

The role of Late Holocene climate variability in the expansion of yellow birch in the western Great Lakes region

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Abstract. Pollen records from the western Great Lakes region of North America show substantial increases in birch pollen percentages during the late Holocene. The vegetational and population dynamics underlying the birch increase have received little attention, in part because of the inability to discriminate among species of birch based on pollen morphology. We used analyses of pollen and plant macrofossils from four lakes in the Upper Peninsula of Michigan to document that the birch pollen increase represents a regional expansion of yellow birch (*Betula alleghaniensis*) populations, which was initiated c. 4500 years ago. Whether yellow birch invaded the region at this time or simply expanded from small, previously established populations is not

clear, although it probably did not grow near our study sites before the expansion. The initial expansion occurred during an independently documented period of high moisture and high water levels in Lake Michigan. A subsequent expansion in yellow birch abundance and distribution occurred c. 3000 years ago, coinciding with a second period of increased moisture and high lake-levels. The yellow birch expansion may have been modulated by millennial-scale climate variability, with most rapid expansion occurring during relatively wet periods.

Key words. Vegetation dynamics, late Holocene, climate variability, plant invasions, Great Lakes region, plant migration.

INTRODUCTION

Four prominent tree species of the mixed conifer/hardwoods forests of the Great Lakes, St Lawrence and Appalachian regions of eastern North America reach their western or north-western range boundaries in the western Great Lakes region (Little, 1971). American beech (*Fagus grandifolia*) does not grow west of eastern Wisconsin and the eastern Upper Peninsula of Michigan. Eastern hemlock (*Tsuga canadensis*) extends to the western end of Lake Superior in northern Wisconsin and Upper Michigan, and has a few scattered populations in north-eastern Minnesota. Eastern white pine (*Pinus strobus*) is widespread west of Lake Superior, with extensive populations in northern Minnesota and adjacent

Ontario. Yellow birch (*Betula alleghaniensis*) is important in forests of northern Michigan and Wisconsin, and has scattered populations in mesic habitats as far west as north-central Minnesota (Braun, 1950) (Fig. 1).

Palynological studies indicate significant Late Holocene changes in the distribution and abundance of white pine, beech and hemlock in the western Great Lakes region. White pine immigrated to the region in the early Holocene, but did not grow west of north-eastern Minnesota until after 4500 yr BP¹, when it expanded west into central Minnesota (Jacobson, 1979). Hemlock established populations in most of Upper Michigan by 6000 yr BP, and expanded southward and westward into northern Wisconsin

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¹ All ages reported in this paper are in calendar years Before Present (yr BP) using the 1950 AD datum, based on the CALIB 4.1 program (Stuiver & Reimer, 1993).

