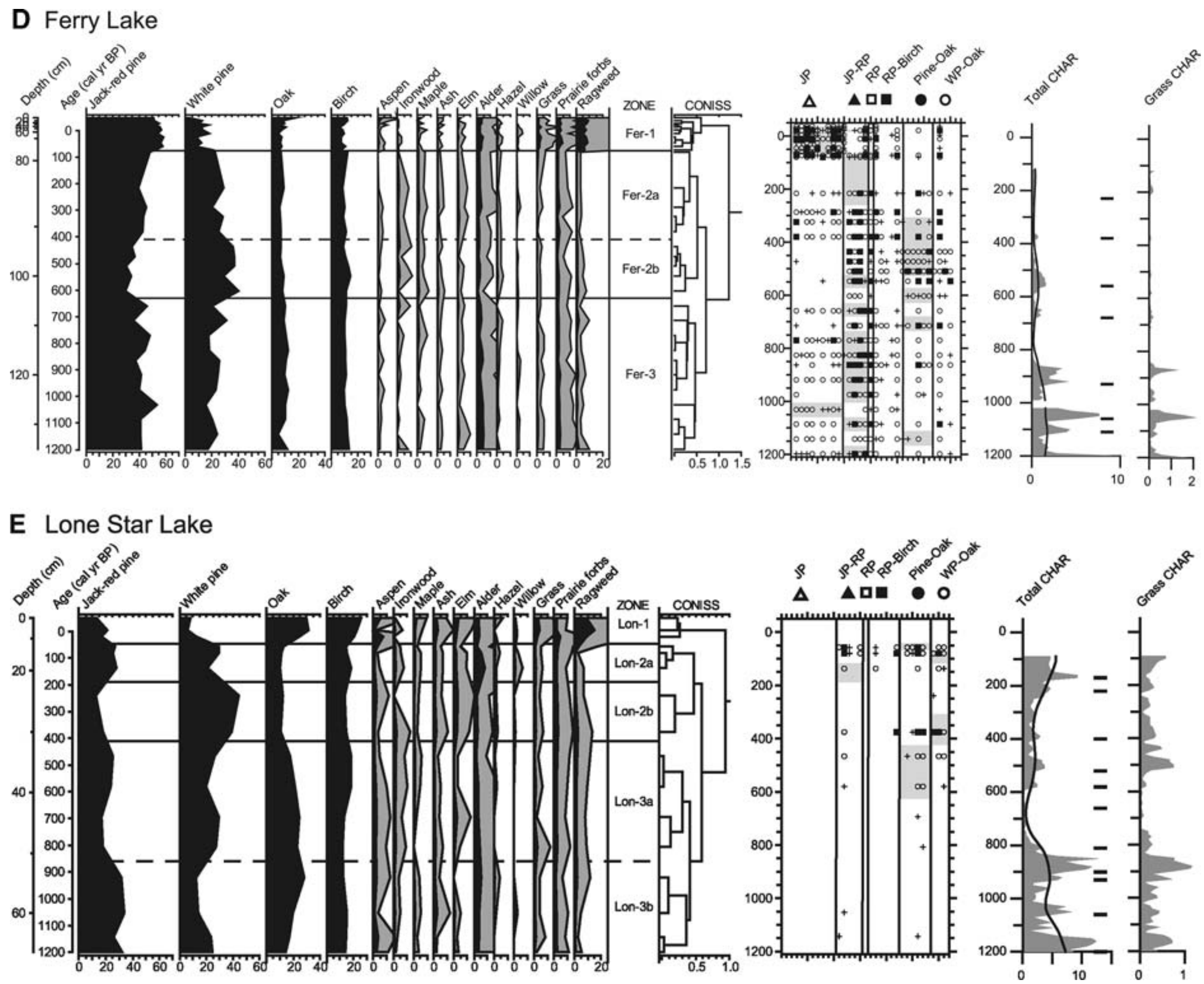

Fig. 4 continued

the record, and was generally increasing during the white pine zone (Lil2b), reaching its highest values during Lil-2a.

