

Holocene forest dynamics in southern Ontario, Canada: fine-resolution pollen data

Janice L. Fuller

Abstract: Holocene fossil pollen data of fine temporal and spatial resolution were obtained from two small, closed lake basins in southern Ontario, Canada. Forest development is recorded in the pollen sequences, which document the invasion and expansion of tree populations during the early Holocene. Subsequent forest dynamics are discussed in terms of the main factors driving vegetation change, including climate, soil development, migration, disturbance regime (abiotic and biotic), and competition, which operate on a species pool with a variety of biological and ecological characteristics. The relative importance of these factors, influencing forest dynamics during the Holocene, appears to have varied over time.

Key words: Fine resolution pollen data, forest dynamics, southern Ontario, Holocene.

Résumé : L'auteur a obtenu des données sur les pollens fossiles de l'holocène avec fine résolution temporelle et spatiale, à partir de deux petits bassins lacustres fermés du sud de l'Ontario, au Canada. Le développement forestier est enregistré dans les séquences polliniques qui retraçent l'invasion et l'expansion des populations d'arbres au début de l'holocène. L'auteur discute la dynamique des forêts subséquentes en termes de facteurs principaux responsables des changements de la végétation, incluant le climat, le développement des sols, la migration, les régimes de perturbation (abiotiques et biotiques) et la compétition, qui agissent sur un ensemble d'espèces avec une variété de caractéristiques biologiques et écologiques. L'importance relative de ces facteurs, influençant la dynamique forestière au cours de l'holocène, semble avoir varié dans le temps.

Mots clés : données polliniques à fine résolution, dynamique forestière, sud de l'Ontario, holocène.
[Traduit par la rédaction]

Introduction

Holocene forest development in the glaciated portion of eastern North America was characterized by a series of invasions of tree taxa, which spread from their full-glacial refugia and re-vegetated this region at the end of the Wisconsin glacial period (Davis 1983; Bennett 1993; Ritchie 1987). Climate was the main factor driving regional vegetation development (Webb 1988), but other factors, which operate on different spatial and temporal scales, may also have been important, including soil development, migration, disturbance regime (wind, fire, disease, people), and biotic interactions (such as competition, herbivory), as well as the biological characteristics of the flora (including seed production, dispersal ability, rate of growth, population dynamics, shade tolerance) (Davis 1981; Davis et al. 1986; Pennington 1986; Bennett 1987, 1993; McAndrews 1988; Clark and Royall 1996; Willis et al. 1997). In this paper I present fine-resolution fossil pollen data from two sites in southern Ontario, Canada, and discuss Holocene forest dynamics in relation to the factors that drive vegetation change and their relative importance.

An understanding of vegetation responses to internal and external driving factors is critical for predicting the impact

of global environmental change, as well as developing a basic understanding of landscape ecology. The paleoecological record provides an extensive data base with which to examine vegetation–climate–environment interactions over time. In addition, a long-term perspective is essential to obtain an understanding of forest ecology (because of the long generation time of most tree species) and processes that occur over long time scales (e.g., succession and tree population dynamics) (Green and Dolman 1988). The coarse temporal and spatial scales represented by many fossil pollen records preclude ecological interpretations of Holocene vegetation dynamics, and instead, broader biogeographic and paleoclimatic questions are addressed. Pollen data of fine temporal resolution allows rates and timing of vegetation change to be determined on ecological time scales, bridging the gap in time scale between paleoecological and ecological studies (Green and Dolman 1988).

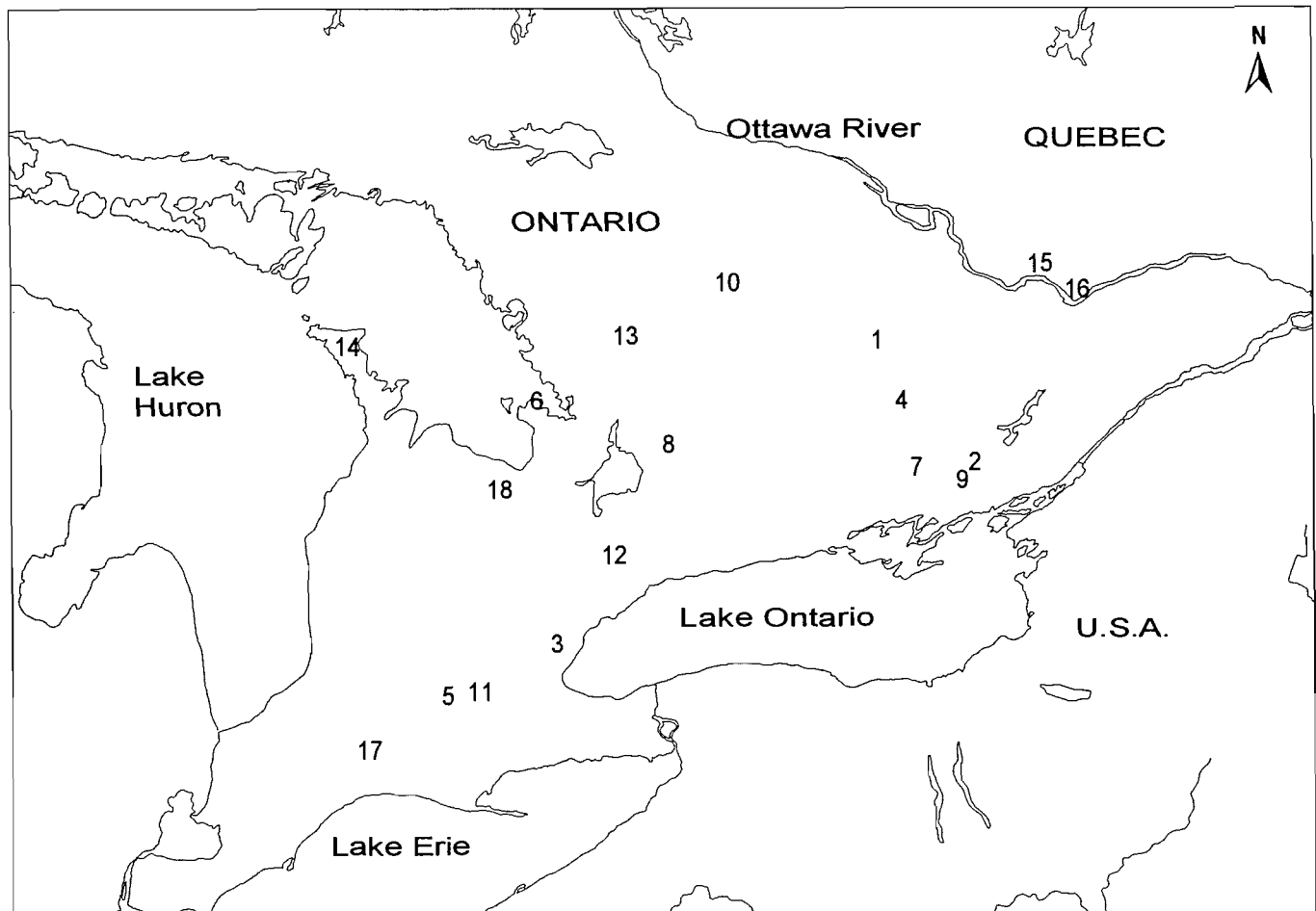
There have been several paleoecological studies of Holocene vegetation history in southern Ontario (reviewed by Liu 1981; McAndrews 1981; Ritchie 1987) that provide much information about forest dynamics in this region. Few studies, however, have utilized pollen accumulation rate (PAR) data (Cwynar 1978; Mott and Farley-Gill 1978, 1981; Terasmae 1980; Bennett 1987; Szeicz and MacDonald 1991), and fewer still have high temporal resolution (exceptions include Cwynar 1978; Boyko-Diakonow 1979). The present study aims to extend our knowledge about Holocene vegetation history in this region and to address the question: what were the main factors driving Holocene forest dynamics in southern Ontario?

Received January 4, 1997.

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Fig. 1. Map of southern Ontario, Canada showing the location of the two study sites: site 1, Graham Lake and site 2, High Lake. Sites from other studies mentioned in the text are also shown: site 3, McAndrews (1988); site 4, McAndrews and Campbell (1993) and J.H. McAndrews, unpublished data; site 5, Mott and Farley-Gill (1978); site 6, Burden et al. (1986); site 7, Fritz et al. (1981); sites 8 and 9, Terasmae (1969); sites 10, 17, and 18, McAndrews (1981); sites 11 and 13, Bennett (1987); site 12, McAndrews (1973); site 14, J.H. McAndrews, unpublished; sites 15 and 16, Mott and Farley-Gill (1981).



