Research paper

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Hemlock (*Tsuga canadensis*) declines at 9800 and 5300 cal. yr BP caused by Holocene climatic shifts in northeastern North America

Yan Zhao,[1] Zicheng Yu[2] and Cheng Zhao[2]

Abstract

We present fossil pollen data from a sediment core at Lake Grinnell in northern New Jersey of the northeastern United States. The 12 500-yr chronology of the sediment record was controlled by seven calibrated AMS radiocarbon dates on terrestrial plant macrofossils. Similar to many pollen profiles in the region, our data show that vegetation changed from *Picea*- and *Pinus*-dominated woodland/forest at 12.5–11.4 ka (1 ka = 1000 cal. yr BP), through *Pinus*-dominated mixed forest at 11.4–9.3 ka, to *Quercus*-dominated forest after 9.3 ka. Some main tree taxa, including *Tsuga*, *Ulmus* and *Acer*, arrived and expanded during the *Quercus* expansion phase at 11.4–9.3 ka in the early Holocene, while other trees, including *Fagus* and *Carya*, established and expanded much later around 9 ka. Pollen data show that major forest shifts were in response to climatic change as independently inferred from oxygen-isotope records in the same core. These responses include major turnovers of tree species at the onset of the Holocene after the Younger Dryas, including the disappearance of *Picea*, declines of boreal taxa *Betula* and *Alnus*, and expansions of most other temperate trees. Our new records show two hemlock (*Tsuga canadensis*) decline events during the Holocene that were both likely caused by climatic change. The early-Holocene hemlock decline centering around 9.5 ka was marked by >10-fold decrease in hemlock populations, which was probably caused by summer high temperature as inferred from high oxygen isotope values. The mid-Holocene hemlock decline from 5.3 ka to 3.0 ka corresponds with a pronounced shift in oxygen isotopes at Grinnell and with a dry climate interval documented from other records in northeastern North America. Our results support the notion that a dry climate caused or triggered the mid-Holocene hemlock decline and that the Appalachian Forest has shown sensitive responses to climatic change in the Holocene.

Keywords

climatic change, fossil pollen, hemlock (*Tsuga canadensis*) decline, Holocene, Lake Grinnell, northeastern North America

Introduction

Deevey's (1939) pioneer fossil pollen analysis from lakes and bogs in Connecticut established a sequence of pollen assemblages that represents the development of forests in the northeastern United States ('New England') since the last deglaciation. Since then, numerous pollen records have become available in this region. Independent lines of evidence from lake sediments provide a climatic framework for understanding New England vegetation histories and their climatic controls (Shuman *et al*., 2004). Shuman *et al*.'s (2004) analysis demonstrates that changes in both the abundance of existing taxa and the arrival of new taxa closely correlate with independently documented changes in regional climate. In southern New England, however, few records that have both robust age controls and high-resolution pollen data (e.g. Davis, 1969; Maenza-Gmelch, 1997; Watts, 1979) contain other independent climate proxy records from the same sites to afford robust discussion of vegetation–climate interactions. As documented in regions around southern New England, independent records for vegetation and water-level changes have shown climate controls of major vegetation changes at multimillennial timescales (Newby *et al*., 2000; Shuman *et al*., 2004; Yu *et al*., 1997). Compared with lithology-based lake-level records, stable isotopes from the same core as pollen data would potentially provide continuous and high-resolution records of temperature and moisture changes (e.g. Huang *et al*., 2002). These paired proxy records from pollen and isotopes would help us investigate how vegetation has responded to climatic changes in the past.

Here we present a high-resolution pollen record from a marl lake in the northeastern United States, to show how vegetation responded to climatic oscillations by comparing the fossil pollen data with stable isotope data from the same core. The objectives of this study were (1) to provide a detailed pollen and vegetation record spanning the Holocene; and (2) to evaluate the responses of forested vegetation to climatic changes in southern New England by comparing with an independent climate record. The results presented here provide not only a detailed Holocene vegetation

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[1] Lanzhou University, China
[2] Lehigh University, USA

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Corresponding author:
Yan Zhao, MOE Key Laboratory of Western China's Environmental System, College of Earth and Environmental Sciences, Lanzhou University, Lanzhou 730000, China
Email: yanzhao@lzu.edu.cn

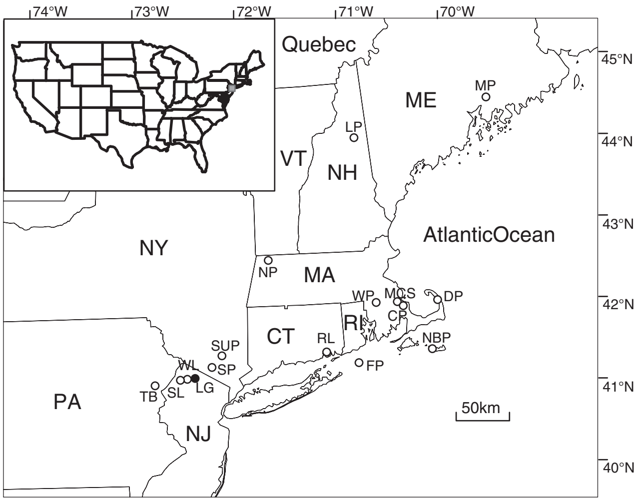

Figure 1. Location map of Lake Grinnell and other paleoclimate sites in the northeastern United States mentioned in the text. Red square in the inset map shows the location of the study site. Site abbreviations: LG, Lake Grinnell (this study); TB, Tannersville Bog (Cai, 2008; Watts, 1979); SL, Silver Lake (Zelanko, 2008); WL, White Lake (Yu, 2007); SP, Spruce Pond (Maenza-Gmelch, 1997); SUP, Sutherland Pond (Maenza-Gmelch, 1997); FP, Fresh Pond (Dunwiddie, 1990); RL, Rogers Lake (Davis, 1969); NBP, No Bottom Pond (Dunwiddie, 1990); CP, Crooked Pond (Shuman *et al*., 2001); WP, Winneconnet Pond (Suter, 1985); MCS, Makepeace Cedar Swamp (Newby *et al*., 2000); DP, Duck Pond (Winkler, 1985); NP, North Pond (Spear *et al*., 1994); LP, Lost Pond (Spear *et al*., 1994); MP, Moulton Pond (Davis, 1981). State abbreviations are: NJ, New Jersey; PA, Pennsylvania; CT, Connecticut; RI, Rhode Island; MA, Massachusetts; NY, New York; VT, Vermont; NH, New Hampshire; ME, Maine

history in northeastern North America but also convincing evidence in support of the climatic interpretation of pollen sequences for southern New England as proposed by Deevey (1939) and Shuman *et al*. (2004). In particular, we discuss the newly documented hemlock decline during the early Holocene and its climatic controls and regional significance.

