THE INFLUENCE OF ARIDITY AND FIRE ON HOLOCENE PRAIRIE COMMUNITIES IN THE EASTERN PRAIRIE PENINSULA

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Abstract. The role of climate and fire in the development, maintenance, and species composition of prairie in the eastern axis of the tallgrass Prairie Peninsula intrigued early North American ecologists. However, evaluation of the long-standing hypotheses about the region’s environmental history has been hampered by the scarcity of paleorecords. We conducted multiproxy analyses on early and middle Holocene sediments from two Illinois, USA, lakes to assess long-term climatic, vegetational, and fire variability in the region. Sediment mineral composition, carbonate δ18O, ostracode assemblages, and diatom assemblages were integrated to infer fluctuations in moisture availability. Pollen and charcoal δ13C were used to reconstruct vegetation composition, and charcoal influx was used to reconstruct fire. Results indicate that fire-sensitive trees (e.g., Ulmus, Ostrya, Fraxinus, and Acer saccharum) declined and prairie taxa expanded with increased aridity from 10 000 yr BP to 8500 yr BP. Between ~8500 yr BP and ~6200 yr BP, aridity declined, and prairie coexisted with fire-sensitive and fire-tolerant (e.g., Quercus and Carya) trees. After ~6200 yr BP, prairie taxa became dominant, although aridity was not more severe than it was around 8500 yr BP. Along with aridity, fire appears to have played an important role in the establishment and maintenance of prairie communities in the eastern Prairie Peninsula, consistent with the speculations of the early ecologists. Comparison of our data with results from elsewhere in the North American midcontinent indicates that spatial heterogeneity is a characteristic feature of climatic and vegetational variations on millennial time scales.

Key words: charcoal; climate change; fire; grasslands; Holocene; paleoecology; pollen; tallgrass Prairie Peninsula.

INTRODUCTION

Unfortunately for the ecologist, the prairies of Illinois were converted into cornfields long before the development of ecology and phytogeography in America, thus forever prohibiting the satisfactory investigation of some questions of the most absorbing interest and also of considerable importance in aiding a clear understanding of American ecology and phytogeography.

—Gleason (1909)

Early North American ecologists were intrigued by the origin and persistence of prairie in the eastern tallgrass Prairie Peninsula (Fig. 1). They considered the region to be capable of supporting forest communities in the absence of frequent fires that were ignited by Native Americans (Gleason 1909, 1913, Cowles 1928, Transeau 1935). However, their studies of remnant prairies could not adequately explain ecological issues of interest to them, such as the species composition of the original prairie communities and the environmental conditions that led to prairie establishment and maintenance. Questions and misconceptions regarding the vegetational history of the Prairie Peninsula were first addressed by what are now considered classic paleoecological studies (e.g., Wright et al. 1963, McAndrews 1966). These, along with numerous subsequent studies (e.g., Clark et al. 2001, Camill et al. 2003, Nelson et al. 2004), demonstrated that prairie expansion in Minnesota, USA occurred during the warmer and drier middle Holocene, rather than during the late-glacial period as was originally hypothesized (e.g., Gleason 1922, Transeau 1935).

However, the extent of Holocene prairie expansion into the eastern Prairie Peninsula, the region of primary interest to Gleason (1909, 1913), Cowles (1928), and Transeau (1935), remains unclear. Wright (1968) extrapolated the pattern of vegetational change at Kirchner Marsh and Lake Carlson in south-central Minnesota (Fig. 1; Wright et al. 1963) by hypothesizing that prairie expanded eastward throughout the Prairie Peninsula ~8000 calibrated 14C years before present (yr BP) because of increased aridity and then gradually
retreated westward during the remainder of the middle Holocene, as aridity declined. Pollen assemblages from Chatsworth Bog in central Illinois (Fig. 1) displayed an expansion of nonarboreal pollen ~8000 yr BP (King 1981) and therefore appeared to confirm the extrapolation of data from Minnesota to the eastern Prairie Peninsula (i.e., Wright 1968). However, pollen assemblages from Roberts Creek (Baker et al. 1992) and stalagmite isotopic evidence from Coldwater Cave (Dorale et al. 1992) in the central region of the Prairie Peninsula (Fig. 1) challenged the hypothesis of Wright (1968) and the results of King (1981). These studies suggested that a steep moisture gradient between southeastern Minnesota and northeastern Iowa prevented prairie from expanding into the central and eastern Prairie Peninsula until after ~6000 yr BP. Evaluation of the two alternative ideas addressing the environmental history of the eastern Prairie Peninsula is difficult because the only available record, from Chatsworth Bog (King 1981), consists solely of pollen assemblages. Furthermore, this record has a chronology based on bulk sediment $^{14}$C dates that may be skewed toward older age estimates (Grimm and Jacobson 2004), thus complicating comparison with other records.