- | | |
|----------------------|-----------------------|
| 1. Graham Lake | 10. Found Lake |
| 2. High Lake | 11. Hams Lake |
| 3. Crawford Lake | 12. Van Nostrand Lake |
| 4. Tonawa Lake | 13. Nutt Lake |
| 5. Maplehurst Lake | 14. Shouldice Lake |
| 6. Second Lake | 15. Ramsay Lake |
| 7. Inglesby Lake | 16. Pink Lake |
| 8. Victoria Road Bog | 17. Pond Mills Pond |
| 9. Harrowsmith Bog | 18. Edward Lake |

Study area

The study area (Fig. 1) is located on the Precambrian Shield in southern Ontario, a landscape covered with shallow, late-Quaternary glacial deposits (Chapman and Putnam 1984). Soils are commonly inceptisols and spodosols in the uplands; gleysols and peats in areas with poor drainage. The forests of southern Ontario are mainly classified within the Great Lakes – St. Lawrence Forest Region, a mixed forest composed of a mosaic of conifer-dominated bogs and swamps, pine plains, and upland hardwoods (Halliday 1937; Braun 1950; Rowe 1977). The two study sites (Graham Lake and High Lake), occur within a subdivision of this forest region, the Middle Ottawa Forest Section (Rowe 1977). Important tree species include *Tsuga canadensis* (L.) Carr., *Fagus grandifolia* Ehrh., *Betula*

alleghaniensis Britt., *Acer rubrum* L., *Acer saccharum* Marsh., *Pinus strobus* L., and *Pinus resinosa* Ait., with varying amounts of *Picea glauca* (Moench) Voss, *Abies balsamea* Mill., *Betula papyrifera* Marsh., *Quercus rubra* L., and *Tilia americana* L. plus other less frequent taxa (Rowe 1977). *Thuja occidentalis* L., *Picea mariana* (Mill.) B.S.P., *Fraxinus nigra* Marsh., and *Ulmus americana* L. are locally abundant in wetlands.

Little is known about the impact, if any, of aboriginal populations on vegetation composition and structure, although it has been suggested that fire, associated with an aboriginal settlement around Crawford Lake in southern Ontario, resulted in a subtle shift in forest composition (Clark and Royall 1995). These changes have also been attributed to climate change (Campbell and McAndrews 1993). Burden et al. (1986) suggest that people of the Huron Indian

culture were present at a site in southern Ontario for most of the Holocene but had little impact on the environment until AD 1450 when they cleared land for agriculture. Release of Crown land for European settlement began in the early 1700s (Gentilcore 1969). The presence of *Ambrosia* pollen in Holocene deposits is an indicator land clearance favouring the increase of herbaceous weeds (Bassett and Terasmae 1962).

Materials and methods

Paleoecological methods

Site selection and description

The selection of study site determines the spatial and temporal detail that can be resolved in paleoecological studies (Jacobson and Bradshaw 1981). To obtain records of local vegetation change on ecological time scales (decades rather than centuries), the lake basins investigated were selected to have a mainly local pollen source area and contain sediments that have undergone minimal disturbance that might blur the temporal resolution. Graham Lake and High Lake (Fig. 1) are, therefore, both small (<2.5 ha area), closed lakes within bedrock basins.

Graham Lake (45°11'N, 77°21'W) is situated within the Algonquin Highlands on the Precambrian Shield (at 381 m a.s.l.), 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 with rock outcrops (<30%) and muck or peat (Gillespie et al. 1963). The rocky slopes on the western shore of Graham Lake are vegetated mostly by *Acer rubrum* with some *Acer saccharum*, *Fagus grandifolia*, *Quercus rubra*, *Tilia americana*, *Betula papyrifera*, and *Tsuga canadensis*. *Picea glauca*, *Abies balsamea*, *Thuja occidentalis*, and *Pinus strobus* are more abundant near the shore. The slopes on the eastern side are dominated by *Pinus strobus* with *Picea glauca* abundant adjacent to the lake edge.

High Lake (44°31'N, 76°36'W) is also located in the Algonquin Highlands at the southern boundary of the Precambrian Shield (at 192 m a.s.l.). 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 *Pinus strobus* on the rocky border of the lake, with some *Picea glauca*, *Tsuga canadensis*, and *Abies balsamea*. *Acer rubrum*, *Acer saccharum*, *Quercus rubra*, *Fagus grandifolia*, *Ostrya virginiana* (Mill.) K. Koch, and *Betula papyrifera* can be found in the surrounding area. *Fraxinus nigra* and *Thuja occidentalis* occur in the less well-drained areas.

The sites were chosen to be comparable in size, elevation, and modern soils to minimize variation between sites for sedimentary reasons. Vascular plant nomenclature follows Gleason and Cronquist (1991).

Lake sediment extraction

Sediments were collected using a modified Livingstone piston corer (Livingstone 1955; Wright 1967) in 1-m segments from the deepest point of the lake; 5 m of sediment were obtained from Graham Lake and 8 m from High Lake. Core segments were extruded in the field; wrapped in plastic film, aluminum foil and thick plastic; and stored at 4°C. The uppermost segment of the core at Graham Lake was extracted with a plastic tube attached to the Livingstone rods (Wright 1980) and stored within the tube until excess water trapped at the top had been siphoned off or evaporated.

Sediment age determination

Six samples of bulk sediment from Graham Lake were selected for conventional radiocarbon age determinations and eight samples from High Lake. The radiocarbon age determinations were calibrated using the program CALIB version 3.0 based on the bidecadal

tree-ring data set combined with the marine coral data set (Stuiver and Reimer 1993). Individual radiocarbon ages fell within a range of calendar years including two SDs. Bennett (1994a) suggests that, to obtain a single corresponding calibrated age, the midpoint between the pair of calendar years that enclose the 95% confidence interval should be estimated. The distance between this age and either of the calendar years was taken as an estimate of the SD.

Sediment analysis

Sediment samples of 0.5 cm³ were taken at regular intervals for determination of dry weight and organic content using the methods of Bengtsson and Enell (1986). A continuous profile of volume magnetic susceptibility was measured for both sedimentary sequences using a Bartington meter with a core-scanning loop sensor (Thompson and Oldfield 1986). Magnetic susceptibility is usually proportional to the concentration of ferrimagnetic minerals in the samples, and since ferrimagnetic minerals are associated with inputs of allochthonous mineral material to the lake, this parameter serves as a useful measure of the relative importance of inorganic materials in lake sediments.

Fossil pollen and charcoal analysis

Sediment samples of 0.5 cm³ were taken at regular intervals (1–4 cm) and processed for pollen and charcoal using a modified version of method B described by Berglund and Ralsa-Jasiewiczowa (1986). A known volume of an exotic marker (calibrated *Eucalyptus* pollen suspension) was added to each sample before preparation to calculate pollen concentrations (Benninghoff 1962). One thousand terrestrial pollen grains and spores were counted per sample to minimize statistical uncertainty (Maher 1972; Faegri et al. 1989). Pollen percentages were calculated on the basis of the terrestrial pollen sum, and pollen accumulation rates (PAR) were estimated using pollen concentrations and sediment deposition time. Charcoal content was estimated using the point-count method (Clark 1982).

Numerical analysis

Zonation

To aid description of the data, the pollen records obtained were zoned numerically using an optimal splitting technique based on pollen counts of taxa recorded at ≥5% of the terrestrial pollen sum using PSIMPOLL version 2.25 (Bennett 1992, 1994b). The splits were made by minimizing information content (variation within the data) within the zones (Bennett 1996). A broken stick model, which tests whether the number of zones accounts for a greater proportion of the variance than predicted using a randomized data set, was used to determine the appropriate number of zones (Bennett 1996).

Rates of change

Rates of change analysis involves measuring the dissimilarity between adjacent pairs of samples (pollen levels) and then relating that to the temporal difference between the samples (Jacobson and Grimm 1986; Bennett and Humphry 1995). Rates of palynological change can be interpreted as a measure of rates of vegetation change (Jacobson et al. 1987). Chord distances were used to measure dissimilarity between samples (Bennett and Humphry 1995) using percent pollen data based on taxa recorded at ≥5% of the terrestrial pollen sum. The data were smoothed (three-point moving window) and interpolated to achieve equal time intervals (100 years) before estimating rates of change (E.C. Grimm, personal communication; Jacobson et al. 1987).