Study region and site

Lake Grinnell is located in northern New Jersey (41°06′N latitude, 74°38′W longitude; ~170 m above sea level; Figure 1) in the northeastern United States. The Laurentide ice sheet retreated from this region at a minimum of ~14 000 years ago (Witte, 2001). Regional climate has been strongly affected by moisture from the Gulf of Mexico and the Atlantic Ocean. The study site is in a humid temperate region, and instrumental records from nearby Charlotteburg Reservoir station (15 km southeast of Lake Grinnell) show a mean annual temperature of 17.6°C and a mean annual precipitation of *c*. 1200 mm. Forests of northern New Jersey are part of the Appalachian Forest Region. They are mainly oak (*Quercus*)-dominated hardwood forests, with high abundances of walnut (*Juglans*), maple (*Acer*), ash (*Fraxinus*), and hickory (*Carya*) (Flora of North America Editorial Committee, 1993).

Lake Grinnell is a small hardwater lake with a surface area of 0.2 km^2 and a catchment area of ~7 km^2. The lake water level was raised artificially about 2.4 m by a dam to form the present impoundment area, with a maximum water depth of about 10.4 m. Lake Grinnell is the headwater lake of a tributary of Wallkill River, which flows northeastward to the Hudson River.

Methods

A 900 cm long sediment core (GL05-1) was taken near the center part of Lake Grinnell in January 2005 at 6.6 m water depth using a Livingstone-Wright piston corer of 5 cm in diameter. Terrestrial plant macrofossils and charcoals were picked from seven samples and sent to Keck Carbon Cycle Accelerator Mass Spectrometry (AMS) Laboratory at University of California, Irvine for AMS ^{14}C dating (see details in Zhao *et al*., 2010). LOI analysis was used to estimate organic matter and carbonate content, and a total of 334 calcite samples were analyzed for oxygen isotopes in the Stable Isotope Laboratory at the University of Minnesota (see Zhao *et al*., 2010, for details on LOI and isotope analysis).

Pollen analysis was carried out on 0.7 cm^3 subsamples at 8 cm intervals. Pollen samples were prepared using a modified standard acetolysis procedure (Fægri and Iversen, 1989), including HCl, KOH, HF and acetolysis treatments (for <3 min in hot water bath to minimize the possible damage to pollen grains), and fine sieving was used to remove clay-sized particles. The concentrate was mounted in silicon oil. A known number of *Lycopodium clavatum* spores (batch # 938934; 10 679±426 spores per tablet) was initially added to each sample for calculation of pollen concentration (Maher, 1981). Pollen sums were mostly >300 terrestrial pollen grains. Pollen percentages were calculated based on the total terrestrial pollen sum. Pollen diagrams were plotted using TGView 2.0 (E. Grimm of Illinois State Museum, Springfield IL, USA). A total of 18 dominant pollen taxa with percentages >2% in at least one sample were used for stratigraphically constrained cluster (CONISS) analysis (Grimm, 1987).

Principle components analysis (PCA), a multivariable statistical method for dimensionality reduction (ordination analysis), was performed on the pollen data set to identify the major pattern of vegetation changes and to facilitate the comparison of vegetation shifts with the isotope-derived climate variations from Lake Grinnell. The same dominant 18 pollen taxa as for CONISS analysis were used in PCA using the CANOCO program (Ter Braak, 1988). We also carried out PCA for other pollen records from the northeastern United States in order to compare fossil pollen assemblages from Lake Grinnell with these records. Pollen data from these sites were obtained from the North American Pollen Database (http://www.ncdc.noaa.gov/paleo/napd.html). We carried out CONISS analysis for major taxa (>2% in any sample) to divide pollen zones at these sites. Mean PCA scores for each of all pollen zones at all these sites were calculated.

Results

Lithology, chronology and isotope results

The core has 230 cm of clay at the bottom (1560–1330 cm below the lake surface). The rest of the core is mostly marl sediment (1330–670 cm), except 10 cm of gyttja at the very top (670–660 cm; Figure 2A). The marl sediment contains >90% carbonate (Figure 2B; Zhao *et al*., 2010), with ~6% organic matter and ~2% silicate (not shown here). The seven AMS dates on plant macrofossils from core GL05-1 were all in stratigraphic order (Zhao *et al*., 2010). The chronology indicates that the analyzed

