



Rapid responses of the prairie-forest ecotone to early Holocene aridity in mid-continental North America

John W. Williams^{a,*}, Bryan Shuman^b, Patrick J. Bartlein^c

^a Department of Geography, 550 North Park St., University of Wisconsin, Madison, WI 53706, USA

^b Department of Geology and Geophysics, 1000 E. University Ave., Laramie, WY 82071, USA

^c Department of Geography, 1251 University of Oregon, Eugene, OR, 97403, USA

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ABSTRACT

The prairie-forest transition in midcontinental North America is a major physiognomic boundary, and its shifts during the Holocene are a classic example of climate-driven ecotonal dynamics. Recent work suggests asymmetrical Holocene behavior, with a relatively rapid early Holocene deforestation and more gradual reforestation later in the Holocene. This paper presents a new synthesis of the Holocene history of the Great Plains prairie-forest ecotone in the north-central US and central Canada that updates prior mapping efforts and systematically assesses rates of change. Changes in percent woody cover (%WC) are inferred from fossil pollen records, using the modern analog technique and surface-sediment pollen samples cross-referenced against remotely sensed observations. For contemporary pollen samples from the Great Plains, %WC linearly correlates to percent arboreal pollen (%AP), but regression parameters vary interregionally. At present, %AP is consistently higher than %WC, because of high background levels of arboreal pollen. Holocene maps of the eastern prairie-forest ecotone agree with prior maps, showing a rapid decrease in %WC and eastward prairie advance between 10,000 and 8000 ka (1 ka = 1000 calibrated years before present), a maximum eastward position of the ecotone from 7 to 6 ka, and increased %WC and westward prairie retreat after 6 ka. Ecotone position is ambiguous in Iowa and southeastern Minnesota, due to a scarcity of modern analogs for early-Holocene samples with high *Ulmus* abundances and for samples from alluvial sediments. The northern prairie-forest ecotone was positioned in central Saskatchewan between 12 and 10 ka, stabilized from 10 to 6 ka despite decreases in %WC at some sites, then moved south after 6 ka. In both east and north, ecotonal movements are consistent with a dry early Holocene and increasing moisture availability after 6 ka. Sites near the ecotone consistently show an asymmetric pattern of abrupt early Holocene deforestation (<300 years) and gradual reforestation after 6 ka. Early Holocene decreases in %WC are faster than the corresponding drops in %AP, because the analog-based %WC reconstructions correct for the high background levels of arboreal pollen types that blur temporal variations in %AP. For example, at Elk Lake, the %AP decline lasts 1000 years, whereas the %WC decline occurs between adjacent pollen samples, approximately 300 years apart. Thus, early Holocene deforestation may have been even more abrupt than previously recognized. Rapid deforestation likely was promoted both by rapid climate changes around 8.2 ka and positive fire-vegetation feedbacks. Non-linear vegetational responses to hydrological variability are consistent with 1) other paleorecords showing rapid die-offs of some eastern tree species in response to aridity and 2) observations of threshold-type ecological responses to recent climate events. The 21st-century trajectory for the Great Plains prairie-forest ecotone is uncertain, because climate models differ over the direction of regional precipitation trends, but future drying would be more likely to trigger threshold-type shifts in ecotone position.

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1. Introduction

This paper examines the Holocene history of the prairie-forest ecotone in the eastern and northern Great Plains. This transition from

open to forested vegetation is one of the most physiognomically important vegetation gradients in North America, because spatial variations in tree cover is a primary determinant of land-surface properties including albedo, surface roughness, canopy density, and depth of root penetration into the water table (Bonan, 2002; Meir et al., 2006). These properties in turn regulate surface-atmosphere exchanges of energy and water, resulting in significant regional feedbacks to climate change (Pielke et al., 1998; Bonan, 1999). During

* Corresponding author. Tel.: +1 608 265 5537; fax: +1 608 265 3991.

E-mail addresses: jww@geography.wisc.edu (J.W. Williams), bshuman@uwyo.edu (B. Shuman), bartlein@uoregon.edu (P.J. Bartlein).

the Holocene, the prairie-forest ecotone was highly mobile, shifting position in response to regional changes in aridity and fire regime (McAndrews, 1966; Grimm, 1983; Webb et al., 1983; Wright, 1992; Baker et al., 2002; Nelson et al., 2004; Umbanhowar et al., 2006). Understanding these Holocene dynamics has long been of interest to ecologists, as a way of gaining insight into the physical, biological, and cultural processes that regulate the position and structure of the ecotone (Gleason, 1922; Transeau, 1935), to synoptic paleoclimatologists documenting the spatiotemporal patterns of long-term hydrological variability (Bartlein et al., 1984, 1998; Harrison et al., 2003), and to atmospheric scientists interested in the effects of land-cover change upon atmospheric circulation and climate variability (Clausen et al., 2001). McAndrews (1966) first demonstrated the dynamism of the prairie-forest border via a transect of pollen records across the prairie-forest ecotone in northern Minnesota that showed that the prairie-forest border during the middle Holocene was about 100 km east of its late-Holocene position. Subsequent mapping efforts of the Holocene history of the prairie-forest ecotone focused on Minnesota and adjacent states and showed that the prairie advanced eastwards between 9000 and 7000 years BP (radiocarbon years before present), then retreated westward from 6000 to 3000 radiocarbon years BP (Wright and Watts, 1969; Bernabo and Webb, 1977; Webb et al., 1983).

Several developments since Webb et al. (1983) make the time ripe to reexamine the Holocene history of the prairie-forest ecotone. First, many new pollen records have been collected, most of which have more precise chronologies and higher-resolution pollen stratigraphies than earlier records (e.g. Whitlock et al., 1993; Camill et al., 2003; Nelson et al., 2004, 2006). In some areas, e.g. Iowa and southeastern Minnesota, these new records have suggested alternate placements of the Holocene prairie-forest ecotone (Baker et al., 1996, 2002). Chronologies have been especially improved by the increased precision of radiocarbon dating, the recognition that radiocarbon dates collected from bulk lake sediments are unreliable (Grimm and Jacobson, 2004), and the establishment of radiocarbon-year to calendar-year calibration curves (e.g. Reimer et al., 2004; Fairbanks et al., 2005). (Note: this paper normally represents time as 1000's of calendar years before present [ka] but occasionally refers to radiocarbon years [rka] when comparing to earlier work.) These new records make it possible to map the past position of the prairie-forest ecotone more precisely than before, and to extend the mapping of the prairie-forest ecotone beyond the region mapped by Webb et al. (1983).

Second, these new high-resolution pollen records suggest that, at individual sites, the Holocene phenomenon of prairie advance then retreat was highly asymmetric (Umbanhowar et al., 2006; Nelson and Hu, 2008), with abrupt deforestations during the early Holocene, then gradual reestablishment of forest during the mid- to late-Holocene. Paleohydrological proxy records suggest that this asymmetry was produced at least in part by a rapid early Holocene drying, followed by a gradual increase in moisture availability (Nelson and Hu, 2008), but there also may be an asymmetry in vegetational sensitivity to increases vs. decreases in moisture availability (Umbanhowar et al., 2006). Umbanhowar et al. (2006) noted that this asymmetry is apparent at other Midwestern pollen records, but there has been no systematic review to determine whether abrupt deforestation is a common phenomenon.

Third, techniques have greatly improved for quantitatively reconstructing the extent and density of tree cover in the past. Traditionally, Holocene prairie-forest dynamics have been inferred from percent pollen abundances: Webb et al. (1983) used the 20% isopoll for prairie forbs (a sum of Asteraceae and Chenopodiaceae/Amaranthaceae) to map the Holocene positions of the prairie-forest ecotone, and palynologists widely use the arboreal pollen sum (%AP) as a proxy for forest density. These palynological proxies, however, are imperfect indicators of tree density, because arboreal pollen types tend to be overrepresented in non-arboreal settings and because arboreal species differ widely in their pollen productivity and

dispersal (Sugita et al., 1999, Table 2). At stand- to landscape-scales, first-principle models of pollen production, atmospheric transport, and deposition provide powerful tools for reconstructing vegetation patterns from networks of pollen records (Sugita, 2007a,b). However, these parameter-intensive models are difficult to apply at broader spatial scales, because they require taxon-specific information on pollen source area, pollen productivity, and regional vegetation composition. At subcontinental to global scales, modern pollen datasets cross-referenced against remotely-sensed observations of forest cover can be used to quantitatively reconstruct past variations in vegetation indices such as fractional woody cover and leaf area (Williams, 2003; Tarasov et al., 2007; Gonzales et al., 2008; Williams et al., 2008). These quantitative indices complement categorical mappings of the past vegetation (Williams et al., 2004; Dyke, 2005; Strong and Hills, 2005) and are useful for land-use and land-cover-change research because they can be compared directly to global satellite-based observations of recent land-cover change (e.g. DeFries et al., 2000; Yang et al., 2006).

