

Late Quaternary dynamics of tundra and forest vegetation in the southern Niagara Escarpment, Canada

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Summary

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- Here, paleoecological studies from southern Ontario, Canada, are detailed to reconstruct vegetation history of the last 13 000 ¹⁴C year, with emphasis on late-glacial treeless vegetation.
- Two sites (Crawford Lake and Twiss Marl Pond) were investigated using combined pollen and plant–macrofossil stratigraphic data. Comparison of multivariate analysis of pollen data with climate variations inferred independently from oxygen isotopes at the same site facilitated systematic evaluations of climate–vegetation interactions during different stages of vegetation development.
- Pollen results show a distinctive successional change from *Alnus–Dryas–Cyperaceae* sparse tundra or periglacial desert to *Salix–Juniperus–Cyperaceae* dense tundra, with abundant arctic/alpine plant macrofossils, during the first few centuries after ice retreat. The area around the two sites was then dominated by *Picea* (c. 12 000–10 000 ¹⁴C BP). Vegetation shifts, summarized by log-contrast principal component analysis of the pollen record, indicated a lagged response of forests to deglacial climate warming. The major vegetation shift at c. 7500 ¹⁴C BP from coniferous *Pinus*-dominated to mixed forests probably corresponded to a major shift from deglacial to full post-glacial climates. Vegetation during the mid- and late Holocene responded more directly to natural (drought-triggered pathogen-induced *Tsuga* decline) and human disturbances (aboriginal and EuroCanadian settlements).
- This study demonstrates that bedrock basins most faithfully recorded the earliest vegetation change because they usually experienced a short delay in lake formation after ice retreat.

Key words: climate change, late Quaternary, oxygen isotopes, paleoecology, plant macrofossils, pollen analysis, principal component analysis, Younger Dryas.

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Introduction

Late Quaternary vegetation history has been well understood at regional and subcontinental scales in eastern North America, with accumulating fossil pollen and macrofossil records over the past several decades (Ritchie, 1987; Webb *et al.*, 1993a; Jackson *et al.*, 1997). Recent paleoecological investigations have increasingly focused on answering ecological questions regarding patterns and processes that require longer periods of time than usually available in neo-ecological studies. This includes studies of climate–soil–vegetation interactions (Brubaker, 1975; Pennington, 1986;

Willis *et al.*, 1997), ecological response to climate change and possible time lags (Pennington, 1986; Clark, 1990; Campbell & McAndrews, 1993; MacDonald *et al.*, 1993; Mayle & Cwynar, 1995), forest response to natural and anthropogenic disturbance (Allison *et al.*, 1986; Foster & Zebryk, 1993; Fuller, 1998) and forest dynamics at fine spatial scales (Bradshaw, 1988; Lynch, 1998). These studies have increased our understanding of issues relevant to global change.

In the Great Lakes region of North America, despite abundant paleoecological sites available, there is still controversy over several aspects of long-term postglacial vegetation dynamics. Was there an initial treeless tundra vegetation

between the last deglaciation and the invasion of trees? Were there time lags in vegetation response to abrupt deglacial climate oscillations? How do the characteristics of soils and topography affect interspecific interactions and vegetation dynamics? Most published paleoecological studies in southern Ontario emphasize forest changes during the Holocene and late glacial (Mott & Farley-Gill, 1978; McAndrews, 1981; Anderson, 1982; Warner *et al.*, 1984; Bennett, 1987, 1992; Szeicz & MacDonald, 1991; Fuller, 1997, 1998; McAndrews & Jackson, 1988). This lack of detailed studies of initial treeless vegetation could be caused for the following reasons: first, lack of sedimentary records for that period owing to delayed development of lake basins after ice retreat (Florin & Wright, 1969; Warner *et al.*, 1991); second, a brief phase of initial treeless vegetation controlled by strong climatic and vegetational gradients immediately south of the retreating ice (COHMAP Members, 1988; Webb *et al.*, 1993a,b; Levesque *et al.*, 1997); and third, complication of interpretation of fossil pollen assemblages due to large proportions of reworked and long-distance transported pollen in sparse tundra environments (Cushing, 1964; McAndrews, 1984; Gajewski, 1995). As a result, only a few sites in southern Ontario recorded the pollen assemblages before the spruce (*Picea*) peak in late glacial (Anderson, 1982; McAndrews & Jackson, 1988). Stable isotope data from this region show a series of climate oscillations during the last deglaciation, including the Younger Dryas, which correlate in remarkable detail with well-documented climate events in the North Atlantic region (Yu & Eicher, 1998, 2001; Yu, 2000). These events, however, appear to be absent in vegetation records, suggesting differential response of natural systems to climate change (Wright, 1984).

