Ecological Impact of the Mid-Holocene Hemlock Decline in Southern Ontario, Canada

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ECOLOGICAL IMPACT OF THE MID-HOLOCENE HEMLOCK DECLINE IN SOUTHERN ONTARIO, CANADA

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Abstract. Hemlock (*Tsuga canadensis*) was an abundant tree species in eastern North America before it declined sharply in abundance ~4700 ^{14}C yr BP (~5400 calendar years BP). The rapid, apparently synchronous, and species-specific nature of the decline suggests that it was the result of a pathogenic outbreak. *T. canadensis* is a highly shade-tolerant, long-lived conifer, and its sudden removal from the canopy is likely to have had an impact on forest composition, structure, and function. The response of forest vegetation to the mid-Holocene hemlock decline at two sites in southern Ontario, Canada was examined using paleoecological methods. At one site, where *T. canadensis* declined sharply, several other forest taxa increased in abundance, resulting in a long-term shift in forest composition. At a second site, pollen percentages of *T. canadensis* did not decrease so dramatically, and less change in forest composition occurred. At both sites, *T. canadensis* took ~2000 yr to recover from the decline and reach former abundance levels. This study suggests that the mid-Holocene decline of a forest dominant may have had a long-term impact on forest composition in northeastern North America.

Key words: fine-resolution pollen analysis; forest dynamics; hemlock decline; pathogenic outbreak; southern Ontario; Tsuga canadensis.

INTRODUCTION

Hemlock (*Tsuga canadensis*) was an abundant tree species in the mixed forests that covered eastern North America in the mid-Holocene (Gaudreau and Webb 1985, Ritchie 1987). Paleoecological evidence suggests that *T. canadensis* declined dramatically in abundance throughout this region ~5000 yr before present (Davis 1978, 1981, Webb 1982). This decline was rapid, more or less synchronous throughout eastern North America, and unique to *T. canadensis* (Davis 1981, Webb 1982, Allison et al. 1986). It is therefore considered to have been the result of a pathogenic outbreak (Davis 1981, Allison et al. 1986), possibly by an insect pest (Bhiry and Filion 1996). In many locations, *T. canadensis* populations recovered 1000–2000 yr after the decline, whereas in others it remained a sparse member of the forest flora (Davis 1978, 1981).

Several studies have focused on the cause of the mid-Holocene hemlock decline (Davis 1981, Allison et al. 1986, Filion and Quinty 1993, Bhiry and Filion 1996), but few have examined the ecological or ecosystem-level consequences. Davis (1978, 1981) notes that *Betula, Fagus grandifolia, Acer saccharum,* and/or *Quercus* increased in abundance after the decline at a number of sites in the Northeast. Hall and Smol (1993) examined communities of diatoms and chrysophytes

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preserved in lake sediments at a number of sites in southern Ontario to determine whether they responded to changes in the watershed vegetation cover during the hemlock decline. They found shifts in algal communities, but only in lakes with large watersheds did they observe a change in lake trophic status, with a short-lived period of eutrophication. The present study examines the impact of the hemlock decline on forest dynamics by investigating the response of other forest taxa using fine-resolution pollen data from two sites in southern Ontario, Canada.

T. canadensis is a long-lived, slow-growing, and highly shade-tolerant conifer, which, along with *F. grandifolia, A. saccharum,* and *Betula alleghaniensis,* is a major component of mature forests throughout the Great Lakes–St. Lawrence and Acadian forest regions (Rowe 1977, Ritchie 1987, Godman and Lancaster 1990). *T. canadensis* is generally found today in regions with cool, humid climates, and it grows on a wide variety of soils that are characterized as moist to very moist but with good drainage (Godman and Lancaster 1990). Its modern distribution is largely a function, at least locally, of recent history and human activity, as it is sensitive to disturbance and tends to be most abundant on sites least impacted by land use (Rogers 1978). *T. canadensis* casts deep shade and produces a thick litter layer, which often restricts the understory vegetation to *T. canadensis* seedlings and saplings (Rogers 1978, Benzinger 1994). Its removal from the forest canopy is, therefore, expected to result in a response from other tree and shrub species, and to influence ecosystem properties.
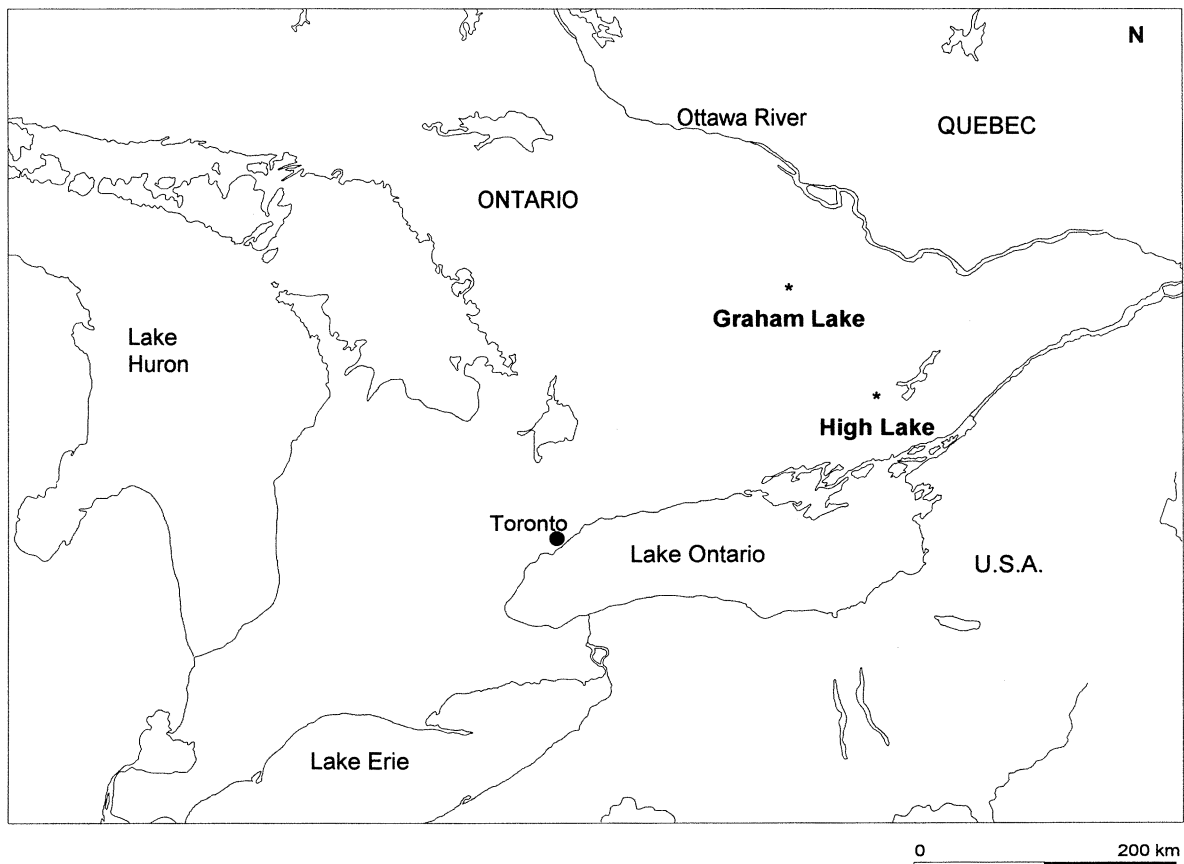
FIG. 1. Map of southern Ontario, Canada showing the location of the two study sites, Graham Lake and High Lake.

It is important to understand the short- and long-term impacts of pests and disease on forest dynamics for conservation and forest management purposes. The hemlock decline provides an opportunity to examine the long-term impact on forest dynamics of a species-specific, pathogenic outbreak. The chestnut decline, which occurred in North America in the early 1900s, due to the fungus *Cryphonectaria parasitica,* and the spread of Dutch elm disease (due to another fungus, *Ceratocytis ulmi*) in Europe and North America, demonstrated the potentially devastating impact of introduced pathogens (Allison et al. 1986, Whitney 1993). Currently *T. canadensis* populations at the southern end of their range are being attacked by the woolly adelgid (*Adelges tsugae*), an introduced insect whose larvae can kill trees through defoliation (McClure 1987). This pest is spreading rapidly and could decimate *T. canadensis* populations in North America (Orwig and Foster 1998).