Understanding spatial and temporal dynamics of middle Holocene plant communities in the eastern Prairie Peninsula has implications beyond Gleason’s desire to improve our knowledge of North American phytogeography. Information on vegetational dynamics during the middle Holocene is invaluable because the prevailing climate was warm and dry, similar to projections of anthropogenic climatic change in the midcontinent of North America (IPCC 2001). Though the paleorecord does not offer a precise analog for anthropogenic change, a long-term perspective into vegetational dynamics during warm and dry conditions provides a context for anticipating future environmental changes, which will likely surpass the historical range of drought severity and variability (Woodhouse and Overpeck 1998) and cause marked vegetational shifts near forest–grassland ecotones (Allen and Breshears 1998).

We analyzed sediment cores from two Illinois lakes for pollen, diatoms, ostracodes, minerals, carbonate $^{13}$C, charcoal influx, and charcoal $^{13}$C. Here we report the results and use them to infer factors influencing the establishment and maintenance of prairie communities. Reliable chronologies based on 17 accelerator mass spectrometry (AMS) $^{14}$C dates facilitate comparison of our records with other well-dated paleorecords from the midwestern United States. This comparison helps clarify long-term climatic, vegetational, and fire variability near the transition between tallgrass prairie and forest.

**Study Sites**

The tallgrass Prairie Peninsula extended from the eastern Dakotas through north-central Illinois prior to European settlement (Fig. 1), which occurred AD 1840 in central Illinois (Transeau 1935, Anderson 1970). Our two sites are located ~130 km apart near the eastern end of this subbiome. Chatsworth Bog (40°40'33" N, 88°19'23" W; 220 m elevation) is located between the Paxton and Gifford moraines in central Illinois. The tillplain soils of the watershed are moderately well drained (Higgins 1996). Chatsworth Bog once covered ~25 ha (King 1981), and it was connected as a second-order watershed to the south fork of the Vermillion River. Although called a “bog,” the site was a fen prior to drainage for agricultural use. Oxidation and humification of sediments have occurred above the drain tiles (~1 m deep); however, the sediments below the upper ~1 m are well preserved. The mean July temperature and mean annual precipitation at Pontiac, Illinois, USA, ~30 km northwest of Chatsworth Bog, were 23.7°C and 87.1 cm, respectively, between 1950 and 2005 (data from the Illinois State Climatologist’s Office of the Illinois State Water Survey [available online]).

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7 (http://www.sws.uiuc.edu/data/climatedb/)
Nelson Lake (41°49'58" N, 88°22'48" W; 211 m elevation) is located in northern Illinois on the western flank of the St. Charles Moraine. Its watershed soils are poorly drained to moderately well drained (Deniger 2004), and the watershed forms the headwaters of a stream that flows to the Fox River. A large stand of fire-sensitive forest existed AD 1840, about five kilometers east of Nelson Lake on the east side of the Fox River, a major fire break (Kilburn 1959). Nelson Lake has an area of ~25 ha with a maximum depth of ~1.2 m. The mean July temperature and mean annual precipitation at Aurora, Illinois, USA, ~11 km south of Nelson Lake, were 22.9°C and 89.7 cm, respectively, between 1950 and 2005 (available online).7

Prior to European settlement, the dominant vegetation in the eastern Prairie Peninsula was tallgrass prairie (Anderson 1970). Abundant prairie grasses included Andropogon gerardii, Schizachyrium scoparium, Elymus canadensis, Sorghastrum nutans, Spartina pectinata, and Hesperostipa spartea (Kucera 1992; nomenclature follows Flora of North America Editorial Committee 1993). Woody species in north-central Illinois grew near waterways and in isolated upland “prairie groves” (Boggess and Geis 1967). The most abundant upland trees were Quercus spp. and Carya spp. Fire-sensitive trees (Curtis 1959, Grimm 1984), such as Acer saccharum, Fraxinus spp., and Ulmus spp., were restricted to sites well protected from fire (Boggess and Geis 1967, Rodgers and Anderson 1979), such as the eastern side of water bodies (Gleason 1912, 1913).

Materials and Methods

We obtained stratigraphically overlapping sediment cores from Chatsworth Bog and Nelson Lake using a square-rod piston corer (Wright 1991). At Chatsworth Bog, we selected a core site in a topographic low point of the former basin near the core location of King (1981) based on historical photographs. We removed the upper sediment from the plow zone with a bucket auger before retrieving the lake sediment below. Nelson Lake was cored in the center of the lake.

Sediment subsamples were sieved with distilled water to isolate terrestrial plant macrofossils for AMS 14C dating. The dates were converted to calibrated ages using CALIB 5.0.1 (available online)8 with the atmospheric decadal calibration data set.