Results

Chronology

The radiocarbon age determinations made for Graham Lake and High Lake are internally consistent (Table 1). Calibrated

Table 1. Conventional radiocarbon age determinations and calibrated age ranges for bulk sediment samples from Graham Lake and High Lake.

| Depth (cm) | Laboratory code | Radiocarbon age (^{14}C years BP) | Calibrated age (calendar years BP) |
|--------------------|-----------------|---|------------------------------------|
| Graham Lake | | | |
| 935–945 | Q-2909 | 1 750 ± 40 | 1 645 ± 110 |
| 995–1005 | Q-2908 | 3 205 ± 45 | 3 445 ± 155 |
| 1061–1071 | Q-2907 | 4 760 ± 45 | 5 520 ± 100 |
| 1113–1123 | Q-2905 | 6 650 ± 50 | 7 475 ± 85 |
| 1155–1165 | Q-2904 | 8 260 ± 60 | 9 195 ± 195 |
| 1212–1232 | Q-2903 | 10 105 ± 85 | 11 570 ± 540 |
| High Lake | | | |
| 717–723 | SRR-4946 | 820 ± 45 | 730 ± 70* |
| 827–833 | SRR-4947 | 1 485 ± 45 | 1 395 ± 105 |
| 937–943 | SRR-4948 | 2 725 ± 45 | 2 845 ± 95 |
| 1057–1063 | SRR-4949 | 4 060 ± 45 | 4 530 ± 120 |
| 1127–1133 | SRR-4950 | 5 200 ± 50 | 5 995 ± 115 |
| 1187–1193 | SRR-4951 | 6 865 ± 50 | 7 660 ± 120 |
| 1257–1263 | SRR-4952 | 8 435 ± 50 | 9 410 ± 90 |
| 1327–1333 | SRR-4953 | 9 415 ± 50 | 10 435 ± 155 |

*Age determination rejected; see text.

age determinations were used to construct age–depth models. An age–depth model for Graham Lake was constructed using a polynomial curve with three terms, of the form (Fig. 2):

$$[1] Y = a + bx + cx^2$$

where x is depth, and y is age, $a = -3.0$, $b = 20$, and $c = 3.5 \times 10^2$.

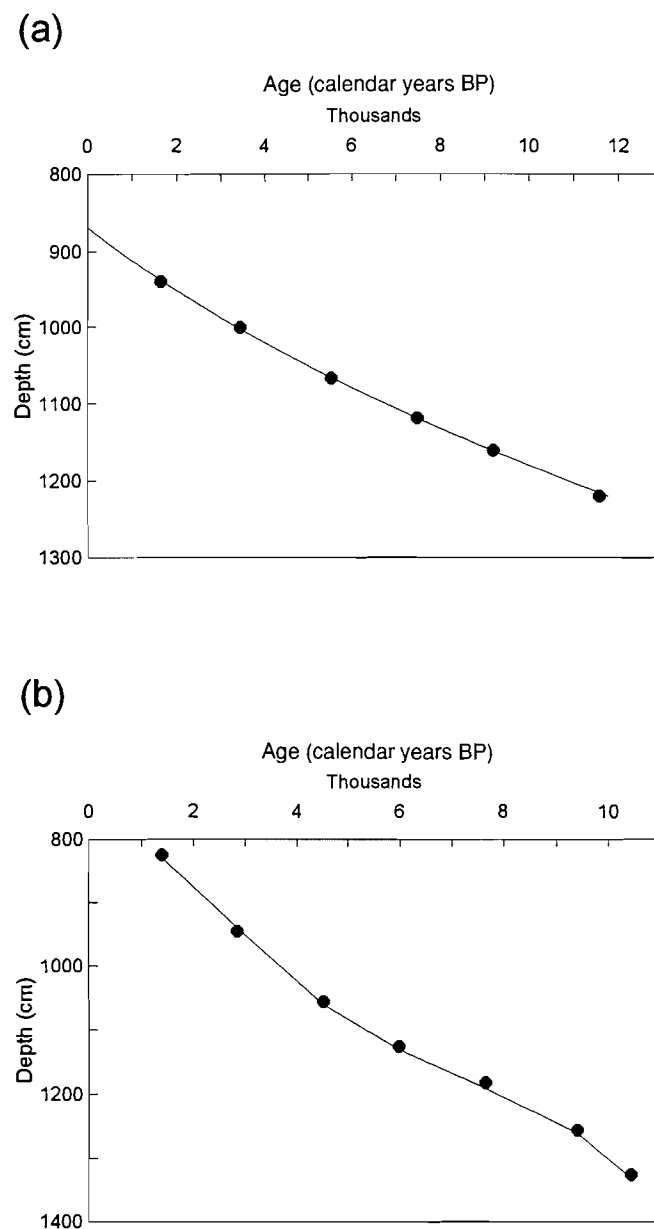
Bennett (1994a) has shown such a method is preferable to linear interpolation (when a good fit can be obtained) as changes in sediment accumulation rate are smooth and not punctuated. The chi-squared value obtained fitting the model is 0.9 and the goodness-of-fit 0.913, which suggests that the model explains the data well (Press et al. 1992; Bennett 1994a). The peak in abundance of *Ambrosia* pollen at the top of the sedimentary sequence (Fig. 3) indicates land clearance after European arrival (beginning approximately 2 centuries ago) and suggests that Graham Lake contains a complete Holocene sequence to the present day. The age of the surface of the sediment was therefore assumed to be 0 years.

In the case of High Lake, a linear interpolation age–depth model was adopted (Fig. 2). The uppermost age determination was rejected as being too old as it produced highly anomalous pollen accumulation rates (by producing estimates of a marked increase in sedimentation rate). There is no evidence from the physical properties of the sediments (magnetic susceptibility or organic content) to indicate a marked increase in sedimentation rate (in which case erosion of inorganic material into the basin might be expected). As there was no significant increase in the abundance of *Ambrosia* pollen, no assumptions were made for the age of the top of the sequence.

Fossil pollen interpretation

Picea glauca and *Picea mariana* pollen types were separated following the criteria of Hansen and Engstrom (1985). *Pinus*

Fig. 2. Age–depth models proposed for (a) Graham Lake and (b) High Lake. Depths were measured from the water surface. Stratigraphic location of dated samples and age ranges are shown in Figs. 3 and 4 and listed in Table 1.