The hemlock decline provides a unique opportunity to investigate long-term forest dynamics in response to a major disturbance event, such as the removal of a single, dominant tree species. The long generation time of most tree species prevents empirical studies of forest succession or tree population dynamics that cover sev-

eral generations (Bennett 1983, Chen 1986). However, a paleoecological approach using fine-resolution fossil pollen analysis can provide records of forest dynamics that span thousands of years (several generations of trees) with a temporal resolution of decades (within the life-span of most tree species). In this paper I address the following questions: What is the impact on forest dynamics of the removal of an abundant tree species? At what rate does vegetation respond to such a disturbance? Are there long-term implications for forest composition of such an historical event?

Study area

The study area is southern Ontario, Canada, the forests of which are mainly classified within the Great Lakes–St. Lawrence Forest Region (Halliday 1937, Rowe 1977), and are composed of a mosaic of conifer-dominated bogs and swamps, pine plains, and upland hardwoods (Braun 1950, Rowe 1977). The two study sites (Fig. 1) occur within a subdivision of this forest region, the Middle Ottawa Forest Section (Rowe 1977). This is an upland forest type, the main components of which include *Acer saccharum, Fagus grandifolia, Betula alleghaniensis, Acer rubrum, Tsuga canadensis, Pinus strobus,* and *Pinus resinosa* (Rowe 1977). *Picea*

TABLE 1. Site parameters for Graham Lake and High Lake.

Parameters	Graham Lake	High Lake
Latitude	45°11′ N	44°31′ N
Longitude	77°21′ W	76°36′ W
Area (ha)	2.5	2.3
Maximum depth (m)	8	7.6
Mean depth (m)	3.2	5.4
Altitude (m)	381	192

glauca, Abies balsamea, Populus tremuloides, Betula papyrifera, Quercus rubra, and Tilia americana occur throughout in varying amounts. Hardwood and mixed wood swamps are common, composed of Thuja occidentalis, Juniperus communis, Picea mariana, Fraxinus nigra, Acer rubrum, and Ulmus americana (Rowe 1977). Vascular plant nomenclature follows Gleason and Cronquist (1991).

The sites are located on the Precambrian shield. Bedrock is covered with Pleistocene glacial deposits and glacial landforms, such as outwash plains, moraines, and lacustrine deposits (Chapman and Putnam 1984). Elevation varies from 75 m in the south to 560 m in the Northeast. Soils are commonly inceptisols and spodosols in the uplands. Gleysols and peat form in areas with poor drainage.

Site selection and description

The two sites were chosen for comparable size, elevation, and soils to minimize variation between their pollen records for sedimentary reasons (Table 1). High Lake is located slightly farther south than Graham Lake (Fig. 1) and experiences a slightly milder and moister climate (Brown et al. 1968). The sites were selected to have a predominantly local pollen source area in order to obtain records of local vegetation change. Several studies have concluded that the smaller the pollen-collecting basin the smaller the pollen source area, providing the basin is closed (Jacobson and Bradshaw 1981, Prentice 1985, Jackson 1990, Sugita 1993). Both sites are therefore small, closed lakes within well-defined bedrock basins that are relatively flat bottomed (Table 1), thus reducing the likelihood of sediment focusing (Davis et al. 1984).

Graham Lake is situated within the Algonquin highlands, a region of locally rough relief (Chapman and Putnam 1984). The bedrock is amphibolite, a metasedimentary rock (Evans and Appleyard 1963). Modern soils around the lake are described as Monteagle sandy loam (Gillespie et al. 1963). The rocky slopes on the western shore of Graham Lake are vegetated mostly by Acer rubrum, with some A. saccharum, F. grandifolia, Q. rubra, T. americana, B. papyrifera, and T. canadensis. P. glauca, A. balsamea, T. occidentalis, and P. strobus are more abundant near the shore. The slopes on the eastern side are dominated by P. strobus, with P. glauca abundant adjacent to the lake edge.

High Lake is also located in the Algonquin highlands, on the edge of the Precambrian shield. Bedrock is granite, and modern soils surrounding the lake are also classified as Monteagle sandy loam (Gillespie et al. 1966). Local vegetation is composed mostly of P. strobus on the rocky border of the lake, with some P. glauca, T. canadensis, and A. balsamea. A. rubrum, A. saccharum, Q. rubra, F. grandifolia, Ostrya virginiana, and B. papyrifera can be found in the surrounding area. Fraxinus nigra and T. occidentalis occur in the less well-drained areas.

METHODS

Paleoecological analysis

Standard paleoecological methods were used to extract cores of lake sediment from the two sites and to analyze them for fossil pollen and charcoal (Benninghoff 1962, Clark 1982, Berglund and Ralska-Jasiewiczowa 1986, Fuller 1995, 1997). Sediment samples (0.5 cm³) were taken at regular intervals (1–2 cm) for pollen analysis. More than 1000 pollen grains and spores were counted per sample to minimize statistical uncertainty (Maher 1972, Faegri et al. 1989). A known volume of an exotic marker (calibrated Eucalyptus pollen suspension) was added to each sample before preparation to calculate pollen concentrations (Benninghoff 1962). Radiocarbon age determinations (expressed as ^{14}C yr) were made on bulk samples of sediment from both sites. The ages were calibrated to calendar years using the program CALIB 3.0 (Stuiver and Reimer 1993, Fuller 1997). Unless otherwise stated, all the ages are expressed as calendar years before present (hereafter abbreviated yr BP). Pollen percentages were calculated based on the terrestrial pollen sum (which included trees, herbs, and pteridophytes). Pollen influx was estimated using pollen concentrations and sediment deposition time. To aid description, the pollen data were zoned numerically (optimal splitting based on information content) using the program psimpoll version 2.25 (Bennett 1994, 1996).

Numerical analyses

1. Rates of change.—Rates of palynological change are an indirect method of assessing rates of vegetation change (Jacobson and Grimm 1986, Jacobson et al. 1987). These rates were used to determine the impact of the hemlock decline on forest dynamics at both sites. This analysis involves measuring the dissimilarity between adjacent pairs of samples (pollen assemblages) divided by the temporal difference between the samples (Bennett and Humphry 1995). Interpolation was used to achieve equal time intervals (300 yr), and dissimilarity between adjacent samples was estimated using chord distances with the program Tilia 2 (Jacobson and Grimm 1986; E. Grimm, personal communication). Tree pollen types that reached values ≥5% of the pollen sum were included in this analysis.

TABLE 2. Conventional radiocarbon age determinations (^{14}C yr BP) and calibrated age ranges (yr BP) for bulk sediment samples from Graham Lake and High Lake.

Depth range (cm)	Laboratory code	Radiocarbon age (^{14}C yr BP)	Calibrated age (yr BP)
Graham Lake			
935–945	Q-2909	1750 ± 40	1645 ± 110
995–1005	Q-2908	3205 ± 45	3445 ± 155
1061–1071	Q-2907	4760 ± 45	5520 ± 100
1113–1123	Q-2905	6650 ± 50	7475 ± 85
1155–1165	Q-2904	8260 ± 60	9195 ± 195
1212–1232	Q-2903	10 105 ± 85	11 570 ± 540
High Lake			
827–833	SRR-4947	1485 ± 45	1395 ± 105
937–943	SRR-4948	2725 ± 45	2845 ± 95
1057–1063	SRR-4949	4060 ± 45	4530 ± 120
1127–1133	SRR-4950	5200 ± 50	5995 ± 115
1187–1193	SRR-4951	6865 ± 50	7660 ± 120
1257–1263	SRR-4952	8435 ± 50	9410 ± 90
1327–1333	SRR-4953	9415 ± 50	10 435 ± 155

2. *Response of individual taxa to the hemlock decline.*—To describe the increase in abundance of other forest taxa after the hemlock decline, an exponential equation was fitted to pollen influx values (N):

$$\ln N = rt + c \tag{1}$$

where r is the rate of increase (yr^{-1}), t is the sample age (years), and c is a constant.

Linear regression analysis was used to fit parameters. The r parameter is not the intrinsic rate of increase for a particular taxon but the observed rate of increase. The exponential model assumes that the only limiting factor to population growth is reproductive potential, which is clearly not realistic in most natural habitats. However, this simple model can be useful in describing the increase in pollen influx values of taxa after a major event such as the hemlock decline.

3. *Ordination.*—Principal components analysis (PCA) was used to determine the pattern and direction of change in forest composition over the period from which *T. canadensis* became relatively abundant in the early Holocene (~7500 yr BP) to the present. Pollen percentage data were analyzed, and only tree taxa that reached ≥5% of the pollen sum were included. The data were square-root transformed prior to analysis.