For ostracode assemblage analysis, sediment subsamples were gently washed through a sieve with 150-μm openings. A minimum of 20 adult valves were identified and counted from each sample (Delorme 1970a, b, 1971). Candona ohiensis valves at Chatsworth Bog were soaked in 50% Clorox for 24 hours, triple rinsed with distilled water, and air-dried. The valves (five, on average) were then ground to a powder to create a composite sample for a given core depth for δ18O analysis. δ18O analysis was performed at the Illinois State Geological Survey Stable Isotope Laboratory (Champaign, Illinois, USA) and the Stanford University Stable Isotope Laboratory (Stanford, California, USA). Samples were reacted with ultrapure phosphoric acid in automated Kiel devices (Finnigan, Bremen, Germany) interfaced with Finnigan MAT 252 isotope ratio mass spectrometers (IRMS, Finnigan, Bremen, Germany). The analytical precision was <0.1% for internal laboratory standards, and the average difference was 0.2% for replicate samples.

The relative abundance of organic matter, carbonate, and other inorganic matter was determined by loss-on-ignition. Mineral composition was determined by X-ray diffraction with a Scintag 0-0 (Scintag, Cupertino, California, USA) diffractometer following conventional procedures (Moore and Reynolds 1997). Sediment subsamples for mineral analysis were washed through a sieve with 150-μm openings to remove ostracode valves. The abundance of each mineral was quantified as the dry mass percentage of total major identified minerals, including aragonite, calcite, dolomite, potassium feldspar, plagioclase feldspar, and quartz (Hughes et al. 1994). We summarized the mineral data using principal component analysis (PCA).

Freeze-dried subsamples from Nelson Lake were treated with 10% HCl and 30% H2O2 for diatom-assemblage analysis. Diatoms were settled onto coverslips and mounted onto microscope slides with Naphrax (a synthetic resin dissolved in toluene). We counted 300 diatom valves per sample at 1000× magnification, except in samples with poor diatom preservation, for which a minimum of 100 valves were counted. Planktonic diatoms (those living within the water column) were identified to the lowest possible taxonomic level, whereas benthic (bottom-dwelling) diatoms were characterized as either small Fragilariaceae spp., Surirella spp., or other pennates (Patrick and Reimer 1975, Krammer and Lange-Bertalot 1991, Lange-Bertalot 1993). We summarized the diatom-assemblage data using PCA.

Sediment subsamples were prepared for pollen analysis with standard methods (Fægri et al. 1989). Tablets of exotic Lycopodium spores (Chatsworth Bog) or polystyrene microspheres (Nelson Lake) were added to each sample to determine pollen densities (Bennninghoff 1962). At least 300 grains were counted per sample at 400× magnification. Pollen accumulation rates of individual taxa show similar patterns as pollen percentages, except where noted, and therefore are not presented. The pollen assemblages at Chatsworth Bog and Nelson Lake were divided into zones using CONISS (a stratigraphically constrained cluster analysis, Grimm 1987) and visual inspection.

We used detrended correspondence analysis (DCA) to compare fossil-pollen assemblages from Chatsworth Bog and Nelson Lake with pre-European-settlement pollen assemblages from sites in the tallgrass prairie or deciduous forest of the midwestern United States. For

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7 Available online: http://CALIB.qub.ac.uk/CALIB
8 Available online: http://CALIB.qub.ac.uk/CALIB
sites with a clear *Ambrosia* rise (see Fig. 6 for sources),
the pollen signature of European settlement in the
region (Grimm 2001, Wright et al. 2004), pollen
assemblages immediately below the *Ambrosia* rise were
included in the DCA. Only taxa with >2% abundance in
at least one sample from Chatsworth Bog and Nelson
Lake were included in the DCA. Pollen percentages of
taxa with >2% abundance were recalculated prior to
performing the DCA. We also compared our pollen
results with other well-dated paleorecords from the
midwestern United States. All statistical analyses were
performed using the program PAST (version 1.27;
Hammer et al. 2001; available online).9

Macroscopic charcoal particles were counted and
results converted into charcoal accumulation rates
(CHAR) following Nelson et al. (2004). At selective
stratigraphic levels, charcoal particles were isolated for
$\delta^{13}$C analysis to estimate the relative abundance of C$_3$
and C$_4$ plants and help constrain our vegetational
reconstruction. C$_3$ and C$_4$ plants possess distinct $\delta^{13}$C
compositions primarily because they use different
enzymes for initial carbon fixation. C$_3$ plants use
ribulose-1,5-bisphosphate for initial carbon fixation,
which discriminates more strongly against $^{13}$C than
phosphoenolpyruvate, the enzyme used for initial
carbon fixation in C$_4$ plants. Each $\delta^{13}$C sample was
composed of 40 randomly selected charcoal particles,
and $\delta^{13}$C analysis was done at the University of
California-Davis Stable Isotope Facility (Davis, Cali-
ifornia, USA) with an elemental analyzer interfaced with
a Europa Hydra 20/20 IRMS (PDZ-Europa, Crewe,
UK). The analytical precision was <0.1‰ for internal
lab standards, and the average difference was
1.2‰ for replicate samples from each core. Given the
1.2‰ error, we focus on the smoothed patterns at
centennial to millennial time scales in the charcoal $\delta^{13}$C
data. To estimate the relative abundance of C$_4$ plants
from charcoal $\delta^{13}$C values, we used a two-end-member
mixing model (Clark et al. 2001) based on the average
$\delta^{13}$C values of C$_3$ (~27‰) and C$_4$ (~13‰) plants
(Cerling 1999).