In the current study I investigated two sites at the edge of the southern part of Ontario's Niagara Escarpment, with detailed stratigraphic pollen and plant-macrofossil data. Combining pollen and plant macrofossils from same sites is a powerful approach to reconstructing history of past flora and vegetation (Watts, 1967; Birks & Birks, 1980; Ritchie, 1995). Oxygen isotopes from one of these sites were used as independent proxy of climate change (Yu & Eicher, 1998). These two sites were selected based on the following considerations. First, they are both in bedrock basins surrounded by shallow and scattered glacial deposits. Thus, these basins were expected to record the earliest vegetation after glacier ice retreat, as bedrock basins usually have a short delay time between ice retreat, lake formation and lacustrine sedimentation (Saarnisto, 1974; McAndrews, 1981). Second, they are both small and steep-sided lakes surrounded by bedrock cliffs, which may funnel macrofossil materials to complement and refine the pollen record. Finally, the Niagara Escarpment could have been important phytogeographically during the postglacial migration and establishment of plant species, so these sites may provide unusual records of migrational patterns and vegetational history for some species along the

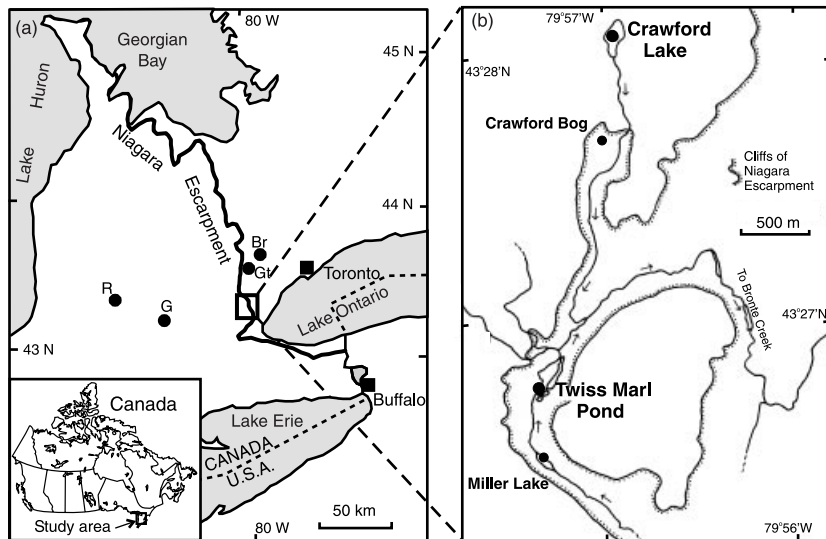
Escarpment (e.g. possible southward migration of *Thuja* along the Escarpment as speculated by Yu, 1997b). The distinct modern plant community along the cliff faces of the Escarpment (e.g. Larson *et al.*, 1989) might be reflected in the fossil record as well.

The objectives of this study were: to reconstruct the late Quaternary history of treeless and forest vegetation using detailed fossil pollen and plant-macrofossil records from two sites along the southern Niagara Escarpment; and to discuss vegetation response to abrupt climate oscillations and possible time lags. Specifically, I undertook this study to answer the following questions. Was the initial vegetation essentially treeless? If so, what species were contributing to this tundra flora? Two bedrock basins were expected to record the earliest vegetation after ice retreat and thus provide conclusive evidence for the nature of initial vegetation. The exposed bedrock settings with shallow soils around the study sites would have supported a genuine tundra vegetation rather than a forest tundra as previously documented in areas with relatively deeper unconsolidated deposits and soils. How did vegetation respond to deglacial climate oscillations? Were there significant time lags in vegetation response? The vegetation shifts as summarized by principal component analysis of pollen record will be compared with isotope-inferred climate history from the same site in answering these questions. Although full pollen and macrofossil data were presented, this paper mostly focuses on late-glacial and early Holocene period.

Study area

The Niagara Escarpment is the dominant physiographic feature of southern Ontario (Fig. 1a). Deglaciation was probably complete by 13 000 ¹⁴C BP in the highland area west of the Escarpment (so-called 'Ontario Island', Chapman & Putnam, 1984). At that time the study sites were located at a junction position of high land west of the Escarpment, water of Glacial Lake Whittlesey in the Erie basin, and ice of the Ontario lobe east of the Escarpment (Barnett, 1979). The Crawford Lake basin was probably formed during the retreat of the glacier ice after the Port Huron advance by a meltwater flood between the ice lobe and exposed land. The bedrock basin was hydraulically excavated at this time (McAndrews & Boyko-Diakonow, 1989) or, at least, glacial deposits in the previously formed basin were washed away by this glacial meltwater. In either case, the bare bedrock basin was emptied for subsequent lacustrine sedimentation. Surficial materials in this area consist primarily of glacial deposits including scattered Wentworth Till west of the Escarpment, extensive Halton Till east of the Escarpment and outwash gravels along the Escarpment (Karrow, 1987). Bedrock outcrops are frequent atop the Escarpment in the study area. Soils of the area consist of loam series developed on the coarse textured tills and stony shallow soils on the bedrock outcrops.

Fig. 1 Maps of study area and sites. (a) Map showing location of study area (open square) along Ontario's Niagara Escarpment and other southern Ontario pollen sites discussed in the text in the context of the late-glacial tundra (small dots). R: Rostock site (McAndrews & Jackson, 1988; McAndrews, 1994a); G: Gage Street site (Anderson, 1982; Schwert *et al.*, 1985; Fritz *et al.*, 1987); Gt: Georgetown site (Warner *et al.*, 1991); Br: Brampton site (Terasmae & Matthews, 1980). Inset map shows location of the study area in Canada. (b) Detailed map of Crawford Lake and Twiss Marl Pond showing relation to the Niagara Escarpment and present drainage pattern. Fossil pollen sites nearby are Crawford Bog (McAndrews, 1994b; also in Karrow, 1987) and Miller Lake (McAndrews, 1994b).