RESULTS

Chronologies

Radiocarbon age determinations are listed in Table 2. A cubic polynomial was used to construct the age–depth model for Graham Lake, based on six calibrated radiocarbon age determinations and assuming modern sediments at the top of the core sequence (Fig. 2). High levels of *Ambrosia* pollen were recorded in the uppermost sediment samples (Fig. 3), indicating forest clearance associated with European agriculture, which started ~200 yr BP. Linear interpolation was used to describe the age–depth relationship at High Lake, based

on seven calibrated radiocarbon age determinations and making no assumptions for the age of the top of the sequence. The proposed age–depth models suggest that sediment has been accumulating at relatively constant rates throughout the postglacial period in both lake basins (Fig. 2). Methods and rationale for constructing age–depth models are discussed in Fuller (1997).

Vegetation history

Pollen percentage data for the main taxa are presented (Figs. 3 and 4) to show vegetation dynamics before, during, and after the hemlock decline at Graham Lake and High Lake, respectively, covering the period 8000 yr BP to the present. Pollen influx data for Graham Lake and High Lake are shown in Fig. 5. The high level-to-level variation in the data reflects the relatively high temporal resolution and suggests that sediment mixing has not resulted in significant smoothing of the data. Charcoal was recorded at extremely low levels in the sediments at both sites. Full Holocene records of vegetation change for each site are described elsewhere
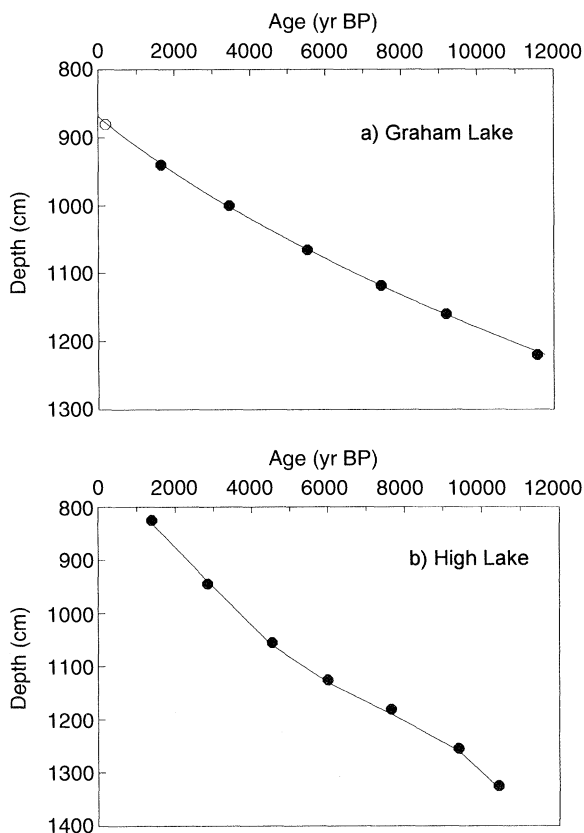

FIG. 2. Age–depth models (based on calibrated radiocarbon age determinations) proposed for the sedimentary sequences from (a) Graham Lake and (b) High Lake (Fuller 1997). Age ranges are provided in Table 2. At Graham Lake, open symbol represents the timing of the increase of *Ambrosia* pollen, which indicates European forest clearance ~200 yr BP. This date was not used to generate the age–depth model.
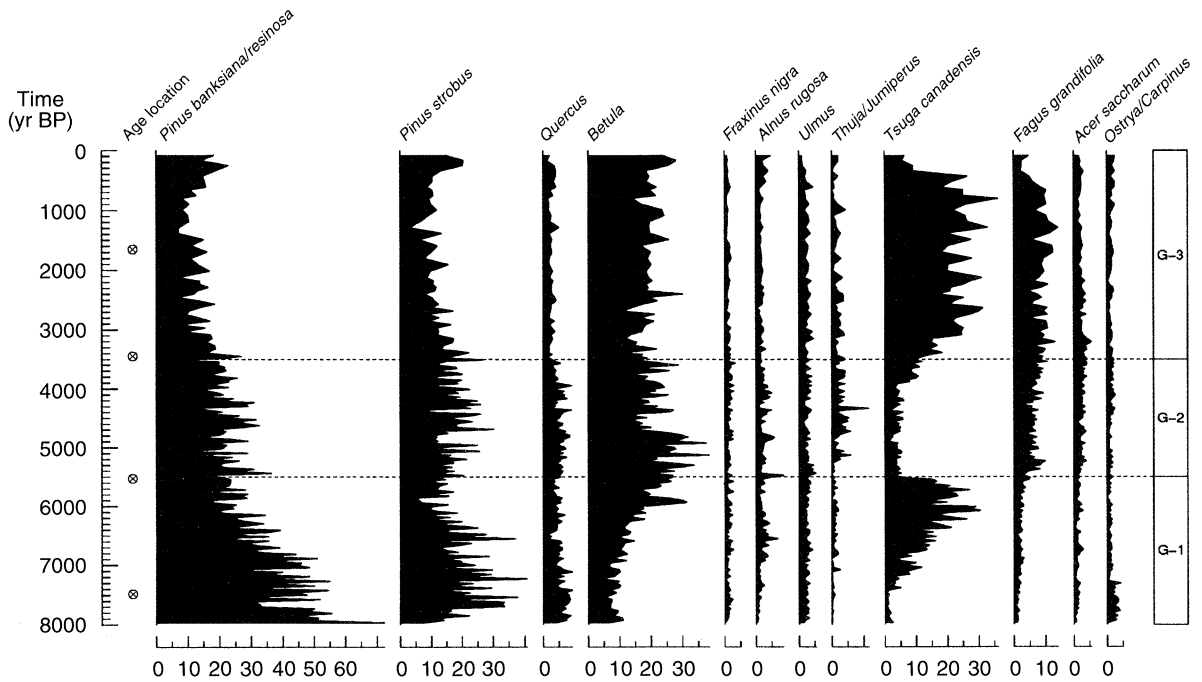
FIG. 3. Pollen percentage data for the main taxa at Graham Lake for 8000 yr BP to the present. The vertical axis shows calibrated radiocarbon years. The data were zoned numerically, and three pollen assemblage zones were identified (denoted by dashed lines). The location of the radiocarbon ages are shown on the left-hand side, next to the time scale.
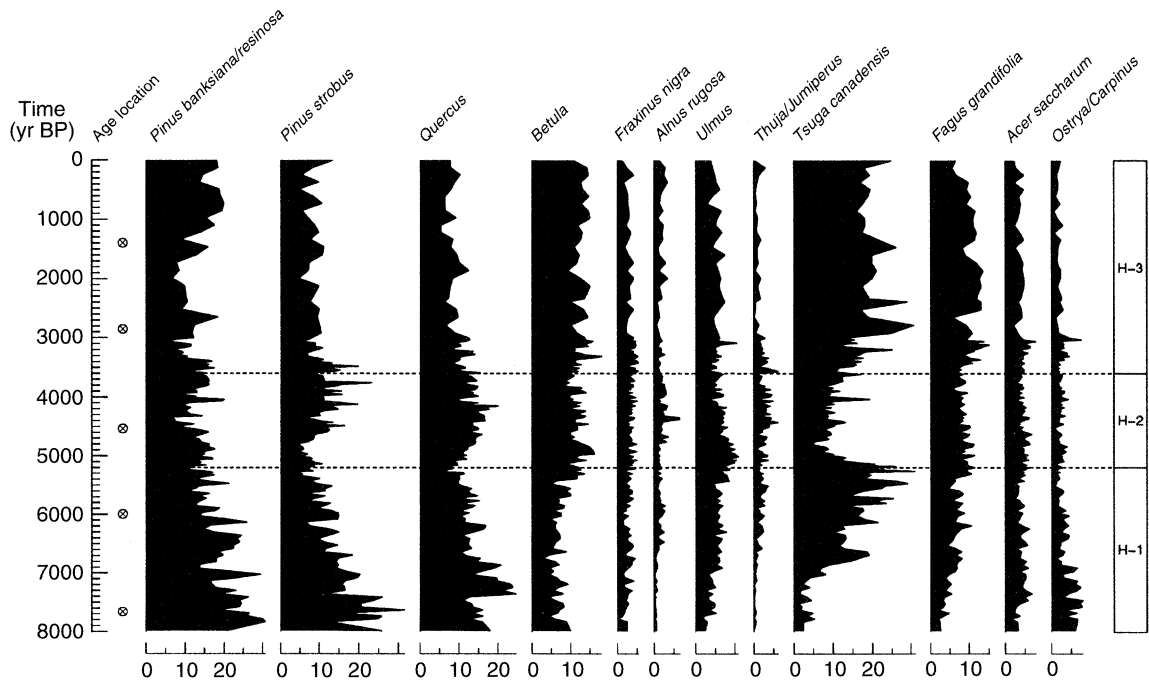