**RESULTS AND INTERPRETATIONS**

**Chronological control**

Seven and thirteen AMS $^{14}$C dates were obtained from
Chatsworth Bog and Nelson Lake, respectively, to
construct age–depth relationships. We fit a mixed-effect
regression model (Heegaard et al. 2005) to the six
youngest dates at Chatsworth Bog and used linear
interpolation between the oldest two dates (Appendix
and Fig. 2a). Three dates on grass macrofossils in the
upper part of the Nelson Lake core were significantly
older than adjacent charcoal dates (Appendix and Fig.
2b). The grass macrofossils appeared to be from *Zizania
aquatica*, an aquatic species. We excluded these dates
from the age–depth model in favor of the charcoal-based
dates, because the dated grass material could have been
affected by a hard-water effect of ~600-1300 years. The
10 remaining dates from Nelson Lake were fit with a
mixed-effect regression model (Heegaard et al. 2005).
Sediment accumulation rates ranged from ~0.04 to 0.79
cm/yr at both sites.

**Aridity reconstruction**

We reconstructed aridity because it is the climatic
variable most important for determining the distribution
of prairie and forest (Changnon et al. 2002), and because
it encompasses the effect of temperature on evapotrans-
piration. We inferred aridity variations from a suite of
biotic and abiotic proxies sensitive to aridity (Fig. 3).
The ratio of the ostracode taxa *Candona* and *Cypridopsis
vidua* correlates with lake-level changes (Kitchell and
Clark 1979, Curry 2003) because *Candona* spp. prefer
profound water, whereas *Cypridopsis vidua* is most
abundant among aquatic vegetation in the littoral zone.
For diatoms, benthic species increase at the expense of
planktonic species when lake levels are lower (Wolin and
Duthie 1999). Finally, increased detrital-mineral input
indicates aridity-induced increases in landscape insta-
bility (e.g., Clark et al. 2002), and carbonate $\delta^{18}$O
increases with aridity because of evaporative enrichment
(Kelts and Hsu 1978). The time spans differ among the
different proxy records at each site, primarily reflecting
the availability of suitable materials for the analysis of a
given proxy (e.g., ostracodes are absent in the early
Holocene sediments of Chatsworth Bog).

These proxies display both similarities and differences
in temporal patterns. As an example of similarities,
peaks ~6100 yr BP and troughs ~6500 yr BP and 5600
yr BP occur in (1) the *Candona* : *Cypridopsis
vidua* ratio at both sites, (2) $\delta^{18}$O composition at Chatsworth
Bog, (3) PCA2 of diatom assemblages at Nelson Lake
(PCA2 explains 22.9% of the diatom variance), with higher
PCA2 scores reflecting increased abundance of benthic
diatoms, and (4) PCA summaries of the mineral data at
both sites, with lower PCA2 scores at Chatsworth Bog
(PCA2 explains 19.9% of the mineral variance) and
higher PCA1 scores at Nelson Lake (PCA1 explains
55.1% of the mineral variance) reflecting higher amounts
of detrital minerals, such as quartz and feldspars (Fig.
3). In contrast, stratigraphic differences exist between
any two individual proxies when compared in detail. For
example, although $\delta^{18}$O and PCA2 of the Chatsworth
Bog mineral data display similar fluctuations from
~6500 to 5000 yr BP, $\delta^{18}$O remains high while PCA2
declines after ~4500 yr BP. Such differences are not
surprising given that proxy sensitivity to aridity may
vary through time and that each proxy may be affected
by variables other than aridity, such as moisture source
($\delta^{18}$O) (Kelts and Hsu 1978), windiness (detrital
minerals) (Clark et al. 2002), and salinity (ostracodes

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9 [http://folk.uio.no/ohammer/past/index.html]
We created a composite aridity record for each site using z scores, a means of standardizing different proxies (e.g., Overpeck et al. 1997, Booth and Jackson 2003). Z scores were calculated for each aridity proxy at each site as the number of standard deviations of a sample from the mean, and z score values of all proxies from a given core depth at each site were averaged to create composite records. Prior to z score calculations, the proxy data from each site was multiplied by $\frac{1}{C_0}$, if necessary, to ensure that aridity fluctuations in proxies with opposing signs were additive in the composite records. The composite records highlight aridity, the control common to all proxies, and mask the influence of other controls. Thus the composite aridity records should provide a more rigorous evaluation of moisture variations than any individual proxy record. More positive z scores indicate wetter conditions, and more negative z scores, drier conditions (Fig. 4). The composite aridity records from Chatsworth Bog and Nelson Lake display strikingly similar patterns, indicating synchronous moisture fluctuations between our sites (Fig. 4). In particular, aridity gradually increased after 10,000 yr BP to reach a peak ~8500 yr BP, and gradually decreased until ~6500 yr BP. Aridity then peaked at ~6100 yr BP, declined to a trough at ~5600 yr BP, and was relatively high after ~5000 yr BP.