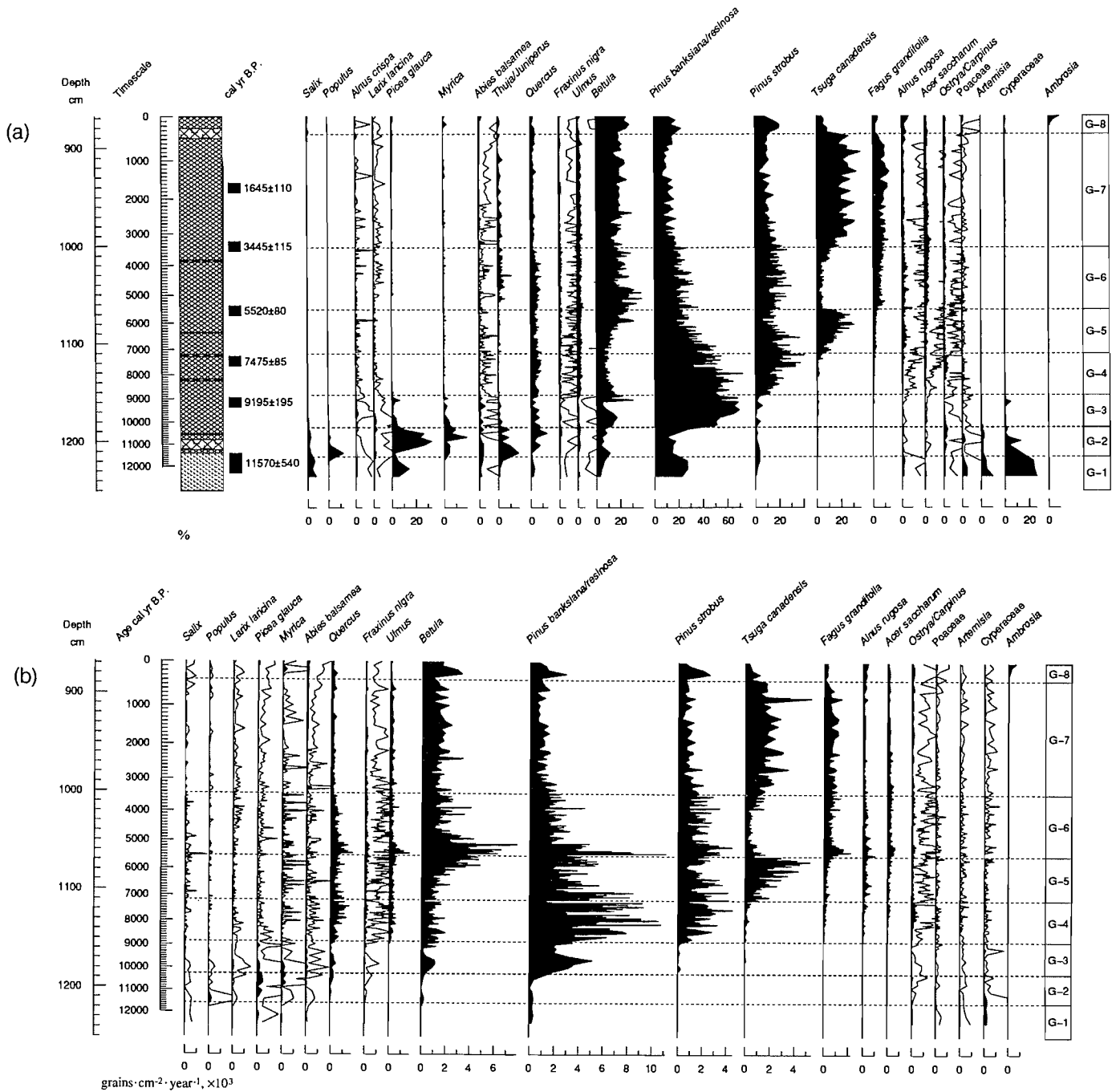


banksiana-resinosa pollen type represents *Pinus banksiana* Lamb. and (or) *Pinus resinosa*. During the early Holocene, *Pinus banksiana* was probably the more abundant of the two, although *Pinus resinosa* was also present (Anderson 1982; Schwert et al. 1985). *Betula* pollen is thought to represent mainly *Betula papyrifera* during the early Holocene and *Betula alleghaniensis* from about 6000 ^{14}C years BP onwards, as macrofossil analyses at Edward Lake (McAndrews 1981) and in northern New England indicate (Davis and Jacobson 1985; Anderson et al. 1986).

Graham Lake and High Lake fossil pollen records

Tables 2 and 3 describe the pollen records and pollen assemblage zones proposed for the Graham Lake (Figs. 3a and 3b)

Fig. 3. (a) Percentages of the most common pollen and spore taxa for Graham Lake plotted against depth. Values for taxa present at low abundances are exaggerated by $\times 10$. A time scale and location of the calibrated radiocarbon ages are plotted on the left next to the lithostratigraphic column (Troels-Smith 1955). (b) Pollen and charcoal accumulation rates for Graham Lake plotted against depth.



and High Lake (Figs. 4a and 4b) sedimentary sequences. The main features of the pollen diagrams are described in relation to the zonation scheme and lithostratigraphy. Only the main pollen and spore taxa are presented. Organic content, magnetic susceptibility, and charcoal accumulation rates for the Graham Lake and High Lake sediments are presented in Figs. 5 and 6, respectively. The Graham Lake sedimentary sequence has an older basal date (11 570 ± 540 calendar years BP) and longer record than the High Lake sequence (10 435 ± 155 calendar years BP) (Fig. 2). As a conse-

quence, the first zone in the High Lake diagram corresponds with the second zone at Graham Lake. The herb-shrub tundra phase (Table 2, zone G-1) was not recorded at High Lake. The increase in abundance of *Ambrosia* pollen, approximately 200 years BP, at Graham Lake signals land clearance associated with the arrival of Europeans and indicates that this record extends to the present day. There is no such marked increase in *Ambrosia* pollen at High Lake suggesting that the most recent portion of the sedimentary sequence was not retrieved and no zone corresponds with G-8.

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Table 2. Description of pollen assemblage zones for Graham Lake sedimentary sequence (Figs. 3a and 3b) and physical properties of sediments (Fig. 5). Age of base sequence uncertain.

| Zone | Depth (cm) | Age (calendar years BP) | Pollen, spore, charcoal, and sediment stratigraphy |
|------|------------|-------------------------|---|
| G-1 | 1250–1210 | ? – 11 600 | High herbaceous pollen frequencies and low total pollen accumulation rates. <i>Pinus banksiana-resinosa</i> pollen percentages high (20%) but PAR low. <i>Salix</i> pollen reached maximum abundances. Sediments dominated by fine sand, silt, and clay. Magnetic susceptibility of sediments high. |
| G-2 | 1210–1186 | 11 600 – 10 300 | Sharp rise in <i>Populus</i> followed by <i>Picea glauca</i> pollen frequencies (30%). <i>Myrica</i> , <i>Thuja-Juniperus</i> , and <i>Abies balsamea</i> pollen types reached maximum percentages. Corresponding decline in <i>Salix</i> pollen and total herbaceous pollen frequencies. Transition from clay dominated sediments to gyttja, interrupted with a band of sand. Magnetic susceptibility of sediments decreased as organic content increased. |
| G-3 | 1186–1146 | 10 300 – 8 600 | <i>Pinus banksiana-resinosa</i> pollen percentages increased sharply (>60%) with a corresponding decline in <i>Picea glauca</i> pollen percentages. <i>Myrica</i> , <i>Salix</i> , <i>Thuja-Juniperus</i> , and total herbaceous pollen types also decreased in abundance. <i>Betula</i> pollen frequencies increased interrupted by a short decrease. Sediment for this zone and rest of sequence dominated by gyttja. |
| G-4 | 1146–1110 | 8600–7200 | <i>Pinus strobus</i> pollen percentages increased to ca. 35% as <i>Pinus banksiana-resinosa</i> pollen frequencies declined gradually along with other arboreal taxa. <i>Ostrya-Carpinus</i> pollen percentages increased to reach maximum levels. <i>Tsuga canadensis</i> pollen percentages increased sharply towards end of zone. |
| G-5 | 1110–1066 | 7200–5600 | <i>Tsuga canadensis</i> pollen percentages continued to rise (ca. 30%). <i>Ostrya-Carpinus</i> , <i>Pinus strobus</i> , <i>Quercus</i> , and <i>Pinus banksiana</i> pollen types decreased in abundance. <i>Betula</i> , <i>Thuja-Juniperus</i> , and <i>Alnus rugosa</i> pollen percentages increased. |
| G-6 | 1066–1002 | 5600–3500 | Sharp decline in pollen percentages of <i>Tsuga canadensis</i> . Corresponding increase of percentages and PAR of several pollen taxa: <i>Pinus strobus</i> , <i>Pinus banksiana-resinosa</i> , <i>Betula</i> , <i>Thuja-Juniperus</i> , <i>Ulmus</i> , <i>Fagus grandifolia</i> , <i>Acer saccharum</i> , and <i>Alnus rugosa</i> . This increase of PAR was short-lived after which they declined again. |
| G-7 | 1002–878 | 3500–200 | <i>Tsuga canadensis</i> pollen percentages increased again with a corresponding decline in pollen frequencies of <i>Pinus strobus</i> , <i>Pinus banksiana</i> , and <i>Quercus</i> . <i>Abies balsamea</i> and <i>Picea glauca</i> pollen percentages start to increase gradually. Pollen frequencies of <i>Tsuga canadensis</i> , <i>Acer saccharum</i> , and <i>Fagus grandifolia</i> started to decrease gradually towards end of zone. |
| G-8 | 878–868 | 200–0 | Sharp increase in <i>Ambrosia</i> pollen percentages. Other herbaceous taxa such as <i>Rumex</i> and Poaceae also increased. Pollen percentages of <i>Tsuga canadensis</i> , <i>Pinus strobus</i> , <i>Pinus banksiana</i> , and <i>Quercus</i> decreased while those of <i>Picea glauca</i> , <i>Salix</i> , <i>Alnus rugosa</i> , <i>Abies balsamea</i> , <i>Betula</i> , and <i>Corylus</i> increased somewhat. |

Rates of change

At Graham Lake, maximum rates of palynological change (Fig. 7a) occurred during the early Holocene, corresponding to the invasion of *Picea glauca* onto open herb–shrub tundra and the subsequent expansion of *Pinus banksiana-resinosa* to form closed woodland. Rates of change increased again during the invasion of *Pinus strobus*. There was a sharp increase in rates of change after the *Tsuga canadensis* decline and during its re-expansion onto the landscape.