FIG. 4. Pollen percentage data for the main taxa at High Lake for 8000 yr BP to the present. The vertical axis shows calibrated radiocarbon years. The data were zoned numerically, and three pollen assemblage zones were identified (denoted by dashed lines). The location of the radiocarbon ages are shown on the left-hand side, next to the time scale.
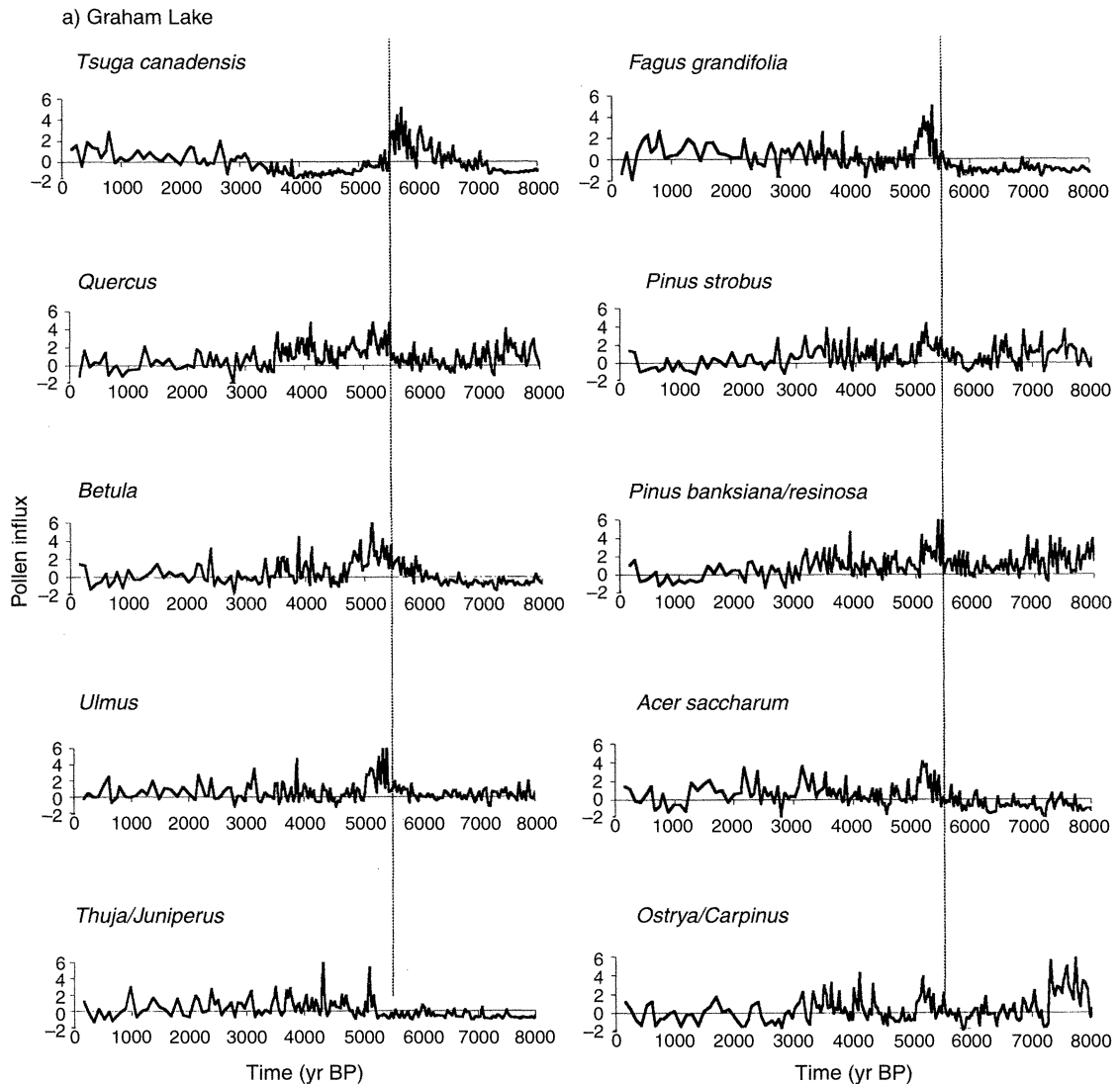
a) Graham Lake

FIG. 5.   Pollen influx data for selected taxa from (a) Graham Lake and (b) High Lake, plotted against calibrated radiocarbon years BP. A dashed line indicates the zone boundary at the hemlock decline. Pollen influx values were transformed into standardized deviates (by subtracting the mean for the sequence and dividing by the standard deviation for each pollen taxon), to determine significant shifts from mean values after the decline.

(Fuller 1997). Three pollen assemblage zones are proposed for the Graham Lake and High Lake records, covering the past 8000 yr. The main features of the pollen records are discussed below in relation to the zonation scheme.

Graham Lake; G-1.—The pollen record from Graham Lake indicates *Tsuga canadensis* first increased in abundance at ~7500 yr BP to become one of the forest dominants, forming mixed forest along with *P. strobus, Betula,* and *Quercus. A. saccharum* and *F. grandifolia* were present at low abundances. *Fraxinus nigra, Ulmus,* and *Alnus rugosa* probably occurred in wet areas. As *T. canadensis* became abundant, pollen influx values of other tree taxa, including *P. strobus, Quercus,* and *P. banksiana/resinosa,* started to decline. Pollen

influx values of *T. canadensis* decreased briefly at ~6000 yr BP, but recovered again (Fig. 5). Pollen influx values of several other forest taxa started to increase at this time.

G-2.—Pollen influx values (Fig. 5) and percentages of *T. canadensis* (Fig. 3) declined sharply (from >20% to <5% of the pollen sum) for a second time at 5500 yr BP (~4700 ^{14}C yr BP), after which they did not recover to reach former levels for nearly 2000 yr. Pollen influx values and percentages of several forest taxa increased further at this time, including *F. grandifolia, P. strobus, A. saccharum, Betula, Thuja/Juniperus, P. banksiana/resinosa, Ulmus,* and *Quercus.*

G-3.—By ~3500 yr BP, pollen percentages of *T. canadensis* had increased again to reach predecline val-