Hellhole Lake

The earliest pollen zone in Hellhole Lake (Hel-3; 1,200–640 cal yr BP) is characterized by abundant jack-red pine pollen (40–50%) (Fig. 4b). Non-arboreal pollen percentages are high at the beginning of the zone (Hel-3b), decreasing after ~900 years ago (Hel-3a). Analogs to pre-European pollen assemblages are generally poor during Hel-3b, but assemblages are increasingly similar to jack pine and jack-red pine vegetation types during Hel-3a. Hel-2 (640–70 cal yr BP) is marked by a sharp decrease in jack-red pine pollen and increase in white pine pollen. Birch (*Betula*) pollen percentages are slightly higher (15–20%) during Hel-2. Analog and ratio interpretations shift to the pine-oak vegetation type in Hel-2b. After 350 cal yr BP (Hel-2a) jack-red pine pollen decreases further as birch and alder increase slightly and there is a slight increase in the strength of analogs in the white pine-oak vegetation type. Hel-1 is defined by the sharp decrease in white pine and increase in ragweed pollen characteristic of the European settlement period.

The recent part of the charcoal record at this site has not yet been analyzed, but influx rates were uniformly low (median = 1.69; range 0.41–4.00 fragments/cm^2/year) from 1,200 to 550 cal yr BP (Fig. 4b). Although many charcoal peaks occur, they are small. Clusters of peaks occur in the time periods 1,000–800 and 650–600 cal yr BP, during pollen zone Hel-3 which is dominated by jack-red pine pollen.

Tomahawk Lake

Abundant jack-red pine pollen (40–50%) characterizes the early record at Tomahawk Lake (Tom-3; 1,200–670 cal yr BP) and analog and ratio interpretations indicate that the vegetation was most similar to pre-European jack pine and jack-red pine vegetation types (Fig. 4c). Alder pollen is also relatively high during this zone. Jack-red pine pollen decreases slightly toward the end of the period where there is a slight rise in white pine and birch pollen percentages. During zone Tom-2 (670–80 cal yr BP) both types of pine pollen remain moderately high (usually ~30% each), although the abundance of white pine pollen peaks early in the zone (Tom-2b). Tom-2 analog and ratio interpretations are primarily in the pine-oak type, with a brief switch to jack-red pine at about 300 cal yr BP. During the European settlement era (Tom-1) ragweed and other non-arboreal pollen types increase. Jack-red pine pollen percentages also increase as white pine decreases and analogs and ratios switch to jack pine and jack-red pine vegetation types. Oak pollen percentages reach their highest values of the last 1,200 years (>20%) in the last several samples, for which there are no pre-European analogs.

Charcoal influx rates are low at Tomahawk (median = 0.95, range 0.26–5.73 fragments/cm^2/year) (Fig. 4c), similar to rates at Hellhole and Ferry lakes (Fig. 4b, d), although prior to 1,200 cal yr BP all three sites had many large (5–10 fragments/cm^2/year) CHAR peaks (data not shown). CHAR is lowest 1,050–650 cal yr BP, a period with jack pine then jack-red pine vegetation (Tom-3). Influx rates are slightly higher after ca. 650 cal yr BP when white pine pollen percentages are increasing (Tom-2b). Both total and grass charcoal influx peak between 450 and 250 cal yr BP (Tom-2a).

Ferry Lake

The pollen record from Fer-3 (1,200–630 cal yr BP; FL-2 in Lynch et al. 2006) has high jack-red pine pollen percentages (~40%) with moderate levels of white pine pollen (~20%) (Fig. 4d). Alder pollen is at its most abundant in this zone. Weak analogs occur to all vegetation types during Fer-3, with strong analogs primarily to jack-red pine samples. Jack-red pine pollen percentages decrease and white pine pollen percentages increase about 650 years ago, at the beginning of Fer-2b. After 400 cal yr BP white pine pollen decreases and jack-red pine pollen increases again, resulting in pollen assemblages that look very much like Fer-3. Samples in Fer-2b lose the weak analogs to jack pine vegetation types and have stronger analogs to pine-oak and white pine-oak vegetation types, with ratio-based interpretations switching to pine-oak type. As white pine pollen decreases in Fer-2a, analog and ratio interpretations again shift toward the jack-red pine vegetation type. The most recent pollen zone (Fer-1) begins with an increase in ragweed and other non-arboreal pollen, and a decrease in white pine pollen percentages.