Here, we build upon these advances with a new synthesis of the Holocene history of the prairie-forest ecotone. The primary variable reconstructed here is percent area occupied by woody cover (%WC), which is inferred from fossil pollen records using the modern analog technique (MAT) (Overpeck et al., 1985; Jackson and Williams, 2004) and a modern calibration dataset consisting of surface pollen samples from Whitmore et al. (2005) linked to remotely-sensed raster maps of %WC (DeFries et al., 2000). Because our temporal reconstructions of %WC ultimately are founded upon the contemporary spatial relationships between %WC and %AP, we first examine these relationships for the northern Great Plains. We show that %AP is high relative to %WC, presumably caused by high levels of background arboreal pollen from long-distance transport of arboreal pollen into non-arboreal settings (Webb et al., 1981; Sugita, 1994), and argue that these high background values cause %AP-based inferences of tree density to underestimate past rates of change. We then map %WC from 11 to 0 ka, use these maps to reconstruct the Holocene movements of the prairie-forest ecotone, and check our reconstructions against prior efforts. Finally, we survey the %WC time series from individual sites (along with $\delta^{13}\text{C}$ records of the relative abundances of C3 and C4 plants) and report that 'abrupt' vegetation responses (<300 years) to early Holocene drying of the mid-continent were widespread. The rates of early Holocene deforestation estimated here are faster than previously reported, and are consistent with recent evidence that climate-mediated shifts in fire regime or pest outbreaks can cause widespread tree die-offs and rapid shifts in forest/woodland ecotones (Allen and Breshears, 1998; Foster et al., 2006; Kurz et al., 2008), whereas reforestation of landscapes tends to span several thousand years (Umbanhowar et al., 2006).

2. Data and methods

2.1. Data

Fossil pollen records are drawn primarily from the Global Pollen Database (Grimm, 2000), and supplemented with recently collected records from the prairie-forest ecotone (Supplementary Table 1). The list of 80 pollen types used in the modern and fossil datasets to calculate %AP and as the basis for the MAT reconstructions of %WC (Supplementary Table 2) is identical to the '64-split' list recommended by Williams and Shuman (2008).

The modern calibration dataset used here is the North American Surface Sample Database (Whitmore et al., 2005, available at <http://www.lpc.uottawa.ca/data/modern/index.html>), cross-referenced with woody cover data derived from the Advanced Very High Resolution Radiometer (AVHRR) (DeFries et al., 2000; Williams, 2003). For each surface pollen sample, the AVHRR tree cover for all raster grid-cells within a 11 km × 11 km search window is averaged and assigned to the surface pollen sample.

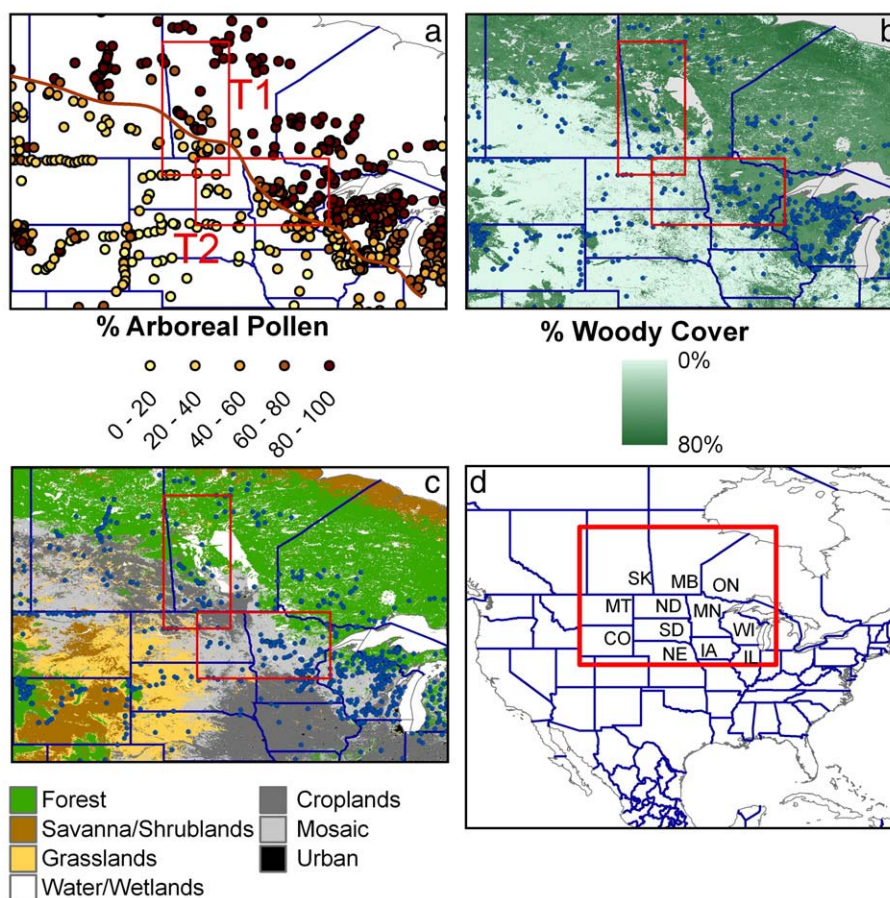


Fig. 1. Current spatial gradients in Midwestern vegetation, as sensed by the surface pollen samples and AVHRR instrument. a) Percent abundance of arboreal pollen (%AP) in surface sediment samples (Whitmore et al., 2005). Brown line indicates the 80% AP isopoll. b) Map of percent woody cover (%WC), from the Global Land Cover Facility at the University of Maryland (DeFries et al., 2000). c) Maps of current vegetation land cover types, including agricultural cover types (Loveland et al., 2000). d) Map of south-central North America, showing location of study region as a red box. State and province names within the study region are indicated using standard two-letter abbreviations. In b) and c), blue dots indicate locations of the surface pollen samples shown in a). In a)–c), Locations of the transects used for %WC vs. %AP comparisons (Fig. 2) are indicated by red boxes. Bounds for Transect 1: 48°N to 56°N, 102°W to 98°W. Bounds for Transect 2: 45°N to 49°N, 100°W to 92°W.

Unlike previous reconstructions of woody cover (Williams, 2003; Williams and Jackson, 2003), this paper did not remove surface pollen samples from regions affected by historical land use, because this would have excluded most Great Plains surface pollen samples. In the Great Plains, human land-use has tended to reduce forest cover. These land-use changes have also affected the composition of recent pollen assemblages, with the increased abundances of *Ambrosia* pollen the most visible signature of European settlement and land clearance. However, despite this land-use history, the prairie-forest ecotone is still clearly present (Fig. 1), and its present position appears to be unchanged from its position prior to European arrival (Ramankutty and Foley, 1999). Moreover, our application of the modern analog technique makes no assumption about why a given site is forested or unforested, so anthropogenic changes to some portions of the modern vegetation should not affect the MAT results, as long as a) potential analog sites from fully forested locations still exist in the calibration dataset and b) anthropogenic impacts on %WC are also reflected in the corresponding modern pollen records. Thus, we believe that our positioning of the Holocene prairie-forest ecotone is not substantially affected by recent land-use, but recognize that our reconstructions of %WC at individual sites might be too low.

2.2. The modern analog technique

The modern-analog technique (Overpeck et al., 1985; Jackson and Williams, 2004) relies on the assumption that compositionally similar pollen samples were produced by compositionally similar bodies of

vegetation. Fossil pollen samples can thus be matched to their closest analogs in modern calibration datasets and assigned the observed vegetation characteristics associated with their modern analogs. This approach is conceptually identical to the widespread application of the MAT to reconstruct past climates from paleoecological data (e.g. Davis et al., 2003; Vau et al., 2006), but does not require assuming that vegetation composition is in equilibrium with climate (Williams, 2003).