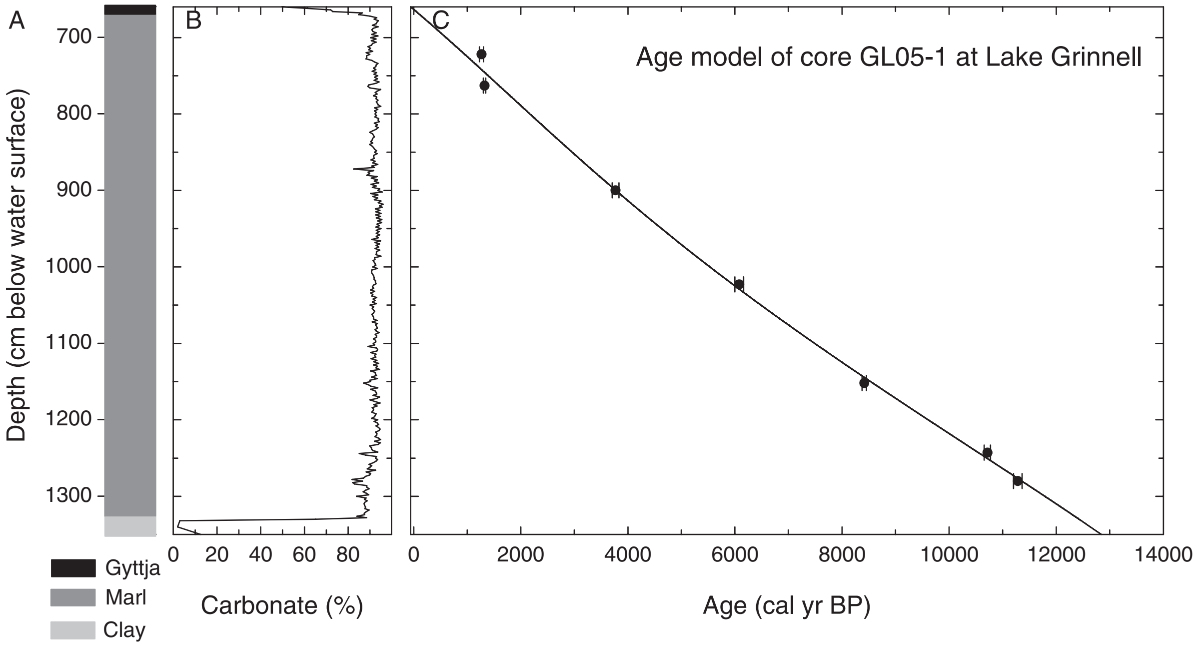

Figure 2. Lithology and chronology of core GL05-1 at Lake Grinnell, New Jersey. (A) Lithology column. (B) Carbonate content (%) (Zhao *et al.*, 2010). (C) Age–depth model based on fourth polynomial curve of calibrated AMS ages (Zhao *et al.*, 2010). Error bars show errors of 2σ range of calibrated ages

core section spanned the last 12 500 years (Figure 2C). The sediment accumulation rates based on the age–depth model are nearly constant throughout the core at *c*. 0.56 mm/yr. The $\delta^{18}O$ values of calcite at Lake Grinnell range from −8.9‰ to −6.7‰ (Zhao *et al.*, 2010).

Fossil pollen assemblages

The sampling resolution of pollen results is about 140 years per sample. We identified 44 pollen types in 85 samples from core GL 05-1 at Lake Grinnell. A summary percentage pollen diagram is shown in Figure 3 (only major taxa with >2% in any sample were shown). *Quercus* (up to 80.2%), *Pinus* (up to 76%), *Carya* (~16%), *Betula* (~39%), and *Tsuga* (18%) are the dominant pollen types. Other pollen/spore types with abundances of <2% (not shown) include *Abies*, *Salix*, Rosaceae, Brassicaceae, *Polygonum*, *Thalictrum*, *Stellaria*, *Artemisia*, other Asteraceae-type, Chenopodiaceae, *Sphagnum*, *Typha*, *Potamogeton* and *Nuphar*. The summary of the pollen diagram shows clear vegetation changes during the last 12.5 ka (1 ka = 1000 cal. yr BP), corresponding with the classic pollen sequence of Deevey (1939) for southern New England (Figure 3). The percentage pollen diagram from core GL05-1 was divided into six pollen assemblage zones, with subzones when necessary, based on CONISS.

Zone GL-1 (Deevey's Regional Zone A4): Pinus-Picea-Betula (12.5–11.4 ka; 1330–1284 cm). Zone GL-1 features high percentages of *Pinus strobus* and *Pinus* undifferentiated pollen (up to 68.7%) together with *Picea* (up to 21%) and *Betula* (up to 38.9%). *Alnus* is also high (up to 12.6%). Pollen concentration fluctuates between 3700 and 455 000 grains/cm^3. This zone mostly corresponds to the Younger Dryas event, as indicated by a prominent *Alnus* peak and declining *Picea* (e.g. Yu, 2007).

Zone GL-2 (Regional Zone B): Pinus-Quercus (11.4–9.3 ka; 1284–1180 cm). Zone GL-2 features high percentages of *Pinus* pollen (up to 46%) and a gradual increase in *Quercus* (from 7% to 61%), as well as high percentages of *Tsuga* pollen (up to 18%). The decline of *Pinus* from its peak is followed by the rise and predominance of *Quercus* in the pollen rain that has continued through the Holocene to the present day. The rise in *Quercus* is accompanied by a steep rise (Subzone 2a) and decline (Subzone 2b) in *Tsuga canadensis*. Pollen concentration is high up to 602 000 grains/cm^3; however, it shows a sharp decrease in Zone 2b when *Tsuga canadensis* declines.

Zone GL-3 (Regional Zone C1): Quercus-Tusga (9.3–5.4 ka; 1180–996 cm). Zone GL-3 is characterized by high *Quercus* percentage (>55%) and high *Tsuga canadensis* pollen percentages (mostly >10%). Several hardwood trees increased in this zone, including *Carya*, *Fagus* and *Ulmus*, while *Quercus* shows a gradual decline. Concentration decreases to 100 000–200 000 grains/cm^3.

Zone GL-4 (Regional Zone C2): Quercus-Carya (5.4–3.3 ka; 996–876 cm). Generally rising but fluctuating values of *Carya* (up to 16.3%) and abrupt decline in *Tsuga* (to mostly <2%) distinguish zone GL-4 from other zones. *Quercus* increases slightly as *Tsuga* decreases. Both *Pinus* and *Betula* increase slightly and *Fagus* shows its highest values. Concentration decreases to 56 000 grains/cm^3.

Zone GL-5 (Regional Zone C3a): Quercus-Carya-Tsuga-Betula (3.3–0.2 ka; 876–676 cm). *Tsuga* shows a gradual recovery from the mid-Holocene decline to percentages of around 10%. *Pinus* and *Betula* have higher values than in zone GL-4. Green algae *Pediastrum* is highest (up to 8.5%) but also highly variable in this zone. Poaceae increases in this zone. Concentration is relatively low at *c*. 100 000 grains/cm^3.