At High Lake, rates of palynological change were also highest in the early Holocene (Fig. 7b). The signal is relatively noisy, but rates of change increase when *Pinus strobus* invades the landscape and after the expansion of *Fagus grandifolia* and *Tsuga canadensis*.

Discussion

Forest history in southern Ontario

Forest development at Graham Lake and High Lake is discussed below in relation to other pollen records from southern

Ontario (see Fig. 1 for site locations). In the text the pollen assemblage zones for Graham Lake (G-1 to G-8) and High Lake (H-1 to H-6) are referred to as they appear on Figs. 3 and 4 and are described in Tables 2 and 3, respectively.

Early Holocene

The early Holocene landscape around Graham Lake (zone G-1) was vegetated by herb–shrub tundra composed mainly of *Salix*, *Artemisia*, Cyperaceae, Poaceae, and Tubuliflorae. Erosion was occurring in the watershed, washing inorganic material into the lake basins suggesting that vegetation cover was sparse initially. Tree and shrub taxa with a modern boreal distribution, such as *Shepherdia canadensis* (L.) Nutt., *Abies balsamea*, and *Larix laricina* (Du Roi) K. Koch, were also present in low abundances. There appears to have been a short-lived increase of *Populus* followed by *Picea glauca* (G-2), which invaded to form open spruce woodland (at ca. 11 200 calendar years BP around Graham Lake). *Picea glauca* was also abundant in the early Holocene around High Lake (H-1). The openness of the vegetation is inferred

Table 3. Description of pollen assemblage zones for High Lake sedimentary sequence (Fig. 4) and physical properties of sediments (Fig. 6). Age of base and top of sequence uncertain.

| Zone | Depth (cm) | Age (calendar years BP) | Pollen, spore, charcoal, and sediment stratigraphy |
|------|-------------|-------------------------|---|
| H-1 | 1415–1350 | ? – 10 750 | High percentages of <i>Picea glauca</i> pollen (25%) initially which decreased towards top of zone. <i>Salix</i> , <i>Myrica</i> , <i>Abies balsamea</i> , <i>Larix laricina</i> , and <i>Thuja–Juniperus</i> pollen types reached maximum abundance for the sequence. Herbaceous pollen types also relatively high. Sediments dominated by clay and magnetic susceptibility high. |
| H-2 | 1350–1220 | 10 750 – 8 400 | Pollen percentages of <i>Pinus banksiana–resinosa</i> increased sharply (50%). <i>Tsuga canadensis</i> , <i>Quercus</i> , and <i>Acer saccharum</i> pollen types started to increase in frequency slowly. There was a sharp transition from sediments dominated by clay to almost pure gyttja. As organic content of the sediments increased, magnetic susceptibility decreased. |
| H-3 | 1120–1164 | 8400–7000 | <i>Pinus banksiana–resinosa</i> pollen percentages decreased as those of <i>Pinus strobus</i> increased. <i>Fagus grandifolia</i> and <i>Acer saccharum</i> pollen frequencies started to increase, while <i>Ostrya–Carpinus</i> and <i>Corylus</i> pollen types reached their maximum values for the sequence. |
| H-4 | 1164–1086.5 | 7000–5100 | Sharp increase in <i>Tsuga canadensis</i> pollen percentages (20%). Corresponding decrease in the pollen frequencies of other tree taxa such as <i>Pinus strobus</i> , <i>Pinus banksiana–resinosa</i> , <i>Acer saccharum</i> , <i>Quercus</i> , <i>Ostrya–Carpinus</i> , and <i>Corylus</i> . |
| H-5 | 1086.5–999 | 5100–3700 | Significant decline in the pollen percentages of <i>Tsuga canadensis</i> (20% to <10%). Corresponding increase in PAR of <i>Pinus banksiana–resinosa</i> , <i>Quercus</i> , <i>Ulmus</i> , <i>Fraxinus nigra</i> , <i>Betula</i> , <i>Fagus grandifolia</i> , <i>Acer saccharum</i> , <i>Ostrya–Carpinus</i> , and <i>Corylus</i> , although in most cases this increase was erratic. |
| H-6 | 999–715 | 3700–? | <i>Tsuga canadensis</i> pollen percentages increased again to former levels. <i>Fagus grandifolia</i> pollen percentages continued to increase gradually. Pollen frequencies of <i>Quercus</i> and <i>Pinus strobus</i> declined gradually although their PAR values were more erratic. <i>Picea glauca</i> , <i>Thuja–Juniperus</i> , and <i>Pinus banksiana–resinosa</i> pollen percentages increased in abundance towards the end of the zone. |

from the continued presence, although at lower abundances, of herbaceous taxa and the relatively high inorganic content and magnetic susceptibility of the lake sediments. As *Picea glauca* woodland expanded, several tree and shrub taxa declined.

There is evidence for early Holocene tundra or forest tundra-like vegetation from other sites in southern Ontario (including Tonawa Lake, Ramsay Lake, Maplehurst Lake, Second Lake, and Pink Lake; Mott and Farley-Gill 1978, 1981; Liu 1981; Burden et al. 1986; McAndrews and Campbell 1993). Mott and Farley-Gill (1978, 1981) suggest that low pollen accumulation rates (similar to those found in modern tundra sites) support evidence of a tundra-like vegetation in the early Holocene. In most cases, open tundra vegetation was invaded by *Populus* followed by *Picea* with a corresponding decline in herbaceous taxa. At other sites in southern Ontario (Inglesby Lake, Victoria Road Bog, Harrowsmith Bog, Found Lake, Hams Lake, Van Nostrand Lake, Nutt Lake) there appears not to have been a tundra phase after deglaciation, and the vegetation was immediately colonized by *Picea* and other arboreal taxa (Terasmae 1969; McAndrews 1973, 1981; Bennett 1987; Fritz et al. 1987). McAndrews (1981) suggests that, at least for those sites that are kettle lakes (such as High Lake), there may have been a lag between deglaciation and melting of buried ice to form the basins, thus the tundra phase may not have been recorded in the sediments.

A decline in *Picea glauca* in the early Holocene occurred at sites throughout southern Ontario (G-3, H-1) approxi-

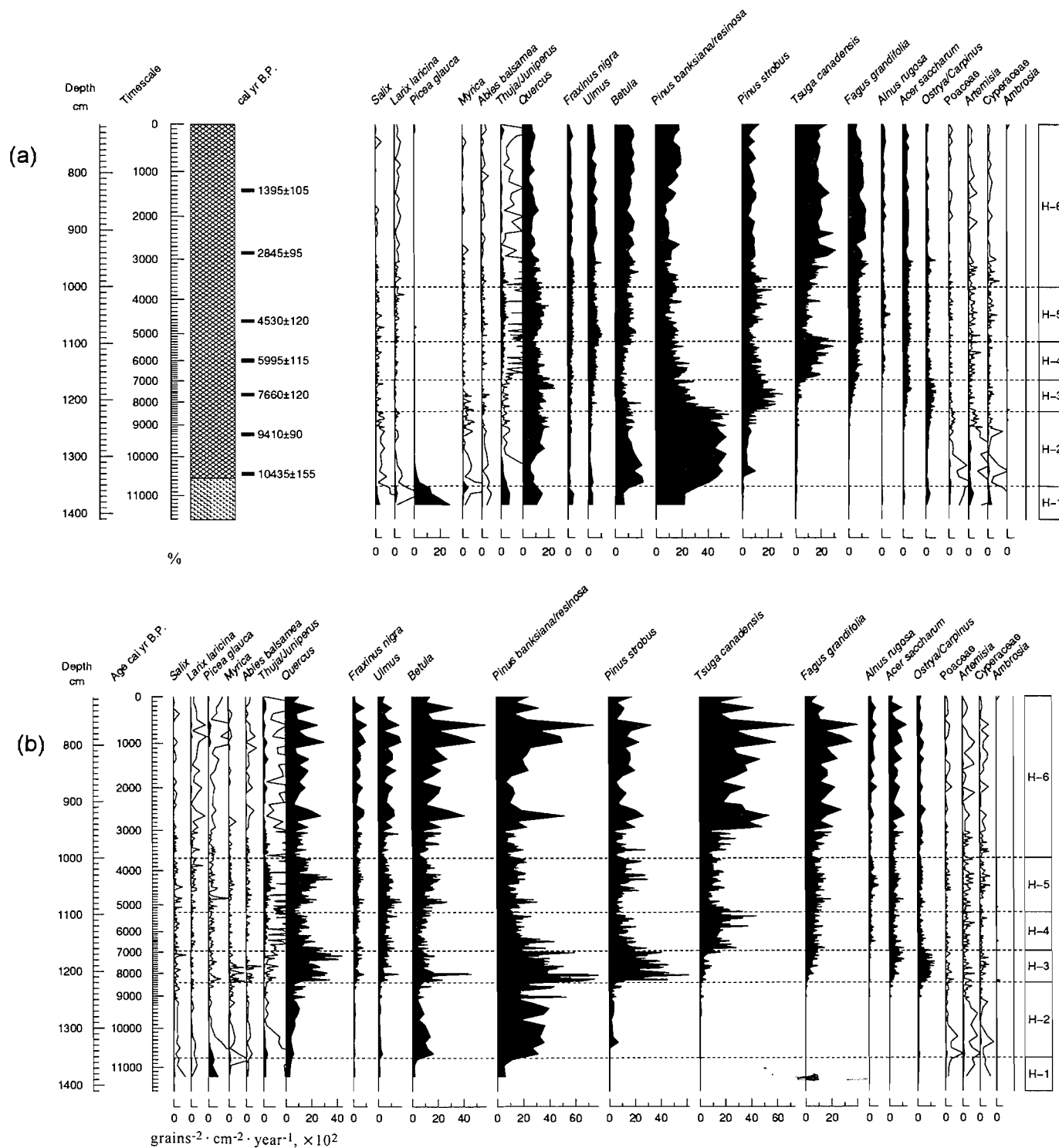
mately between 10 500 and 9500 ¹⁴C years BP (Terasmae 1969; McAndrews 1973, 1981; Mott and Farley-Gill 1981; Burden et al. 1986; McAndrews and Campbell 1993; Bennett 1987; Fritz et al. 1987). There was a corresponding increase in *Pinus banksiana–resinosa* and *Betula* (probably mainly *Betula papyrifera*) at Graham Lake, High Lake (G-3, H-2), and several other sites (McAndrews 1973, 1981; Mott and Farley-Gill 1981; Burden et al. 1986; Bennett 1987; McAndrews and Campbell 1993). A sharp decline in the proportion of inorganic material in the sediments at Graham Lake and High Lake (Figs. 4 and 6), while *Pinus banksiana–resinosa* and *Betula* increased in abundance, suggests that continuous forest cover had developed. *Pinus banksiana–resinosa* and *Betula* appear to have been more abundant at Graham Lake than at High Lake, based on their pollen percentages.

