Research paper

The Holocene
22(1) 71–78

DOI: 10.1177/0959683611409774
hol.sagepub.com
SAGE

Middle-Holocene dynamics of *Tsuga canadensis* (eastern hemlock) in northern New England, USA

W. Wyatt Oswald[1,2] and David R. Foster[2]

Abstract

The abrupt, range-wide decline of *Tsuga canadensis* ~5500 calibrated years before present (cal. yr BP) is one of the most-studied events in North American paleoecology. Little attention, however, has been given to an earlier *Tsuga* decline, dated to ~6000 cal. yr BP in southern Ontario, Canada. To investigate whether this event occurred elsewhere in eastern North America, we analyzed the middle-Holocene interval of a lake-sediment record from Knob Hill Pond, located in northern Vermont, USA, an area of historically high *Tsuga* abundance. A dramatic, short-lived drop in *Tsuga* pollen abundance does occur at ~6000 cal. yr BP in the Knob Hill Pond record, indicating that *Tsuga* populations declined in various parts of its range. We hypothesize that both middle-Holocene declines of *Tsuga* were caused by the deleterious effects of pronounced droughts on this moisture-sensitive tree. Close examination of pollen data from a transect of sites across New England reveals that the earlier decline of *Tsuga* is present in other records, although some aspects of the event appear to have varied geographically. While northern and higher-elevation sites exhibit a nearly full recovery of *Tsuga* populations between the two declines, records further to the south are characterized by a stair-step pattern of progressive decline. At sites near its southern range limit, relatively warm conditions between ~6000 and 5500 cal. yr BP were apparently not conducive to the reestablishment and survival of *Tsuga*, and thus it was unable to recover between the drought events.

Keywords

climate, hemlock, paleoecology, pollen, *Tsuga canadensis*, Vermont

Introduction

The middle-Holocene decline of *Tsuga canadensis* is one of the most-studied events in the postglacial vegetation history of eastern North America (e.g. Allison et al., 1986; Bennett and Fuller, 2002; Bhiry and Filion, 1996; Calcote 2003; Davis, 1981; Foster, 2000; Foster and Zebryk, 1993; Foster et al., 2006; Fuller, 1998; Haas and McAndrews, 2000; Hall and Smol, 1993; Heard and Valente, 2009; Shuman et al., 2004; St Jacques et al., 2000; Webb, 1982; Yu and McAndrews, 1994; Zhao et al., 2010). Most research has focused on the precipitous drop in *Tsuga* pollen percentages at ~5500 calibrated years before present (cal. yr BP), a widespread pattern interpreted as an abrupt, range-wide crash in *Tsuga* populations (e.g. Bennett and Fuller, 2002; Davis, 1981; Webb, 1982). A study by Fuller (1998), however, suggested that *Tsuga* also underwent an earlier, short-lived decline, dated to ~6000 cal. yr BP in a high-resolution lake-sediment pollen record from Graham Lake, located in southern Ontario, Canada (Figure 1). The earlier *Tsuga* decline has not been documented unambiguously in other paleoecological studies in the region, but few pollen records feature the sampling resolution required to detect and define a century-scale event.

In this paper we present and discuss a post-glacial pollen record from Knob Hill Pond, located in northern Vermont, USA (Figure 1), an area of historically high *Tsuga canadensis* abundance (e.g. Cogbill et al., 2002). Century-scale analysis of the middle-Holocene interval of the record allows us to investigate whether the ~6000 cal. yr BP decline of *Tsuga* documented by Fuller (1998) occurred elsewhere in eastern North America. We also explore the spatial patterns and possible causes of middle-Holocene vegetation changes across New England.

Study area

Tsuga canadensis is currently found across a large area of eastern North America, ranging from the Great Lakes region east to Nova Scotia, and south along the Appalachian Mountains to northern Georgia and Alabama (Little, 1971; Thompson et al., 1999). *Tsuga* is common in northern Vermont, where it occurs with *Acer saccharum*, *A. rubrum*, *Fagus grandifolia*, *Betula alleghaniensis*, *B. papyrifera*, *Pinus strobus*, *Quercus rubra*, *Fraxinus americana*, *Picea rubens*, *Abies balsamea*, *Larix laricina*, and *Thuja occidentalis* (Thompson and Sorenson, 2000). Northern New England is characterized by cold winters (mean January temperature is −8°C at St Johnsbury, Vermont, for example) and cool summers (mean July temperature is 21°C). Mean annual precipitation is 99

[1] Emerson College, USA
[2] Harvard University, USA

Received 9 August 2010; revised manuscript accepted 28 February 2011

Corresponding author:
W. Wyatt Oswald, Emerson College, Department of Communication Sciences and Disorders, Boston MA 02116, USA.
Email: w_wyatt_oswald@emerson.edu