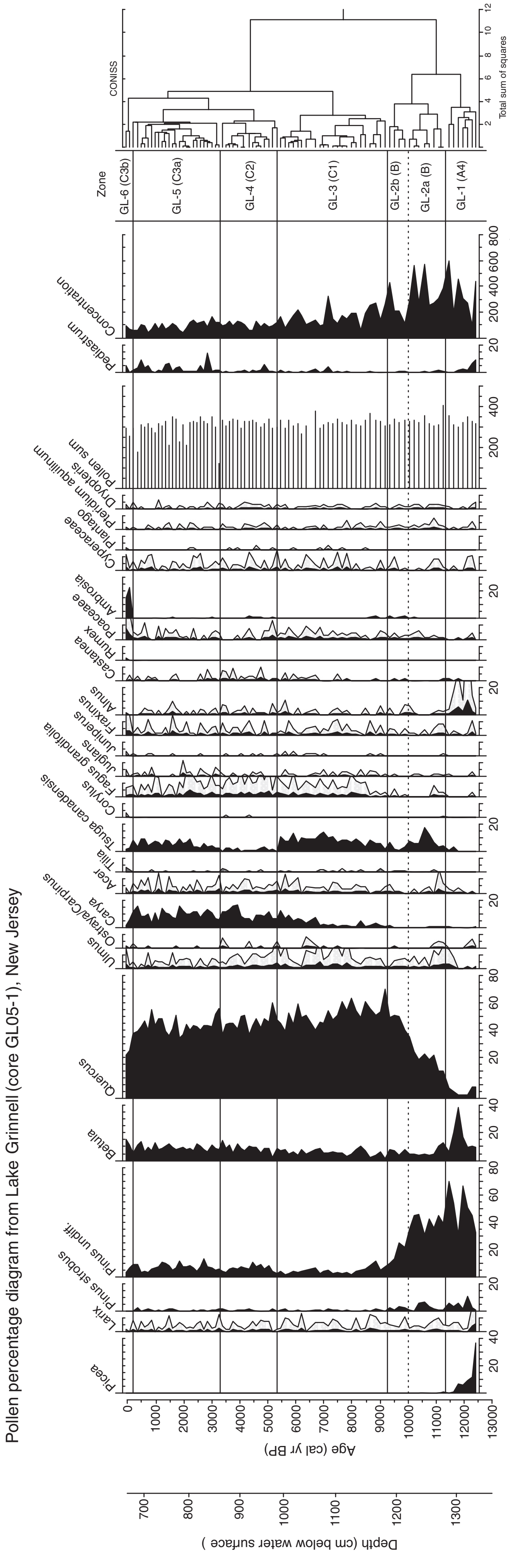

Figure 3. Pollen percentage diagram from Lake Grinnell (core GL05-1), New Jersey. Only selected taxa (with percentage of >2% in any one sample) are shown. Open curves for minor taxa are 5× exaggeration

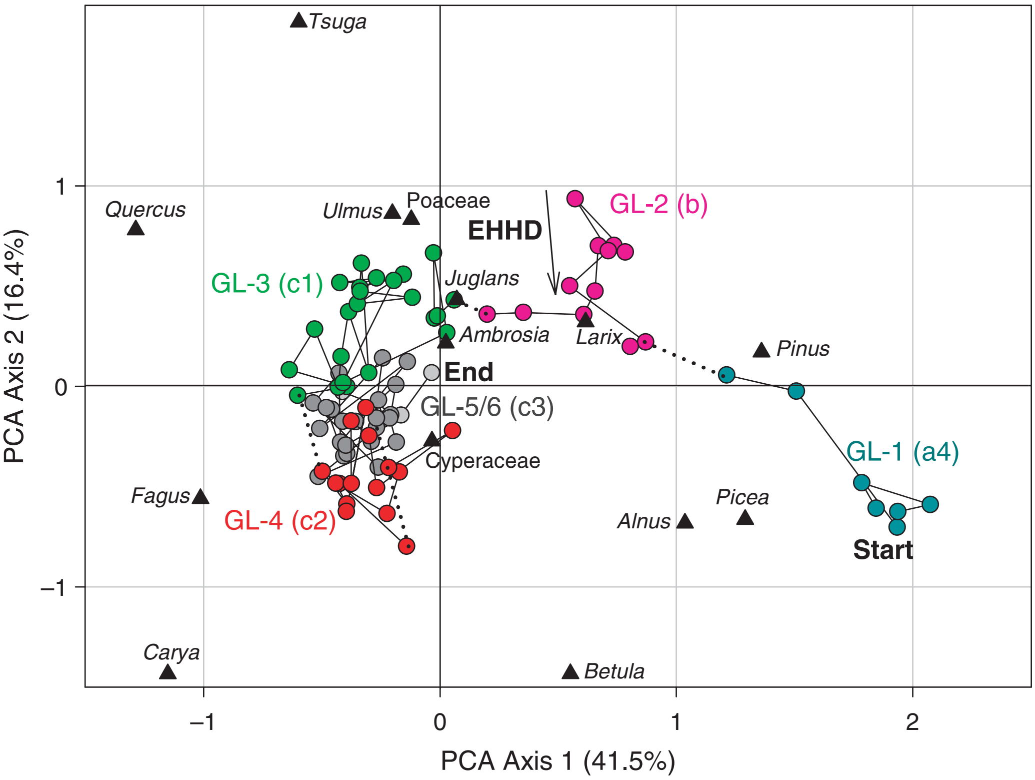

Figure 4. PCA results of fossil pollen data from Lake Grinnell (core GL05-1). PCA scores based on pollen types (in black triangles); PCA scores based on fossil pollen samples (in filled dots); colors representing different pollen zones, with pollen zones labeled. EHHD, early-Holocene Hemlock Decline

Zone GL-6 (Regional Zone C3b): Quercus-Ambrosia-Poaceae (the last 250 years; 676–660 cm). *Pinus*, *Tsuga*, *Carya* and *Quercus* values decrease. Accordingly, large increases in the percentages of *Ambrosia* (up to 22.5%) and Poaceae distinguish zone GL-6 from GL-5. *Plantago* is also present. Concentration is still low (<100 000 grains/cm^3).