Mid-Holocene

Pinus strobus invaded the landscape around Graham Lake and High Lake at ca. 8500 calendar years BP (G-4, H-3), resulting in a marked shift in vegetation regionally (Ritchie 1987). Hardwood components of the forested landscape at this time included *Quercus*, *Fraxinus*, *Ulmus*, *Ostrya–Carpinus*, and *Corylus*. *Tsuga canadensis*, *Fagus grandifolia*, and *Acer saccharum* were also present at low abundances. *Ostrya–Carpinus* reached maximum abundances between ca. 8500 and 7000 calendar years BP.

Pinus strobus was eventually replaced as one of the forest dominants by more shade tolerant, species characteristic of

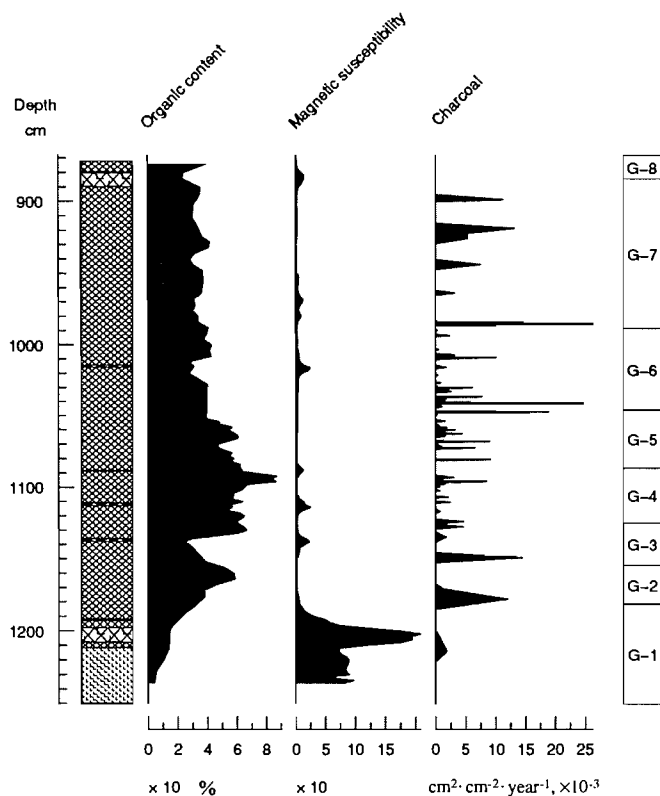
Fig. 4. (a) Percentages of the most common pollen and spore taxa for High Lake plotted against depth. Values for taxa present at low abundances are exaggerated by $\times 10$. A time scale and location of the calibrated radiocarbon ages are plotted on the left next to the lithostratigraphic column (Troels-Smith 1955). (b) Pollen and charcoal accumulation rates for High Lake plotted against depth.



modern temperate forests (G-5, H-4), such as *Tsuga canadensis*, *Fagus grandifolia*, and *Acer saccharum* (Liu 1981; McAndrews 1981; Ritchie 1987; Bennett 1987), which invaded closed-canopy woodland after ca. 7000 calendar years BP at Graham Lake and High Lake. *Fagus grandifolia* and *Acer saccharum* appear to have been more abundant at

High Lake than at Graham Lake throughout the Holocene. High Lake is situated further south than Graham Lake, and a slightly milder climate may account for such differences in the relative abundance of taxa. As these long-lived, highly competitive tree species increased, other taxa, including *Ostrya-Carpinus*, *Quercus*, and *Pinus banksiana-resinosa*

Fig. 5. Organic content (as a percentage of dry weight), magnetic susceptibility (uncalibrated units), and charcoal accumulation rates of Graham Lake sediments.



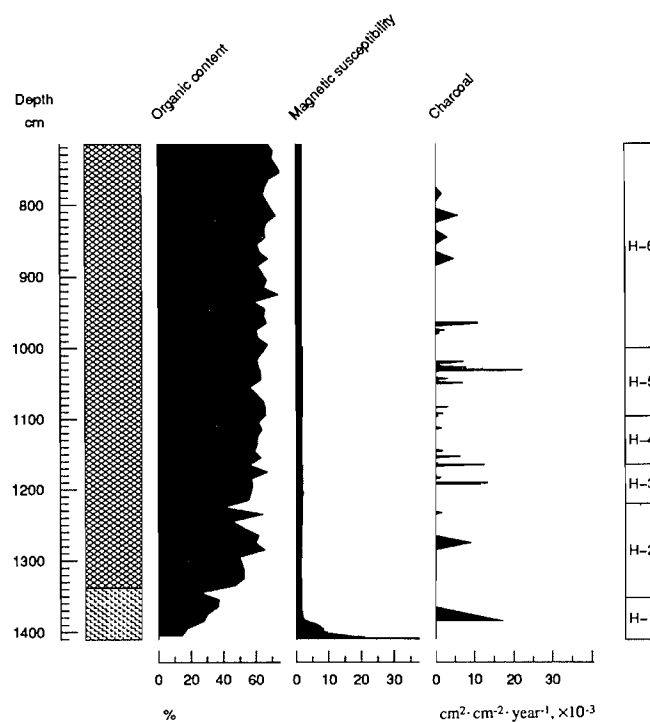
as well as *Pinus strobus*, declined (McAndrews 1973; Mott and Farley-Gill 1978; 1981; Burden et al. 1986; Bennett 1987).

In the mid-Holocene, there was a dramatic decline in the abundance of *Tsuga canadensis* throughout eastern North America, which is recorded in most pollen diagrams from this region (Davis 1981; Liu 1981; McAndrews 1981; Webb 1982; Allison et al. 1986; Ritchie 1987; Bennett 1993), including Graham Lake and High Lake (G-6, H-5). *Tsuga canadensis* remained at lower abundances for ca. 1500 years, after which it increased again to become one of the forest dominants (G-7, H-6). At Graham Lake, as *Tsuga canadensis* populations expanded, other taxa, such as *Quercus*, *Pinus strobus*, *Pinus banksiana-resinosa*, and *Thuja-Juniperus*, declined.