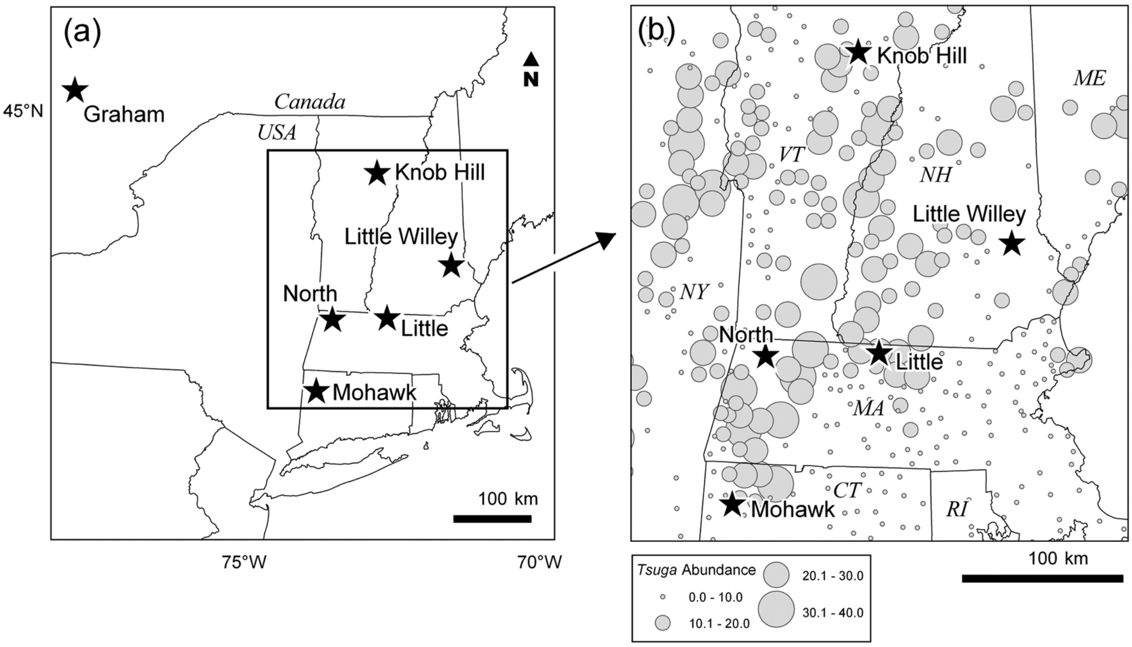

Figure 1. (a) Map showing locations of Knob Hill Pond and other key sites mentioned in the text. (b) Map of New England showing site locations and pre-settlement relative abundance (percentage values in witness-tree data set) of *Tsuga canadensis* (Cogbill et al., 2002)

cm, distributed relatively evenly throughout the year (Easterling et al., 1996).

Knob Hill Pond (44.3605°N, 72.3737°W, 370 m elevation) is located in the town of Marshfield in northern Vermont, USA (Figure 1). The 7.1 ha, 4.2 m deep pond has a single outlet that flows west towards the Winooski River. Much of this region was cleared for agriculture in the late eighteenth century and has reforested over the last century (Foster, 2002). There remain actively used agricultural fields southwest of Knob Hill Pond, whereas the landscape northwest of the pond is forested. The pond is located on the Waits River Formation, which consists of mica schist and phyllite interbedded with crystalline limestone (Doll et al., 1961). Soils in the 41 ha Knob Hill Pond watershed have developed on thick glacial till. Knob Hill Pond is ~8 km southeast of South King Pond, analyzed by Ford (1990) in a study of long-term ecosystem acidification.

Methods

We collected an 857 cm long sediment core from the center of Knob Hill Pond (water depth 4.2 m) in August 2001. Upper sediments, including an undisturbed sediment–water interface, were collected with a plastic tube fitted with a piston. The surface core was transported to the laboratory and extruded vertically in 1 cm segments. Lower sediments were raised in 1 m drive lengths using a modified Livingstone piston sediment sampler. Those core segments were extruded horizontally in the field and wrapped in plastic and aluminum foil. All samples were subsequently refrigerated.

Chronological control is provided by ^{210}Pb analysis of recent sediments (Binford, 1990), pollen evidence for European settlement, and accelerator mass spectrometry ^{14}C analysis of nine bulk-sediment samples (Table 1). ^{14}C dates were converted to calibrated years before present (cal. yr BP) using CALIB 5.0

Table 1. Chronological data for the Knob Hill Pond sediment core

Type	Depth (cm)	^{14}C lab code[a]	δ^{13}C (‰)	^{14}C date ± 1 SD	Cal. age 2σ range (cal. yr BP)	Age[b]
Surface	0–1					−51
^{210}Pb[c]	56–57					87
ESH[d]	90–91					160
^{14}C	115–116	Beta-174850	−26.8	880 ± 80	699–915	794
	143–144	Beta-174851	−27.5	1280 ± 80	1089–1292	1221
	185–186	Beta-174852	−28.1	1840 ± 80	1638–1875	1777
	274–275	OS-52811	−28.1	3180 ± 80	3336–3477	3406
	473–474	OS-52854	−28.0	5050 ± 70	5668–5906	5819
	603–604	OS-52857	−29.1	6740 ± 110	7507–7680	7604
	653–654	OS-52858	−29.6	7770 ± 100	8429–8631	8546
	753–754	OS-52859	−33.7	10 200 ± 130	11 613–12 145	11 899
	803–804	OS-52860	−32.7	11 950 ± 140	13 673–13 981	13 814

[a]Beta, Beta Analytic, Miami FL, USA; OS, National Ocean Sciences Accelerator Mass Spectrometry Facility, Woods Hole MA, USA.
[b]Median calibrated age for ^{14}C dates.
[c]Oldest of 15 ^{210}Pb age assignments.
[d]ESH, European settlement horizon.

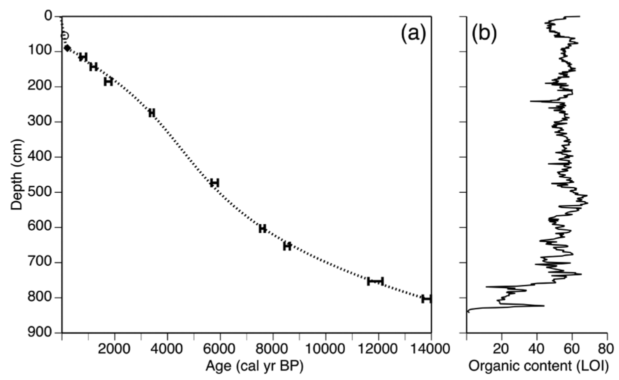

Figure 2. (a) Age–depth model for the sediment core from Knob Hill Pond; the 2σ cal. age ranges are plotted for the ^{14}C dates; the black diamond is the European settlement horizon and the open circle is the lowermost ^{210}Pb age assignment. (b) Organic content (percent weight loss-on-ignition; LOI) of the sediment core

(Reimer et al., 2004; Stuiver and Reimer, 1993). Sediment organic content was estimated for 1 cm^3 samples at selected depths by percent weight loss-on-ignition (LOI) at 550°C; we also calculated accumulation rates (influx; g/cm^2 per yr) for the organic and inorganic sedimentary fractions. Sediment samples of 1–2 cm^3 were prepared for pollen analysis following standard procedures (Faegri and Iversen, 1989), and tablets containing *Lycopodium* spores were added to the samples to estimate pollen accumulation rates (influx; Stockmarr, 1971). Pollen residues were mounted in silicone oil and analyzed at 400× magnification. At least 450 pollen grains and spores of upland plant taxa were counted for each sample, and pollen percentages were calculated relative to that sum. Low pollen concentrations prevented analysis of samples below 823 cm.