b) High Lake

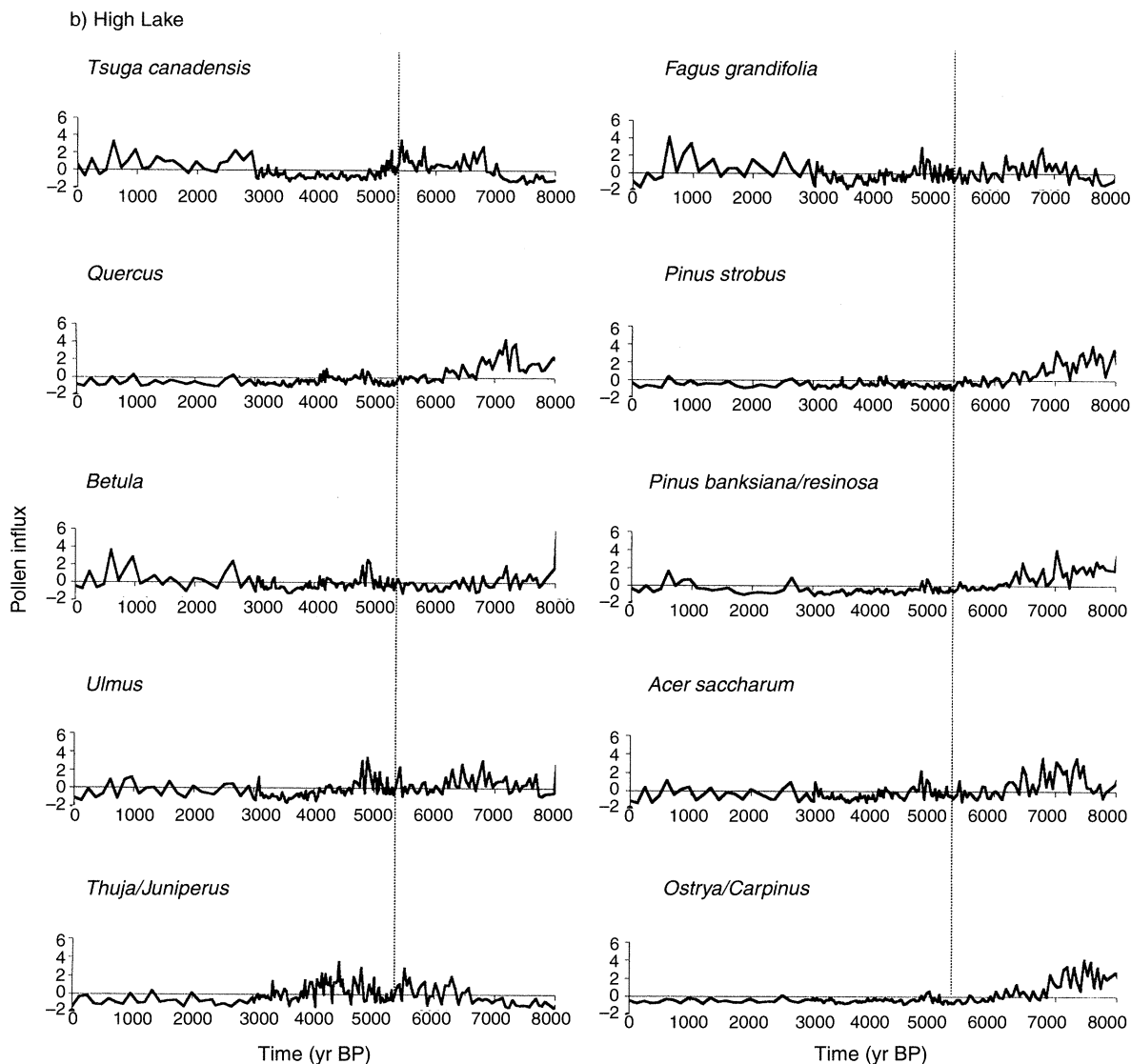FIG. 5. Continued.

ues. As *T. canadensis* populations re-expanded there was a gradual decrease in pollen influx values of *P. strobus, P. banksiana/resinosa,* and *Quercus,* whereas *F. grandifolia* and *A. saccharum* did not decrease. Pollen percentages of *T. canadensis* increased to predecline levels, whereas pollen influx for this taxon was lower than prior to the decline.

High Lake; H-1.—*T. canadensis* increased in abundance (pollen influx and percentages) at High Lake at ~7000 yr BP to form mixed forest with *A. saccharum, F. grandifolia, P. strobus, P. banksiana/resinosa,* and *Betula.* As *T. canadensis* pollen percentages increased, there was a decrease in pollen percentages and influx values of *P. strobus, P. banksiana/resinosa, Quercus,* and *A. saccharum. Ulmus, F. nigra, A. rugosa,* and *Thuja/Juniperus* were also present, probably occurring in the wet-

ter areas. Pollen percentages and influx values of *T. canadensis* started to decline toward the end of this zone.

H-2.—*T. canadensis* pollen influx values and percentages declined (from >20% to ~10% of pollen sum) at ~5100 yr BP, ~400 yr later than at Graham Lake. As at Graham Lake, pollen percentages declined, increased briefly, and declined again. The decline (in terms of pollen percentages) was less marked than that at Graham Lake (where pollen percentages fell from 20% to < 5%). Pollen influx values of *Ulmus, F. grandifolia, A. saccharum,* and *Betula* increased somewhat.

H-3.—*T. canadensis* increased in abundance again to reach former pollen percentages after 3600 yr BP. Pollen percentages of *F. grandifolia* and *Betula* also increased, while those of *Quercus* and *Thuja/Juniperus* declined.
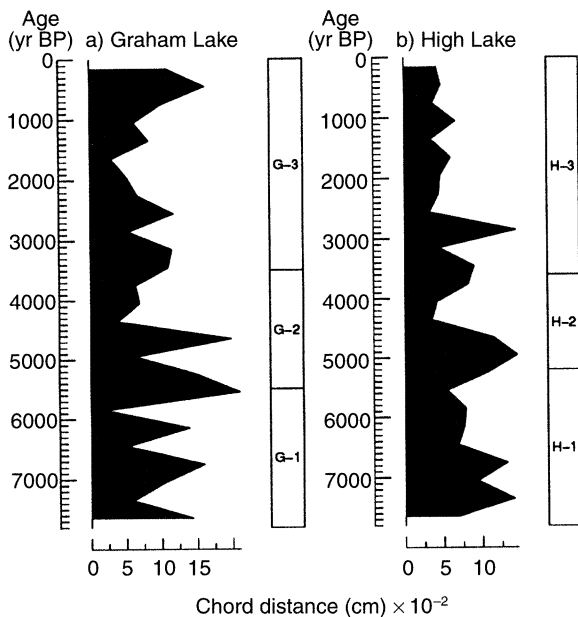
FIG. 6. Rates of palynological change for (a) Graham Lake and (b) High Lake. The dissimilarity measure used was chord distances. The pollen assemblage zone boundaries for each site are also indicated.The vertical axes show calibrated radiocarbon years.

Response to the hemlock decline

Graham Lake.—Rates of change increased at the time of the hemlock decline at Graham Lake as other forest taxa increased in abundance (Fig. 6). Most taxa appear to have started to increase after the initial decline of hemlock at ~6000 yr BP (Fig. 5), and they continued to increase once hemlock populations declined further after 5500 yr BP. Pollen influx values for several taxa increased exponentially after the decline (Fig. 7, Table 3). The increase of *F. grandifolia, P. strobus, Quercus, Betula,* and *A. saccharum* were described relatively well by the exponential equation. Pollen influx values of some tree taxa, such as *F. nigra* and *Ostrya/Carpinus,* did not increase after the hemlock decline. *P. banksiana/resinosa* pollen influx values were highly variable with some short-lived increases.

The ordination plot in Fig. 8a shows the pattern of vegetation change at Graham Lake over the period of the hemlock decline. The samples (individual pollen levels reflecting vegetation composition around the site at certain time intervals) fall into three clusters (as delineated by numerical zonation) that represent three phases of the decline: before (7500–5500 yr BP), during (5500–3500 yr BP), and after (3500–1000 yr BP). Forest composition changed markedly during the period of the hemlock decline, represented by the distinct cluster of samples in ordination space during this period (Fig. 8a). However, when *T. canadensis* populations recovered and increased to former levels of abun-

dance, after ~2000 yr, pollen assemblages did not return to the pre-decline composition; *F. grandifolia* and *A. saccharum* pollen influx values were higher, suggesting they were more abundant on the landscape, and *Pinus* and *Quercus* species appear to have become less abundant than prior to the decline. The samples covering this time period also fall into a distinct cluster (Fig. 8a).

High Lake.—Rates of change increased after the hemlock decline at High Lake, but the values were lower than those estimated for Graham Lake. Pollen percentages and influx values of *T. canadensis* did not decline as markedly at High Lake. *Ulmus* appears to have been the main pollen taxon that increased exponentially after the decline. The increase of other forest taxa was not highly significant and/or explained well by the exponential equation. *Ulmus, Betula, F. grandifolia,* and *A. saccharum* were the main tree taxa to increase.

PCA shows the pattern of vegetation change during the hemlock decline at this site (Fig. 8b). There was a shift in forest composition after the decline of hemlock; however, unlike the pattern observed at Graham Lake, once *T. canadensis* populations recovered, the pollen assemblage was not markedly different from that present prior to the decline. There is considerable overlap between the pre- and postdecline samples.

DISCUSSION

Nature of the hemlock decline

Paleoecological data from numerous sites in northeastern North America record the rapid decline of *Tsuga canadensis* in the mid-Holocene (Davis 1981, Webb 1982, Ritchie 1987). At Graham Lake there appears to have been a double decline in the abundance of *T. canadensis* during the mid-Holocene. Pollen influx values dropped sharply ~6000 yr BP, recovered briefly, and then declined further at 5500 yr BP (Fig. 5). *T. canadensis* remained at low levels for ~1500 yr before recovering to reach former abundances. The apparent double hemlock decline recorded at Graham Lake may reflect an initial outbreak of a pathogen, followed by recovery, and then a further wave of infestation, which wiped out the already weakened population. Bhiry and Filion (1996) found in situ hemlock macrofossils and insect remains in a paludified dunefield in Québec. Their evidence suggests that two defoliation events occurred during the mid-Holocene hemlock decline at the site in Québec, which may also have been the case at other sites, including Graham Lake, depending on the pathogen dynamics and resistance of the hemlock populations.