Vegetational change inferred from pollen assemblages

Pollen assemblages show similar stratigraphic patterns between Chatsworth Bog and Nelson Lake, indicating regionally synchronous changes in vegetation composition (Figs. 5–7). In zone 1 (from 10,000 to 9000 yr BP) at both sites, pollen of fire-sensitive woody taxa, including Ulmus, Ostrya, Fraxinus nigra, and Acer saccharum (Curtis 1959, Grimm 1984), are relatively abundant (Fig. 5). The DCA1 score of this zone is the
lowest of the pollen zones at each site because DCA1 primarily separates woody from herbaceous pollen types and these zones have a high proportion of arboreal pollen (Fig. 6). On DCA1, zone 1 at both sites overlaps with pre-European-settlement pollen assemblages from Kimble Pond (Camill et al. 2003), which was surrounded by closed deciduous forests in the Big Woods region of southern Minnesota (Grimm 1984). Vegetation composition at Nelson Lake was probably more similar to that of Kimble Pond than at Chatsworth Bog, as suggested by the higher DCA2 score at Nelson Lake, because mesic and fire-sensitive taxa (e.g., *Acer saccharum* and *Ostrya*-type) have more positive values on DCA2 than taxa with a greater tolerance of drier conditions and fire (e.g., *Quercus* and *Carya*).

Around 9000 yr BP, woody taxa decline and herbaceous taxa begin to increase in the pollen diagrams of both sites (Fig. 5). The herbaceous taxa include

![Fig. 3. Records of proxies used to infer aridity at Chatsworth Bog (CB) and Nelson Lake (NL). Ostracode samples containing *Candona* spp., but no *Cypridopsis vidua*, were assigned a value equal to the highest ratio of any sample that contained *Candona* spp. and *Cypridopsis vidua*. The log scale of the *Candona* : *Cypridopsis vidua* ratio reduces the magnitude of data variation. Mineral percentages for the CB PCA were calculated without calcite because of a significant declining trend in carbonate after ~8.7 cal. ka BP (Fig. 2a), which resulted in inflated values for the other minerals (a “percentage effect”); no strong declining trend in carbonate occurred at NL (Fig. 2b), so carbonate was not removed. Raw data are represented by circles and squares, and curves represent three-sample moving averages of the raw data. Gaps in the diatom PCA curve of Nelson Lake represent periods of >300 years during which the sediments are void of diatoms.](image)

![Fig. 4. Comparison of composite aridity records from Chatsworth Bog and Nelson Lake with other data. Raw data are represented by circles and squares, and the curves represent three-sample moving averages of the raw data. More positive z scores indicate wetter conditions, and more negative z scores, drier conditions. Solar insolation was calculated using Analyses [http://www.ncdc.noaa.gov/paleo/softlib/softlib.html]. The percentage of the last glacial maximum ice area of the Laurentide Ice Sheet followed Shuman et al. (2002). The aragonite : calcite (solid curve) and carbonate δ¹³O (dashed curve) data from West Olaf Lake (WOL) and Steel Lake (SL), respectively, indicate patterns of regional aridity in west-central Minnesota (Nelson et al. 2004).](image)
Ambrosia, Poaceae, Cyperaceae, Chenopodiaceae/Amaranthaceae, and Asteraceae subf. Asteroidae undiff. These pollen changes indicate a decline of closed deciduous forest and an initial expansion of prairie species throughout the region. Pollen of the fire-sensitive woody taxa from zone 1 at both sites, as well as Quercus and Carya, remains moderately abundant in zone 2, ~8900–7800 yr BP at Chatsworth Bog and 8900–7400 yr BP at Nelson Lake. Zone 2 has higher DCA1 scores than zone 1 at both sites because of higher percentages
of herbaceous pollen (Figs. 5–7). The transitions from
zone 1 to zone 2 show a trend towards DCA1 scores of
pre-European-settlement pollen assemblages from Lake
Mendota (Winkler et al. 1986) and Devils Lake (Baker
et al. 1992) in south-central Wisconsin (Fig. 6), where
the vegetation was largely open Quercus woodlands
and prairie (Curtis 1959). However, Quercus pollen was more
abundant at the Wisconsin sites than in zone 2 at
Chatsworth Bog and Nelson Lake. These data indicate a
mosaic of prairie and woodland in Illinois, somewhat
similar to that at European settlement in this region,
except that the woodland patches were richer in fire-
sensitive trees during the early portion of the middle
Holocene. The DCA1 scores of pollen zone 2 at our sites
are also similar to that of Wolfsfeld Lake (Grimm 1983)
in the Big Woods of Minnesota, but the DCA2 scores
are farther from that of Wolfsfeld Lake than from those
of the Wisconsin sites.