Results

The base of the Knob Hill Pond sediment core dates to ~14 000 cal. yr BP (Figure 2; Table 1). The age–depth model for the record involves a third-degree polynomial fit to the ^{14}C dates and linear interpolation between the sediment–water interface, the lowermost ^{210}Pb age assignment, the European-settlement date, and the uppermost ^{14}C date (Figure 2). We extrapolate the age–depth model beyond the lowermost ^{14}C date (~13 800 cal. yr BP at 803 cm). The dating of bulk-sediment samples may be complicated by carbon-reservoir effects (e.g. Grimm et al., 2009), but comparison of our results with other records from New England (e.g. Oswald et al., 2007) suggests this age–depth model is reasonable. Sediments dated to ~14 000–11 500 cal. yr BP have high influx of inorganic material, low organic influx, and low LOI values (0–40%; Figures 2–4). LOI is ~50% from 11 500 cal. yr BP to the surface, peaking at >65% during ~6200–5800 cal. yr BP. Organic and inorganic accumulation rates track each other closely after 11 500 cal. yr BP, although organic influx values are higher than those of the inorganic fraction during the ~6200–5800 cal. yr BP interval of elevated LOI (Figures 2–4). We divided the pollen record into seven zones and subzones (Figures 3–4); the zones correspond with those of Deevey (1939).

Zone A: 14 000–11 500 cal. yr BP

Pollen assemblages in samples dating to ~14 000–13 000 cal. yr BP feature *Picea* (~30%), *Pinus* (~30%), *Betula* (~10%), and Cyperaceae (~5%; Figure 3). Between ~13 000 and 11 500 cal. yr BP, *Picea* and Cyperaceae pollen percentages decline while *Alnus*, *Betula*, *Quercus*, *Larix*, and *Abies* percentages increase in abundance. Pollen accumulation rates are low (~2000 grains/cm^2 per yr) in Zone A (Figure 4).

Zone B1: 11 500–10 200 cal. yr BP

Picea, *Alnus*, *Larix*, and *Abies* pollen percentages are low after ~11 500 cal. yr BP (Figure 3). *Betula* increases abruptly at the beginning of Zone B1, peaking at ~40% at 11 200 cal. yr BP. *Quercus* increases gradually during this interval to reach ~20% by 10 200 cal. yr BP. *Pinus* pollen percentages increase to ~50%; most of the identified *Pinus* grains are *Pinus* subgenus *Strobus*. *Ulmus* pollen is present at low percentages (~3%). Pollen accumulation rates increase to ~10 000 grains/cm^2 per yr (Figure 4).

Zone B2: 10 200–8400 cal. yr BP

Pinus remains abundant in Zone B2 (~50%), and as in the previous zone, the identified *Pinus* pollen grains are *Pinus* subgenus *Strobus* (Figure 3). *Betula* percentages are lower than in Zone B1

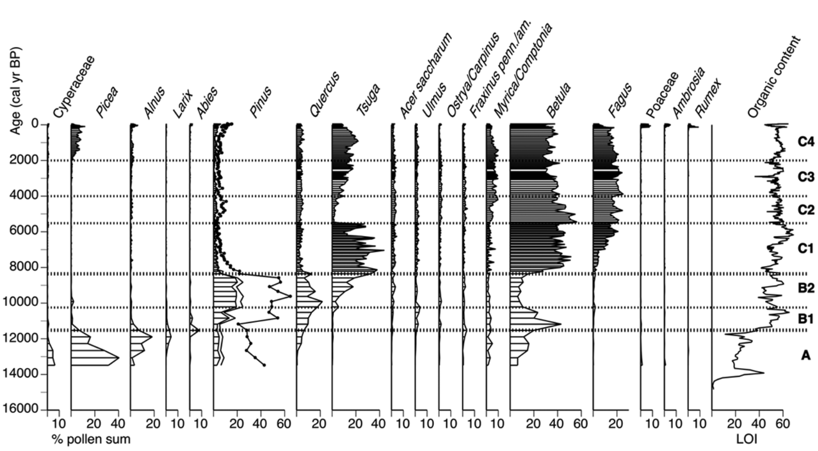

Figure 3. Pollen percentage diagram for Knob Hill Pond showing selected taxa; for the *Pinus* graph, line with symbols = total % of *Pinus* pollen, area with horizontal drop lines = % pollen identified as *Pinus* subgenus *Strobus*, and open area = % pollen identified as *Pinus* subgenus *Pinus*. Organic content (percent weight loss-on-ignition) is also plotted

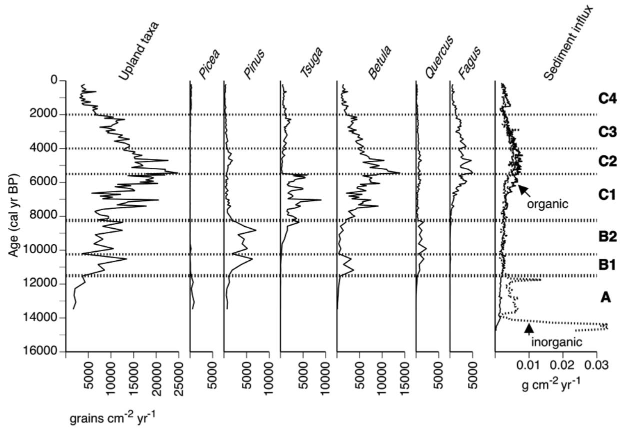

Figure 4. Pollen accumulation rate diagram for Knob Hill Pond showing total influx for upland taxa and selected individual pollen types. Influx values for the organic (solid line) and inorganic (dotted line) fractions of the core are also plotted. Data for the interval of European settlement (<160 cal. yr BP) are not shown; influx values increase unrealistically due to the abrupt change in the rate of sedimentation during the settlement era (Figure 2)

(~10%), *Quercus* remains at ~10%, and *Tsuga* percentages increase gradually, reaching ~40% by ~8400 cal. yr BP. *Acer saccharum* pollen is present at low percentages (<3%). Pollen influx values remain at ~10 000 grains/cm^2 per yr (Figure 4).

Zone C1: 8400–5500 cal. yr BP

Pinus pollen percentages drop abruptly from >50% to ~20% at the beginning of Zone C1, then continue to decline to ~5% by ~7000 cal. yr BP (Figure 3). *Betula*, on the other hand, increases from ~10% to ~40% between 8400 and 7900 cal. yr BP. *Fagus* pollen is present at <5% after ~8400 cal. yr BP, then increases to 10–20% between ~7000 and 5500 cal. yr BP. *Tsuga* abundance is relatively high during Zone C1 (20–40%), but declines from ~35% to ~20% at ~8000–7500 cal. yr BP, and drops precipitously to <10% during ~6200–5800 cal. yr BP. Pollen accumulation rates fluctuate from ~7000 to 20 000 grains/cm^2 per yr during this zone (Figure 4). Low *Tsuga* influx values coincide with the percentage declines at ~7700 and 6000 cal. yr BP, and also occur at ~7000–6600 cal. yr BP.