Median CHAR at Ferry Lake was low (0.44; range 0–10.65) and declined at ca. 850 cal yr BP from values of 5–10 fragments/cm^2/yr to near 0 for the rest of the record (Fig. 4d). The decrease in CHAR comes 200–300 years before the pollen zone boundary between Fer-3 and Fer-2b when white pine increases. Grass charcoal influx decreased at the same time. This decline in CHAR coincides with the change from jack-red pine to a period with fluctuations between jack-red pine and pine-oak vegetation types. The frequency of charcoal peaks is low throughout the record (150–200 years between peaks is common). There is a slight increase in CHAR from ~650 to 450 cal yr BP, corresponding to the period with highest white pine pollen percentages (Fer-2b).

Lone Star Lake

The earliest pollen zone at Lone Star (Lon-3; 1,200–410 cal yr BP) has two distinct subzones (Fig. 4e). Lon-3b (1,200–860 cal yr BP) is characterized by moderately high jack-red pine and oak pollen percentages, followed by moderately high white pine and oak in Lon-3a. Analogs to pre-European samples are poor throughout Lon-3 due to the high oak pollen percentages. At the beginning of Lon-2b white pine pollen increases further (to ~40%), as jack-red pine decreases again and oak decreases to the lowest levels of the sequence. Strong analogs remain rare, but occasionally occur in pine-oak or white pine-oak vegetation types. Better analogs appear toward the end of Lon-2a just before European settlement. Lon-1 is characterized by the rise in ragweed pollen and decrease in white pine found in all our sites at the beginning of European settlement. Oak, ragweed and aspen increase during this period.

The charcoal record at this site is similar to the record at Lily Lake, with relatively high influx levels (median = 2.31; range 0.10–12.77 fragments/cm^2/year) (Fig. 4e). It differs from the Lily Lake record, however, in that CHAR drops earlier (ca. 830 cal yr BP) as white pine increases at the beginning of Lon-3a. Both total and grass charcoal influx rates are lowest 800–600 cal yr BP. CHAR gradually increases ca. 600 cal yr BP to European settlement, before the increase in white pine pollen in Lon-2a. Charcoal peaks occur about once every 100–150 years throughout the record.

Discussion

Regional response to climatic change 700–600 cal yr BP

A vegetation change occurred between 700 and 600 cal yr BP at most of our sites (Fig. 4). White pine pollen percentages increase and jack pine and jack-red pine vegetation types become pine-oak or white pine-oak types at this time. Oak pollen percentages remain the same or decrease, suggesting that the primary vegetation change leading to the shift in vegetation analogs is increased white pine abundance (Fig. 4a–e). Increasing white pine and decreasing jack-red pine on the coarse-textured soils of the sand plain strongly suggest increased moisture and lower fire frequency. An increase in pollen of other relatively mesic taxa such as ironwood (*Ostrya–Carpinus* pollen type) occurs in several sites at about the same time. The interpretation of a climatic shift to more mesic conditions is supported by the decrease in charcoal accumulation during the LIA, although the decreases in CHAR are not as synchronous among sites as the vegetation changes (Fig. 4). Decreases in CHAR could also be caused by reduced fuel loads in response to more xeric conditions during the growing season; however, this interpretation is contradicted by changes in the pollen assemblages to more mesic vegetation.

The interpretation that the vegetation change 700–600 cal yr BP indicates the beginning of more mesic conditions is consistent with other vegetation histories from the region. The development of the Big Woods in southern Minnesota was originally estimated to have taken place only 400–300 cal yr BP (Waddington 1969; Grimm 1983, 1984), but has more recently been dated at about 700 cal yr BP (Umbanhowar 2004). Swain (1978) also interpreted increased white pine and hemlock (*Tsuga canadensis*) pollen and a decreased ratio of charcoal to pollen in Hell's Kitchen in north-central Wisconsin about 600 cal yr BP as the beginning of more mesic conditions.