The study area has a moist continental climate with warm summers and cold winters. The nearest climate station (Milton Kelso) has mean July and January temperatures of 20.6°C and −6.8°C, respectively, and annual precipitation of 875 mm (Environment Canada, 1982). There is about 50 mm more precipitation annually near the Escarpment than on either side (Environment Canada, 1982; Yu, 1997a), which may be caused by orographic effects. The study area lies on the boundary between deciduous forest and the Great Lakes – St. Lawrence mixed forest (Rowe, 1972). Forests of the area mainly consist of *Acer saccharum*, *Betula lutea*, *B. papyrifera*, *Carya cordiformis*, *Fagus grandifolia*, *Fraxinus americana*, *F. pennsylvanica*, *Ostrya virginiana*, *Pinus strobus*, *Quercus rubra*, *Thuja occidentalis*, *Tilia americana*, *Tsuga canadensis* and *Ulmus americana*.

Study sites

Crawford Lake (43°28' N; 79°57' W) is situated atop the Niagara Escarpment at an altitude of 278 m above sea level (Fig. 1b). The lake has a surface area of 2.4 ha (*c.* 250 × 150 m) and a maximum depth of 24 m. The lake is partly surrounded by dolomite cliffs of up to 6 m above the lake surface that are mostly covered with white cedar (*Thuja occidentalis*) (Fig. 2). Crawford Lake is meromictic (partial circulation of water), and has varved (annually laminated) sediments for the last several millennia. The top varved sediment spanning the past *c.* 2000 yr has been studied in detail for fossil pollen (Boyko, 1973; McAndrews & Boyko-Diakonow, 1989), for microscopic charcoal (Clark & Royall, 1995), and for testing climate-driven forest dynamics using simulation modeling (Campbell & McAndrews, 1993).

Twiss Marl Pond (informal name, 43°27' N; 79°57' W) is located 2.5 km south of Crawford Lake at an altitude of 256 m in a glacial spillway containing outwash gravels (Karrow,

1987). The site is bordered by cliffs (Fig. 1b). Presently the site is occupied by three man-made ponds and surrounded by wet swamps (Yu, 2000 for detailed description of the site).

Methods

Field sediment coring

The Crawford Lake core (core DC) presented in this paper was taken from the deepest part of the lake (22.2 m water) on 15 March 1994, with a modified Livingstone piston sampler of 5 cm diameter (Wright, 1967); a plastic tube sampler fitted with a piston was used for taking the top 70 cm of soft sediments. The core penetrated to bedrock. The Twiss Marl Pond core was taken from a residual berm between two ponds (Fig. 1b; Yu, 2000) on 17 January 1995. The core penetrated to outwash gravel. The sediment was described, and the core segments of 1 m long each were wrapped in plastic and aluminum foil in the field.

Radiocarbon dating

Two bulk sediment samples and two plant-macrofossil samples from the Crawford core were dated at Brock University Radiocarbon Laboratory using the conventional method and at the US Livermore National Laboratory using AMS ¹⁴C dating, respectively. Eight plant-macrofossil samples from the Twiss core were dated by AMS at IsoTrace Laboratory of the University of Toronto (Table 1).

Loss-on-ignition analysis

The organic matter and carbonate contents of sediments were estimated with loss-on-ignition analysis (Dean, 1974), as dry weight loss at 550°C for 1 hr and 1000°C for 1 hr,