Zone C2: 5500–4000 cal. yr BP

The pronounced decline of *Tsuga* pollen percentages (from >25% to <1% in <70 years) at ~5500 cal. yr BP marks the beginning of Zone C2 (Figure 3). *Betula* abundance increases to >50% from the time of the *Tsuga* decline to ~4900 cal. yr BP, while percentages of *Pinus* pollen (mainly *Pinus* subgenus *Strobus*) increase slightly in the middle of this zone. *Fagus* pollen percentages remain at ~20%, and minor taxa exhibit little variability. Pollen accumulation rates reach a peak of 25 000 grains/cm^2 per yr at 5500 cal. yr BP, then decline to ~15 000 grains/cm^2 per yr by the end of Zone C2 (Figure 4).

Zone C3: 4000–2000 cal. yr BP

Tsuga pollen abundance increases gradually from the end of Zone C2 to the end of Zone C3, reaching >15% by ~2000 cal. yr BP (Figure 3). *Betula* pollen percentages decrease slightly during this interval, while other taxa have stable percentage values. Pollen influx values continue to drop during this zone, declining to ~10 000 grains/cm^2 per yr (Figure 4).

Zone C4: 2000 cal. yr BP to present

Several notable pollen-assemblage changes take place after 2000 cal. yr BP. *Picea* pollen percentages increase at the beginning of Zone C4, reaching ~10% (Figure 3). *Tsuga* increases to >20% at ~900 cal. yr BP, then steadily declines towards the present-day. *Fagus* pollen percentages decrease gradually during Zone C4, while *Pinus* percentages rise slightly after ~700 cal. yr BP. European deforestation and settlement appear clearly in the uppermost sediments, where *Tsuga*, *Betula*, and especially *Fagus* decline in abundance and herbaceous taxa, including *Rumex*, *Ambrosia*, and Poaceae, increase sharply. A peak in *Alnus* pollen coincides with the rise in herbaceous taxa, while *Pinus* percentages increase during the twentieth century. Pollen influx declines to ~3500 grains/cm^2 per yr before rising abruptly at the time of European settlement (not shown in Figure 4). We attribute this unrealistic increase in pollen influx values to the change in the rate of sedimentation during the settlement era (Figure 2).

Discussion

Postglacial ecological and environmental history of northern Vermont

The postglacial changes in vegetation revealed by the Knob Hill Pond pollen record resemble those seen at other sites in this part of northern New England (e.g. Davis et al., 1980; Likens and Davis, 1975; Mott, 1977; Shuman et al., 2005; Spear, 1989; Spear et al., 1994), including nearby South King Pond (Ford, 1990). Boreal forests featuring *Pinus banksiana* and *Picea* species occurred across the region during the Lateglacial interval (e.g. Oswald et al., 2007), with a compositional shift ~13 000 cal. yr BP from open-canopy *Picea glauca* woodland to a denser forest with *Picea mariana*, *Alnus*, *Larix*, and *Abies* (e.g. Lindbladh et al., 2007). This transition has been attributed to abrupt cooling at the beginning of the Younger Dryas event (e.g. Cwynar and Levesque, 1995; Cwynar and Spear, 2001; Levesque et al., 1993; Mayle et al., 1993; Shuman et al., 2002b).

The sharp increase in sediment organic content (LOI) ~11 500 cal. yr BP marks the beginning of the Holocene and the onset of warmer, drier conditions (Cwynar and Spear, 2001; Davis et al., 1980; Shuman et al., 2005). Summer insolation was high and a strong glacial anticyclone prevented moisture from reaching northern New England (Shuman et al., 2002a). *Pinus strobus* dominated the regional vegetation between ~11 500 and 8000 cal. yr BP, with relatively abundant *Quercus* at many sites (e.g. Ford, 1990; Richard, 1978; Spear, 1989; Spear et al., 1994), including Knob Hill Pond. *Tsuga canadensis* expanded gradually after ~10 000 cal. yr BP, presumably as the influence of the Laurentide Ice Sheet weakened and climate ameliorated (Shuman et al., 2005).

Lake-level studies across the region indicate a rise in moisture availability after 8000 cal. yr BP (Almquist et al., 2001; Lavoie and Richard, 2000; Muller et al., 2003; Newby et al., 2000; Shuman et al., 2001), presumably due to the collapse of the Hudson Bay ice dome at that time and its influence on circulation patterns (Barber et al., 1999). At Knob Hill Pond and several other sites, *Pinus strobus* and *Quercus* are replaced by mesic taxa, including *Betula*, *Tsuga canadensis*, *Acer saccharum*, and *Fagus grandifolia* (e.g. Ford, 1990; Richard, 1978; Shuman et al., 2005; Spear et al., 1994). In most pollen diagrams from southern New England, *Fagus* increases sharply at ~8000 cal. yr BP, immediately reaching levels that would be maintained throughout the Holocene (e.g. Oswald et al., 2007; Whitehead and Crisman, 1978). *Fagus* was present at Knob Hill Pond beginning at ~8000 cal. yr BP, but its population levels were relatively low until it expanded after ~7000 cal. yr BP. This pattern of late expansion appears to have been prevalent across northern New England and southern Quebec (e.g. Bennett, 1985).

While *Tsuga canadensis* experienced a steady increase in abundance across the early Holocene, it also exhibits a pronounced decline at ~8000 cal. yr BP in the Knob Hill Pond record. After reaching a peak (>35%) at the beginning of Zone C1, *Tsuga* pollen percentages are relatively low (~20–25%) for a period of several centuries. This pattern may represent the deleterious effects of the cold, dry 8200 cal. yr BP climatic event (e.g. Alley and Ágústsdóttir, 2005; Alley et al., 1997; Kurek et al., 2004) on *Tsuga* populations in New England, as was proposed by Shuman et al. (2004).