Multivariate analysis results

For core GL05-1 from Lake Grinnell, the first three PCA axes account for 67.1% of the total variance in the pollen data (Figure 4). PCA axis 1 mostly shows a major vegetation transition at ~ 9 ka from *Pinus-Picea* assemblages to *Quercus*-other hardwood trees and further separation of Zones 1 and 2; PCA-2 predominantly reflects the percentage change in *Quercus, Tsuga* and other hardwood trees during the later half of the Holocene; and PCA-3 emphasizes the *Ambrosia* increase at the top of the diagram (Figures 4 and 5G). Several clusters of pollen samples can be separated by PCA scores on the first two axes (Figure 4), corresponding with pollen zones described above. For example, the closely clustered zone GL-1 samples were characterized by the dominance of *Picea*, *Pinus*, *Betula* and *Alnus* (Figure 4), whereas zone GL-3 samples were clustered together and characterized by the dominance of *Quercus* and *Tsuga*.

Discussion

Responses of tree migration and forests to climatic changes during the last 12 500 years

Changes in δ^{18}O values at Lake Grinnell have been interpreted as changes in summer air temperature, after examining the lake hydrology and evaluating the lake water geochemistry (see detailed interpretation in Zhao *et al*., 2010). The low δ^{18}O values at 12.5–11.4 ka indicate a cold climate, corresponding to the Younger Dryas event (YD). However, the extrapolated onset and ending ages for the YD at Lake Grinnell are younger than most other records for the YD (e.g. Shuman *et al*., 2002; Yu, 2007), probably because of the lack of direct dating of our record before the Holocene. Holocene climate warming after 11.4 ka is indicated by the highest δ^{18}O values in the oxygen isotope record, showing that warmer climate prevailed from 11 to 5.8 ka, with large multi-centennial-scale oscillations. After 5.8 ka, the δ^{18}O values shifted from a value fluctuating around −7.4‰ to a gradual and steadily decreasing trend, reflecting a cooling climate.

Several paleoclimatic records from the northeastern United States revealed moisture change over the Holocene. For example, increased peat decomposition in a core at Tannersville Bog in northeastern Pennsylvania (Cai, 2008) suggests a dry climate at 10–9 ka. Lithology and macrofossil records from Silver Lake, New Jersey indicate a drier early Holocene with multiple lake-level oscillations (Zelanko, 2008). Evidence from other paleoclimatic records in New England and the surrounding regions (e.g. Davis *et al*., 1980; Huang *et al*., 2002; Jackson and Whitehead, 1991; Newby *et al*., 2000; Shuman *et al*., 2004; Spear *et al*., 1994) also support a generally dry climate in the early Holocene before *c*. 9 ka. Lake-level records from the northeastern United States indicate that the climate became dry again at 5.4–3 ka after the warm and wet period from 9 to 5.4 ka (Shuman, 2003; Shuman *et al*., 2001). Based on the temperature signal inferred from δ^{18}O data at Lake Grinnell and moisture change indicated by other regional records as discussed above, the combination of temperatures and moisture around the Lake Grinnell region can be summarized as a series of four climatic phases: cold climate during the Younger Dryas; cool/dry (but warmer than YD) at 11.4–9 ka; warm/wet at 9–5.4 ka; and cool/dry since 5.4 ka.