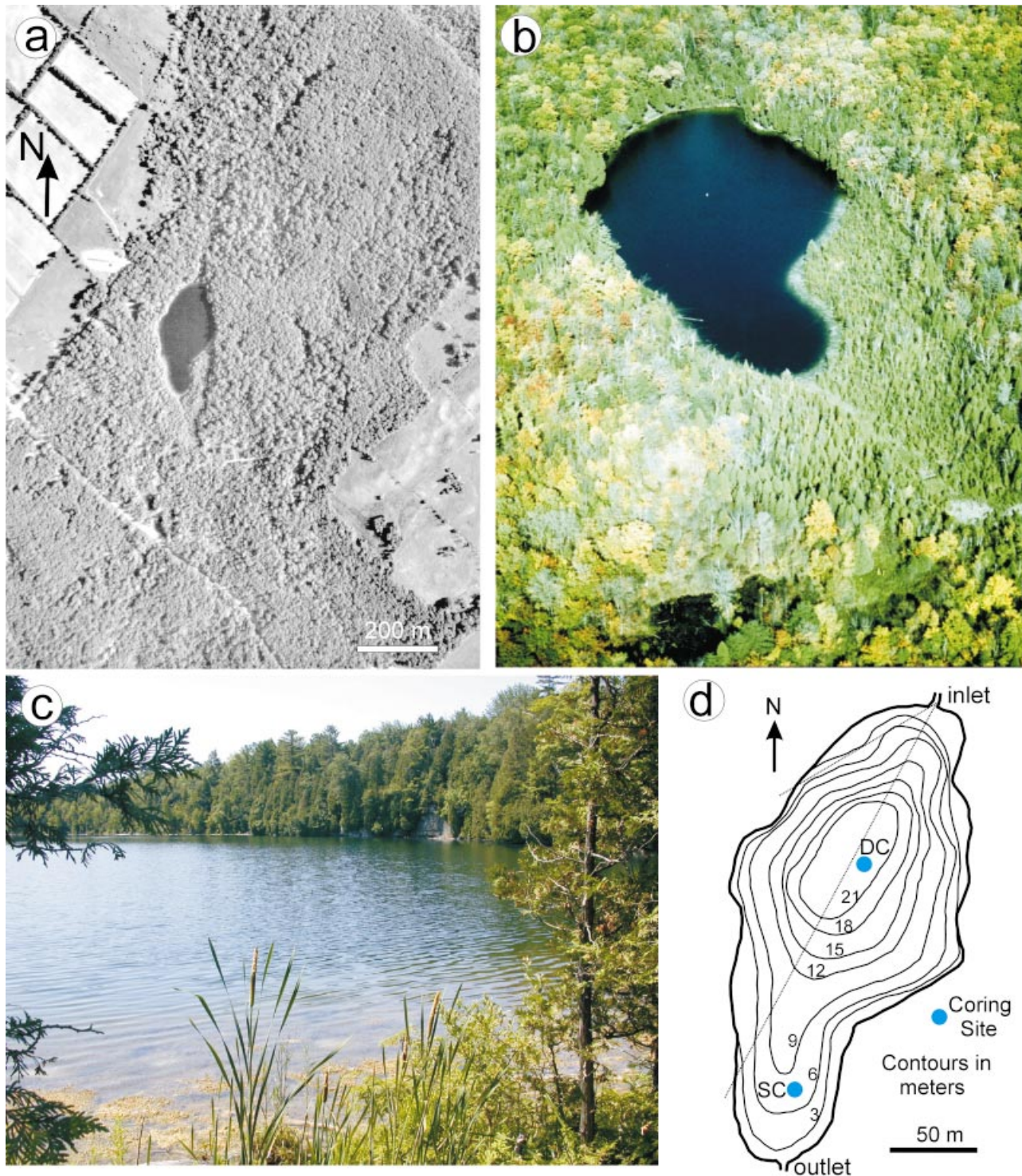


Fig. 2 Photos and bathymetry of Crawford Lake. (a) Aerial photograph of the Crawford Lake area. The forested areas are generally with shallow soils on the bedrock outcrops, whereas the patterned areas on south-east and north-west are farmlands on till deposits. The Niagara Escarpment is visible in the north-eastern corner of the photo. Courtesy of Ontario Ministry of Natural Resources, Canada; photo #78-4333/57-100 (1978). (b) Oblique aerial photograph of Crawford Lake. The lake is partially surrounded by dolomite cliffs, which are dominated by eastern white cedar (green belt around the lake). Photo courtesy of Conservation Halton, Ontario, Canada. (c) Crawford Lake looking in the south-west direction from the inlet area in the north of the lake. Rock cliffs are visible at the west side of the lake. Photo taken on 14 July 2002 by the author. (d) Bathymetry of Crawford Lake also showing locations of core DC, from which pollen and plant-macrofossil data were presented in this paper, and core SC, which provided detailed oxygen-isotope record as an independent climatic proxy (Yu *et al.*, 1997; Yu & Eicher, 1998, 2001). The dotted lines show approximate view from the inlet as shown in the photo of Fig. 2 (c).

Table 1 Radiocarbon (^{14}C) dates from Crawford Lake and Twiss Marl Pond, Ontario, Canada

Sample depth (cm)	Material daed (Method)	Carbon (mg)	Lab number ^a	^{14}C date ^b (BP \pm 1 SD)
Crawford Lake				
DC 92–97	Organic fraction of marly gyttja (bulk)	1059.4	BGS 1741	2 130 \pm 140
DC 130–135	Organic fraction of marly gyttja (bulk)	1100.1	BGS 1742	3 540 \pm 150
DC 345–347	<i>Larix</i> needles (AMS)	0.39	CAMS 16062	9 620 \pm 60
DC 355–357	<i>Larix</i> needles, wood fragments, charcoal fragments and Compositae seed (AMS)	0.22	CAMS 16061	9 670 \pm 70
Twiss Marl Pond (from Yu, 2000)				
TP 170–190	30 <i>Pinus strobus</i> needles/fragments (AMS)	2.44	TO-5834	7 900 \pm 70
TP 390–400	3 <i>Larix</i> needles, 1 <i>Betula</i> bract and unidentified charcoal fragments (AMS)	0.15	TO-5504	8 750 \pm 200 ^c
TP 400–415	20 <i>Picea</i> and 40 <i>Larix</i> needle fragments (AMS)	0.80	TO-6106	9 670 \pm 100^d
TP 480–490	9 <i>Picea</i> needles and 1 <i>Picea</i> seed (AMS)	1.27	TO-5505	10 920 \pm 80
TP 510–520	4 <i>Picea</i> needles and 1 <i>Larix</i> needle (AMS)	0.63	TO-5506	10 550 \pm 140 ^e
TP 560–570	30 <i>Dryas</i> and 26 <i>Salix</i> leaf fragments (AMS)	0.14	TO-5835	10 250 \pm 250 ^f
TP 570–590	90 <i>Dryas</i> and 15 <i>Salix</i> leaf fragments (AMS)	0.41	TO-6107	7 810 \pm 140 ^d
TP 600–610	27 <i>Dryas</i> leaves, 60 <i>Dryas</i> leaf fragments, 4 <i>Salix</i> leaves (AMS)	0.24	TO-5836	10 190 \pm 160 ^f

^aBGS: Brock University Radiocarbon Laboratory, Canada; CAMS: Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, USA; TO: IsoTrace Laboratory, University of Toronto, Canada. ^bAll IsoTrace (TO) dates were corrected for natural and sputtering fractionation to a base of $\delta^{13}\text{C} = -25\%$. The dates are uncalibrated conventional radiocarbon dates in years before present (BP), using Libby ^{14}C meanlife of 8033 years. The errors represent 68.3% confidence limits. ^cRejected as too young. This sample was badly preserved and yielded very little datable carbon. Probably biased by charcoal fragments or by contaminants. ^dLimited Acid-Alkali (AAA) pretreatment for 4 hr (TO-6106) and 2 hr (TO-6107). TO-6107 is rejected as too young. ^eRejected as too young. Perhaps the *Larix* needle was intrusive. ^fRejected as too young. These two samples were very small after pre-treatments and produced insufficient datable carbon.

respectively, after drying at 105°C overnight. The sampling intervals were usually 5 or 10 cm with close sampling (1–2 cm) for some levels.