Our usage of the MAT follows the recommendations made by Williams and Shuman (2008), who systematically explored the parameter space for the MAT to identify which combinations of parameters provided the most accurate and precise climate and vegetation reconstructions from the North American Surface Sample Dataset. We used 63 pollen types with 14 of these types split into regional varieties (Supplementary Table 2, Williams and Shuman, 2008). *Ambrosia* was not included. In the MAT, these regional splits effectively act to exclude surface pollen samples from floristically distinct regions (Williams et al., 2006; Williams and Shuman, 2008). We used the squared-chord dissimilarity (SCD) metric to measure the compositional differences among modern and fossil pollen samples (Gavin et al., 2003). We set an analog/no-analog threshold of 0.3, limited the maximum number of modern analogs per fossil sample to 7, and calculated an unweighted average for %WC from the modern analog samples (Williams and Shuman, 2008). Fossil samples were declared to have no modern analog if the SCD to the closest modern analog was greater than the analog/no-analog threshold (0.3), and were declared to have few modern analogs if the number of modern

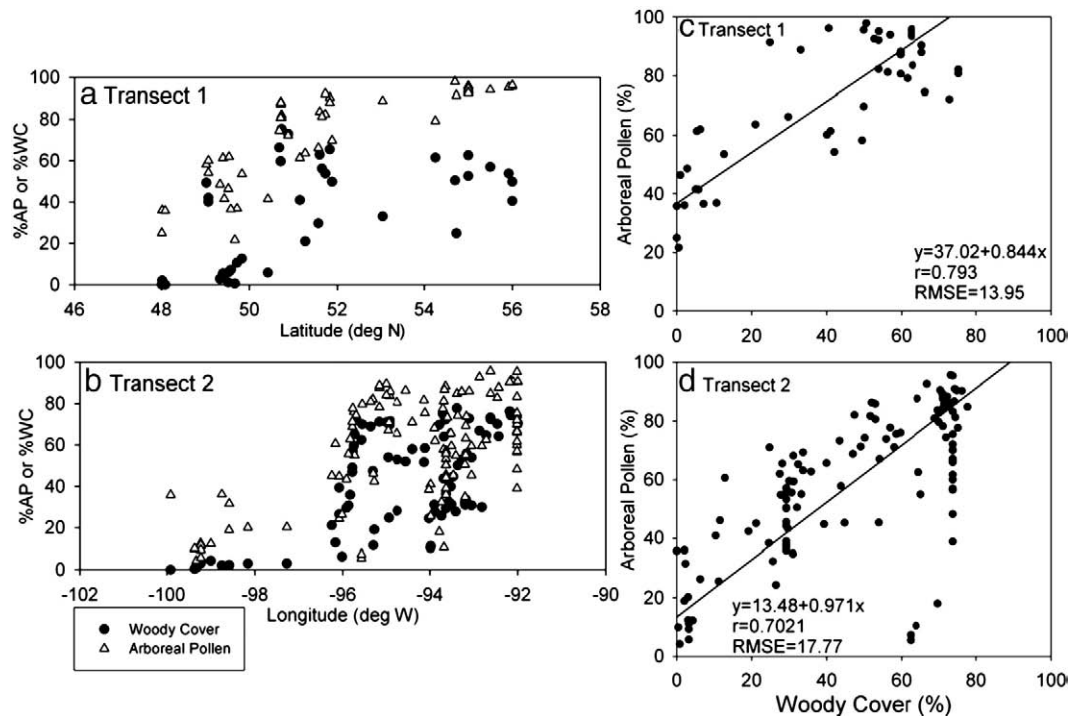


Fig. 2. Relationships between %AP and %WC for two transects crossing the prairie-forest ecotone (Fig. 1). Left-hand plots show the distribution of %AP and %WC for a latitudinal transect across the northern prairie-forest border and a longitudinal transect across the eastern prairie-forest border (see Fig. 1). Right-hand plots show scatter plots of %AP versus %WC for both transects. In both transects, an approximately linear relationship exists between %AP and %WC, but the form of the relationship varies due to differences in species composition between the two transects. In both transects, the y -intercept is >0 , indicating a consistent overrepresentation of arboreal pollen. There are 49 data points in Transect 1 and 119 in Transect 2.

analogs with SCD's below the analog/no-analog threshold was <7 . We did not infer %WC for fossil samples with no modern analog.

Note that %AP itself is not a predictor variable in the MAT-based reconstructions of %WC, although its constituent pollen types are (Supplementary Table 2). Therefore, although %WC and %AP are related indices of forest density, there is no direct relationship between the two.

In our maps, we use the 20% WC isoline to mark the position of the prairie-forest ecotone. Because the ecotone is a patchy mosaic of variable width (Marschner and Heinzelman, 1974), a swath admittedly would be a more appropriate representation, but for visual clarity we use a line. In many places and times, the %WC gradient is steep enough that the precise choice of isoline is not very important (Fig. 1b); in the Discussion we note places where the 20% isoline alone fails to capture key changes in forest cover.

2.3. Defining abruptness

To analyze the rapidity of early Holocene vegetation changes, we visually assessed the %WC time series to identify the early Holocene transition from high to low %WC. We define this transition as 'abrupt' if the duration of the transitional period is <300 years. This definition is a bit broader than used by Williams et al. (2002), who identified rapid changes as <200 years. The broader definition used here is a compromise between matching the standard set by Williams et al. (2002), versus the counterpoint that we are casting a wider net to map the prairie-forest ecotone and so the pollen dataset has wide intersite variations in sampling resolution and dating precision. We highlight instances where well-dated and high-resolution pollen records show evidence of changes substantially less than 300 years, or show changes between adjacent pollen samples; i.e. at the limit of detection. Changes are 'moderate' if the duration of transition is <1000 but >300 years. Transitions lasting >1000 years are 'gradual.' Sites showing no change in %WC during the early Holocene are classified as 'no

signal.' This is a narrow definition of no signal, because many of the 'no signal' sites show changes in the abundances of individual pollen types that are not reflected as changes in %WC (e.g. Grimm, 2001).

3. Results

3.1. Modern relationships of %WC and %AP in the northern Great Plains

The present position of the prairie-forest ecotone is clearly apparent in the AVHRR-based mapping of fractional woody cover (Fig. 1b). Although the ecotone appears as a fairly sharp line in these maps, at finer scales the ecotone is a patchy mosaic, characterized by a high landscape-scale heterogeneity in forest cover caused by local- to landscape-scale variations in climate, position of fire breaks, and edaphic conditions (Wells, 1965; Grimm, 1984). The prairie-forest ecotone persists, although in many areas agricultural land cover has replaced prairie vegetation (Fig. 1c). The distribution of %AP in the northern Great Plains (Fig. 1a) is qualitatively similar to the %WC patterns, with low values in the interior of the Great Plains, and rapidly increasing values at the prairie-forest ecotone. The 60% isopoll for %AP (Fig. 1a, line) approximates the position of the prairie-forest ecotone (Fig. 1b).

Two transects across the prairie-forest ecotone, one trending north from North Dakota to Manitoba (Transect 1) and the other trending east from the Dakotas to eastern Minnesota (Transect 2), permit a more direct analysis of the relationship between %AP and %WC. As in the maps, plots of %AP and %WC along these transects clearly trend from low values within the Great Plains to high values north and east of the prairie-forest ecotone (Fig. 2a,b). In Transect 1, the increase in woody cover is fairly gradual and linear (Fig. 2a), whereas in Transect 2 the prairie-forest ecotone is clearly placed at ca. 96°W (Fig. 2b). In both transects, %AP values are systematically higher than %WC values, indicating that arboreal taxa are consistently overrepresented in the surface pollen samples (Fig. 2a,b).

The relationship between %AP and %WC is approximately linear in both transects (Fig. 2c,d), and in both transects the slope of the relationship does not significantly differ from the 1:1 line (Transect 1: 95%CI = 0.6524 to 1.0799; Transect 2: 95%CI = 0.8049 to 1.1701). RMSE is 13.95 for the %AP vs. %WC regression in Transect 1 and 17.77 for Transect 2, indicating a moderate amount of scatter around the regression line. The column of points apparent at the right side of Fig. 2d is particularly discrepant. They are all from a single site – Thinn Lake, MN – in which a set of surface pollen samples were collected from a range of local vegetation types and depositional settings (Swain, 1979). If the Thinn Lake samples are removed from Transect 2, the regression fit improves but the regression parameters do not qualitatively change, i.e. $y = 11.9 + 1.08x$, the 95%CI for slope is 0.91 to 1.21, $r = 0.75$, and $RMSE = 17.44$. Deviations from the model presumably are caused by differences among sites in plant community composition (and differences among taxa in their pollen over/underrepresentation), a higher sensitivity of the pollen sensor to plants adjacent to the sample location, and vegetation changes between the time of pollen-sample collection and time of AVHRR-image collection (Williams and Jackson, 2003).

For both transects the y -intercept is large, indicating that many sites with essentially no tree cover still contain substantial quantities of arboreal pollen. This combination of a slope close to one and a positive y -intercept suggests that the high %AP values are due to high levels of background pollen caused by long-distance transport of arboreal pollen from trees outside the 20 km window (Webb et al., 1981). The higher levels of background pollen in Transect 1 (i.e. higher y -intercept) is likely due to differences in pollen productivity and dispersal among the arboreal species found in the two transects, particularly for notoriously overrepresented taxa such as *Pinus*, *Alnus*, and *Betula* (Sugita et al., 1999; Williams and Jackson, 2003) that are more common in the north. Thus, even within the Great Plains the parameters vary for the %AP vs. %WC regression, and these parameters should not be applied outside the Great Plains. Although we report linear regressions here, we do not expect a linear relationship between %WC and %AP for all regions and spatial scales.