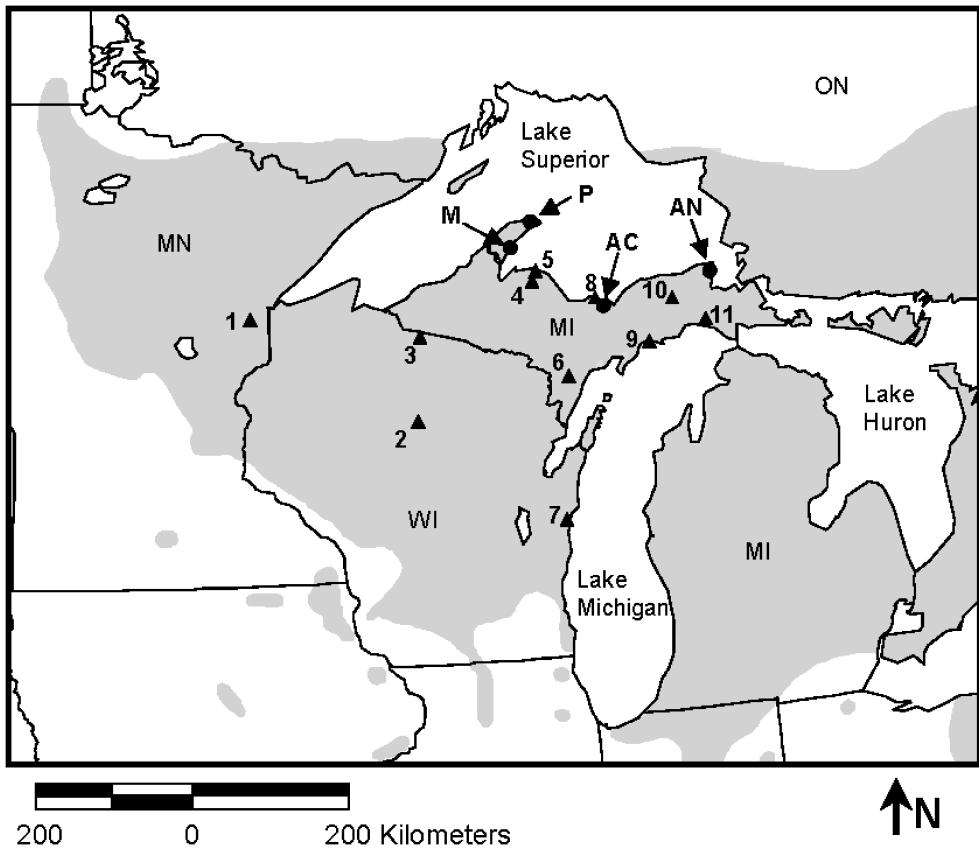


Fig. 1 Map of western Great Lakes region showing modern distribution of *Betula alleghaniensis* (shaded), study sites (circles), and other sites mentioned in text (triangles). Sites are numbered as follows: (1) Jacobson Lake (Wright & Watts, 1969), (2) Wood Lake (Heide, 1984), (3) Lake Mary (Webb, 1974), (4) Camp 11 Lake (Brubaker, 1975), (5) Canyon Lake (Davis, 1981), (6) Kitchner Lake (Woods & Davis, 1989), (7) Gass Lake (Webb, 1987), (8) Spirit Lake (Woods & Davis, 1989), (9) Manistique swale complex (Singer, 1996), (10) Wolverine Lake (Futyma, 1982), (11) Ryerse Lake (Futyma, 1982), (M) Mud Lake (Booth *et al.*, 2002), (P) Partridge Lake, (AN) Andrus Lake, (AC) Ackerman Lake. Modern range map is based on Thompson *et al.* (2000).

c. 3000 yr BP (Davis *et al.*, 1986, 1998; Davis, 1987; Parshall, 2002). Beech occurred over much of the Lower Peninsula of Michigan by 8000 yr BP, and colonized the eastern Upper Peninsula and eastern Wisconsin after 4500 yr BP, where regional populations expanded 3000–2500 yr BP (Davis *et al.*, 1986; Woods & Davis, 1989).

Pollen analysis has been successful in documenting these expansions because both beech and hemlock are monotypic in the region, and because white pine pollen can be differentiated morphologically from other eastern North American pine species. Unfortunately, pollen of yellow

birch is morphologically similar to that of paper birch (*Betula papyrifera*), a forest tree, and bog birch (*B. pumila*), a peatland shrub. Both species are widespread in the region.

Pollen sequences from the western Great Lakes region show a mid-Holocene rise in birch pollen percentages. This increase begins at most sites between 5000 and 4500 yr BP, and at many sites is followed by a second increase between 3000 and 2000 yr BP (Fig. 2). The birch increase is accompanied by a decline in pine (particularly white pine) pollen percentages, with hemlock pollen also decreasing at some sites. Although