Pollen-analytical method

Pollen samples of 0.8 cm³ (1.6 cm³ for the basal clay samples) were taken at varying intervals between 1 and 10 cm, depending on the degree of resolution desired. Pollen was concentrated using a modified standard acetolysis procedure (Fægri & Iversen, 1989), with fine-sieving to remove clay/silt-sized particles for highly mineral basal samples (Cwynar *et al.*, 1979). The concentrate was stained with safranin and mounted in silicone oil. A known number of *Lycopodium clavatum* spores (batch #710961, mean = 13 911 \pm 306 spores per tablet) was initially added to each sample for calculation of pollen concentration (Benninghoff, 1962). Each pollen sample was counted under a light microscope at $\times 400$ magnification in regularly spaced transverses; $\times 1000$ magnification was used for critical determination. Pollen sums are usually more than 300 (from 228 to 685) terrestrial plant pollen grains and spores for the Crawford core and more than 250 grains (from 211 to 407), but only 113–164 grains for the top 30-cm of woody peat, from the Twiss core. Identifications followed McAndrews *et al.* (1973) aided by the modern reference collection.

Plant macrofossil analysis

During the subsampling for macrofossil analysis the outer 1–2 mm of each core segment was scraped off to remove possible contaminant macrofossils. All nonhorizontally oriented macrofossils on or near the sediment surface were also removed for the same purpose (Jackson, 1989). Samples of mostly 10-cm-long sediment core segments (about 200 ml in volume) were dispersed by gentle agitation in water and then washed on a 500- μm mesh to concentrate macrofossils. Identifiable materials were picked under a stereomicroscope at $\times 8$ magnification. Seeds and other plant organs were identified by comparison with the modern reference collection.

Multivariate analysis

Ordination analysis was carried out on pollen assemblages to facilitate the comparison of the vegetation shifts with the climate variation from Crawford Lake. I reduced the dimensionality of fossil pollen data through an indirect gradient (ordination) analysis (Prentice, 1980). I used the percentages of 27 pollen types that reached a value of at least 2% in one sample for numerical analysis using CANOCO program (Ter Braak, 1988). Because pollen data are 'closed' compositional data (as percentages) and they have constant

sum problem, a log-transformation was applied to the data (Aitchison, 1986). To check the linearity of the data, a detrended correspondence analysis (DCA) was carried out initially. DCA results show the gradient lengths of the ordination axes are less than 2.5 standard deviations (maximum 2.04 for the first axis), suggesting that most of the response curves (or surfaces) are linear or at least monotonic (Ter Braak, 1987). Thus the use of a linear method such as principal component analysis (PCA) is more appropriate (Ter Braak, 1987). Log-contrast PCA is an alternative form of PCA using log-transformation and centering both by samples and by pollen types (doubling centering), which provides better representation of real 'ecological distance' between samples. The selected 27 major pollen types from Crawford pollen data fill most of the pollen-sample spaces (*c.* 75%), which is another reason that warrants the use of PCA because PCA emphasizes quantitative variation in pollen percentages whereas DCA emphasizes qualitative variation (presence/absence) (Ter Braak, 1987). Similar analysis was performed on pollen data from Twiss Marl Pond, but with only 22 major pollen types.

Results

Radiocarbon dates and chronology

Four ^{14}C dates from Crawford Lake and eight dates from Twiss Pond were used for chronological control of the paleoecological records (Table 1). The AMS dates from Twiss Pond were expected to provide a reliable chronology for late-glacial pollen and macrofossil records. Unfortunately, five of these dates were rejected as too young due to insufficient datable carbon after pretreatment and possible contaminants. One sample (TO-6107) with limited pretreatment still yielded insufficient carbon for reliable dating and produced an even younger date presumably due to persistent contaminants (see notes in Table 1). The other dates for major pollen transitions in south-western Ontario were estimated from nearby dated pollen sequences (Mott & Farley-Gill, 1978; Terasmae & Matthews, 1980; McAndrews, 1981; Bennett, 1987; McAndrews & Boyko-Diakonow, 1989; Szeicz & MacDonald, 1991; Yu, 2000). The age models used for the two sites were shown in the age-depth plots (Fig. 3), which represents a tentative chronology, especially for the record older than 11 000 ^{14}C BP. Although the age estimates for the earlier record are regarded as tentative and may be in error, the effect of a potentially erroneous chronology will be small because the discussion on this period focuses on the nature and sequence of initial vegetation and afforestation, rather than on the timing and rates of their changes. Twiss Pond provided a sedimentary record only for the late glacial and early Holocene because there was a sediment hiatus of several thousand years in the mid- and late Holocene, indicated by a sharp lithologic contact and missing pollen zones (see the following two subsections). All ages in this