3.2. Holocene shifts in the prairie-forest ecotone

In the east (Minnesota, southern Manitoba, and Iowa), the prairie expanded eastwards from 11 to 7 ka, with the largest declines in %WC and fastest ecotone movement between 10 and 8 ka (Figs. 3 and 4). From 11 to 10 ka, the initial prairie expansion was limited to southeastern Minnesota (Fig. 3). From 10 to 8 ka, deforestation and prairie expansion was rapid and widespread along the eastern ecotone (Figs. 3–5). The fastest movement of the prairie-forest ecotone (as marked by the 20% WC isoline) occurred between 10 and 9 ka, whereas between 9 and 8 ka, %WC decreased substantially in northern Minnesota but the 20% isoline did not move much (Figs. 3 and 5). From 8 to 7 ka, the rate of prairie expansion continued but greatly slowed, with localized expansion in southeastern Minnesota. By 7 ka, the prairie-forest ecotone had reached its maximum eastward extent, and it remained there through 6 ka. Then, from 6 to 2 ka, the prairie retreated west, reaching its present position by ca. 2 ka. This retreat was pervasive along the eastern prairie-forest ecotone, but was somewhat irregular, due to intersite differences in the rate and timing of reforestation.

In a series of papers, Baker et al. (1996, 2002) suggested that the mid-Holocene prairie-forest ecotone in Iowa and southeastern Minnesota was sharp and west of the position mapped by Webb et al. (1983). Our results are ambiguous with respect to the mid-Holocene position of the prairie-forest ecotone in this region (Figs. 3–4 and 6), but generally suggest a more diffuse, rather than sharp, ecotone. The %WC reconstructions for Kirchner Marsh (Wright et al., 1963), Money/Pine Creeks (Baker et al., 2002), and Roberts Creek (Baker et al., 1996) suggest that at all three sites, woody cover was low

(ca. 20%) from 10 to 4 ka, when woody cover gradually increased (Fig. 6). The reconstruction of ca. 20% woody cover at all three sites creates uncertainty in the placement of the 20% isoline (Fig. 4), but contraindicates the existence of a sharp ecotone between these sites. However, our placement of the prairie-forest ecotone in this region is complicated by no-analog samples (Fig. 6, see Discussion). In the eastern Prairie Peninsula, in Illinois, intersite differences between Nelson Lake and Chatsworth Bog in their charcoal, $\delta^{13}C_{\text{charcoal}}$, and pollen records also contraindicate a sharp ecotone, instead indicating a mosaic of forest and grassland patches during the middle Holocene (Nelson et al., 2006).

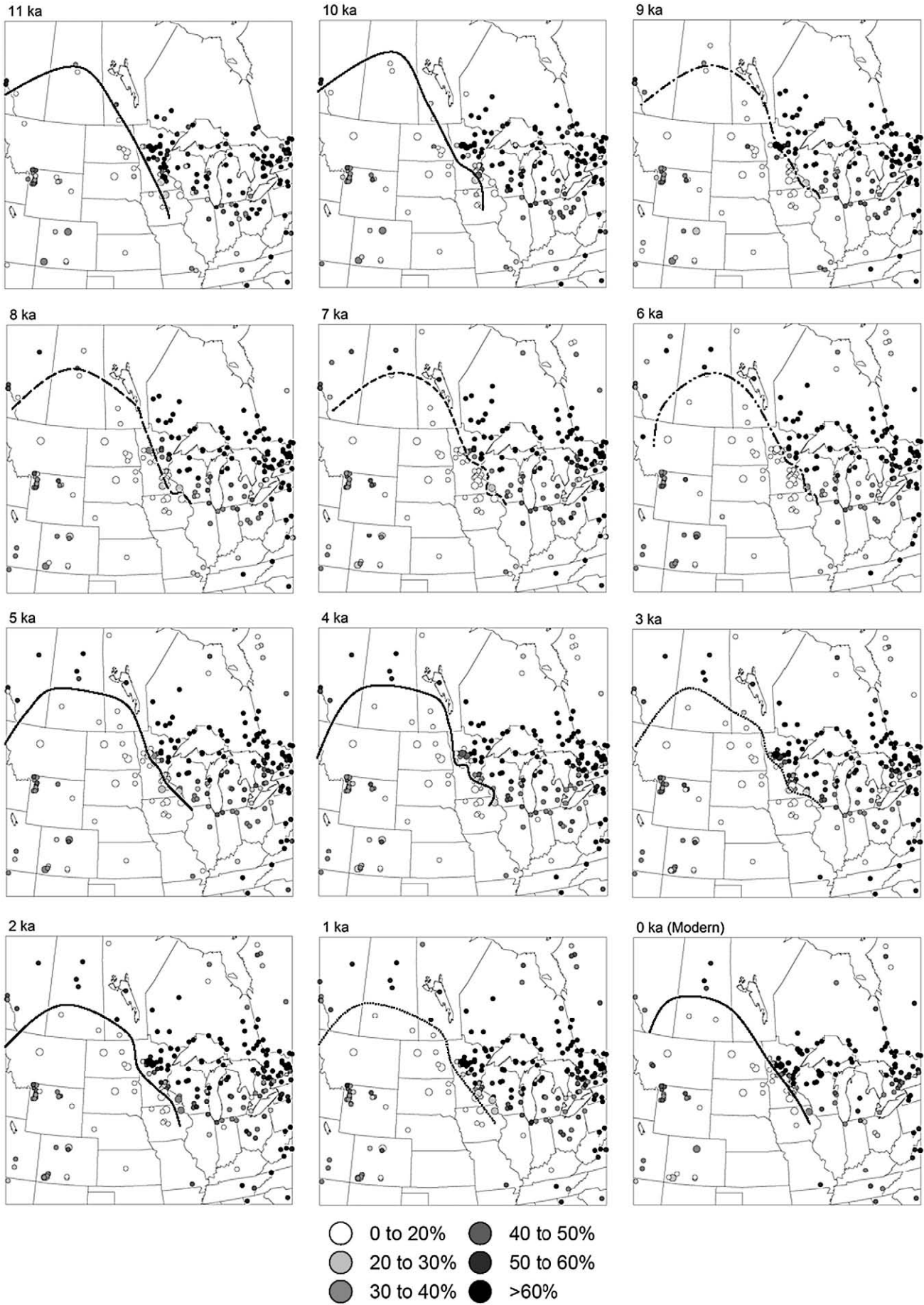
The history of the northern prairie-forest ecotone (Alberta, Saskatchewan, and central Manitoba) is less well constrained than the eastern ecotone, but nonetheless a general trajectory can be reconstructed. During the end-Pleistocene and early Holocene, evidence for the position of the prairie-forest ecotone comes from %WC reconstructions for a few key sites, particularly Lake A and Lake B in central Saskatchewan (Mott, 1973) and Lake E and Glenboro Lake in southern Manitoba (Ritchie and Lichti-Federovich, 1968; Ritchie, 1969). These records indicate that %WC was moderate to high at the end of the Pleistocene, then declined between 12 and 10 ka (Fig. 7). From 10 to 6 ka, the northern prairie-forest ecotone appears to have been fairly stable, except in Manitoba where the prairie expanded eastwards in concert with the adjacent expansion in Minnesota (Figs. 3 and 4). However, the site density used here is so low that some early Holocene movements in the northern prairie-forest ecotone may be undetected. From 6 to 2 ka, %WC increased and the prairie-forest border moved southwards, with a time-transgressive increase in woody cover apparent at Lake A, Lake E, and Glenboro Lake (Figs. 3, 4 and 7).

To summarize, the Holocene histories of eastern and northern prairie-forest ecotone show similar but non-identical trajectories. In the east there is a clear reversal in direction, with prairie expansion from 11 to 7 ka and prairie retreat from 6 to 2 ka. Conversely, in the north, the prairie-forest ecotone apparently alternated between periods of stasis (10 to 6 ka and 2 to 0 ka) and periods of prairie retreat (6 to 2 ka), but no reversals are apparent.

3.3. Rapidity of the early Holocene prairie advance and deforestation

Two key results emerge from the time series of %WC and %AP at individual sites (Figs. 5–8). First, the asymmetrical pattern noted by Umbanhowar et al. (2006) is widespread, with abrupt early Holocene declines in %WC and gradual mid- to late-Holocene reforestation apparent at many sites (Fig. 8, Supplementary Table 1). Of the 46 pollen records showing an early-Holocene decline in %WC, nearly half (21) indicate that the decline was abrupt (Supplementary Table 1). Sites recording abrupt conversions from forest to grassland are concentrated at the prairie-forest ecotone, whereas sites recording moderate or gradual deforestation are distributed more widely (Fig. 8). This pattern suggests that the prairie-forest ecotone is particularly sensitive to environmental change. However, rapid early-Holocene vegetation changes are not limited to the prairie-forest ecotone: $\delta^{13}C$ records also show rapid increases in the relative abundances of C4 plants (Fig. 8, Supplementary Table 1).