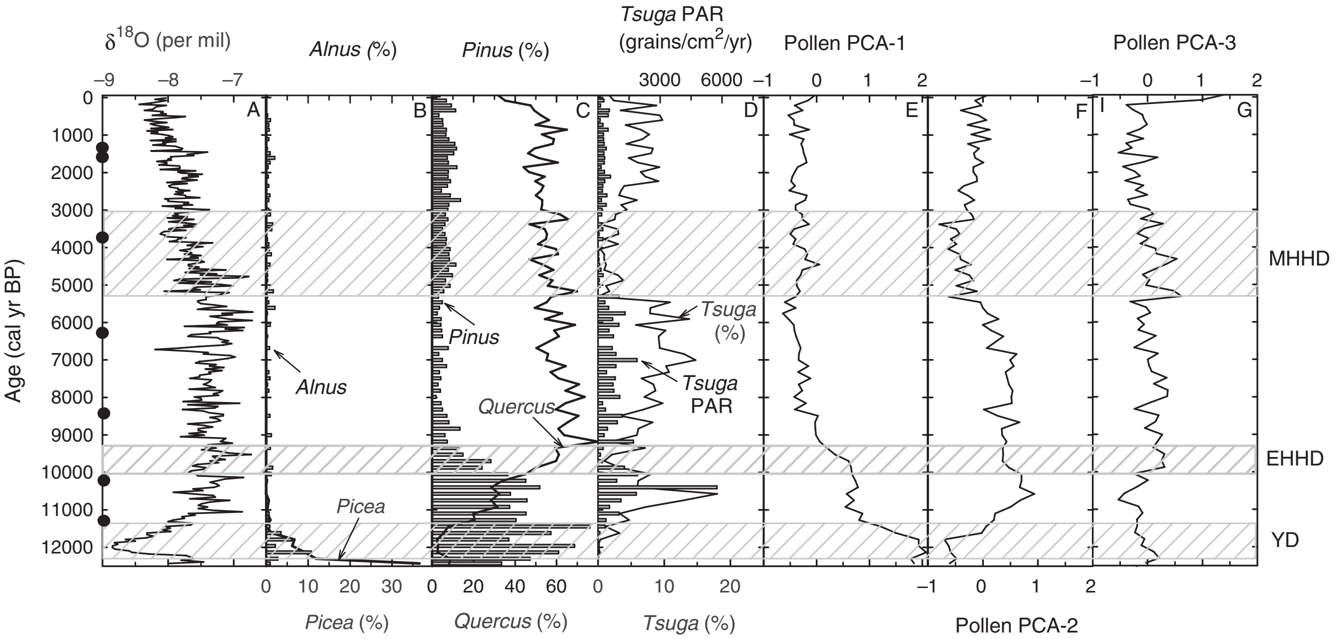

Figure 5. Correlation of pollen data with the $\delta^{18}O$ values from Lake Grinnell (core GL05-1), New Jersey. (A) $\delta^{18}O$ (‰ relative to VPDB) (from Zhao *et al.*, 2010). AMS dating positions marked by black dots. (B) *Picea* (%; curve) and *Alnus* (%; bars). (C) *Quercus* (%; curve) and *Pinus* (%; bars). (D) *Tsuga* (%; curve) and *Tsuga* pollen accumulation rate (PAR; grains/cm^2 per yr; bars). (E) Pollen sample PCA axis 1 scores. (F) Pollen sample PCA axis 2 scores. (G) Pollen sample PCA axis 3 scores. YD, Younger Dryas; EHHD, early-Holocene Hemlock Decline; MHHD, mid-Holocene Hemlock Decline

The pollen diagram together with PCA scores from Lake Grinnell shows the classic sequence of vegetation change and response to major climate oscillations. The YD period clearly corresponds with a peak of alder (*Alnus*) and birch (*Betula*) and also high spruce (*Picea*) percentage. All these trees are cold-tolerant species (Thompson *et al.*, 1999). The increase in birch at the YD suggests that it would more likely be shrub birch (probably *Betula nana* or *B. fruticosa*) than paper birch, which is a boreal-temperate tree. An alder peak is a good regional pollen signal for the YD in New England and Atlantic Canada (e.g. Mayle *et al.*, 1993; Yu, 2007), as alder is a fast-growing shrub (likely *Alnus fruticosa*) or small tree rather than a long-lived tree.

The early-Holocene forest was characterized by expanding oak (*Quercus*) populations and by successive immigration of other tree species. Spruce decreased sharply at 11.4 ka and disappeared altogether at 10.5 ka when climate became warmer. In the meantime, alder and birch declined. Pine (*Pinus*), preferring warmer and drier conditions than spruce (Shuman *et al.*, 2004), was a dominant pollen type at that time when moisture availability was low. As conditions became warmer and wetter, pine pollen percentages at Lake Grinnell declined after 9.3 ka. Oaks then became the predominant trees on the landscape, as oaks, mostly white oaks (*Quercus alba*) and red oaks (*Quercus rubra*) in this region, require more moisture and warm temperature than pines, but less moisture than hemlock (*Tsuga*) and beech (*Fagus*) (Shuman *et al.*, 2004; Thompson *et al.*, 1999).

Between 9.3 and 5.4 ka, hemlock and beech populations, which require greater moisture availability than pine populations (Shuman *et al.*, 2004; Thompson *et al.*, 1999), became abundant as pine populations decreased and moisture availability rose in the Grinnell region. *Tsuga canadensis* arrived at 11.6 ka (age for the beginning of a continuous occurrence of hemlock pollen), followed by *Fagus grandifolia* at 9.5 ka, and hickory (*Carya*) at 9.2 ka. Beech requires warmer climate than hemlock (Thompson *et al.*, 1999). Hickory populations tolerate warmer and drier conditions than other New England trees. The highest hickory pollen percentages at Lake Grinnell were reached after the mid-Holocene hemlock decline when climate became dry. Once drought-tolerant hickory was established in the forest, it continued to be an important component in the vegetation. Because none of these trees contributes large amounts of pollen before 9 ka, it is difficult to pinpoint the exact timing of the tree immigration in the absence of macrofossil data and additional radiocarbon dates.

The mean pollen sample PCA scores for each zone (zones 1–5) from Lake Grinnell show a similar pattern to the ones from Spruce Pond in southeastern New York and Tannersville Bog in Pennsylvania over the last 12.5 ka (Figure 6A). At Spruce Pond, vegetation changed from *Quercus-Pinus* at *c.* 11.9–11.2 ka, through *Quercus-Tsuga* at 11.2–7.1 ka, *Quercus-Carya* at 7.1–3.8 ka, *Quercus-Castanea* at 3.8–0.35 ka, to *Ambrosia*-Poaceae since 0.35 ka (Maenza-Gmelch, 1997). At Tannersville Bog, development of *Pinus*, *Quercus*, *Betula* and *Tsuga* show a similar pattern as at Lake Grinnell and Spruce Pond, though with slight age differences due probably to dating uncertainties (Watts, 1979). The similar vegetation sequence in general among these three records suggests relatively uniform regional vegetation change and strong climatic control of general vegetation history in New England as argued by Shuman *et al.* (2004).

The large magnitude decline of hemlock after its initial expansion in the early Holocene

At approximately 11.2 ka, hemlock pollen percentage reached 3%. Roughly 2% hemlock pollen occurs at sites in northern New Jersey and southern Connecticut at about the same time (Peteet *et al.*, 1990, 1993). However, modern pollen assemblages show that 2% hemlock pollen can be found outside the range of this at some sites