At High Lake, pollen data suggest that *T. canadensis* populations declined in the mid-Holocene, although perhaps not as dramatically as recorded at Graham Lake (Fig. 5) or other sites in the region (McAndrews 1981, Ritchie 1987). Heterogeneous dispersal, distribution,
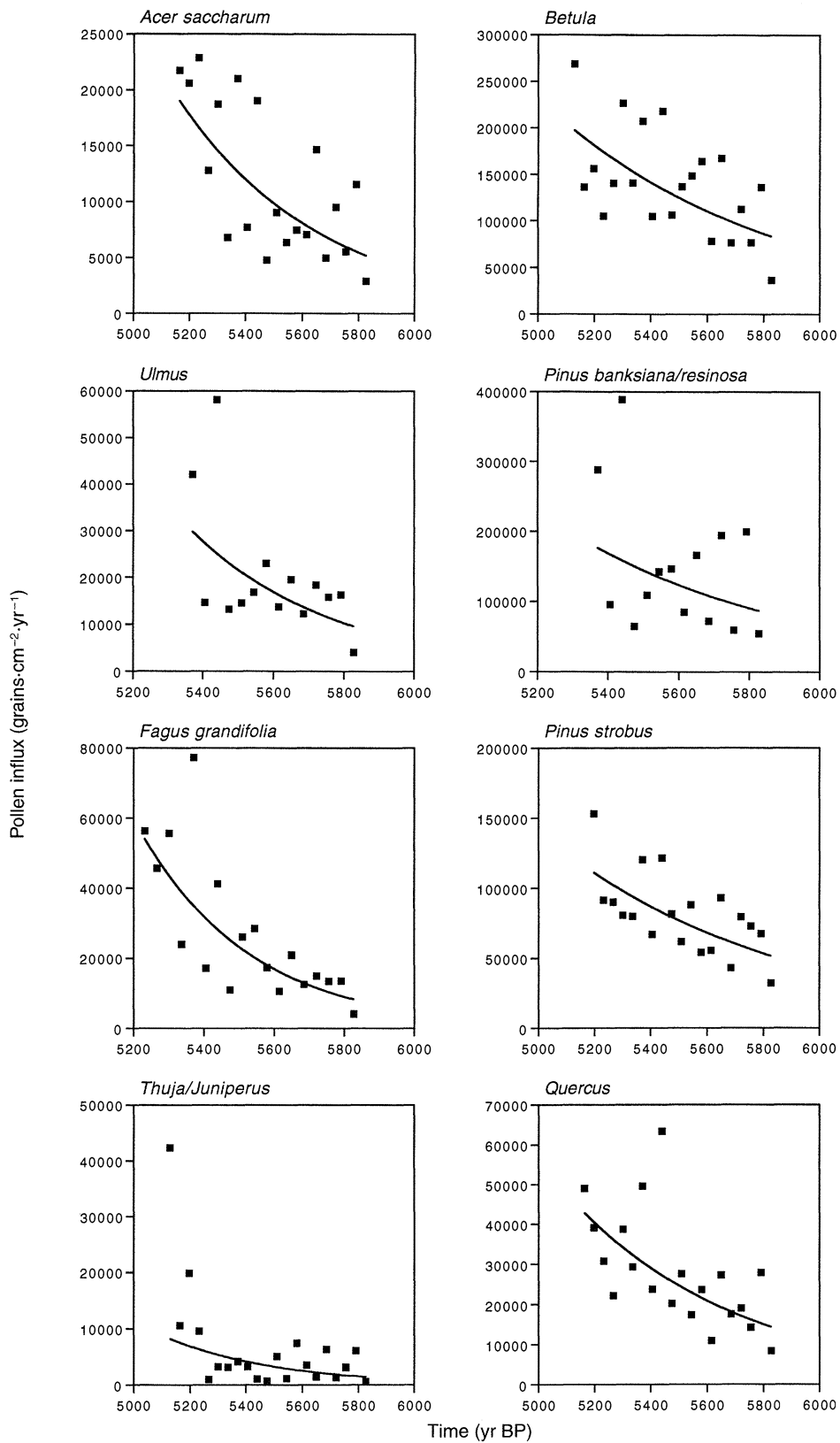
FIG. 7.   Exponential increase of pollen influx values of several tree taxa after the hemlock decline at Graham Lake plotted against calibrated radiocarbon years.

TABLE 3. Results of fitting exponential equation to pollen accumulation rate data following the hemlock decline at Graham Lake and High Lake, where r is the rate of increase and r^2 is the coefficient of determination.

Location and taxon	Rate of increase			
	r	SE	r^2	P
Graham Lake				
Quercus	0.002	<0.001	0.45	0.001
Betula	0.001	<0.001	0.35	0.005
Ulmus	0.002	0.001	0.36	0.023
Thuja/Juniperus	0.003	0.001	0.24	0.024
Pinus strobus	0.001	<0.001	0.43	0.002
Pinus banksiana/resinosa	0.002	0.001	0.14	0.182
Acer saccharum	0.002	0.001	0.45	0.001
Fagus grandifolia	0.003	0.001	0.64	0.000
High Lake				
Quercus	0.002	<0.001	0.40	0.002
Betula	0.002	0.001	0.28	0.017
Ulmus	0.002	0.001	0.44	0.001
Thuja/Juniperus	0.001	0.001	0.14	0.075
Pinus strobus	0.001	<0.001	0.25	0.005
Pinus banksiana/resinosa	0.001	<0.001	0.25	0.019
Acer saccharum	0.001	0.001	0.20	0.040
Fagus grandifolia	0.001	0.001	0.11	0.126

and impact of the pathogen that caused the decline (assuming this was the cause) may have resulted in variation with respect to mortality. There also appears to have been a double decline in *T. canadensis* pollen abundances at this site (Fig. 5).

Vegetation response to the hemlock decline

The fine temporal resolution of the pollen influx and pollen percentage data from Graham Lake and High Lake provide detailed records of vegetation change during the mid-Holocene. It is advantageous to examine both pollen influx and pollen percentage data when investigating forest dynamics, such as those during the hemlock decline, to obtain data that are not dependent on other taxa (as percentages are) and to separate out the effects of changes in sedimentation rates (which affect pollen influx values).

Rates of change increased at both sites as forest composition shifted in response to the disappearance of hemlock across the landscape (Fig. 6). Jacobson et al. (1987) describe a similar increase in rates of change at the time of the hemlock decline at Gould Pond, Maine. This increase in rates of change was greater at Graham Lake, where several tree taxa appear to have increased in abundance following the hemlock decline, including *F. grandifolia, A. saccharum, Ulmus, Quercus, Betula, P. strobus,* and *Thuja/Juniperus.* The exponential equation describes the increase of pollen influx of several of these tree taxa at Graham Lake (Fig. 7). In most cases, these taxa appear to have started to increase in abundance after the initial short-lived decline of hemlock ~6000 yr BP, and continued after the second, long-term decline of hemlock. Forest succession was probably initiated locally and across the region (Fig. 9). At High Lake, taxa such as *Ulmus, Betula,*

F. grandifolia, and *A. saccharum* increased after *T. canadensis* declined, although the magnitude of the increase in pollen influx appears to have been less than that observed at Graham Lake (with the exception of *Ulmus*) and, in general, was not well explained by the exponential equation.