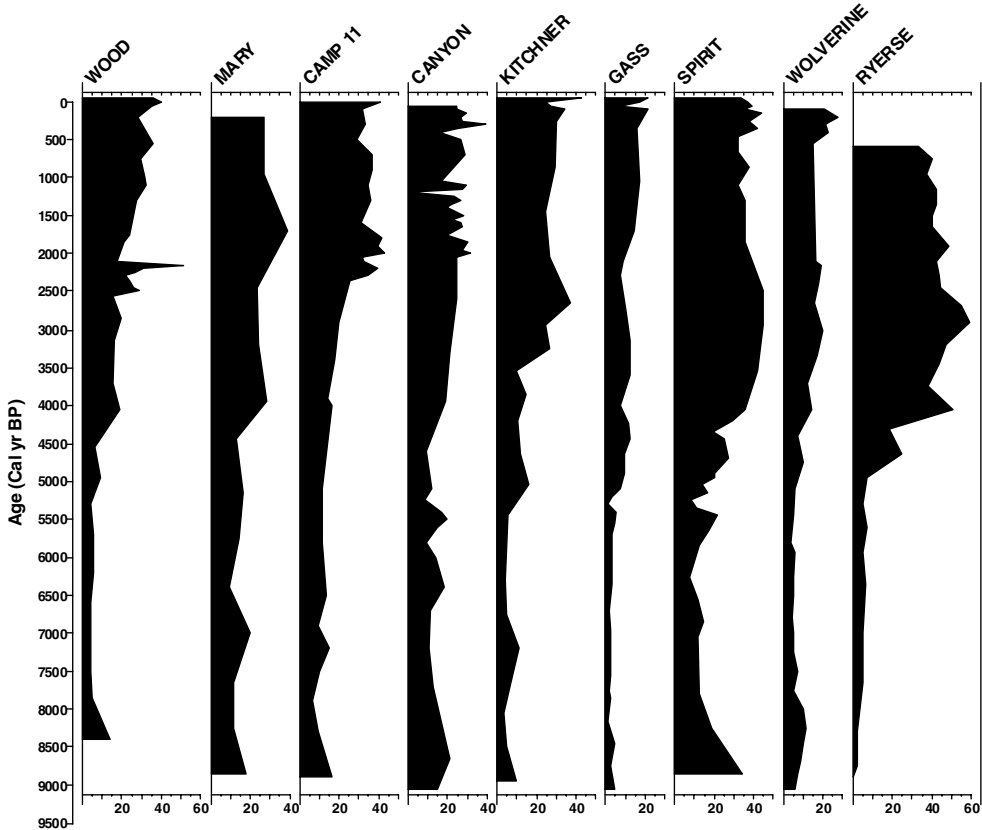


Fig. 2 *Betula* pollen percentages (based on a sum of total arboreal pollen) from previously published sites in northern Wisconsin and Upper Michigan (see Fig. 1 caption for citations). Most show increases in *Betula* pollen between 5000 and 4000 yr BP, and several show additional increases between 3000 and 2000 yr BP. Age models were calculated by converting ^{14}C dates from each site to calendar year ages using the Intcal 98 calibration curve (Method A) from Calib 4.3 (Stuiver & Reimer, 1993), and applying linear interpolation. Dates assigned to each horizon are rounded to the nearest 50-year increment. Data obtained from the North American Pollen Database (NAPD).

the pollen record does not permit identification of the birch species involved, birch macrofossils, particularly fruits and female catkin bracts, can be identified to species.

Macrofossils document occurrence of paper birch throughout the Great Lakes region since at least 10 000 yr BP (Jackson *et al.*, 1997). However, few macrofossil records of yellow birch exist in the western Great Lakes region. Singer (1996) reported yellow birch macrofossils dating *c.* 1850 and 2750 yr BP from coastal wetlands in Upper Michigan, but the sites are young (basal ages 2750 and 4100 yr BP, respectively) and yellow birch trees are scarce in local vegetation. Yellow

birch macrofossils are sparse in Late Holocene sediments (< 3000 yr BP) of Jacobson Lake in north-eastern Minnesota (Wright & Watts, 1969), and are reported in fluvial sediments dating to 3260 yr BP in south-eastern Minnesota (Baker *et al.*, 2002).