The major decline of *Tsuga canadensis* at ~5500 cal. yr BP occurred rapidly, spanning <70 years at Knob Hill Pond and <10 years in the pollen record from the laminated sediments of Pout Pond, located in central New Hampshire (Allison et al., 1986). This event has been attributed to *Tsuga* mortality caused by a pathogen (e.g. Allison et al., 1986; Davis, 1981) or insect pest (Bhiry and Filion, 1996), but mounting evidence indicates that climate change was likely the primary driver (e.g. Foster et al., 2006; Haas and McAndrews, 2000; Shuman et al., 2004, 2009; Yu et al., 1997; Zhao et al., 2010). In the Knob Hill Pond record, the coincident rise in *Betula* likely represents the replacement of *Tsuga* by the shade-tolerant and long-lived *Betula alleghaniensis* (Fuller, 1998; Thompson and Sorenson, 2000). Early successional species such as *Betula papyrifera* may also have experienced a brief, positive response to the decline of *Tsuga* (Fuller, 1998), as has recently been the case in southern New England as *Tsuga* mortality due to *Adelges tsugae* has favored *Betula lenta* (e.g. Orwig and Foster, 1998). Elevated abundance of *Pinus strobus* during the ~5500–4000 cal. yr BP interval of low *Tsuga* abundance, also observed in New Hampshire (Davis, 1981; M. Lindbladh et al., unpublished data, 2011), may be attributable to climatic conditions or successional changes (Allison et al., 1986).

Lake-level evidence from across the region suggests that moisture availability increased during the late Holocene (Almquist et al., 2001; Lavoie and Richard, 2000; Muller et al., 2003; Newby et al., 2000; Shuman et al., 2001, 2005), perhaps due to a rise in winter precipitation (Carcaillet and Richard, 2000). Cooler and moister conditions at Knob Hill Pond likely enabled the increases in *Tsuga* after ~4000 cal. yr BP and *Picea* after ~2000 cal. yr BP. Similar late-Holocene changes have been observed in pollen records across northern New England (e.g. Shuman et al., 2005; Spear, 1989) and southern Quebec (e.g. Webb et al., 1983). *Tsuga* pollen increases gradually to reach a peak at ~900 cal. yr BP, then declines steadily. This also appears to be a region-wide trend, perhaps attributable to a shift to colder or drier conditions during the 'Little Ice Age' (e.g. Fuller et al., 1998; Gajewski, 1987).

The impacts of eighteenth- and nineteenth-century European forest clearance and agricultural activities are clearly evident in the sediments of Knob Hill Pond. The declines in *Fagus*, *Betula*, and *Tsuga* reflect the widespread logging of the major tree species, while the corresponding increases in *Rumex*, *Ambrosia*, Poaceae, and *Alnus* indicate open and disturbed vegetation (e.g. Brugam, 1978). The uppermost sediments of Knob Hill Pond record the establishment of old-field *Pinus strobus*, which over the last century has become more abundant than any time in the previous ~7000 years.

Middle-Holocene dynamics of Tsuga canadensis

The brief, pronounced decline of *Tsuga canadensis* at ~6000 cal. yr BP observed by Fuller (1998) in the Graham Lake pollen record from southern Ontario also appears in the record from Knob Hill Pond. The earlier decline is of the same magnitude (>25% drop in *Tsuga* pollen) as the better-known ~5500 cal. yr BP event. Fuller (1998) suggests that, like the ~5500 cal. yr BP *Tsuga* decline, the earlier event was caused by an insect outbreak. This interpretation is supported by evidence for two middle-Holocene defoliation events in Quebec (Bhiry and Filion, 1996). However, various studies now suggest that the decline of *Tsuga* at ~5500 cal. yr BP was driven by climate (e.g. Foster et al., 2006; Shuman et al., 2004; Yu et al., 1997; Zhao et al., 2010), including a lake-level reconstruction from New Long Pond, located in southeastern Massachusetts (Shuman et al., 2009). In that record, middle-Holocene sand layers are thought to represent a series of drought events that initiated and then sustained the low abundance of moisture-sensitive *Tsuga canadensis* from ~5500 to 4000 cal. yr BP (Shuman et al., 2009). We hypothesize that the ~6000 cal. yr BP *Tsuga* decline was also caused by a brief interval of dry climate, reflected in the sediments of Knob Hill Pond by the peak in organic content at ~6200–5800 cal. yr BP (Figures 3–4). For a relatively small, shallow lake like Knob Hill Pond, a drop in water level might result in increased abundance of near-shore macrophytes, which in turn would contribute additional organic matter to the sediment. On the other hand, there is not a corresponding sedimentary change at 5500 cal. yr BP, as might be expected if there were two droughts within a few centuries of each other. However, the record from Shephard Lake, Ontario (Haas and McAndrews, 2000) does feature evidence of two middle-Holocene drought events that are roughly coincident (~5800 and 5300 cal. yr BP) with the double *Tsuga* declines at Knob Hill Pond and Graham Lake (Fuller, 1998).

To explore the spatial pattern of the ~6000 cal. yr BP decline of *Tsuga canadensis* in New England, we analyzed pollen data from a transect of sites (Figure 1), starting at Knob Hill Pond in northern Vermont and moving south along the regional environmental gradient (e.g. Cogbill et al., 2002). Close examination of the records from North Pond in the Berkshires of western Massachusetts (Whitehead and Crisman, 1978), Little Willey Pond in southeastern New Hampshire (M. Lindbladh et al., unpublished data, 2011), Little Pond in north-central Massachusetts (Oswald et al., 2007), and Mohawk Pond in western Connecticut (Gaudreau, 1986), all of which have middle-Holocene *Tsuga* pollen percentages >20% and adequate sampling resolution to evaluate fine-scale changes during that interval, suggests that the ~6000 cal. yr BP decline of *Tsuga canandensis* did occur in other parts of New England, although some aspects of middle-Holocene *Tsuga* dynamics appear to have varied geographically (Figure 5). While northern and higher-elevation sites, including Knob Hill Pond, North Pond (Whitehead and Crisman, 1978), and Graham Lake in southern Ontario (Fuller, 1998), exhibit a nearly full recovery of *Tsuga* populations between the ~6000 and 5500 cal. yr BP