Good examples of the abrupt early Holocene deforestation and gradual reforestation at the eastern ecotone (Fig. 5) include Elk Lake (Whitlock et al., 1993), Steel Lake (Nelson et al., 2004; Wright et al., 2004), and Little Bass Lake (Swain, 1979). At Elk and Steel Lakes, forests completely converted to grasslands at ca. 8 ka. Note that the 1000-year offset between the Elk Lake and Steel Lake chronologies argued for by Wright et al. (2004) is not apparent in the %WC reconstructions. However, the chronological offset is most apparent for the end-Pleistocene spruce decline (ca. 11 ka at Steel Lake and 10 ka at Elk Lake); the pollen diagrams show no obvious discrepancy in the early Holocene rise in non-arboreal pollen abundances



(Whitlock et al., 1993; Wright et al., 2004). At Steel Lake non-arboreal pollen percentages gradually rise at 9 ka and accelerate at 8.0 ka (Wright et al., 2004, Fig. 4) versus a gradual increase between 8.6 and 7.9 ka at Elk Lake (Whitlock et al., 1993, Fig. 2). At Little Bass Lake, further to the east, the decline in %WC is abrupt but the magnitude is smaller, suggesting that forest openness increased but did not result in a complete conversion to grasslands. Sites at the northern ecotone also record abrupt deforestation and gradual reforestation (e.g. Lake A, E Lake; Fig. 7c,d). Lake B apparently remained forested throughout the Holocene, except perhaps between 10 and 9 ka, and Glenboro Lake shows a rapid decline in forest cover at the end of the Pleistocene but also a moderately rapid reforestation after 4 ka. In both transects (Figs. 5 and 7), the variable timing of the forest decline is consistent with a time-transgressive expansion of prairie.

Second, the early Holocene deforestation may have been much more abrupt than previously recognized. At almost all sites, %WC decreases much more quickly than %AP. At Elk Lake, for example, the decline in %AP spans 1000 years, whereas the decline in %WC lasts ca. 300 years (Fig. 5c). At Steel Lake, the %AP decline spans 1400 years, versus 275 years for the %WC decline (Fig. 5d). Relatively rapid declines in %WC can be seen at the other sites shown in Figs. 5 and 6, as well as for other sites not shown here. This difference between the temporal rates-of-change for %WC and %AP can be linked directly to their present spatial distributions (Fig. 1), and in particular, the overrepresentation of arboreal pollen in non-arboreal communities (Fig. 2). Just as the overrepresentation of arboreal pollen blurs the present-day prairie-forest ecotone, it also limits the range of variation possible in arboreal pollen diagrams from the Great Plains. Grassland sites such as Moon Lake still have 10 to 20% arboreal pollen (mostly *Quercus*, *Betula*, and *Picea*) (Laird et al., 1996) during the Holocene, and ecotonal sites such as Elk Lake and Steel Lake rarely drop below 40% arboreal pollen during the Holocene (Fig. 5c,d). Modern analogs for the mid-Holocene fossil samples from these sites are near to but west of the modern ecotone, where %AP is moderate but %WC is very low. In this way, the modern analog technique corrects for the overrepresentation of arboreal pollen.

Lake B is an informative exception. Unlike the other sites, %AP rapidly drops at ca. 11 ka, contrasted with variable but increasing %WC from 12 to 10 ka (Fig. 7b). The high %AP mainly represents *Picea* (Mott, 1973). Modern analogs for these high-*Picea* samples are found north of Arctic treeline, where locally low pollen productivity combined with long-distance transport of *Picea* results in high %AP despite low %WC. High %AP and low %WC values also occur in the basal sediments of Lake A and E Lake (Fig. 7c,d), suggesting that landscapes were initially open following deglaciation, then boreal forests established as temperatures increased, then %WC decreased again in response to increasingly dry conditions. Note that calibrating from %AP to %WC can also shift the apparent timing of the early Holocene deforestation: at E Lake, %AP decreases at 11 ka, whereas %WC decreases at 10 ka.

4. Discussion

4.1. Checking the reconstructions of the prairie-forest ecotone

Our maps of the Holocene history of the prairie-forest ecotone generally match the earlier mapping efforts of Webb et al. (1983), although there are important differences in detail (Fig. 4). The general patterns are similar: a large advance during the early Holocene (10 to 8 ka; 9 to 8 rka), a maximum eastward position by the mid-Holocene (7 to 6 ka; 7 to 6 rka), and prairie retreat westward after 6 ka. However, the range of movement shown here is somewhat smaller than in

Webb et al. (1983), and in our reconstructions the prairie-forest ecotone never advanced into southwestern Wisconsin, contrary to the patterns mapped by Webb et al. (1983) (Fig. 4). However, this apparent disagreement is partially due to our choosing the 20% isoline to map the prairie-forest ecotone: the %WC reconstructions indicate that the Holocene prairie-forest ecotone in southern Minnesota and Wisconsin was gentler than in northern Minnesota (Fig. 3), and the moderate mid-Holocene %WC values mapped for southern Wisconsin are consistent with prior inferences of lowered lake levels and oak savannas during the middle Holocene (Winkler et al., 1986). The early Holocene prairie expansion eastwards indicated by both maps (Fig. 4) is consistent with a wide variety of independent climate proxies (e.g. eolian, lake-level, paleosalinity, and $\delta^{13}\text{C}$ records) indicating that the Great Plains became warmer and dryer during the early Holocene (Forman et al., 2001; Dean et al., 2002; Shuman et al., 2002; Miao et al., 2007). The general consistency between these %WC-based maps of the prairie-forest ecotone and prior work reinforces our confidence in the %WC reconstructions.

A key limitation on the accuracy of these maps is the availability of well-dated pollen records from the midcontinent (Grimm, 2001). Our mapped position of the prairie-forest ecotone is best constrained in Minnesota and Iowa (Fig. 3) by a series of recently analyzed and well-dated sites (Baker et al., 1996, 2002; Camill et al., 2003; Wright et al., 2004; Nelson and Hu, 2008). In other areas, the mapped position of the ecotone may change somewhat as new sites with better chronological controls become available.

Our %WC reconstructions in southeastern Minnesota and Iowa are complicated, however, by the presence of no-analog samples, which have two causes. First, high abundances of *Ulmus* pollen at many early Holocene sites have no equivalent in surface pollen samples (Wright, 1992; Camill et al., 2003; Williams et al., 2004). Second, we suspect that the frequent Holocene no-analog samples at Roberts Creek and Money/Pine Creeks (Fig. 6) result from their collection from alluvial depositional environments. From a theoretical perspective, small creeks have a very high perimeter-to-area ratio, such that the pollen in alluvial sediments is presumably sourced mostly from the adjacent riparian vegetation (Fall, 1987; Sugita, 1994). In eastern Iowa prior to European settlement, riparian vegetation primarily consisted of gallery forests composed of *Quercus*, *Carya*, *Populus*, and other mesophytic trees (Küchler, 1964), and these pollen types presumably are highly upweighted relative to upland prairie taxa. Moreover, pollen assemblages are sorted when transported by water, affecting the relative abundance of pollen types in alluvial sediments (Holmes, 1994). The different depositional settings of the samples from Money/Pine Creeks and Roberts Creek versus the reference sample dataset (mostly from lakes and mires) likely causes the lack of identifiable modern analogs, and reduces confidence in the analog-based %WC reconstructions. Given these considerations, we have low confidence in pollen-based placements of the prairie-forest ecotone in eastern Iowa.

This paper presents, to our knowledge, the first detailed mapping of the northern prairie-forest border (but see Williams et al., 2004; Strong and Hills, 2005). The generally similar Holocene histories for the northern and eastern prairie ecotones suggest that both responded to a common climate forcing, i.e. dryer-than present conditions during the early Holocene and increasing moisture availability after 6 ka. The cause of the interregional differences in the early Holocene dynamics (i.e. stasis in the north and prairie advance in the east) is unknown, but we have three hypotheses. First, the apparent stasis of the northern prairie-forest ecotone simply may be an artifact of a low site density relative to the high density of

Fig. 3. Maps of percent woody cover (%WC) for the Holocene, based on modern-analog reconstructions applied to fossil pollen records. For each 1-ka time period, a black line marks the inferred position of the prairie-forest ecotone. We use the 20% isoline for woody cover to mark the position of the prairie-forest border. The line symbology (dashed, solid) is identical between this figure and Fig. 4. Larger circles mark sites with particularly strong chronological controls i.e., they either have 1) five or more AMS ^{14}C dates or other high-precision Holocene age controls, 2) two or more high-precision dates within 500 years of the early-Holocene decline in %WC recorded at that site, or 3) 10+ accurate but less-precise Holocene dates such as OSL or conventional ^{14}C of terrestrial plant fossils.