In this paper, we present evidence from plant macrofossil records from four lakes in the Upper Peninsula that the late Holocene birch-pollen increase in the region represents invasion and/or expansion of yellow birch. We also provide evidence that the yellow birch expansion and other vegetational events in the region may have been paced by millennial-scale climate

Table 1 Site characteristics

Site	Location	Elevation (m)	Surface area (ha)	Maximum depth (m)
Ackerman Lake	46°19'53"N 86°47'47"W	87	6	13.0
Andrus Lake	46°42'04"N 85°02'17"W	190	14	8.0
Mud Lake	47°07'44"N 88°19'04"W	190	72	3.0
Partridge Lake	47°25'11"N 88°00'26"W	301	3	10.5

variability, which is documented from independent evidence.

METHODS

We obtained palaeoecological records from four lakes in Upper Michigan (Table 1), using pollen analysis to track regional vegetational history, plant macrofossils to verify local establishment and identity of species, and accelerator mass spectrometry (AMS) dating to provide chronological control. The easternmost site, Andrus Lake, is near the eastern shore of Whitefish Point (Fig. 1). The lake apparently originated when a lagoonal feature formed during the Nipissing II highstand (*c.* 4500 yr BP) of Lake Superior was isolated during the subsequent lake-level decline (T. A. Thompson, personal communication). Forests of the surrounding sandy lake plain are dominated by white pine, red pine (*Pinus resinosa*), jack pine (*P. banksiana*), and paper birch. Populations of yellow birch are sparse. This lake yielded a poor record of yellow birch macrofossils, so we use it primarily to verify patterns from the other sites.

Ackerman Lake is a deep kettle lake near Munising Bay (Fig. 1). Steep slopes on the south side, near the coring site, are forested by mixed stands of northern hardwoods (sugar maple (*Acer saccharum*), yellow birch, beech) and conifers (hemlock, white pine). Mud Lake is a shallow lake formed from a cut-off embayment of Lake Superior at the base of the Keweenaw Peninsula (Booth *et al.*, 2002). Sandy lacustrine soils are dominated by white pine, black spruce (*Picea mariana*), white spruce (*P. glauca*), white pine, paper birch and yellow birch. Partridge

Lake is a kettle near the tip of the Keweenaw Peninsula (Fig. 1). Steep slopes around the lake are forested by sugar maple, yellow birch, white pine, white spruce and red oak (*Quercus rubra*).

Each lake was cored from a floating platform using a modified Livingstone piston corer. We used a 7.5-cm diameter barrel except for the compact, deeper sediments (> 2.5 m) of Partridge Lake, where we used a 5-cm core barrel. Cores were extruded and described in the field. Pollen samples comprised *c.* 1 cm³, each spanning 1 cm of sediment depth, and macrofossil samples (30–80 cm³) each spanned 1–3 (usually 2) cm of sediment depth. We used standard techniques for pollen and plant macrofossil analyses from the cores (Jackson, 1999). Pollen samples were counted to a minimum sum of 250 arboreal grains, and percentages were calculated based on a sum of all arboreal types. Macrofossil counts were standardized to a sample volume of 50 cm³. We present only pollen and macrofossil data for birches in this paper. Complete data from these sites have been (Booth *et al.*, 2002) or will be presented in other papers.

Age-models are based on AMS dates of plant macrofossils (Table 2). Dates and age-model information for Mud Lake are presented in Booth *et al.* (2002). Age-models for the other sites are based on linear interpolation between dates, using the sediment surface (–50 yr BP) as an additional benchmark. At Ackerman Lake, we also used the initial mid-Holocene increase of *Tsuga* pollen as a stratigraphic marker, which is dated at 6400 yr BP at other sites in the region (Woods & Davis, 1989; Booth *et al.*, 2002). We used two cores from Partridge Lake. The upper metre of sediment was collected from shallow