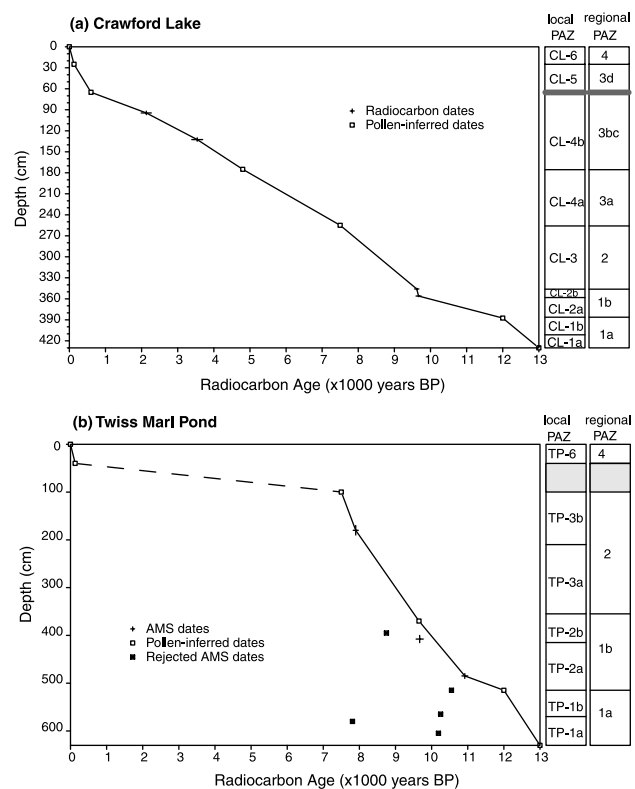


Fig. 3 The age-depth plots and age models for (a) Crawford Lake and (b) Twiss Marl Pond (TMP). Crosses are ^{14}C dates, open squares are pollen-inferred dates, and crossed squares are rejected AMS dates from TMP (see notes in Table 1). Inferred ^{14}C dates are 0 BP for sediment surface; 100 ^{14}C BP for *Ambrosia* rise (CL-5/CL-6 boundary corresponding with European settlement; McAndrews & Boyko-Diakonow, 1989); 600 BP for *Fagus* decline (CL-4b/CL-5; McAndrews & Boyko-Diakonow, 1989); 4800 BP for the mid-Holocene *Tsuga* decline (CL-4a/CL-4b; interpolated; Davis, 1981; Webb, 1982); 7500 BP for the mid-Holocene *Pinus-Fagus* transition (CL-3/CL-4a; extrapolated from TMP; Bennett, 1987); 9650 BP for *Picea* recurrence at Twiss Marl Pond (AMS dates from Crawford Lake; see Table 1); 12 000 BP for the extrapolated lower boundary of *Picea* zone (1b/2a; Mott & Farley-Gill, 1978, Terasmae & Matthews, 1980, Szeicz & MacDonald, 1991); and 13 000 BP for the base of the records (extrapolated; local deglaciation: Barnett, 1979; Calkin & McAndrews, 1980; Karrow, 1987). Local and regional pollen assemblage zones (PAZ) are also shown on the right of both plots. The date of 9670 ± 100 (TO-6106) from TMP is not used in the age model, because it could be too young due to limited pretreatment of the sample (Table 1). Dashed line indicates a sediment hiatus at TMP.

paper are radiocarbon ages (^{14}C BP, or ka = 1000 ^{14}C BP) unless stated otherwise.

Sediment lithology

For both Crawford Lake and Twiss Marl Pond cores, loss-on-ignition data were presented in Fig. 4 and their lithology was summarized in Table 2. The sediment of both cores shows a

Table 2 Sediment lithology at Crawford Lake and Twiss Marl Pond, Ontario, Canada

Core	Depth (cm)	Age (¹⁴ C ka)	Description
Crawford Lake	0–185	0–4.8	Organic-rich marl: > 70% organic matter, laminations disappeared at 170–165 cm and at 138–112 cm
	185–360	4.8–10	Marl: mostly > 60% carbonate, dark banded/laminated marl bracketing a distinct 6.5-cm thick light-color sediment layer at 354–347.5 cm, laminated sediments initiated at 208 cm
	360–387	10–12	Clayey marl: > 50% carbonate
	387–430	12–13	Clay: 20% carbonate and low organic matter, top clay indistinctly laminated
	430+		Impenetrable, likely bedrock
Twiss Marl Pond	0–35	0–0.3	Woody peat: 50% organic matter
	35–525	7.5–12	Marl: 80–90% carbonate
	525–565	12–12.5	Clayey marl
	565–630	12.5–13	Clay: slightly banded reddish and grey clay
	630+		Impenetrable, probably gravel deposit

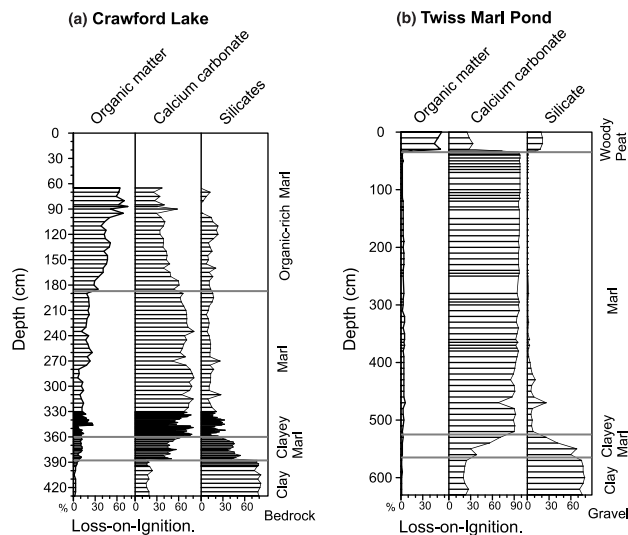


Fig. 4 Sediment composition estimated from loss-on-ignition analysis for (a) Crawford Lake and (b) Twiss Marl Pond. The horizontal lines indicate the sampling levels, with close sampling at 395–330 cm from Crawford Lake.

typical lithology sequence from clay, through transitional clayey marl, to marl.