Beginning ~7700 yr BP at Chatsworth Bog and 7300
yr BP at Nelson Lake, prairie pollen types decline,
although not to pre-9000 yr BP levels, while fire-sensitive
woody taxa such as Ulmus, Ostrya, and Juglans nigra
increase (Fig. 5). Pollen of Acer saccharum increases at
Nelson Lake, but not at Chatsworth Bog. Correspond-
ing to the decline in herbaceous pollen, pollen zone 3
(7700–6300 yr BP at Chatsworth Bog and 7300–6300 yr
BP at Nelson Lake) at both sites is located between
zones 1 and 2 on DCA1 (Fig. 6). These changes in pollen
assemblages indicate a decline of prairie and an
expansion of forest.

About 6200 yr BP, woody taxa generally decline and
prairie taxa, particularly Poaceae, increase in pollen
abundance (Figs. 5–7). The DCA1 scores of zone 4
(~6200–3000 yr BP) are the highest at both sites (Fig. 6),
and they trend toward those of French Lake (Grimm
1983), near the western edge of Minnesota’s Big Woods,
Sharkey Lake (Camill et al. 2003) in oak woodland
adjacent to the Big Woods, and Clear Lake (Baker et al.
1992) in the tallgrass prairie of north-central Iowa, USA
(Figs. 1 and 6). However, Artemisia was more abundant
and Poaceae less abundant at the Minnesota and Iowa
sites. Zone 4 at neither site has DCA1 scores as high as
the pre-European-settlement pollen assemblages from Moon Lake (Laird et al. 1996) in eastern North Dakota, USA (Figs. 1 and 6), where woody taxa were rare. These data indicate that after \( \sim 6200 \) yr BP the eastern Prairie Peninsula was dominated by tallgrass prairie and woody plant communities containing primarily *Quercus* and *Carya*.

Despite their broad similarity in temporal patterns, as described above, differences exist between the pollen records of Chatsworth Bog and Nelson Lake. These differences probably reflect vegetational variation at local scales. Pollen from fire-sensitive taxa such as *Ostrya*, *Acer saccharum*, and *Tilia* were generally more abundant at Nelson Lake than at Chatsworth Bog, whereas pollen from more fire-tolerant taxa such as *Quercus* was generally more abundant at Chatsworth Bog (Figs. 5 and 6). A greater abundance of fire-sensitive taxa at Nelson Lake probably resulted from the facts that the soils are more poorly drained and that fire breaks, such as rivers, are more abundant near this site. After \( \sim 6200 \) yr BP, Cyperaceae pollen was more abundant at Chatsworth Bog than at Nelson Lake, which is probably related to local fen development at the former site. This interpretation is supported by the presence of aquatic snail taxa that live on or near aquatic vegetation, such as *Gyraulus*, *Helisoma*, *Physa*, and *Valvata* (Fig. 2a; Clarke 1981).

**Abundance of C\(_3\) and C\(_4\) plants estimated from charcoal \( \delta^{13}C \)**

Charcoal \( \delta^{13}C \) data show different temporal patterns between our two sites, suggesting local variation in the C\(_4\) plant abundance of burned vegetation. For example, C\(_4\) abundance declined from \( \sim 75\% \) around 7600 yr BP to \( \sim 40\% \) around 6600 yr BP at Nelson Lake, but only small fluctuations in C\(_4\) abundance occurred during this same period at Chatsworth Bog (Fig. 7). Nonetheless, several similarities in the two charcoal \( \delta^{13}C \) records help enhance our vegetational reconstruction. These records reveal that C\(_4\) plants, probably C\(_4\) tallgrasses, were continually present on the landscape no later than 9000 yr BP (Fig. 7). C\(_4\) plant abundance did not increase at either site following the pollen-inferred increase in prairie vegetation \( \sim 6200 \) yr BP. This result seems counterintuitive given the fact that C\(_4\) grasses are abundant in tallgrass prairies today. It also contradicts
A stalagmite $\delta^{13}C$ record from northeastern Iowa which suggests a large expansion of C4 plants after $\sim$6000 yr BP (Fig. 8a; Dorale et al. 1992).

The lack of a major charcoal $\delta^{13}C$ shift at our sites $\sim$6200 yr BP probably indicates that C4 plants were relatively abundant in burned areas before that time, consistent with pollen evidence that prairie taxa were present by $\sim$9000 yr BP. Many mesic tree taxa (C3) such as Ulmus, Ostrya, Fraxinus, and Acer saccharum, which were abundant prior to $\sim$6200 yr BP, are fire-sensitive. Similar to the Big Woods region of southern Minnesota, a buffer zone of fire-tolerant oaks may have existed between the fire-sensitive trees and the highly flammable prairie (Grimm 1984, Camill et al. 2003). Thus, prior to $\sim$6200 yr BP, fires that did occur in the eastern Prairie Peninsula were probably patchy. These fires primarily consumed herbaceous plants, including C4 grasses, which were likely most abundant in frequently burned areas. Unlike charcoal $\delta^{13}C$, stalagmite $\delta^{13}C$ depends on the relative contributions of C3 trees, shrubs, and herbaceous plants, as well as C4 grasses, to soil organic matter. Therefore it is not surprising that stalagmite and charcoal $\delta^{13}C$ records show different temporal patterns of C4 plant abundance.