Late Holocene

At Graham Lake (G-8), *Tsuga canadensis* and *Fagus grandifolia* started to decline at ca. 1000 calendar years BP. There was a corresponding increase in abundance of *Pinus banksiana-resinosa*, *Salix*, *Picea glauca*, *Abies balsamea*, and *Alnus rugosa* (Du Roi) Spreng. A similar shift in forest composition has been noted by other authors for this region and eastern North America (Liu 1981; McAndrews 1988; Gajewski 1987; Campbell and McAndrews 1991, 1993; Clark and Royall 1995; J. Fuller unpublished data). The increase of *Ambrosia* pollen type around 2 centuries ago signals land clearance after European settlement and the spread of agriculture. Several tree species declined markedly, including *Tsuga canadensis* and *Fagus grandifolia*.

Fig. 6. Organic content (as a percentage of dry weight), magnetic susceptibility (uncalibrated units) and charcoal accumulation rates of High Lake sediments.

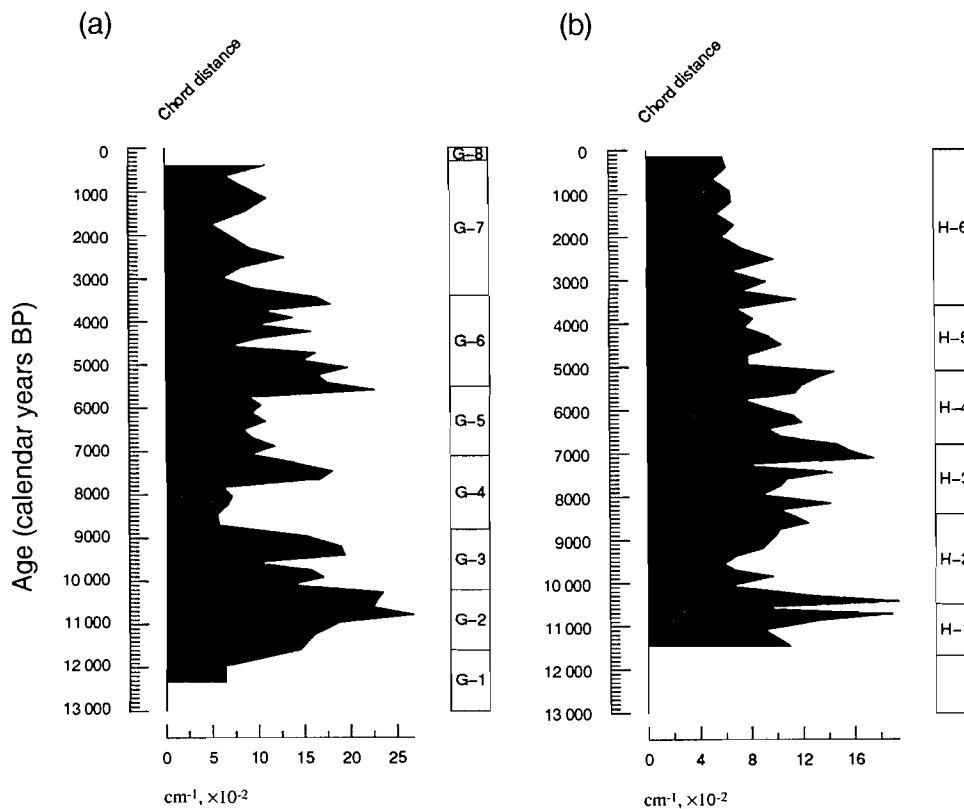


Driving factors of forest development

The above discussion details forest history for southern Ontario. What were the main factors driving vegetation change during the Holocene? Vegetation composition and structure is ultimately controlled by climate (Woodward 1990). However, vegetation response to climatic change, such as that at the end of the Wisconsin glaciation, is modified by topography, edaphic factors, species biology, disturbance regime, and historical factors (Ritchie 1986), introducing lags and leads to the spread of vegetation. The effects of climate on vegetation can be indirect, and the response of vegetation to climate change is not necessarily linear. Climate indirectly affects vegetation by influencing disturbance regimes (e.g., fire, wind), competitive balance between taxa and soil development, as well as directly affecting plant growth, reproduction, and mortality. In addition, aspects of soil development, history (e.g., past disturbances, geological events), and chance (e.g., location of full glacial refugia) are independent of climate (Pennington 1986).

General circulation models (GCMs) suggest that summer solar radiation increased after 18 000 years BP to reach a maximum at 9000 years, by which time southern Ontario was ice free (Prest 1970; Kutzbach 1987). GCMs suggest that climate in northeastern North America was 2°C warmer than today between 9000 and 6000 years BP, and this warmer climate scenario is supported by paleoecological data (Davis et al. 1980; Bartlein and Webb 1985; Kutzbach 1987). High levels of charcoal and high abundances of *Pinus* in sedimentary records covering the early Holocene period are interpreted as indicative of a climate with warmer and drier summers than at present (Green 1982; Ritchie 1987; Spear et al. 1994). Several studies indicate that climate has become cooler and moister in the latter part of the Holocene

Fig. 7. Rates of palynological change (using chord distance as a dissimilarity measure) for (a) Graham Lake and (b) High Lake.



(Davis et al. 1980; Jackson 1989, Spear et al. 1994). Climate was, therefore, not constant during the Holocene and undoubtedly influenced vegetation dynamics. Holocene forest history in southern Ontario is discussed below in relation to climate change and the other factors driving vegetation change.

Climate, soil development, and disturbance

In the early Holocene, during the transition from a mainly herbaceous vegetation cover to a wooded landscape, rates of vegetation change increased sharply at both Graham Lake and High Lake to reach levels higher than any previous or subsequent periods during the Holocene, reflecting the marked shift in vegetation composition in response to climatic warming. Jacobson et al. (1987) found similarly high rates of change for a number of sites in eastern North America during the early Holocene. Early colonizers spread onto recently deglaciated soils that were low in organic matter (Mott and Farley-Gill 1978). Environmental conditions, therefore, controlled vegetation development, as well as climate, as many species cannot tolerate soils with low organic content. Although not well represented in the pollen record, one of the early colonizers appears to have been *Populus* (Mott and Farley-Gill 1981) (probably *Populus balsamifera* L.), a pioneering taxon that has a modern boreal distribution, produces high amounts of well-dispersed seeds, and has the ability to germinate on bare mineral soils (Zasada and Phipps 1990).

Picea subsequently invaded to form open spruce woodland. This tree species does not have several of the typical characteristics of pioneers, such as short life-span, shade intolerance, prolific seed production etc., but it can tolerate a broad range of climatic and soil conditions and has the abil-

ity to establish on mineral soils (Nienstadt and Zasada 1990). *Picea glauca* is highly shade tolerant and long lived (Nienstadt and Zasada 1990) providing strong competition for other arboreal taxa and shading out herbs. As it spread on the landscape, several herbaceous and arboreal taxa declined in abundance.

Picea was abundant on the landscape for approximately 1000 years, after which it declined and remained at low levels for most of the rest of the Holocene. Several authors suggest that this decline of *Picea* is indicative of a climatic change (warming event) at this time (Mott and Farley-Gill 1981; Liu 1981; Spear et al. 1994). Spear et al. (1994) consider that climate change produced conditions which were "too warm" for *Picea* to thrive. Climatic warming in the early Holocene allowed forest taxa to extend their ranges. *Picea* populations may have been restricted by competition from the advancing taxa, reducing its range. *Picea* appears, however, to have been replaced mainly by early successional species such as *Pinus banksiana* and *Betula papyrifera*, both of which are highly shade intolerant and relatively short lived (Rudolph and Laidly 1990; Safford et al. 1990). All three of these taxa now have mainly boreal distributions that overlap to a large extent (Nienstadt and Zasada 1990; Rudolph and Laidly 1990; Safford et al. 1990). Changes in the fire regime (related to climate, fuel loading, and ignition frequency; Clark 1990) resulting in increased fire frequency and (or) intensity may have facilitated the invasion of species that regenerate vigorously after fire, such as *Pinus banksiana* and *Betula papyrifera* (Rudolph and Laidly 1990; Safford et al. 1990).

Pinus banksiana was abundant in southern Ontario for 1000–2000 years in the early Holocene, as recorded by most

sites in the region (Liu 1981; McAndrews 1981; Ritchie 1987). In the absence of fire or other disturbances, this early successional tree is replaced by more shade-tolerant species (Rudolph and Laidly 1990), and it is therefore likely that some form of regular disturbance was occurring during this period to maintain pine populations. There is no evidence for higher charcoal frequencies at Graham Lake or High Lake, although fires may still have been occurring but went unrecorded in the sedimentary record. Spear et al. (1994) found higher levels of charcoal in the sediments of Mirror Lake, New Hampshire, during the period between 11 000 and 9000 ^{14}C years BP when pine species dominated the tree flora. They suggest that maximum solar radiation in the early Holocene (as predicted by Milankovitch theory) may have resulted in hot, dry summers promoting fire. Anderson et al. (1986) also find high charcoal values between 9800 and 7500 ^{14}C years BP (ca. 10 900 – 8200 calendar years BP) at a site in Maine where pine was abundant.