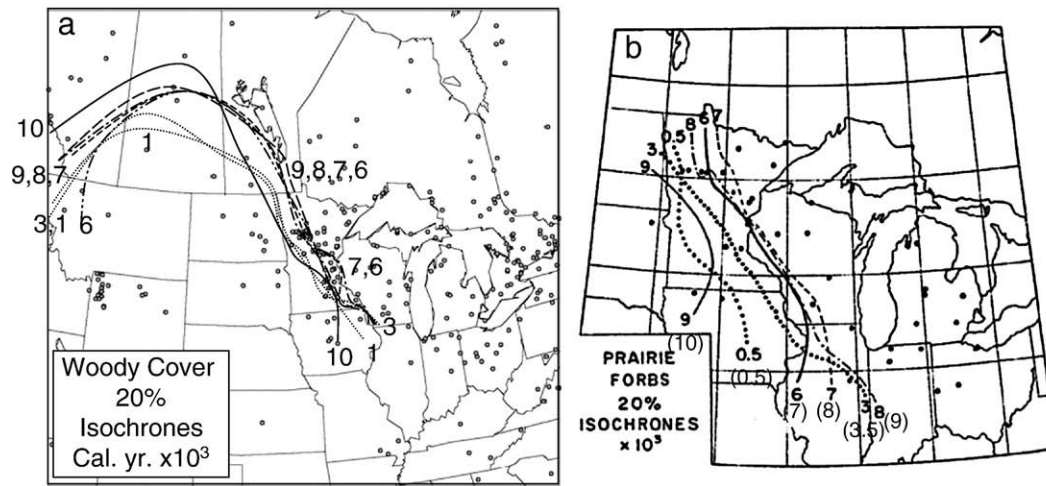


Fig. 4. Mapped shifts in the prairie-forest ecotone during the Holocene, based on a) reconstructions of fractional woody cover (this paper) and b) the 20% isopoll for prairie forb taxa (the sum of *Ambrosia*, *Artemisia*, other Asteraceae, and Chenopodiaceae/Amaranthaceae) (Webb et al., 1983). Numbers indicate 1000's of years before present, as calendar years in a) and ^{14}C years in b). In b), the calendar-year equivalents of the radiocarbon ages are shown in parentheses (all calendar ages are rounded to the nearest quarter-millennium). Note also that the northern position of the prairie-forest ecotone is not well constrained during the early Holocene (Fig. 3).

eastern sites. Second, early Holocene drying may have been less severe in the north. This hypothesis is supported by regional climate simulations for 6 ka (Diffenbaugh et al., 2006, Fig. 1, S3) but contraindicated by eolian and lake-level records indicating a dry early Holocene, with many northern Plains lakes entirely dried out (Barnosky et al., 1987; Sauchyn and Sauchyn, 1991; Schweger and Hickman, 1993; Wolfe et al., 2002). Third, these regional differences may have been caused by spatially varying interactions between temperature and moisture availability. The early Holocene warming and drying may have more strongly increased evapotranspiration rates (Almendinger, 1993) and reduced soil moisture in the east than in the north.

4.2. Abrupt declines in early Holocene forest cover

Our findings indicate that abrupt deforestation and gradual reforestation (Umbanhowar et al., 2006) were common but not universal phenomena at the prairie-forest ecotone during the Holocene (Fig. 8). Both our definition of 'abrupt' change — a step change in the vegetation lasting less than 300 years — and our identification of sites experiencing abrupt change are conservative. Our ability to detect abrupt changes is primarily limited by the pollen-sampling resolution at individual sites, and by the accuracy and precision of the available age models. For many pollen records, even sites with fairly high sampling resolution, the decline in %WC occurs between adjacent samples, e.g. at Elk Lake (Fig. 5c). At other sites, especially sites in southern Minnesota (e.g. Sharkey Lake and Kimble Pond) the %WC reconstructions were confounded by no-analog and few-analog results for early Holocene samples with high *Ulmus* abundances (Wright, 1992; Umbanhowar et al., 2006), so %WC estimates are less precise for these sites. However, other proxies at these sites often suggest rapid ecological change, e.g. at Sharkey Lake, a large change in charcoal influx occurring in <100 years suggests a step-change in fire regime and vegetation at 8 ka (Camill et al., 2003). (Changes in pollen and charcoal are more gradual at Kimble Pond, presumably due to differential landscape controls on fire regime.) Similarly abrupt shifts are observed in the relative abundances of C3 and C4 plants (Fig. 8, Supplementary Table 1), suggesting that rapid vegetation responses to early Holocene aridity are not limited to the prairie-forest ecotone. The $\delta^{13}\text{C}$ records are most common west of the prairie-forest ecotone, where fewer pollen records are available.

The reconstructed decreases in %WC are more abrupt than previous estimates based on %AP. For example, the 'gradual' vegeta-

tion responses to early Holocene drying reported for Elk Lake (Dean and Schwab, 2002, p. 1776) is considerably more rapid when the pollen data are calibrated against the modern %WC observations (Fig. 5c). Comparison of the present %AP and %WC gradients across the prairie-forest ecotone (Figs. 1 and 2) helps show why the MAT-based early Holocene drops in %WC — are more rapid than for the corresponding %AP curves. Arboreal pollen is diffused across the prairie-forest ecotone such that sites west of the present prairie-forest ecotone can have %AP values close to 40%, but %WC values close to zero (Fig. 2b). This present-day blurring of the prairie-forest ecotone presumably occurred in the past as well, and acts to minimize the range of variation in the %AP time series. The analog technique corrects for this blurring effect and in essence translates the present abrupt spatial gradient in %WC into abrupt temporal changes at many sites (Figs. 2 and 5–7). Thus, these quantitative reconstructions of past forest cover suggest that vegetation responses to early Holocene drying may have been faster than previously recognized.

What caused the rapid forest-to-prairie conversion? For some sites, the abrupt loss of forest cover may be a direct response to rapid drying of the continental interior. Paleoclimatic records suggest widespread drying in the interior during the end-Pleistocene and early Holocene, with a pulse of rapid drying along the prairie-forest ecotone around 8 ka (Nelson and Hu, 2008; Williams et al., in review). Possible triggers for rapid regional climate change include changes in atmospheric circulation caused by the collapse of the Laurentide Ice Sheet at 8.2 ka (Shuman et al., 2002; Nelson and Hu, 2008) and/or altered regional hydrology caused by the simultaneous outburst drainage of Lake Agassiz (Hu et al., 1997; Clarke et al., 2004). Positive vegetation feedbacks to summer precipitation may have further accelerated regional drying (Gallimore et al., 2005). Many sites show abrupt deforestation near to the 8.2 event, particularly for the more recent and well-dated records (Figs. 5 and 6). However, other sites show abrupt vegetation changes as early as 11 ka and continuing until 6 ka (Figs. 5 and 6; Williams et al. in review), so the 8.2 event cannot be the sole driver of abrupt vegetation change. Conversely, the gradual forest expansions during the middle to late Holocene likely were driven by correspondingly gradual increases in moisture availability (Nelson and Hu, 2008). Increasing moisture availability after ca. 6 ka is widely indicated by higher (but variable) lake-levels, reduced lake salinity, and reduced eolian activity (Laird et al., 1996; Forman et al., 2001; Shuman et al., 2002; Miao et al., 2007). At centennial to millennial timescales, paleohydrological variations appear to have regulated variations in forest composition and the expansion of tree