Table 2 Radiocarbon dates for Ackerman (AC), Andrus (AN) and Partridge (P) Lakes

Site	Depth (cm)	Material Dated	Laboratory Number	¹⁴ C yr BP	Calibrated Age (yr BP)
AC	174–176	Yellow birch fruits	GX-28720	3320 ± 40	3564 (3680–3465)
AC	275–277	White pine needles	GX-28719	7120 ± 40	7885 (8012–7842)
AN	73–77	White pine needles	NSRL-12635	2130 ± 30	2119 (2297–2002)
AN	178–180	White pine needles	NSRL-12140	4060 ± 40	4564 (4806–4420)
P1	77–80	White pine needles	NSRL-12632	1240 ± 40	1174 (1274–1059)
P1	187–188	White pine needles	NSRL-12633	2950 ± 35	3128 (3241–2967)
P1	449–451	Paper birch fruits	NSRL-12634	8250 ± 40	9167 (9419–9032)
P2	86–88	White pine needles	GX-28717	480 ± 40	516 (548–476)

water (5 m depth) and comprises the last 500 years. The rest of the sediments (starting at *c.* 25 cm depth) were collected from the deepest part of the lake. These cores, which overlap in time represented, were correlated based on their inferred ages and pollen stratigraphy.

RESULTS

Birch pollen percentages at Andrus, Ackerman and Mud Lakes increase 4500 yr BP, level off or decline slightly, and increase again between 4000 and 3000 yr BP (Fig. 3). At Partridge Lake, birch pollen does not increase until 3000 yr BP (Fig. 3). The birch increases at all of the sites are accompanied by corresponding decreases in pine percentages, particularly white pine.

Paper birch macrofossils are well-represented in sediments dating before 4500 yr BP, and decline or remain steady in number as birch pollen increases at all four sites (Fig. 3). Yellow birch macrofossils are absent from all sites before 4100 yr BP. They first appear at Mud Lake *c.* 4100 yr BP, and are consistently represented there after 3500 yr BP. Yellow birch macrofossils first occur at Ackerman 4000 yr BP, and increase rapidly in number; they are particularly abundant between 3500 and 2000 yr BP. Yellow birch macrofossils are rare at Andrus Lake, occurring only *c.* 3600 and 2600 yr BP. Their scarcity probably stems from the large lake size combined with sparse populations on the lakeshore, but their occurrences after the birch pollen increase is consistent with the other sites. Yellow birch macrofossils appear for the first time at Partridge Lake 3200 yr BP, coinciding with the pollen increase there, and are consistently represented in all younger sediments. Paper birch macrofossils

become abundant again at Partridge Lake after 2200 yr BP, but not at the other sites.

DISCUSSION

The advent of yellow birch in the fossil record: invasion or expansion?

Documentation of plant invasions has been a long-standing goal of palaeoecology (Davis *et al.*, 1991). Application of pollen analysis to determine species range limits and identify colonizing populations is hampered by widespread pollen dispersal and by low pollen representation from small, isolated populations (Davis *et al.*, 1991). These factors can lead, respectively, to false positive and false negative outcomes with respect to presence of a species at a site. The problems can be surmounted to some extent when sampling grids are dense, pollen-source area is limited (e.g. small basins), and sites are situated in particularly favourable habitat for colonizing populations (Davis *et al.*, 1991; Clark *et al.*, 1998). The latter approaches have been variously applied to the Holocene history of white pine, hemlock and beech in the western Great Lakes, where increases in pollen from zero or trace amounts to substantial percentages could be interpreted straightforwardly as indicating establishment of local or regional populations (Jacobson, 1979; Davis *et al.*, 1986; Woods & Davis, 1989; Parshall, 2002). These patterns cannot exclude the possibility that earlier colonizing populations were missed by the sampling array, a problem common to all spatial sampling of dispersed, fine-grained entities.