Betula papyrifera has the ability to invade old-growth stands of *Picea glauca* growing on modern flood plains in Alaska by establishing in openings created by the death and uprooting of *Picea glauca* (Safford et al. 1990). It can persist in some modern *Picea glauca* stands because of physical smothering of spruce seedlings by birch foliage. In addition, the chemical properties of the ashes of *Betula papyrifera* following fire are thought to inhibit seedlings of *Picea glauca* (Safford et al. 1990). Therefore, *Betula* may have invaded senescent stands of *Picea* or after fire.

Another event that may have been driven by climate and (or) disturbance was the subtle change in forest composition recorded at Graham Lake ca. 1000 calendar years BP, as *Tsuga canadensis* and *Fagus grandifolia* declined, while other more cold-tolerant and (or) early successional taxa increased, such as *Pinus strobus*, *Quercus*, *Abies*, and *Picea*. Similar changes seen elsewhere have been ascribed to climatic cooling associated with the Little Ice Age (Gajewski 1987; Campbell and McAndrews 1993) and aboriginal activity (Clark and Royall 1995). Disturbance associated with human activity after European arrival (e.g., logging and agriculture) markedly changed the relative abundance of several forest taxa, as disturbance-tolerant species became more abundant.

Climate, migration, and competition

At several sites in southern Ontario, including Graham Lake and High Lake, the mid-Holocene expansion of *Pinus strobus* appears to be associated with a decline of *Pinus banksiana-resinosa*, suggesting competitive displacement (Mott and Farley-Gill 1978, 1981; Liu 1981; McAndrews 1981). *Pinus strobus* is more shade tolerant and long lived than *Pinus banksiana* or *Pinus resinosa*. *Pinus strobus* populations expanded within the matrix of woodland already present. Other arboreal taxa also declined at this time at Graham Lake and High Lake, including *Betula*, *Picea glauca*, *Larix laricina*, and *Abies balsamea*. The corresponding increase in rates of change at Graham Lake and High Lake reflect this shift in forest composition.

Ostrya-Carpinus reached maximum abundances for the Holocene during a period when *Pinus strobus* and *Pinus banksiana-resinosa* formed significant components of the

forest vegetation with lesser amounts of *Quercus* and *Ulmus*. *Ostrya virginiana* and *Carpinus caroliniana* T. Walt. are forest understorey species that are more commonly found today in the understorey of hardwood forests (Metzger 1990a, 1990b). During the Holocene, it is likely that *Ostrya virginiana* was more abundant than *Carpinus caroliniana*, which has a more southerly modern distribution in the deciduous forest region (Metzger 1990a, 1990b). *Ostrya-Carpinus* declined in abundance in the pollen record as *Tsuga canadensis*, *Fagus grandifolia*, and *Acer saccharum* populations expanded. At Graham Lake and High Lake, changes in the nature of the forest, with the expansion of long-lived taxa that cast a dense shade, may have caused this decline. It has been suggested that non-analogue climatic conditions (heightened seasonality) allowed *Ostrya-Carpinus* to reach maximum abundances for the Holocene (Delcourt and Delcourt 1994). Percent pollen records from other sites in southern Ontario, most of which have coarser temporal resolution, do not show this period of increased abundance of *Ostrya-Carpinus*, except at Pond Mills Pond (McAndrews 1981) and Mary Lake (Bennett 1992). However, the timing and patterns of change were different at these sites.

As *Tsuga canadensis*, *Acer saccharum*, and *Fagus grandifolia* populations expanded, other less shade-tolerant taxa declined in abundance. These highly competitive tree species can remain as seedlings or saplings in shaded conditions for a considerable time, but they need a small light gap to allow them to reach the canopy (Godman and Lancaster 1990; Godman et al. 1990; Tubbs and Houston 1990). Small-scale disturbances must have been a feature of the landscape, providing gaps in the closed-canopy forest to allow these taxa to invade. Disturbance regime was therefore important in facilitating invasion, as well as maintaining the abundance of shade-intolerant species.

Disease

At both Graham Lake and High Lake and other sites in the northeast (Jacobson et al. 1987), there was an increase in rates of change after the mid-Holocene *Tsuga canadensis* decline reflecting the shift in forest composition. Assuming that the decline was the result of a pathogen, as proposed by Davis (1981) and supported by evidence from Bhiry and Fillion (1996), individuals and stands would have been killed, creating gaps within the forest canopy. The decline of *Tsuga canadensis* probably resulted in forest succession. Changing abundances of other forest taxa can be observed in the pollen record at Graham Lake, although the spatial replacement dynamics cannot be determined (Fuller 1995). *Alnus rugosa* was one of the first taxa to increase, followed by *Ulmus*, *Quercus*, *Pinus banksiana-resinosa*, *Thuja-Juniperus*, *Betula*, *Fagus grandifolia*, and finally *Acer saccharum*. The decline of *Tsuga canadensis* at High Lake was less dramatic and the response less marked, but several taxa did increase in abundance. Davis (1981) notes broad successional patterns after the demise of *Tsuga canadensis* at Mirror Lake, New Hampshire; *Betula* was one of the first taxa to increase, followed by *Fagus grandifolia*, *Acer saccharum*, and *Ostrya-Carpinus* (Davis 1981). *Tsuga canadensis* remained at low levels for approximately 1500 years before its populations recovered. These observations demonstrate the importance

of competition in controlling forest dynamics and suggest that pathogenic outbreaks can have catastrophic and long-lasting impacts on forest dynamics.

Conclusions

Holocene pollen records from southern Ontario document a series of invasions of tree taxa triggered by climate warming following the last glacial maximum. The first taxa to arrive (e.g., *Picea*, *Populus*, *Pinus banksiana-resinosa*) had the ability to establish on bare mineral soils, the capacity to spread quickly across the landscape (rapid relative growth rates, efficient long distance dispersal, etc.), and wide environmental tolerances. Once complete forest cover was established, the disturbance regime (fire, wind) probably played an important role by providing gaps in which invading taxa could establish and maintaining abundance of shade-intolerant species. Competition-driven dynamics were important as more shade-tolerant taxa arrived (e.g., *Tsuga canadensis* and *Fagus grandifolia*) and expanded on the landscape. Rates of vegetation change increased during periods of invasion at both sites investigated, reflecting shifts in forest composition. In the mid-Holocene, the dramatic decline of one of the forest dominants, *Tsuga canadensis*, demonstrates the role of competition as several other forest taxa increased in abundance at the same time. In addition, the catastrophic nature and longevity of the decline may point to the importance of disease as an influence on forest dynamics. During and for a period after the decline, it appears forest composition and dynamics were in disequilibrium with climate because of this nonclimatic disturbance. More recent changes in forest composition occurring over the last 1000 years may be attributed to climate cooling and (or) human activity.

The forests of southern Ontario have been highly dynamic during the Holocene, responding not only to changes in climate but also to several other factors. Vegetation dynamics during postglacial periods are the result of a (complex) interplay between climatic factors, soils, various disturbance regimes (fire, wind, disease), biotic interactions, and the biological and ecological characteristics of the species pool. Changes seen in pollen records cannot always be related directly to shifts in climatic parameters such as temperature and precipitation. The effects of these parameters may be indirect and the responses nonlinear (Bennett 1993).

Acknowledgements

Special thanks go to Keith Bennett for advice and support. Michalis Averof, Keith Bennett, Grace Brush, David Foster, Susie Lumley, Jason McLachlan, and Tom Webb III gave helpful comments on earlier drafts of the manuscript. Radiocarbon age determinations were provided by V.R. Switsur, Radiocarbon Laboratory, Cambridge and the National Engineering Research Council Radiocarbon Facility, East Kilbride. Ben Slater helped draft Fig. 1. Financial support was provided by a W.A. Meek scholarship, Corpus Christi College, Cambridge, and the British Federation of Women Graduates. Pat Anderson, Keith Bennett, Roslyn Case, Chris Larsen, Glen MacDonald, Katrina Moser, Jim Ritchie, and Linda Taylor are gratefully acknowledged for help coring Graham Lake and High Lake.

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