Our pollen and charcoal $\delta^{13}C$ data together suggest that once prairie patches became established $\sim$9000 yr BP, they coexisted with communities dominated by Quercus, Carya, and mesic deciduous woody species. Such coexistence would have been facilitated by firebreaks and spatial separation of vegetational types with different flammability and fire tolerance, similar to the landscape in southern Wisconsin (Curtis 1959) and Minnesota (Grimm 1984) prior to European settlement.

**Fire reconstruction**

Prairie ecosystems burn on annual to interannual time scales (Gleason 1913, Anderson 1990). In these systems, the high background values of charcoal accumulation rates (CHAR), along with the relatively slow sedimentation rates, make it difficult, if not impossible, to distinguish individual fire events in lake-sediment charcoal records. Thus CHAR in grasslands provide a measure of changes in relative fire importance, which reflects several controlling factors, such as fuel availability, fuel moisture, vegetational type, and/or ignition frequency (Clark et al. 2001, Brown et al. 2005).

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**Fig. 8.** Comparison of paleovegetational records. (a) Summary of vegetational changes at well-dated sites in the central and eastern Prairie Peninsula. The curves are three-sample moving averages of the raw data from each site, with the exception of Roberts Creek, for which the raw data are shown because of its relatively low temporal resolution. NAP stands for non-arboreal pollen; VPDB stands for Vienna PeeDee Belemnite. Stalagmite $\delta^{13}C$ data from Coldwater Cave (Fig. 1) were obtained from the NOAA paleoclimatology web site (ftp://ftp.ncdc.noaa.gov/pub/data/paleo/speleothem/northamerica/usa/iowa/coldwater_cave.txt). (b) Percentage of non-arboreal pollen from well-dated lake-sediment cores spanning a northwest–southeast transect along the tallgrass prairie–forest border prior to European settlement. These sites are represented by the stars in Fig. 1: ML, Moon Lake; WOL, West Olaf Lake; SH, Sharkey Lake; KP, Kimble Pond; CB, Chatsworth Bog; NL, Nelson Lake.
At Chatsworth Bog and Nelson Lake, CHAR increased with the initial establishment of prairie taxa after ~9000 yr BP (Fig. 7). CHAR remained overall low to moderate at both sites prior to ~7000 yr BP, which is consistent with the interpretation that fires were patchy and unimportant during the early part of the middle Holocene. Fire importance increased ~6700 yr BP at Chatsworth Bog and 7200 yr BP at Nelson Lake, as suggested by elevated CHAR values. CHAR remained relatively high for the remainder of the record at Nelson Lake, but dropped markedly ~6200 yr BP at Chatsworth Bog. Although site-specific differences in fire regimes (Gavin et al., in press; Hu et al., in press) may account for this difference between our two CHAR records, it is more likely that the CHAR decline at Chatsworth Bog resulted from the development of the lake into a fen at this time, which filtered runoff entering the basin. This interpretation is supported by the fact that, similar to CHAR, the total influx of pollen and minerals also declined at Chatsworth Bog ~6200 yr BP (data not shown). Thus, after ~6200 yr BP, low CHAR values at Chatsworth Bog resulted from sedimentary processes, whereas high CHAR values at Nelson Lake reflected increased fire importance.

Fuel availability was probably not a limiting factor of fire occurrence at our sites because CHAR values were lowest prior to ~9000 yr BP, when woody species and biomass were abundant. In the eastern Prairie Peninsula, woody and herbaceous biomass was likely adequate for fire occurrence throughout the early and middle Holocene, in contrast to the northwestern Prairie Peninsula and the Great Plains, where aridity was greater and fuels were more limiting (e.g., Nelson et al. 2004; Brown et al. 2005). However, it is difficult to tease apart the relative importance of the other factors controlling fire occurrence.

**DISCUSSION**

This study provides the first multiproxy data set with solid chronologies from the eastern Prairie Peninsula for climate, vegetational, and fire reconstructions. These data allow us to address the two alternative hypotheses concerning the timing and causes of prairie establishment in the region. They also help answer questions of early North American ecologists concerning the development and persistence of prairie following the last glaciation.

Pollen-assemblage and charcoal $\delta^{13}C$ data from Chatsworth Bog and Nelson Lake revealed that the initial pulse of prairie development in the eastern Prairie Peninsula was coeval with the early Holocene expansion of prairie in Minnesota about 9000 yr BP (Fig. 8b; Camill et al. 2003, Wright et al. 2004). The probable causes for this prairie development were increased temperature and decreased moisture resulting from high summer insolation and the waning influence of the Laurentide ice sheet (Fig. 4; Baker et al. 1992, Shuman et al. 2002). However, this pulse of prairie development lasted only ~1500 years. The abundance of trees, including fire-sensitive taxa such as *Ulmus*, increased after ~7700 yr BP at Chatsworth Bog and ~7300 yr BP at Nelson Lake, and the full expansion of prairie did not occur until ~6200 yr BP.