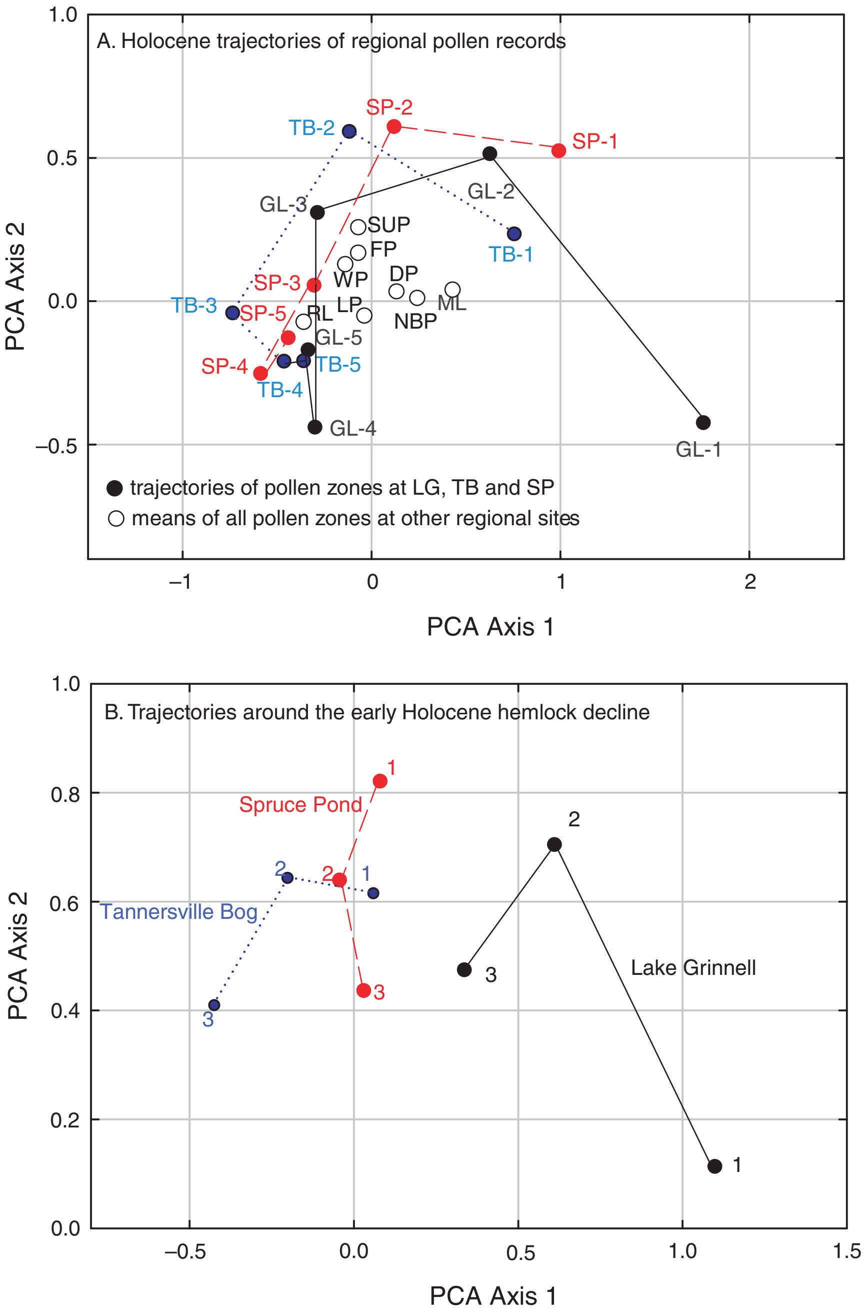

Figure 6. PCA results of pollen assemblages from Lake Grinnell and other sites from northeastern North America. The mean PCA score for each zone is shown. Pollen data from other sites were obtained from the North American Pollen Database (http://www.ncdc.noaa.gov/paleo/napd.html). (A) PCA scores of all pollen zones for the last 12.5 ka, showing mean PCA for each pollen zone at Lake Grinnell, Spruce Pond and Tannersville Bog, and the means of all pollen zones at other sites. Abbreviations of pollen sites included in the PCA are the same as shown in Figure 1. (B) PCA scores of pollen zones around the early Holocene hemlock decline at three sites (Grinnell, Spruce and Tannersville): 1, means of samples before the decline; 2, means of samples during the hemlock decline; and 3, means of samples after the decline

in eastern North America (Davis and Webb, 1975). The threshold value for the establishment of small populations of *Tsuga canadensis* around Lake Grinnell remains unclear due to the lack of plant macrofossil records. Both hemlock percentage and hemlock pollen accumulation rate (PAR) reached the highest values of the entire Holocene (up to 18%) at 10.5 ka (Figure 5D). After the hemlock maximum at 10.5 ka, hemlock percentage declined to <2% from 9.8 to 9.3 ka at Lake Grinnell (Figure 7). Hemlock PAR also shows an abrupt decrease at the same time. This decline corresponds with low total pollen concentration (Figure 3) as well as low pollen accumulation rates. PCA scores of pollen zones around the early Holocene also indicate obvious change (from Zones 2 to 3) reflecting hemlock decline at Lake Grinnell, as well as at other sites, including Tannersville Bog and Spruce Pond (Figure 6B). The decline occurred during the later half of major early-Holocene forest transformation from pine-dominated to oak-dominated forest in the period from 11 ka to 9 ka.

Hemlock has the highest moisture preference and lowest temperature maximum among the dominant trees in the region today (Thompson *et al*., 1999). δ^{18}O from Lake Grinnell shows low values around 10.5 ka, suggesting a cool climate interval (Figure 7), while the highest δ^{18}O value occurred at 9.5 ka in the middle of the