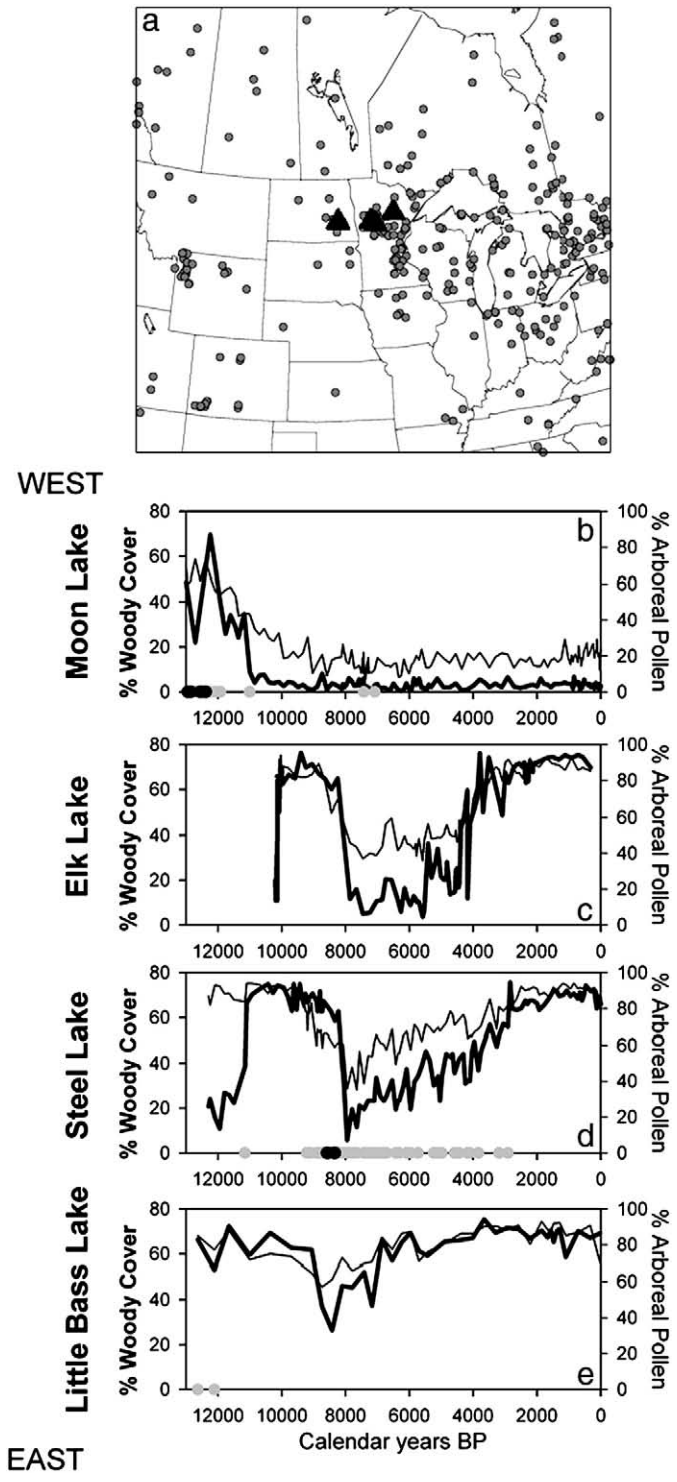


Fig. 5. Holocene time series of %AP and %WC for four lake-sediment records from a transect crossing the eastern prairie-forest ecotone: Moon Lake (Laird et al., 1996), Elk Lake (Whitlock et al., 1993), Steel Lake (Nelson et al., 2004; Wright et al., 2004), and Little Bass Lake (Swain, 1979). Black circles on the time axis indicate fossil samples with no modern analog and gray circles indicate samples with few modern analogs. Samples with no modern analog are included in the %AP curve but not the %WC curve.

taxa in the Great Lakes (Booth et al., 2002, 2004) and New England (Shuman et al., 2004).

Alternatively, rates of drying may have been gradual, but abrupt deforestation was triggered by positive ecological feedbacks. Fire is an obvious candidate mechanism, because in semi-arid ecosystems the relative densities of trees and grasses are strongly mediated by fire regime (Whelan, 1995; Bond and Van Wilgen, 1996) and because pre-

historical distributions of forests and grasslands at the prairie-forest ecotone were regulated by the position of firebreaks (Wells, 1965; Grimm, 1984). Charcoal influxes to lake sediments increased in concert with increased prairie extent during the early Holocene, suggesting a positive feedback loop in which a shift to grassland fuels leads to an increase in fire frequency, which further accelerates the conversion from forest to prairie (Camill et al., 2003; Nelson et al., 2004, 2006). Increased fire severity and/or frequency may also have increased evaporation rates, by reducing litter cover and increasing canopy openness, which would have further facilitated the from forests to grasslands (Cochrane et al., 1999; Umbanhowar et al., 2006).

Whatever the precise mechanism, climate likely played a role in the abrupt early Holocene deforestation because pollen records represent an integrated signal of the surrounding landscape (with a

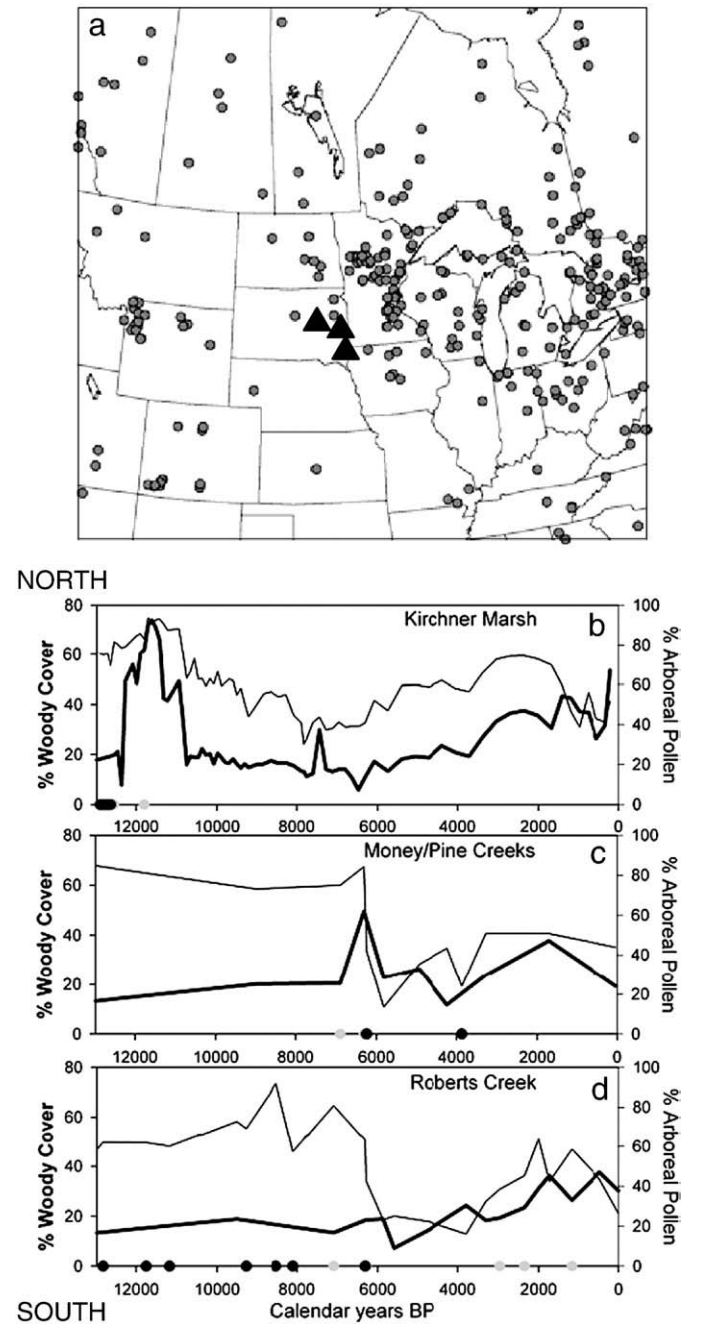


Fig. 6. Holocene time series of %AP and %WC for four lake-sediment records from sites in southeastern Minnesota and Iowa: Kirchner Marsh (Wright et al., 1963), Roberts Creek (Baker et al., 1996), and Money/Pine Creeks (Baker et al., 2002). Format follows Fig. 5.