Despite the nearly synchronous initial increase of prairie taxa ~9000 yr BP in Minnesota and Illinois, major differences existed in the patterns of climatic change and prairie development between these regions. For example, mineral, $\delta^{18}O$, and magnetic data from several sites in Minnesota (Fig. 4; Camill et al. 2003, Nelson et al. 2004) indicate that maximum aridity occurred ~7800 yr BP, which led to the full expansion of herbaceous taxa adapted to relatively high moisture deficits. Following the peak aridity of the early middle Holocene, aridity gradually decreased as summer insolation declined (Fig. 4), which allowed woody plants to become more abundant in Minnesota (Fig. 8b; also see Wright et al. 2004). These data are consistent with the suggestion by Wright (1968) that aridity gradually declined in Minnesota during the middle Holocene, but they contrast with the two-step expansion of prairie in Illinois where prairie did not fully expand until after ~6200 yr BP. To the west of the tallgrass prairie at Moon Lake, conditions were dry enough to support herbaceous taxa throughout the Holocene (Fig. 8b), although the driest conditions prevailed from ~9000 yr BP to 5000 yr BP (Laird et al. 1996). Thus, considerable spatial variability existed in climatic and vegetational histories of the early and middle Holocene.

The pattern of prairie development in the eastern Prairie Peninsula inferred from our new data is more complicated than previously thought. On the basis of pollen data from Roberts Creek and Devils Lake (Baker et al. 1992) and speleothem isotopic data from Coldwater Cave (Dorale et al. 1992), previous studies argued that prairie development did not occur until after ~6000 years ago. Our data, on the other hand, revealed an early pulse of prairie development that was interrupted by mesic conditions until the major expansion of prairie ~6200 yr BP. Nonetheless, the Roberts Creek data do show a small increase in non-arboreal pollen about 8500 yr BP (Fig. 8a), but the samples are widely spaced in time and a possible early pulse of prairie development may have been missed. In addition, Roberts Creek is in the hilly driftless area of northeastern Iowa, which was more forested than northeastern and central Illinois at the time of European settlement (Fig. 1). Similarly, a small increase in non-arboreal pollen occurred ~9000 yr BP at Devils Lake (Fig. 8a), even though this site was always within the deciduous forest. Webb et al. (1983) produced a series of isopoll maps for “prairie forbs” that showed the two-phase development of prairie in the eastern Prairie Peninsula. These maps were anchored in Illinois by King’s (1981) pollen data from Chatsworth Bog, and our study supports this interpretation of early Holocene prairie development.
In addition to aridity, fire may have exerted an important control on the establishment and maintenance of prairie communities in the eastern Prairie Peninsula. Our CHAR profiles from Chatsworth Bog and Nelson Lake suggest that fire activity became elevated ~500–1000 years prior to the full establishment of prairie, ~6200 yr BP. Because this change in fire importance did not coincide with any major shifts in our aridity and vegetational records, it is possible that increased fire ignitions resulted in more burns, contributing to prairie expansion in the eastern Prairie Peninsula. Both Native Americans and lightning might have been important ignition sources, but evidence of ignitions beyond the historical record is conjectural. Fires may have also been important for the maintenance of prairies. For example, a marked increase in effective moisture occurred ~5800–5400 yr BP, as evidenced by changes in all proxy indicators at both of our sites (Fig. 3). This change, however, did not cause woody taxa to expand and prairie taxa to decline, probably because fires remained important. These interpretations lend support to the suggestion by early 20th century ecologists that frequent fires prevented forest communities from dominating the region (Gleason 1912, 1913, Cowles 1928, Transeau 1935).

Our results have implications for understanding future climatic change and ecological response in the eastern axis of the tallgrass Prairie Peninsula. Spatial variations in early and middle Holocene climatic conditions across the Prairie Peninsula are consistent with instrumental records. For example, whereas the 1930s drought devastated native and agricultural ecosystems throughout most of the midcontinent, the 1950s and 1980s droughts were primarily restricted to the south-central and northern Great Plains, respectively (Woodhouse and Overpeck 1998). Thus, spatial variability in climatic change appears to be a common feature of the North American midcontinent on annual to millennial scales, and it is therefore prudent to anticipate a wide range of complex sub-biome ecosystem responses to future climatic change. Furthermore, our results suggest that fire regimes interacted with climatic change to exert dominant controls over vegetational dynamics in the eastern Prairie Peninsula. However, anthropogenic domination will undoubtedly surpass the ecological role of fires in any future change of the regional landscape.

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APPENDIX
A table of 14C dates from Chatsworth Bog and Nelson Lake (Ecological Archives E087-152-A1).