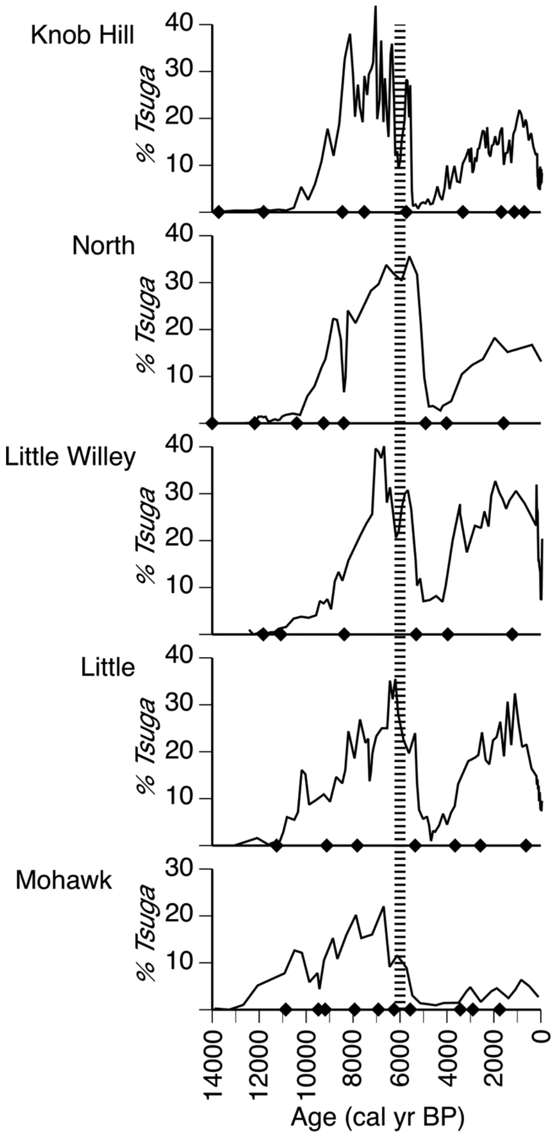

Figure 5. Abundance of *Tsuga* pollen for Knob Hill Pond, North Pond (Whitehead and Crisman, 1978), Little Willey Pond (M. Lindbladh et al., unpublished data, 2011), Little Pond (Oswald et al., 2007), and Mohawk Pond (Gaudreau, 1986). Black diamonds plotted along x-axes are ^{14}C ages

declines, the sites further to the south are characterized by a stair-step pattern of decline, with drops in *Tsuga* pollen percentages at ~6000 and 5500 cal. yr BP but no intervening increase in *Tsuga* abundance (Gaudreau, 1986; Oswald et al., 2007; M. Lindbladh et al., unpublished data, 2011). This spatial pattern suggests varying responses in *Tsuga* across the regional environmental gradient (e.g. Cogbill et al., 2002). In the northern part of the region where climate is relatively cool and *Tsuga* has been abundant through time, *Tsuga* populations were able to recover rapidly. At sites in southern New England, on the other hand, where climate is relatively warm and *Tsuga* exists at its range limit, conditions between ~6000 and 5500 cal. yr BP were not conducive to the reestablishment and survival of *Tsuga*, and thus it was unable to rebound between the drought events.

Tsuga dynamics associated with the ~5500 cal. yr BP decline exhibit less geographic variability; sites in both northern and southern New England experienced the major decline at ~5500 cal. yr BP and a subsequent ~1500 year interval of low *Tsuga* abundance (Figure 4). Even though we hypothesize that both *Tsuga* declines are attributable to abrupt, short-lived periods of dry conditions, some aspect of these droughts must have differed so that the geographic pattern present during the ~6000 cal. yr BP event was less prominent at ~5500 cal. yr BP. For example, it may be the case that the drought at ~5500 cal. yr BP was more severe than at ~6000 cal. yr BP, such that *Tsuga* populations across the region, even in the cooler, northern part of New England, were unable to recover before the onset of the next drought a few centuries later (Shuman et al., 2009). We also recognize that there has been little systematic effort to investigate whether insect pests played a role in either *Tsuga* decline (e.g. Bhiry and Filion, 1996), and therefore it remains a possibility that biotic factors influenced the magnitude and regional details of these events.

Conclusions

Analyses of a lake-sediment pollen record from Knob Hill Pond, Vermont, USA, provide insights into the postglacial history of vegetation in northern New England, including the dynamics of *Tsuga canadensis* during the middle Holocene. In addition to the well-known decline of *Tsuga* at ~5500 cal. yr BP (e.g. Bennett and Fuller, 2002), a pronounced, short-lived drop in *Tsuga* pollen abundance also occurs a few centuries earlier, indicating that the ~6000 cal. yr BP *Tsuga* decline documented in southern Ontario by Fuller (1998) also occurred in other parts of eastern North America. Comparison of the Knob Hill Pond pollen record with paleoclimatic evidence (e.g. Haas and McAndrews, 2000) suggests that both of the middle-Holocene declines of *Tsuga* were triggered by dry conditions. Earlier, short-lived declines of *Tsuga canadensis* may have taken place across eastern North America in response to early-Holocene climatic events (e.g. Futyma and Miller, 2001; Toney et al., 2003; Zhao et al., 2010), including the ~8200 cal. yr BP event (e.g. Alley et al., 1997; Shuman et al., 2004), but additional records with high sampling resolution are needed to better define changes in vegetation during that interval. In general, these findings support the hypothesis of Shuman et al. (2009) that abrupt changes in climate played a critical role in the postglacial history of vegetation in New England. This study also highlights the sensitivity of *Tsuga candensis* to climate and provides long-term context for understanding the present-day dynamics of *Tsuga* as it experiences various stressors, including the introduced insect *Adelges tsugae* (e.g. Albani et al., 2009; Orwig and Foster, 1998; Orwig et al., 2002, 2008).

Acknowledgements

We thank: the Mullen family for allowing access to Knob Hill Pond; Barbara Hansen, Natalie Drake, Sylvia Barry Musielewicz, Susan Clayden, and Elaine Doughty for assisting with field and laboratory work; Brian Hall for drafting Figure 1; and Bryan Shuman, Joe Mason, and two anonymous referees for constructive reviews of the manuscript. This research was supported by the National Science Foundation (DEB-0815036).

References

Albani M, Moorcroft PR, Ellison AM, Orwig DA and Foster DR (2009) Predicting the impact of hemlock woolly adelgid on carbon dynamics of Eastern U.S. forests. *Canadian Journal of Forest Research* 40: 119–133.

Alley RB and Ágústsdóttir AM (2005) The 8k event: Cause and consequences of a major Holocene abrupt climate change. *Quaternary Science Reviews* 24: 1123–1149.

Alley RB, Mayewski PA, Sowers T, Stuiver M, Taylor KC and Clark PU (1997) Holocene climatic instability: A prominent, widespread event 8200 years ago. *Geology* 25: 483–486.

Allison TD, Moeller RE and Davis MB (1986) Pollen in laminated sediments provides evidence for a mid-Holocene forest pathogen outbreak. *Ecology* 67: 1101–1105.