Pollen assemblage zones

Crawford Lake The percentage pollen diagram was divided into six local pollen assemblage zones (PAZ) with subzones if necessary, based on stratigraphically constrained cluster analysis (CONISS; Grimm, 1987) (Fig. 5). The regional pollen zones for southern Ontario of McAndrews (1981, 1994a) were also included for ease of comparison with other pollen diagrams. Table 3 summarizes each zone or subzone.

Twiss Marl Pond The pollen diagram was divided into four local pollen assemblage zones (PAZ) with subzones if necessary, based on cluster analysis (Grimm, 1987). The zones were comparable with those of the Crawford Lake core, although there is a sediment hiatus in this core (Fig. 6). Table 4 summarizes each zone or subzone.

Pollen concentrations at Crawford Lake are about 5-fold higher than at Twiss Marl Pond (Fig. 7), which were summarized for each zone/subzone in Tables 3 and 4. Late-glacial and early Holocene portion of Crawford Lake percentage pollen diagram was presented also on time scale for ease of the following discussions (Fig. 8).

Plant macrofossils

Crawford Lake The macrofossil concentration diagram (Fig. 9) was divided into five local zones, with subzones if necessary based on CONISS (Grimm, 1987). The data were summarized in Table 5.

Twiss Marl Pond The Twiss macrofossil concentration diagram was divided into four local macrofossil assemblage zones with subzones (Fig. 10), based on CONISS (Grimm, 1987), summarized in Table 6.

Multivariate analysis

Log-PCA results of pollen types and samples of the Crawford Lake and Twiss Marl Pond data (Figs 12 and 13) reflect the characteristics of the pollen diagrams and summarize the vegetation dynamics. At Crawford Lake, the pollen type ordination separates along the first axis the temperate deciduous trees (e.g. *Acer*, *Fagus*, *Carya*, *Quercus*, *Betula*) and *Tsuga* on the negative end from other conifers, shrubs and herbs (Fig. 12b). The second axis separates late-glacial taxa (herbs, shrubs, *Picea*) from early Holocene conifers (*Pinus*,