The history of yellow birch, however, presents a unique problem, in that pollen percentages

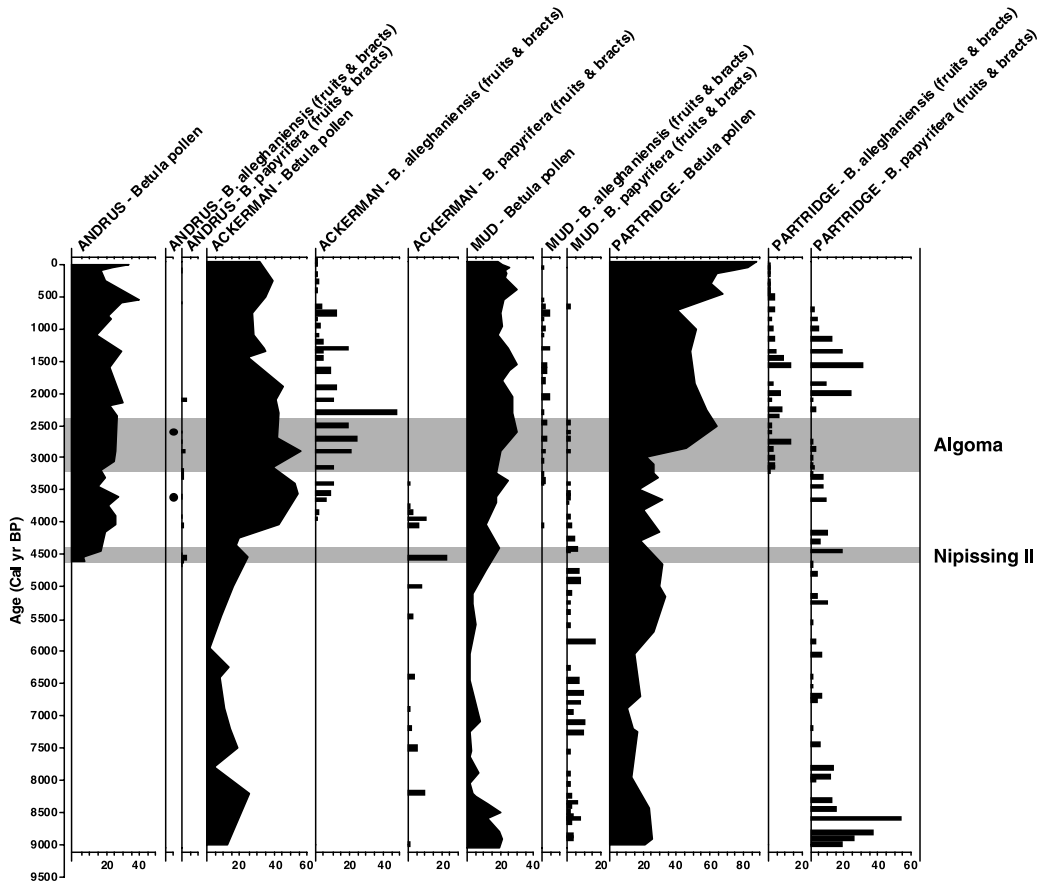


Fig. 3 *Betula* pollen percentage profiles and *Betula* macrofossil concentrations (numbers per 50 cm³ sediment) for Andrus, Ackerman, Mud and Partridge Lakes. Shading represents periods of Lake Michigan highstands (from Baedke & Thompson, 2000).

were substantial (5–30%) well before the late Holocene increase (Figs 2 & 3). For that reason, we relied on plant macrofossils to document yellow birch establishment at the sites. Our application raises the issue of what the macrofossil data signify. The first occurrence of yellow birch macrofossils in a stratigraphic sequence may alternatively represent initial establishment of populations near the lake or expansion of small, pre-existing populations. Macrofossils are more locally dispersed than pollen, which confers advantages in detection of local populations. However, plant organs dispersing from one or a few individual trees are subject to the same problems of dilution and representation as pollen. Does absence of macrofossils from sediments

indicate absence of the species from vegetation near the lake?