Almquist H, Dieffenbacher-Krall AC, Flanagan-Brown R and Sanger D (2001) The Holocene record of lake levels of Mansell Pond, central Maine, USA. *The Holocene* 11: 189–201.

Barber DC, Dyke A, Hillaire-Marcel C, Jennings AE, Andrews JT, Kerwin MW et al. (1999) Forcing of the cold event of 8,200 years ago by catastrophic drainage of Laurentide lakes. *Nature* 400: 344–348.

Bennett KD (1985) The spread of *Fagus grandifolia* across eastern North America during the last 18000 years. *Journal of Biogeography* 12: 147–164.

Bennett KD and Fuller JL (2002) Determining the age of the mid-Holocene *Tsuga canadensis* (hemlock) decline, eastern North America. *The Holocene* 12: 421–429.

Bhiry N and Filion L (1996) Mid-Holocene hemlock decline in eastern North America linked with phytophagous insect activity. *Quaternary Research* 45: 312–320.

Binford MW (1990) Calculation and uncertainty analysis of ^{210}Pb dates for PIRLA project cores. *Journal of Paleolimnology* 3: 253–267.

Brugam RB (1978) Human disturbance and the historical development of Linsley Pond. *Ecology* 59: 19–36.

Calcote R (2003) Mid-Holocene climate and the hemlock decline: the range limit of *Tsuga canadensis* in the western Great Lakes region, USA. *The Holocene* 13: 215–224.

Carcaillet C and Richard PJH (2000) Holocene changes in seasonal precipitation highlighted by fire incidence in eastern Canada. *Climate Dynamics* 16: 549–559.

Cogbill CV, Burk J and Motzkin G (2002) The forests of presettlement New England, USA: Spatial and compositional patterns based on town proprietor surveys. *Journal of Biogeography* 29: 1279–1304.

Cwynar LC and Levesque AJ (1995) Chironomid evidence for late-glacial climatic reversals in Maine. *Quaternary Research* 43: 405–413.

Cwynar LC and Spear RW (2001) Late-glacial climate change in the White Mountains of New Hampshire. *Quaternary Science Reviews* 20: 1265–1274.

Davis MB (1981) Outbreaks of forest pathogens in Quaternary history. In: Bharadwaj D, Vishnu-Mittre and Maheshwari H (eds) *Proceedings of the Fourth International Palynological Conference, Volume 3*. Lucknow: Birbal Sahni Institute of Paleobotany, 216–227.

Davis MB, Spear RW and Shane LCK (1980) Holocene climate of New England. *Quaternary Research* 14: 240–250.

Deevey ES Jr (1939) Studies on Connecticut lake sediments. I. A postglacial climatic chronology for southern New England. *American Journal of Science* 237: 691–724.

Doll CG, Cady WM, Thompson JB Jr and Billings MP (1961) *Centennial Geologic Map of Vermont*. Vermont Geological Survey.

Easterling DR, Karl TR, Mason EH, Hughes PY and Bowman DP (1996) *United States Historical Climatology Network (US HCN) Monthly Temperature and Precipitation Data, ORNL/CDIAC-87*. Oak Ridge: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy.

Faegri K and Iversen J (1989) *Textbook of Pollen Analysis*. Fourth edition. Chichester: John Wiley and Sons.

Ford MSJ (1990) A 10 000-yr history of natural ecosystem acidification. *Ecological Monographs* 60: 57–89.

Foster DR (2000) Hemlock's future in the context of its history: An ecological perspective. In: McManus K (ed.) *Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America*. USDA Forest Service General Technical Report NE-267, 1–4.

Foster DR (2002) Thoreau's country: A historical-ecological perspective to conservation in the New England landscape. *Journal of Biogeography* 29: 1537–1555.

Foster DR and Zebryk TM (1993) Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in New England. *Ecology* 74: 982–998.

Foster DR, Oswald WW, Faison EK, Doughty ED and Hansen BCS (2006) A climatic driver for abrupt mid-Holocene vegetation dynamics and the hemlock decline in New England. *Ecology* 87: 2959–2966.

Fuller JL (1998) Ecological impact of the mid-Holocene hemlock decline in southern Ontario, Canada. *Ecology* 79: 2337–2351.

Fuller JL, Foster DR, McLachlan JS and Drake N (1998) Impact of human activity on regional forest composition and dynamics in central New England. *Ecosystems* 1: 76–95.

Futyma RP and Miller NG (2001) Postglacial history of a marl fen: Vegetational stability at Byron-Bergen Swamp, New York. *Canadian Journal of Botany* 79: 1425–1438.

Gajewski K (1987) Climatic impacts on the vegetation of eastern North America for the past 2000 years. *Vegetatio* 68: 179–190.

Gaudreau DC (1986) Late-Quaternary vegetational history of the Northeast: Paleoecological implications of topographic patterns in pollen distributions. PhD thesis, Yale University.

Grimm EC, Maher LJ Jr and Nelson DM (2009) The magnitude of error in conventional bulk-sediment radiocarbon dates from central North America. *Quaternary Research* 72: 301–308.

Haas JN and McAndrews JH (2000) The summer drought related hemlock (*Tsuga canadensis*) decline in Eastern North America 5700 to 5100 years ago. In: McManus K (ed.) *Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America*. USDA Forest Service General Technical Report NE-267, 81–88.

Hall RI and Smol JP (1993) The influence of catchment size on lake trophic status during the hemlock decline and recovery (4800 to 3500 BP) in southern Ontario lakes. *Hydrobiologia* 269/270: 371–390.

Heard MJ and Valente MJ (2009) Fossil pollen records forecast response of forests to hemlock woolly adelgid invasion. *Ecography* 32: 881–887.

Kurek J, Cwynar LC and Spear RW (2004) The 8200 cal. a BP cooling event in eastern North America and the utility of midge analysis for Holocene temperature reconstructions. *Quaternary Science Reviews* 23: 627–639.

Lavoie M and Richard PJH (2000) Postglacial water-level changes of a small lake in southern Quebec, Canada. *The Holocene* 10: 621–634.

Levesque AJ, Mayle FE, Walker IR and Cwynar LC (1993) A previously unrecognized late-glacial cold event in eastern North America. *Nature* 361: 623–626.

Likens GE and Davis MB (1975) Post-glacial history of Mirror Lake and its watershed in New Hampshire, USA: An initial report. *Internationale Vereinigung fuir theoretische und angewandte Limnologie, Verhandlungen* 19: 982–993.