The timing of the climate and vegetation changes in northern Wisconsin coincides with the beginning of the LIA in Europe. Although the classic LIA is sometimes considered to begin several hundred years later, recent analysis indicates an abrupt beginning to cooler conditions ~650 cal yr BP (~1,300 A.D., Matthews and Briffa 2005). Moisture reconstructions based on testate amoebae suggest high variability 1,000–700 cal yr BP in the western Great Lakes region, with most sites showing lower variability and both testate amoebae and diatoms recording relatively moist conditions after 600 cal yr BP (Brugam et al. 1998; Booth et al. 2004, 2006; Booth and Jackson 2003). While the timing of climatic change is approximately synchronous across this region, the nature of the changes may be spatially heterogeneous (Bradbury and Dieterich-Rurup 1993).

The synchronous changes in vegetation we observed 700–600 cal yr BP suggest that vegetation response to increasing moisture is quite predictable at time scales of several hundred years across the southern sand plain, but at finer temporal and spatial scales, vegetation and fire regimes are much less predictable. As in other studies from the upper Midwest, we found no consistent pattern in the timing of changes in charcoal influx or peak frequency relative to vegetation changes (Umbanhowar 2004; Lytle 2005; Lynch et al. 2006). At Ferry Lake charcoal influx decreased 150–200 years before the increase in white pine, suggesting that the change in fire regime allowed successional vegetation change (Fig. 4d; Lynch et al. 2006). At Lone Star Lake the changes in CHAR and vegetation were roughly synchronous at 800 cal yr BP (Fig. 4e). At Lily Lake the decrease in CHAR and in frequency of charcoal peaks lags the increase in white pine pollen percentages by about 100 years (Fig. 4a), suggesting that vegetation feedbacks could have contributed to the change in fire regime. While these complexities in the interactions among climate, vegetation, and fire regimes are not unexpected (Wilson and Agnew 1992; Turner and Dale 1998; Platt et al. 2002), they underscore the difficulty in predicting the response of sand plain ecosystems to management of fire regimes at time scales of one or two generations of trees.

Vegetation change 500–300 cal yr BP

Vegetation changes in the last 500 years are less uniform in type or timing than changes 700–600 cal yr BP. White pine-oak vegetation is established at Lily Lake by 650 cal yr BP and stays relatively constant for 500 years, but other sites have a gradual decrease in white pine after 600 cal yr BP and/or a change in vegetation type between 500 and 300 cal yr BP (Fig. 4). Hellhole, Tomahawk, Ferry, and Lone Star Lakes all have a pollen/vegetation zone boundary between 450 and 350 cal yr BP, but the direction of change is not consistent. At Lone Star Lake a renewed increase in white pine pollen abundance occurs at 400 cal yr BP, but at Ferry and Tomahawk Lakes white pine pollen decreases slightly and analogs shift to the jack-red pine vegetation type. Changes in CHAR also vary; Lily and Tomahawk Lakes both show an increase in CHAR around 400 cal yr BP while other sites experience little or no change (Fig. 4). Several studies from sites near the sand plain suggest mesic vegetation increased in the last 500 years. Hemlock pollen abundance increased at four forest hollows about 25 km east of the sand plain within the last 500 years (Parshall 2002), and Gajewski et al. (1985) reported decreased jack-red pine and increased white pine and ironwood pollen about 500 years ago in varved lakes on glacial till about 60 km southeast of Hellhole Lake. Both of these vegetation changes are consistent with either the onset of more mesic climatic conditions or reduced human populations and less anthropogenic burning.