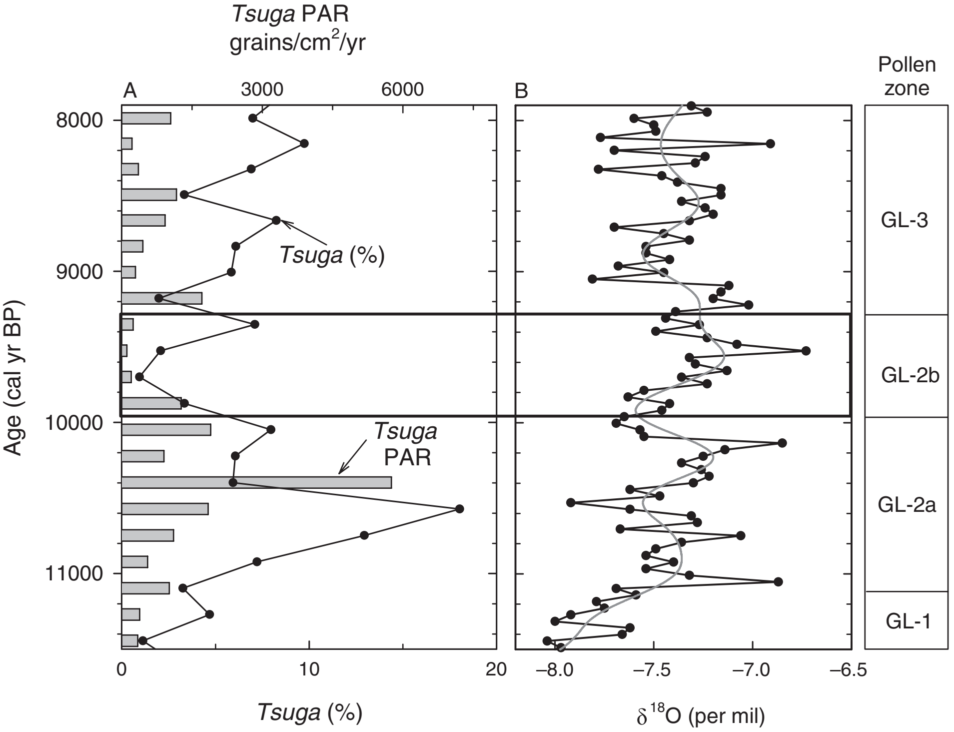

Figure 7. Close-up of the early Holocene hemlock decline and oxygen isotopes as climatic indicators. (A) *Tsuga* percentage (as curve) and pollen accumulation rate (PAR; shown in bars) at Lake Grinnell. (B) The $\delta^{18}O$ values (dots) and five-point smoothed curve from the same core at Lake Grinnell (Zhao *et al.*, 2010)

early-Holocene hemlock decline, suggesting a warmer condition. *Tsuga* percentages in general show a negative relationship with the $\delta^{18}O$ values in the early Holocene, with high *Tsuga* percentages corresponding with low $\delta^{18}O$ values. Thus, the summer warmth at ~9.5 ka as indicated by the high $\delta^{18}O$ value likely caused summer droughts in the region, triggering the hemlock decline, as proposed for the mid-Holocene hemlock decline (e.g. Foster *et al.*, 2006; Shuman *et al.*, 2004; Yu *et al.*, 1997). This dry interval was also indicated by lithology and macrofossil evidence from Silver Lake in New Jersey (Zelanko, 2008) and Tannersville Bog in northeastern Pennsylvania (Cai, 2008). At the same time, summer was too warm to be suitable for pines that were dominant earlier in the Holocene, forcing the retreat of pines northward from the region. Oaks probably took advantage of warm and dry summers and became the dominant trees. As a result, there are no apparent responses from other trees to the early-Holocene hemlock decline at Lake Grinnell (Figure 3).

The mid-Holocene hemlock decline

The mid-Holocene hemlock decline was abrupt at 5.3 ka, and the low hemlock pollen production lasted until 3.0 ka in our Grinnell record, as shown in both pollen percentages and accumulation rates (Figure 5D). The general consistency between hemlock percentages and PAR throughout the record indicates that the percentage change reflects change in tree populations. The general decline in hemlock PAR at Grinnell Lake might represent the real change in hemlock population, as the sedimentation rate is almost constant throughout the core. The mid-Holocene decline has been recorded throughout northeastern North America between 5.5 and 3 ka (Bhiry and Filion, 1996; Davis, 1981, 1983; Foster *et al.*, 2006; Webb, 1981). The decline has been attributed to a pest or pathogen outbreak (Allison *et al.*, 1986; Bhiry and Filion, 1996; Davis, 1981; Webb, 1981). Fossil insect remains indicate that phytophagous insect activity may have been an important agent in the decline (Bhiry and Filion, 1996). Davis (1981) suggested that the prolonged (>1000 years) period of low hemlock abundance following the decline could have resulted from the slow evolution of resistance to disease. However, many researchers examining long-term vegetation and climate dynamics have questioned Davis' interpretation and have suggested that broad-scale climatic change may have led to the decline by favoring a pathogen outbreak and/or stressing hemlock populations (e.g. Calcote, 2003; Foster *et al.*, 2006; Haas and McAndrews, 2000; Yu *et al.*, 1997). Our record at Lake Grinnell shows that the mid-Holocene hemlock decline corresponds to the negative isotope shift in the same core. This isotopic shift is interpreted as indication of a shift in atmospheric circulation that induced a cool and dry climate at that time at Lake Grinnell (Zhao *et al.*, 2009), as at sites from southern Ontario, New England, and the Atlantic Coast (e.g. Shuman, 2003; Shuman *et al.*, 2001; Yu *et al.*, 1997). Given the similar timing of the decline and dry conditions, climatic conditions were probably an important factor in causing or at least triggering the decline and recovery of hemlock populations.

Conclusions

(1) A high-resolution and well-dated pollen record from New Jersey shows that vegetation changed from *Picea*- and *Pinus*-dominated forest at 12.5–11.4 ka, through *Pinus*-dominated mixed forest at 11.4–9.3 ka, to *Quercus*-dominated forest after 9.3 ka. Other dominant trees, including *Tsuga*, *Fagus* and *Carya*, show expansions during the initial *Quercus* phase

at different times, reflecting their respective migration histories in eastern North America. Pollen data document rapid forest response to Holocene climatic changes, inferred from the oxygen isotopic record from the same core, confirming the notion that the pollen sequence as first identified by Deevey (1939) closely corresponds with climatic changes in southern New England (Shuman *et al*., 2004).

(2) The early Holocene hemlock decline occurred at 9.8–9.3 ka at Lake Grinnell as well as at other nearby sites in southeastern New York and eastern Pennsylvania. This decline was probably caused by summer droughts induced by high air temperature as indicated by independent climate proxy from oxygen isotopes during the period of the major forest transformation in the early Holocene.

(3) The hemlock decline and reduction during the mid-Holocene was long-lasting from 5.3 to 3.0 ka at Lake Grinnell, as at most other sites in northeastern North America. Our new record of combined pollen, oxygen-isotope data and other regional records further confirms that a dry climate in the mid Holocene, probably caused by a major shift in atmospheric circulation patterns, was an important causal factor or at least a trigger of the hemlock decline.

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