Lindbladh M, Oswald WW, Foster DR, Faison EK, Hou J and Huang Y (2007) A late-glacial transition from *Picea glauca* to *Picea mariana* in southern New England. *Quaternary Research* 67: 502–508.

Little EL Jr (1971) *Atlas of United States Trees, Volume 1, Conifers and Important Hardwoods*. US Department of Agriculture Miscellaneous Publication 1146.

Mayle FE, Levesque AJ and Cwynar LC (1993) Accelerator-mass-spectrometer ages for the Younger Dryas event in Atlantic Canada. *Quaternary Research* 39: 355–360.

Mott RJ (1977) Late-Pleistocene and Holocene palynology in southeastern Québec. *Géographie physique et Quaternaire* 31: 139–149.

Muller SD, Richard PJH, Guiot J, de Beaulieu JL and Fortin D (2003) Postglacial climate in the Saint Laurence lowlands, southern Quebec: Pollen and lake level evidence *Palaeoceanography, Palaeoclimatology, Palaeoecology* 193: 51–72.

Newby PC, Killoran P, Waldorf M, Shuman B, Webb T III and Webb RS (2000) 14,000 years of sediment, vegetation, and water level changes at Makepeace Cedar Swamp, southeastern Massachusetts. *Quaternary Research* 53: 352–368.

Orwig DA and Foster DR (1998) Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *Journal of the Torrey Botanical Society* 125: 59–72.

Orwig DA, Cobb RC, D'Amato AW, Kizlinski ML and Foster DR (2008) Multi-year ecosystem response to hemlock woolly adelgid infestation in southern New England forests. *Canadian Journal of Forest Research* 38: 834–843.

Orwig DA, Foster DR and Mausel DL (2002) Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *Journal of Biogeography* 29: 1475–1487.

Oswald WW, Faison EK, Foster DR, Doughty ED, Hall BR and Hansen BCS (2007) Post-glacial changes in spatial patterns of vegetation across southern New England. *Journal of Biogeography* 34: 900–913.

Reimer PJ, Baillie MGL, Bard E, Bayliss A, Beck JW, Bertrand CJH et al. (2004) IntCal04 terrestrial radiocarbon age calibration, 26–0 ka BP. *Radiocarbon* 46: 1029–1058.

Richard PJH (1978) Histoire tardiglaciaire et postglaciaire de la végétation au mont Shefford, Québec. *Géographie physique et Quaternaire* 32: 81–93.

Shuman B, Bartlein P, Logar N, Newby P and Webb T III (2002a) Parallel climate and vegetation responses to the early Holocene collapse of the Laurentide Ice Sheet. *Quaternary Science Reviews* 21: 1793–1805.

Shuman B, Bravo J, Kaye J, Lynch JA, Newby P and Webb T III (2001) Late-Quaternary water-level variations and vegetation history at Crooked Pond, southeastern Massachusetts. *Quaternary Research* 56: 401–410.

Shuman BN, Newby P and Donnelly JP (2009) Abrupt climate change as an important agent of ecological change in the Northeast U.S. throughout the past 15,000 years. *Quaternary Science Reviews* 28: 1693–1709.

Shuman B, Newby P, Donnelly JP, Tarbox A and Webb T III (2005) A record of late-Quaternary moisture-balance change and vegetation response from the White Mountains, New Hampshire. *Annals of the Association of American Geographers* 95: 237–248.

Shuman B, Newby P, Huang Y and Webb T III (2004) Evidence for the close climate control of New England vegetation history. *Ecology* 85: 1297–1310.

Shuman B, Webb T III, Bartlein P and Williams JW (2002b) The anatomy of a climatic oscillation: Vegetation change in eastern North America during the Younger Dryas chronozone. *Quaternary Science Reviews* 21: 1763–1916.

Spear RW (1989) The late Quaternary history of high-elevation vegetation in the White Mountains of New Hampshire. *Ecological Monographs* 59: 125–151.

Spear RW, Davis MB and Shane LCK (1994) Late Quaternary history of low- and mid-elevation vegetation in the White Mountains of New Hampshire. *Ecological Monographs* 64: 85–109.

St Jacques JM, Douglas MSV and McAndrews JH (2000) Mid-Holocene hemlock decline and diatom communities in van Nostrand Lake, Ontario, Canada. *Journal of Paleolimnology* 23: 385–397.

Stockmarr J (1971) Tablets with spores used in absolute pollen analysis. *Pollen et Spores* 13: 615–621.

Stuiver M and Reimer PJ (1993) Extended ^{14}C database and revised CALIB radiocarbon calibration program. *Radiocarbon* 35: 215–230.

Thompson EH and Sorenson ER (2000) *Wetland, Woodland, Wildland: A Guide to the Natural Communities of Vermont*. Middlebury: Middlebury College Press.

Thompson RS, Anderson KA and Bartlein PJ (1999) *Atlas of the Relations Between Climatic Parameters and the Distribution of Important Trees and Shrubs in North America*. Professional Paper 1650-A, B. Denver: US Geological Survey.

Toney JL, Rodbell DT and Miller NG (2003) Sedimentologic and palynologic records of the last deglaciation and Holocene from Ballston Lake, New York. *Quaternary Research* 60: 189–199.

Webb T III (1982) Temporal resolution in Holocene pollen data. *Third North American Paleontological Convention, Proceedings* 2: 569–571.

Webb T III, Richard P and Mott RJ (1983) A mapped history of Holocene vegetation in southern Quebec. *Syllogeus* 49: 273–336.

Whitehead DR and Crisman TL (1978) Paleolimnological studies of small New England (U.S.A.) ponds. Part I. Late-glacial and postglacial trophic oscillations. *Polskie Archiwum Hydrobiologii* 25: 471–481.

Yu ZC and McAndrews JH (1994) Holocene water levels at Rice Lake, Ontario, Canada: Sediment, pollen and plant-macrofossil evidence. *The Holocene* 4: 141–152.

Yu Z, McAndrews JH and Eicher U (1997) Middle Holocene dry climate caused by change in atmospheric circulation patterns: Evidence from lake levels and stable isotopes. *Geology* 25: 251–254.

Zhao Y, Yu ZC and Zhao C (2010) Hemlock (*Tsuga canadensis*) declines at 9800 and 5300 cal. yr BP caused by Holocene climatic shifts in northeastern North America. *The Holocene* 20: 877–886.