This period is approximately synchronous with the classical LIA in Europe (Matthews and Briffa 2005) and our results are consistent with a continued cool/wet climate (relative to the climate before 700 cal yr BP). Occasional dry periods within an otherwise relatively cool and moist LIA, however, may have acted as catalysts for vegetation changes at some sites, and account for the inconsistency of the apparent direction of climate change from different sites. Tomahawk, Ferry, and Lone Star Lakes have peaks in CHAR ~400 cal yr BP and Lily and Tomahawk Lakes have prominent peaks in CHAR ~350 cal yr BP. Nearby sites also have charcoal peaks 400 cal yr BP (Gajewski et al. 1985). South Rhody peatland in the Upper Peninsula of Michigan, which has generally higher water levels 600–200 cal yr BP, shows a short but marked drought at 400 cal yr BP (Booth et al. 2004), coincident with evidence for severe droughts throughout western North America (Laird et al. 1996; Woodhouse and Overpeck 1998; Stahle et al. 2000).

Effects of Native American land use

The synchronicity of vegetation change among sand plain sites 700–600 cal yr BP suggests a regional change in climate, human land-use practices, or both. Although we focus our discussion of the causes of vegetation and fire regimes on climatic change, we recognize that the behaviors of native peoples, including their land management practices and changes in population size and density, also may have contributed to changes in vegetation composition and fire regimes. Contemporaneous changes in cultural behavior and vegetation may be unrelated, one may cause the other, or both may be affected by a common external change such as climate. It is not possible to differentiate effects of changing human land use from climatic effects on the sand plain without additional well-dated archeological sites (Harrison 1990).

Building on analogies with ethnographic studies, Day (1953) suggested that Late Woodland, Oneota and protohistoric cultures of the Upper Midwest used burning as a land management tool, but the degree to which they influenced the regional pre-European vegetation and fire regimes is controversial, and changes in the use of fire by successive cultures in the region remain unknown. Paleoecological studies in New England suggest that human land use had a relatively minor influence on vegetation and fire before European settlement (Fuller et al. 1998;

Parshall et al. 2003). However, Loope and Anderton (1998) estimated that fires ignited by humans may have accounted for more than half of the fires in coastal areas of northern Michigan immediately before and after Euro-American settlement, suggesting that humans may have played an important role in controlling fire regimes and vegetation in this region.

Several periods of cultural change in the upper Midwest may roughly correlate with the timing of vegetation change on the sand plain. Although temporal correlation should not be interpreted as causation, especially in the absence of local archaeological data, the Late Woodland period in southern Wisconsin begins about 1,500 cal yr BP (Stevenson et al. 1997), approximately when the vegetation surrounding Ferry Lake (Fig. 1) changed from oak to pine dominated woodland (Lynch et al. 2006). Elsewhere in eastern North America, increasing population density, greater prevalence of permanent settlements, and the rapid spread of the bow and arrow during the Late Woodland period (Harrison 1990; Stevenson et al. 1997) may have affected vegetation composition. It is unclear to what degree the sand plain was used by Late Woodland people, although Clam River sites in the southern sand plain probably date from the Late Woodland period (Stevenson et al. 1997).

Late Woodland cultural traditions may have persisted in some parts of the upper Midwest, including northern Wisconsin, until European contact, as they did in the Northeast. However, to the south and east of the sand plain, the Oneota cultural tradition emerged between about 1,000 and 750 cal yr BP (Stevenson et al. 1997; Brown and Sasso 2001; Theler and Boszhardt 2003; Sasso 2003), corresponding to the timing of fire and vegetation changes on the sand plain. Oneota people south and east of the sand plain were practicing maize agriculture by this time (Boszhardt 1994; Overstreet 1997; Theler and Boszhardt 2003), which may have entailed more active management of vegetation on the landscape, but there is little evidence for agriculture or sedentism on the sand plain.

Native American populations and settlement patterns changed dramatically in the last 500 years due to many causes, including warfare, migration, and the introduction of European diseases (Overstreet 1997; Schroeder 2004). The Ojibwa moved into the sand plain area around 400–300 cal yr BP, displacing Sioux and Fox tribes (Swanton 1952; White 1991), contemporaneous with changes in vegetation at Hellhole, Tomahawk, Ferry, and Lone Star Lakes on the sand plain (Fig. 4). The Ojibwa collected wild rice, maple sugar, and berries, and fished and hunted, occupying seasonal habitations, and they used fire to promote forage for wildlife, drive game, and promote berry and nut production (Murphy 1931; Loope and Anderton 1998). While little archaeological evidence of land use practices is available from the sand plain, temporal correlations between regional cultural change and local vegetation change on the sand plain invite further investigation.