Ulmus and *Quercus* pollen influx values increased exponentially after the hemlock decline at Graham Lake. Both pollen taxa cannot be identified beyond the level of genus. *Ulmus* spp. found today in southern Ontario, *U. americana* and, to a lesser extent, *U. thomassi* and *U. rubra,* have intermediate shade tolerances

■ G-1 7500–5500 yr BP
○ G-2 5500–3500 yr BP
▨ G-3 3500–0 yr BP

■ H-1 7500–5100 yr BP
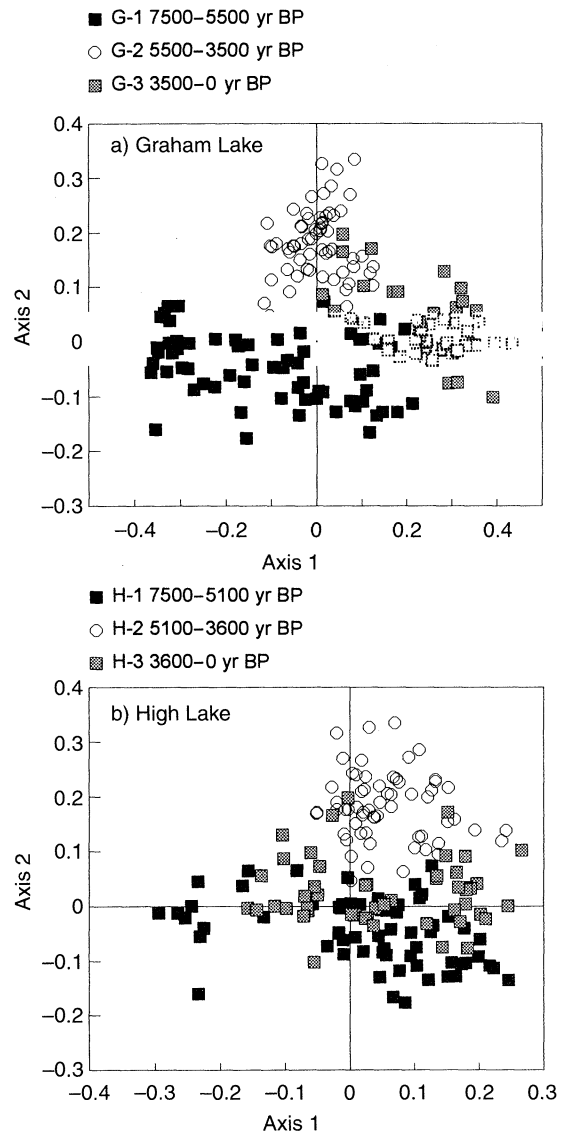○ H-2 5100–3600 yr BP
▨ H-3 3600–0 yr BP

FIG. 8. Principal components ordination plots for (a) Graham Lake and (b) High Lake. The samples have been coded according to the pollen assemblage zones identified for each sequence independently. Time periods are expressed as calibrated radiocarbon years.
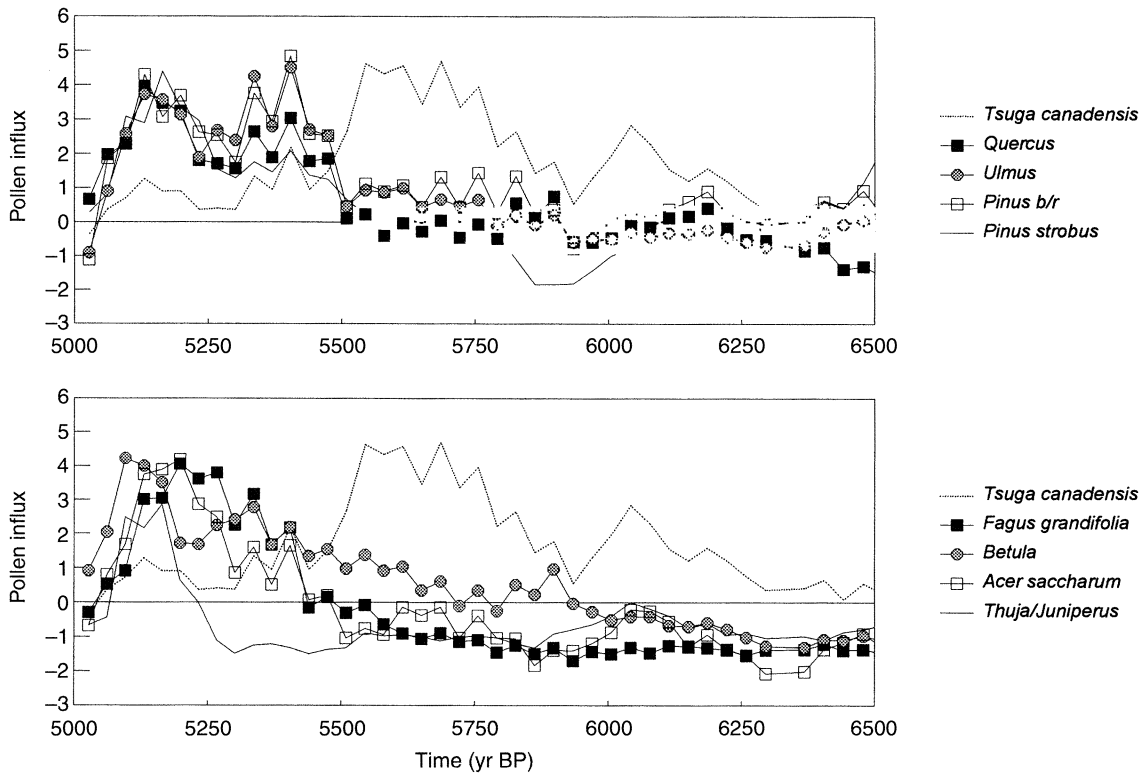
FIG. 9. Forest dynamics after the hemlock decline at Graham Lake as recorded by pollen data. The data for each taxon are plotted as normal standardized deviates in order to present them on comparable scales and plotted against calibrated radiocarbon years BP.

and occur as secondary species (Ritchie 1987). *Quercus* pollen is represented mainly by *Q. rubra, Q. alba,* and *Q. macrocarpa,* which are all classified as intermediate in shade tolerance (Johnson 1990, Rogers 1990, Sander 1990). Species of *Ulmus* and *Quercus* can reproduce vegetatively, as well as by seeds or release of advance regeneration. *Ulmus* and *Quercus* also appear to have increased exponentially at High Lake, although the magnitude of the increase of *Quercus* was low.

There was also an increase in *Pinus banksiana/resinosa* pollen influx values in parallel with *Ulmus* and *Quercus* soon after the hemlock decline at Graham Lake. *P. banksiana* and *P. resinosa* are relatively shade intolerant and do not usually persist for long in mixed forest in the absence of disturbance, especially fire (Rudolf 1990, Rudolph and Laidly 1990). The increase of *P. banksiana/resinosa* pollen influx values at Graham Lake was erratic and may reflect a change in the pollen source area after the removal of *T. canadensis* from the canopy and/or possibly recruitment of new individuals that seeded into gaps.

P. strobus pollen influx values increased exponentially after the initial decline of *T. canadensis* at Graham Lake, and remained higher but variable until *T. canadensis* populations recovered ~3500 yr BP. *P. strobus* is characterized as having intermediate shade

tolerance (Wendel and Smith 1990) but probably could not compete well with vegetative reproduction by hardwoods, such as species of *Quercus, Acer, Ulmus,* and *Fagus.* Neither *Pinus* pollen taxa increased significantly at High Lake. *Pinus* spp. were more abundant at Graham Lake than High Lake prior to the hemlock decline. The nature of the gaps produced (size, substrate exposed, surrounding vegetation, etc.) may have affected their suitability for colonization by light-demanding species.

Betula pollen represents mainly two species, *B. alleghaniensis* and *B. papyrifera,* and it is difficult to determine the extent to which each of these species was contributing to the pollen rain at that time. *Betula* was increasing before the hemlock decline, possibly reflecting the mid-Holocene expansion of *B. alleghaniensis.* Other studies from the region using macrofossil evidence (McAndrews 1981, Davis and Jacobson 1985, Anderson et al. 1986) have shown that *B. alleghaniensis* was probably the most abundant *Betula* species after 6000 ^{14}C yr BP. *Betula* appears to have increased in abundance further after the hemlock decline at Graham Lake and High Lake, although the increase in pollen influx was not described well by the exponential equation. *B. alleghaniensis* is relatively long-lived and slow growing, with intermediate shade tolerance (Erdmann 1990). It is a common gap-phase

component of northern hardwood forests, often associated with *T. canadensis, A. saccharum,* and *F. grandifolia* (Erdmann 1990). *B. alleghaniensis* is therefore likely to have responded to the demise of *T. canadensis. B. papyrifera,* on the other hand, is a highly shade-intolerant species, commonly found as an early-successional species that usually persists for only a single generation in a successional sequence (Safford et al. 1990). *B. papyrifera* seeds can germinate on bare mineral soil or fallen logs, and this species may also have played some role in the succession that took place immediately after the hemlock decline. Both *Betula* species may have contributed to the pollen rain during this time, although *B. alleghaniensis* may have been more abundant. Current stands of *T. canadensis,* which have been killed by the woolly adelgid in Connecticut, are being replaced by *B. lenta* (Orwig and Foster 1998).