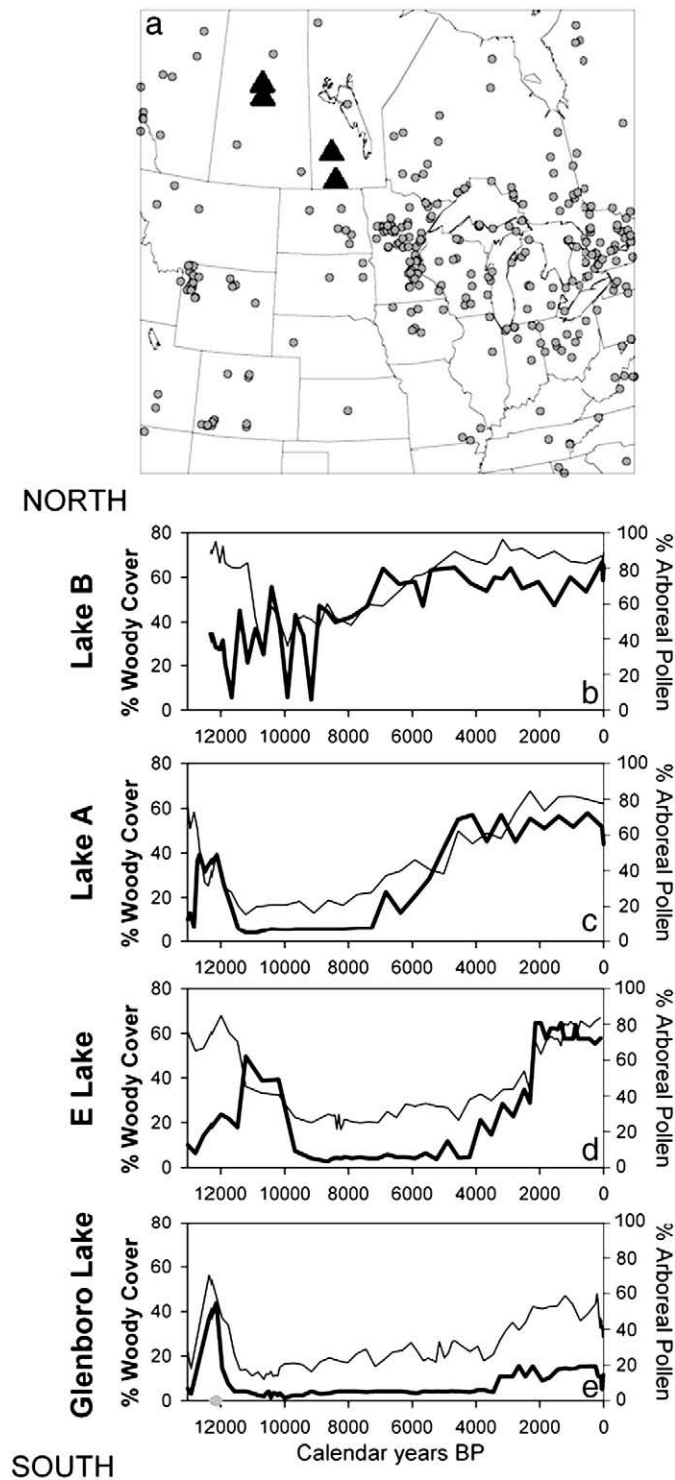


Fig. 7. Holocene time series of %AP and %WC for four lake-sediment records from a transect crossing the eastern prairie-forest ecotone: Lake B (Mott, 1973), Lake A (Mott, 1973), E Lake (Ritchie, 1969), and Glenboro Lake (Ritchie and Lichti-Federovich, 1968). Format follows Fig. 5.

source radius on the order of 10's of kilometers). Hence, abrupt changes in fossil pollen records suggest a widespread and rapid conversion of the surrounding landscape, presumably synchronized by regional climate change. Conversely, the more gradual increase in %WC during the middle to late Holocene suggests that trees gradually infilled the landscape, presumably governed by the interaction between increasing regional moisture availability and local controls on population dynamics.

The rapid decreases in forest cover reported here are consistent with recent papers from both the paleoecological and global change literature that indicate that rapid vegetation change can result from high rates of tree mortality caused by interactions between climate variations and disturbance agents (Breshears et al., 2005; Kurz et al., 2008). In these die-offs, fire, pest, or pathogen outbreaks are usually the direct cause of mortality, but climate variations exert a strong indirect influence, by reducing the resistance of the trees to infection, herbivory, or burning, by altering the population dynamics of the pathogen, or by increasing the frequency and severity of fires. In recent pine- and bark-beetle outbreaks in the western US and Canada, outbreak severity has been amplified by warmer and dryer conditions, which has expanded the range of beetle species, reduced their time of reproduction, and reduced the ability of trees to defend against beetle attacks (Allen and Breshears, 1998; Breshears et al., 2005; Kurz et al., 2008). Because the spread of fire, pests, and pathogens are all density-dependent processes, the severity of fires and pest outbreaks should be highest where tree densities are highest (and where the climatic stresses are strongest), which may explain why most of the early-Holocene abrupt changes are recorded at the prairie-forest ecotone (Fig. 8). Conversely, it is possible that increases in moisture availability during the middle to late Holocene, were also abrupt, but that these changes were masked by gradual establishment of tree populations and infilling.

In the eastern US, the well-known *Tsuga* decline at 5.5 ka (Davis, 1981; Bennett and Fuller, 2002) follows a pattern qualitatively similar to the %WC trends in the Great Plains, with an abrupt decline in *Tsuga* abundances followed by a gradual recovery lasting several thousand years. The *Tsuga* decline is widely attributed to a pest or pathogen outbreak, likely hemlock looper (Davis, 1981; Bhiry and Filion, 1996), was apparently synchronous across the range of *T. canadensis*, and was extremely rapid, occurring within 7–8 years at individual sites (Allison

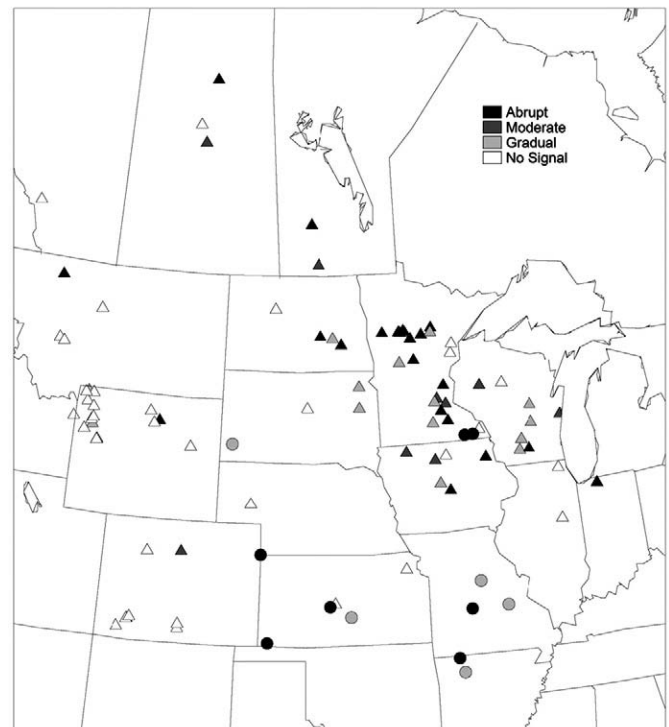


Fig. 8. Map of paleovegetational sites categorized according to the abruptness of the vegetation change during the early Holocene. Most sites are %WC reconstructed from fossil pollen records (triangles) but some represent changes in C3 and C4 plant abundances from $\delta^{13}\text{C}$ records from soil profiles, lake-sediment records, and speleothems (circles). See Methods for the definition of abrupt, moderate, and gradual rates of change. Data from Williams et al. in review.

et al., 1986). Here again, climate variations have been implicated as an indirect cause, based on coincident drops in lake levels and decreased *Quercus* pollen abundances in southern New England (Yu et al., 1997; Shuman et al., 2004; Foster et al., 2006). We speculate that this coincidence in pattern between the %WC and *Tsuga* trends (i.e. rapid declines and gradual recoveries) indicates similar processes are governing the mortality and regrowth of tree species in these two systems, although this simply may be coincidence.

Recent work thus counters the traditional perception that temperate forests, because they are composed of long-lived organisms and create their own microclimates, have weak and lagged responses to climate change (e.g. Davis and Botkin, 1985). It is true that mature trees tend to be more resistant to the direct effects of adverse climates (e.g. drought stress, winter chill) than juveniles, thus climate variability can limit recruitment and colonization without affecting the persistence of mature individuals (Lyford et al., 2003). In classic forest-gap models, the persistence of mature trees increases the resilience and inertia of vegetation responses to climate variations (Davis and Botkin, 1985). However, early versions of these models did not include fire- and pest-related mechanisms and thus omitted the indirect effects of climate variations on disturbance regime and tree mortality. Vegetation models incorporating fire-vegetation and pest-vegetation feedbacks suggest that these processes critically affect the rate of tree mortality and species turnover (Hoffman et al., 2002; Moorcroft et al., 2006; Kurz et al., 2008). More broadly, reviews of the responses of ecological systems to recent climate variations show that non-linear threshold-type responses to climate change are common (Burkett et al., 2005). Thus, both paleorecords from the Great Plains and recent ecological dynamics point to the existence of thresholds, beyond which forests quickly change composition or locally convert to grasslands.

4.3. Implications for the future

Future hydrological trends for the northern Great Plains are uncertain. Half of the climate models from the Fourth Assessment Report of the Intergovernmental Panel on Climate Change predict that summer precipitation will increase in the northern Great Plains during this century (see Fig. 11.12 in Christensen et al., 2007) and half predict a decrease. (A majority predicts winter precipitation will increase.) Nonetheless, climate models consistently indicate an increase in hydrological variability, with more severe rain events interspersed with longer dry periods (see Fig. 10.18 in Meehl et al., 2007). Climate models also consistently indicate that the intensity and frequency of heat waves and other extreme events will increase over this century (Meehl and Tebaldi, 2004; Diffenbaugh et al., 2005), which should further increase the variability of moisture availability at the prairie-forest ecotone. The importance of fire as a landscape process has been reduced by human land-use and fire suppression (Cardille et al., 2001), but pests and pathogens such as Dutch elm disease, beech bark disease, chestnut blight, butternut canker, and emerald ash borer are transforming the composition of eastern forests (Gibbs, 1978; Castello et al., 1995; Schlarbaum et al., 1997). It is possible, therefore, that the key mechanisms governing future ecotonal responses to hydrological variability may shift from fire-climate-vegetation mechanisms to the interactions between climate, vegetation, and pests and pathogens. Although the future trajectory for the Great Plains prairie-forest ecotone cannot be predicted confidently until there is more consistency among climate simulations, both paleorecords and recent events suggest that future drying trends would be more likely to trigger abrupt vegetational responses.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.gloplacha.2008.10.012.

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