Range of natural variability in time and space

The modern vegetation of the sand plain, like most regions, is greatly altered by modern land use practices (Radeloff et al. 1998, 1999), leading to the implicit assumption in much of ecological and conservation thinking that before these recent changes there was a "natural vegetation" that occurred in equilibrium with climate, soil, and ecological interactions. Paleoecological methods applied to landscape-scale vegetation and fire histories offer exciting potential for providing a long-term context for modern and historical data. How variable is "natural vegetation" over time? How constant are landscape patterns over hundreds of years? What is the range of restoration goals that are appropriate to the spatial, temporal and climatic variability of the present and future?

This study shows that the vegetation and fire regimes of the sand plain are sensitive to relatively small climatic changes. At Ferry and Lily Lakes the PLS vegetation type occurred during only about half of the past 1,200 years; Tomahawk, Hellhole, and Lone Star Lakes were surrounded by their PLS vegetation types for shorter times (Fig. 4). Even within the more recent LIA period ($\sim$600–150 cal yr BP) the PLS vegetation types were present less than half the time at Lily, Hellhole, and Ferry Lakes, while Lone Star and Tomahawk Lakes were rarely surrounded by their PLS vegetation types. At Lone Star, Tomahawk, and Hellhole Lakes the PLS vegetation type was in place for less than 100 years before the PLS survey was conducted (Fig. 4). These results suggest the PLS survey recorded transitory vegetation at these sites. Precise interpretation of vegetation changes in the last 100 years before European settlement will require higher temporal resolution paleoecological data. Our estimates of vegetation change within the last 100 years before European settlement may be conservative, because we used both the increase in *Ambrosia* pollen and the decrease in white pine pollen as markers of land clearance and European settlement. This strategy is more likely to set the settlement horizon too early than too late, avoiding the overestimate of pre-European vegetation change that could occur if sediments that accumulated after European land clearance began were included in the pre-European period.

In addition to detecting changes over time, our network of five sites allows us to investigate the stability of the broad spatial patterning of vegetation across the study area. Even though the vegetation at individual sites has changed, we might expect that edaphic and topographic features would have imposed a relatively stable landscape pattern in the distribution of vegetation types. Some aspects of the spatial pattern were persistent through time. Lily and Lone Star, the westernmost lakes, consistently have higher abundance of oak pollen than Ferry, Tomahawk and Hellhole Lakes. This difference is most apparent before 700 cal yr BP, but continues throughout the LIA period (Fig. 4). Overall, however, the landscape vegetation pattern observed in our study area did not remain consistent over the past 1,200 years (Fig. 5). Ferry and Tomahawk Lakes, which had the same PLS vegetation type, differed in vegetation many times over the past 1,200 years (Figs. 4, 5). While there were periods when a vegetation pattern similar to the PLS pattern was observed (e.g. 400 cal yr BP Lily and Lone Star Lakes share a vegetation type, as do Hellhole, Tomahawk, and Ferry), there were no periods when all five sites showed the same geographic pattern of vegetation as they did in the PLS data (Fig. 5).