The answer to the latter question varies among species depending on productivity, dispersibility and preservability of plant organs representing potential macrofossils. In the case of yellow birch, large numbers of highly dispersible seeds and catkin bracts are produced, which are well-represented in sediments of lakes with yellow birch trees near shore. Yellow birch fruits and/or catkin bracts were found in 40 of 46 surface sediment samples (100 cm³ each) in an array of transects across Heart Lake (surface area 11.4 ha) in northern New York (Jackson, 1989; unpublished data). Most of the samples lacking yellow birch macrofossils were from deep waters

50–100 m from shore. Yellow birch macrofossils occurred in surface sediment samples (100 cm³ each) from 14 out of 15 small lakes (0.1–2.0 ha) in northern New York that had yellow birch populations within 100 m of the lake margin (S.T. Jackson, unpublished data). Yellow birch comprised 0.5–35% (median 11%, lower and upper quartiles 2% and 14%) of total basal area in forests within 100 m of the sites. The single site where yellow birch macrofossils were not observed had no individuals within 20 m of the lakeshore, and very sparse populations (0.5% basal area) within 100 m.

By virtue of their small size and steep slopes, Ackerman and Partridge Lakes are particularly well suited to accumulating yellow birch macrofossils from small local populations. Accordingly, the likelihood that local populations of yellow birch went undetected before the appearance of macrofossils in sediments is very small. Mud and Andrus Lakes are larger, with gentler slopes along their shores, so the probability of undetected local populations is higher.

Our data, taken together with the pollen evidence that hemlock and beech, two close associates of yellow birch with similar distributions, invaded the region in the late Holocene (Davis *et al.*, 1986; Davis, 1987; Woods & Davis, 1989), suggests that the yellow birch pattern also represents an invasion rather than expansion. However, our data set is smaller and our sampling array coarser than those for beech and hemlock. A denser site grid, including more sites that represent particularly suitable habitat for yellow birch (like Ackerman and Partridge), is necessary to increase confidence that the pollen increase represents a regional invasion.

Climate variability and the expansion of yellow birch

The late Holocene represents a period of increasing effective moisture in the western Great Lakes region (Webb *et al.*, 1993, 1998; Davis *et al.*, 2000). This climatic trend, resulting ultimately from Milankovitch forcing (Webb *et al.*, 1998; Bartlein *et al.*, 1998), was in turn ultimately responsible for the westward expansions of yellow birch, hemlock and beech.

Late Holocene climatic change was not monotonic at sub-Milankovitch time scales, however.

The western Great Lakes and adjacent regions experienced alternating wet and dry periods at centennial to millennial time scales during the past 5000 years (Laird *et al.*, 1996; Forman *et al.*, 2001; Booth *et al.*, 2002). Beach-ridge sequences and dune palaeosols along the Lake Michigan coast show significant lake-level fluctuations at decadal to millennial time scales (Thompson & Baedke, 1997; Baedke & Thompson, 2000; Loope & Arbogast, 2000). The Lake Michigan highstands of highest magnitude (Nipissing II (4500 yr BP), Algoma (3200–2400 yr BP), unnamed (2000–1200 yr BP)) correspond to periods of increased effective moisture inferred from independent evidence in the region (Brugam *et al.*, 1998; Booth & Jackson, 2002; Booth *et al.*, 2002). This correspondence indicates that the highstands record regional climatic variations.

Climatic variability at annual, decadal and centennial time scales affects recruitment, productivity and mortality in plant populations (Willis *et al.*, 1995; Villalba & Veblen, 1997; Allen & Breshears, 1998; Swetnam & Betancourt, 1998; Gilbert *et al.*, 2001). It is at these relatively fine time scales that individual plants experience climate, and hence population responses at successively larger time scales must represent an aggregate of responses to variability at finer time scales. The ecological significance of centennial, millennial and Milankovitch-scale climatic trends may lie in shifts in interannual and decadal climate variability. For example, a millennial-scale population expansion in response to increasing effective moisture may be driven by an increase in the frequency of individual years in which growing season conditions are sufficiently moist to ensure seedling survival.

Yellow birch expansion in the western Great Lakes region may represent a case in which shifts in high frequency climate variability were responsible for a low frequency response. Yellow birch seedlings are particularly sensitive to transient droughts (1–5 weeks) during the growing season, particularly in the first 2–3 years after germination (Linteau, 1948; Godman & Krefting, 1960; Winget & Kozlowski, 1965; Hatcher, 1966; Houle, 1994). Establishment at a site is contingent on absence or low frequency of such droughts, and the probability of colonization and rate of expansion should be inversely related to drought frequency. Thus, the late Holocene

increase in effective moisture may have been experienced by yellow birch primarily as a decrease in summer drought frequency.