Pollen influx values of *F. grandifolia* and *A. saccharum,* both long-lived, highly shade-tolerant tree species, increased exponentially after the hemlock decline at Graham Lake. *F. grandifolia* had the fastest rate of increase ($r = 0.003$; Table 3) of all the taxa examined. Bennett (1988) found similar rates of increase for *F. grandifolia* at a site in southern Ontario, located near Graham Lake. As *F. grandifolia* and *A. saccharum* pollen influx values increased exponentially, those of *Quercus* and *Ulmus* declined somewhat. *A. saccharum* and *F. grandifolia* produce seedlings that can tolerate shade for some time (Godman et al. 1990, Tubbs and Houston 1990). *A. saccharum* can produce abundant seed crops, and its seedlings can respond quickly to a light gap (Godman et al 1990). *F. grandifolia,* on the other hand, is not prolific in its production of seedlings and does not respond as rapidly to light (Tubbs and Houston 1990), but seedlings of *F. grandifolia* can generally persist in the understory longer (Godman et al. 1990, Tubbs and Houston 1990). These taxa probably increased in abundance after the hemlock decline through advance regeneration in the understory, as well as vegetative reproduction. *A. saccharum* and *F. grandifolia* also increased somewhat at High Lake, although the increase was not described well by the exponential equation.

Thuja/Juniperus appears to have increased in abundance after the initial increase by other forest taxa at Graham Lake, possibly replacing *T. canadensis* in the wetter locations. *Thuja occidentalis* is underrepresented in the pollen record, and as it is shade tolerant (Johnston 1990), may have become quite abundant following the hemlock decline.

Similar increases in abundance of several forest taxa have been recorded at other sites in the Northeast. Mirror Lake in New Hampshire records an increase in pollen influx of several taxa after the hemlock decline: *Betula* appears to have been one of the first pollen taxa to increase, followed by *F. grandifolia, A. saccharum,* and *Ostrya/Carpinus* (Davis 1978, 1981). Sediments from Nutt Lake, Ontario record a small increase in

pollen influx of *F. grandifolia* and *A. saccharum* after the decline (Bennett 1987), whereas pollen percentages of *Betula, Quercus,* and *Larix laricina* increased at Found Lake, Ontario (McAndrews 1981). As Davis (1978) suggests, the patterns of forest dynamics after the decline vary regionally. This is probably a reflection of differences in environmental conditions, species composition, and/or variation in the nature of the decline. The taxa that most commonly appear to have increased after the hemlock decline include *Betula, F. grandifolia, Acer,* and *Quercus* (Davis 1978, 1981, McAndrews 1981, Mott and Farley-Gill 1981, Bennett 1987).

Pollen data thus indicate that the hemlock decline triggered an increase in abundances of several other forest taxa. The sharp increase in pollen influx of several tree taxa at Graham Lake, however, appears to have been short-lived. Before *T. canadensis* populations recovered, pollen influx values of most the taxa that had previously increased at Graham Lake, declined again (Figs. 5 and 9). The decline was not synchronous for all taxa, and there is no evidence from the age–depth model for a marked increase in sediment accumulation rates at this time that might account for this trend. On the other hand, the pollen percentages of these taxa did not decrease markedly, indicating that the decrease in pollen influx may have been due to sedimentary changes. The death of numerous individuals of *T. canadensis* throughout the landscape must have provided a large number of potential sites for the establishment of other taxa. The creation of this newly available space may have been followed by a burst of regeneration and growth of other tree species. Although some species would have responded more quickly than others, a more or less even-aged stand may have developed. It seems plausible, therefore, that the decline in pollen influx values of several taxa (after their initial increase) observed at Graham Lake may have been due simply to the aging of these populations (Bormann and Likens 1979) and their subsequent thinning. Thinning is a natural phase of forest development, during which competition is intense, establishment of new seedlings is minimal, and stem density steadily decreases, as there is not sufficient space for all the offspring produced (Peet 1992). It is probable that the observed decline in pollen influx values at Graham Lake was the result of a combination of changes in sedimentation rates, competitive interactions among taxa, and thinning.

In summary, at Graham Lake several forest taxa appear to have increased in abundance following the hemlock decline, probably resulting in forest succession. By contrast, at High Lake, pollen percentages of *T. canadensis* did not reach levels as low as at Graham Lake, and there was a less dramatic response by other forest taxa. Pollen influx values of most taxa examined did not appear to increase exponentially at High Lake, unlike the situation at Graham Lake, indicating that there was less mortality of hemlock.

Recovery of hemlock populations

At both Graham Lake and High Lake, *T. canadensis* remained at lower abundances for ~1500 yr before increasing to reach former abundances. A similar pattern is seen at other sites in southern Ontario (Mott and Farley-Gill 1978, Liu 1981, McAndrews 1981, Bennett 1987, Ritchie 1987). Why did *T. canadensis* take such a long time to recover? It seems unlikely that the populations of the pathogen remained at high levels after *T. canadensis* stands had been killed throughout its mid-Holocene range, although pathogens may have maintained *T. canadensis* populations at low levels for some time. Principal Components Analysis indicates that forest composition around Graham Lake, after *T. canadensis* populations recovered and re-expanded on the landscape, was different from that prior to the hemlock decline. *F. grandifolia* and *A. saccharum* were more abundant, whereas *P. strobus, P. banksiana/resinosa,* and *Quercus* were less common. This difference may be due in part to a shift in the climatic regime, associated with long-term changes suggested to have occurred during the Holocene. Several studies indicate that climate in northeastern North America has become cooler and moister in the latter part of the Holocene (Davis et al. 1980, Kutzbach 1987, Jackson 1989, Spear et al. 1994). However, after it had declined, *T. canadensis* reinvaded a forest type different from that which it invaded in the early postglacial period. *T. canadensis* populations re-expanded within a closed-canopy forest with high abundances of shade-tolerant species, such as *F. grandifolia* and *A. saccharum.* In addition, life history constraints would have affected rates of population expansion. *T. canadensis* is a slow-growing tree that does not reach reproductive maturity until at least 40 yr of age and has specific requirements for germination (Godman and Lancaster 1990).

By contrast, at High Lake, *T. canadensis* does not appear to have declined dramatically, and forest composition in the late Holocene was not markedly different from that prior to the hemlock decline. This suggests that where *T. canadensis* declined significantly, there was a long-term impact of the decline on forest composition. Whereas at High Lake, although climate and environmental conditions may have changed during the mid- to late Holocene, forest composition did not appear to change as markedly as it did at Graham Lake. Comparable data from other sites are required to explore the possible long-term effects of the hemlock decline on forest composition.

CONCLUSIONS

Several forest taxa appear to have increased in abundance following the hemlock decline, suggesting the importance of competition in controlling forest composition. Assuming that forest composition changed in response to the decline across a wide region, the disappearance of *Tsuga canadensis* on the landscape may

have had a profound impact on forest composition, structure, and function. The hemlock decline undoubtedly had implications for ecosystem properties; hemlock, as a long-lived conifer, which has a strong influence on microclimate, forest floor conditions, and soil chemistry (Benzinger 1994), was replaced to a large extent by hardwoods, including *Quercus, Ulmus, Fagus grandifolia, Acer saccharum,* and *Betula.*

The response to the decline probably depended on the species pool present, landscape patterns of *T. canadensis* abundance, and the extent of damage. A comparison of two sites in Ontario, which varied in the extent of the hemlock decline, suggests that, where *T. canadensis* declined markedly, there was a long-term impact on forest composition. This indicates that catastrophic pathogenic outbreaks can be a rare but important factor influencing forest dynamics. Peglar (1993) has shown in a similar study that the mid-Holocene elm decline in Europe was probably caused by a combination of disease and human activity. *T. canadensis* did not recover for 1000–2000 yr after the decline. This slow recovery may have been controlled by pathogen dynamics, in addition to relatively slow growth rates of *T. canadensis,* narrow requirements for regeneration (Godman and Lancaster 1990), and competition from other highly shade-tolerant and long-lived taxa such as *F. grandifolia* and *A. saccharum.* Forest composition may not have been in equilibrium with climate for 1000–2000 yr due to this nonclimatic disturbance event.

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