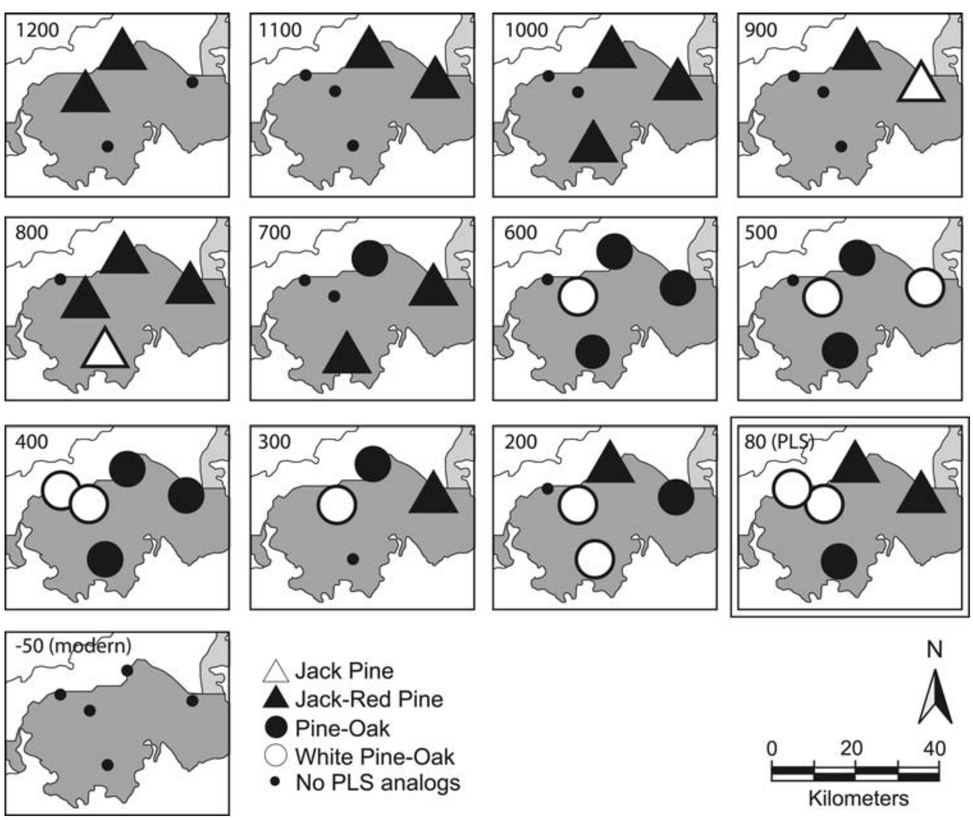

Fig. 5 Changes in vegetation pattern over 1,200 years. Age intervals in cal yr BP, where −50 cal yr BP is modern. *Maps* indicate the vegetation interpretation of the pollen assemblage that is nearest to each 100-year interval. *Symbols* represent PLS vegetation types as in Fig. 1. If no pollen assemblage was analyzed within 45 years of each 100-year interval, no interpretation is plotted

The dynamic nature of the vegetation, both at single sites and in the broad spatial patterning of vegetation types, has important implications for conservation strategies that depend on establishing benchmarks for restoration. The idea that vegetation persisted as a stable entity over long periods in North America before European settlement has been largely abandoned as ecologists came to understand the constant variability of climate and ecological responses to it (Davis 1986; Sprugel 1991; Tilman and El Haddi 1992; Gillson and Willis 2004) and the importance of disturbances in producing a mosaic of vegetation types (Heinselman 1973; Pickett and White 1985). The PLS data are a valuable source of detailed information about the landscape before extensive logging and agriculture, but they represent a particular period in time; in the case of northwestern Wisconsin, that period may be a time of climatic change at the end of the LIA.

Conclusions

Our results suggest that applying paleoecological methods to a network of sites across a landscape can provide long-term perspective on the natural variability of vegetation, complementing the more detailed snapshot available from PLS data. A longer perspective is essential for landscape-scale conservation and ecological studies (Gillson and Willis 2004; Mladenoff et al. 2002; Anderson et al. 2006).

(1) White pine pollen increased and charcoal influx decreased across the study area about 600–700 years ago, suggesting a regional response to cooler/wetter conditions associated with the LIA.
(2) There is another period of change at most sites around 300–500 cal yr BP, but rates, timing, strength and the type of change varied from site to site.
(3) The PLS pattern of vegetation is not representative of the past 1,200 years; both the type of vegetation at a given site and the spatial pattern of vegetation types across the landscape have changed.
(4) The vegetation of the sand plain is sensitive to small climatic changes, and the complex interaction of climate, vegetation and fire leads to changes in fire regimes that are not necessarily synchronous with vegetation changes.

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