The moisture variations represented by the Lake Michigan highstands may have modulated expansion of yellow birch. The initial birch pollen increase at Andrus, Ackerman and Mud Lakes coincided with the Nipissing II highstand (4500 yr BP) (Fig. 3), and birch pollen increases at many other sites in the region fall within 500 year of the highstand (Fig. 2), within the error bounds of ^{14}C -based age-models. These initial pollen increases are followed at most sites by levelling or moderate decline (Figs 2 & 3). The birch pollen increase at Partridge Lake, however, was delayed until 3000 yr BP, during the Algoma highstand (Fig. 3). Birch pollen percentages at Andrus, Ackerman and Mud are all elevated during the Algoma period (Fig. 3), a pattern observed at other sites in the region (Fig. 2; see also Davis *et al.*, 2000).

We propose the following sequence of events to account for the spatial and temporal patterns of yellow birch expansion. Increased effective moisture during the Nipissing II highstand c. 4500 yr BP led to widespread establishment of yellow birch populations over much of eastern and central Upper Michigan. Relatively dry conditions following the Nipissing II period led to slowing or interruption of the expansion, which resumed as moisture increased towards the Algoma highstand. During this long-duration moist phase, yellow birch built up substantial populations over the region and expanded into new territory (e.g. the Keweenaw Peninsula). This scenario is admittedly speculative and will require additional studies to evaluate. The spatial and temporal patterns can be validated and refined using a denser network of well-dated pollen and macrofossil sites from the region and adjacent regions². Independent palaeoclimate records from various proxies (e.g. Brugam *et al.*, 1998; Baedke & Thompson, 2000; Booth & Jackson, 2002) are necessary to link biotic and climatic events.

The role of sub-Milankovitch climatic variation in influencing species invasions and expansions

has received insufficient attention from Quaternary ecologists. Such variation may play a critical role in spatial and temporal patterns of migration (Lyford *et al.*, 2002b), accounting for much of the spatial and temporal variability observed in migration rates (King & Herstrom, 1997; Clark *et al.*, 1998). Effects of centennial and millennial variations are more subtle than Milankovitch-scale effects because they are realized at finer spatial and temporal scales, and often represent lower magnitudes of forcing and response. Spatial smoothing imposed by pollen dispersal together with low site density can mask low-magnitude, fine-scale biotic responses.

Populations of woody plants, once established, can often persist in the face of adverse environmental conditions, and so climatic 'reversals' may not be marked by local extinction or widespread range contraction. Rather, established populations may decline in density or simply fail to invade new sites during adverse periods. The late Holocene invasion of Utah juniper (*Juniperus osteosperma*) in the central Rockies consisted of alternation between rapid expansion during relatively dry periods and quiescence during wet periods (Lyford, 2001; Lyford *et al.*, 2002a, 2002b). Similar episodic patterns of rapid invasion and/or expansion interspersed with periods of population stasis or decline are apparent in pollen and macrofossil records for white pine (Jacobson, 1979), beech (Woods & Davis, 1989), hemlock (Davis *et al.*, 1994; Parshall, 2002; Booth & Jackson, unpublished) and yellow birch (this paper) in the western Great Lakes region. These dynamics may be linked to millennial-scale climatic variability in the region. Such linkages can be clarified by continued accretion of multiple, independent palaeoclimate records and well-dated pollen and macrofossil records. These linkages will remain vague, however, in the absence of ecological studies of the climatic constraints on recruitment, mortality and other relevant population processes. Understanding of the mechanisms that trigger population and range expansions and standstills will be useful in global change planning and mitigation.

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² We note that a recently published record from Nelson Lake (eastern Upper Michigan) shows first appearance of yellow birch macrofossils at 4411 yr BP (Delcourt *et al.*, 2002).

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