(a) Crawford Lake: Percentages of trees and shrubs

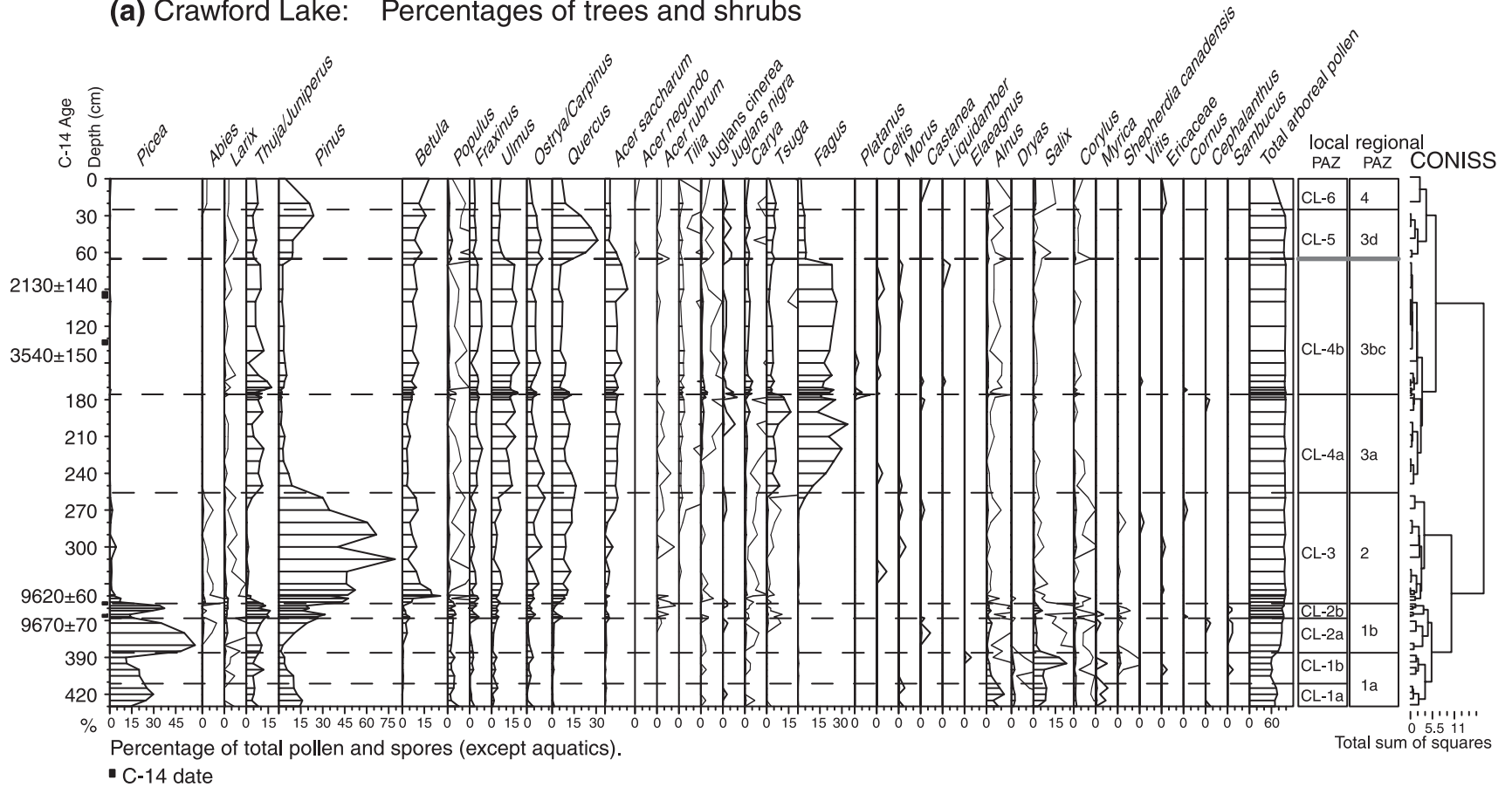


Fig. 5 Percentage pollen diagrams of Crawford Lake. (a) Trees and shrubs; and (b) Herbs and ferns. Open curves for some pollen types are 10x exaggeration. There might be a sedimentary gap in the CL-4b/CL-5 boundary, where the Livingstone core and the plastic-tube core are joined. Regional pollen zones followed McAndrews (1981, 1994a).

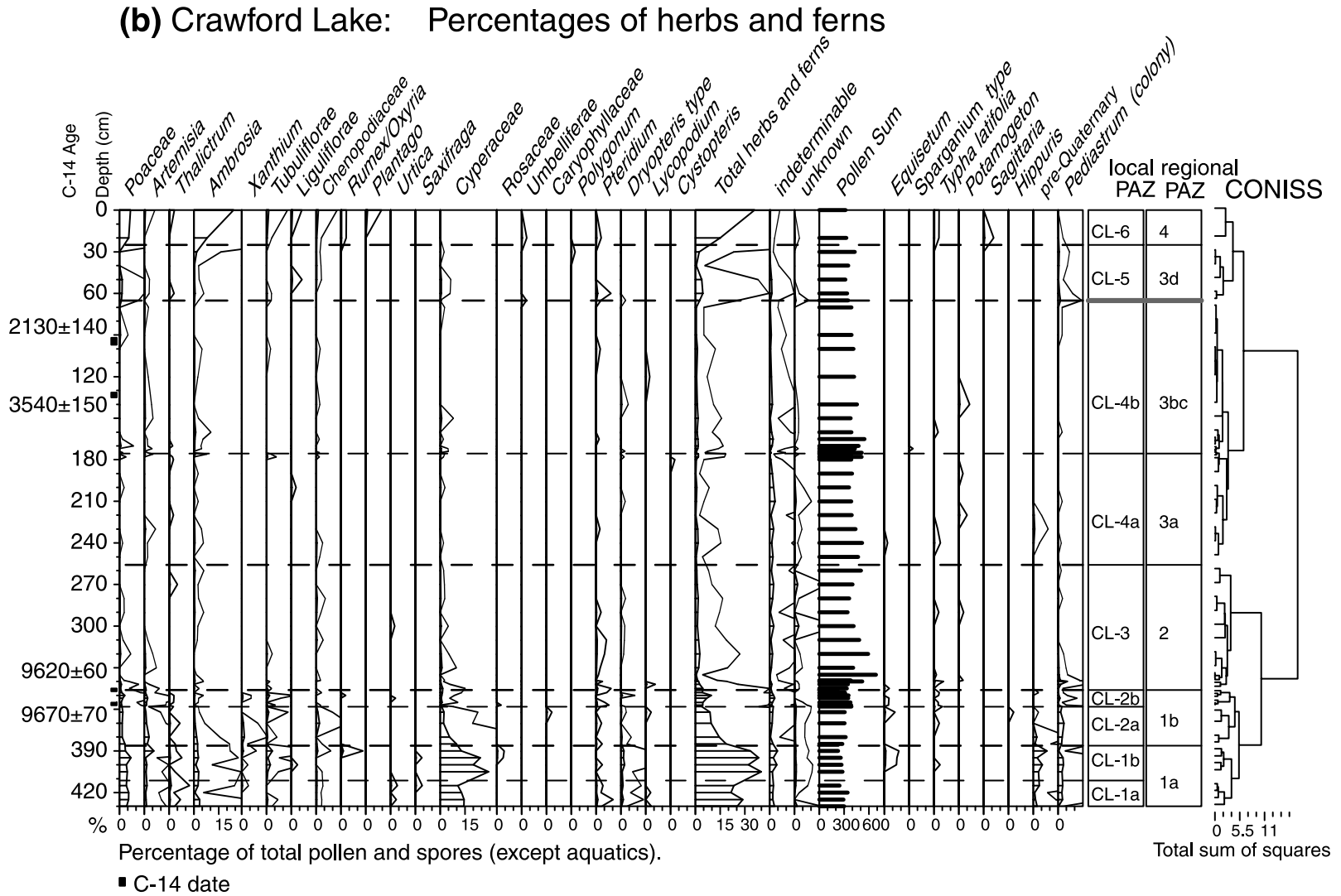


Fig. 5 Continued.

Table 3 Pollen assemblage zones at Crawford Lake, Ontario, Canada

Zone/Subzone	Depth (cm)	Age (^{14}C ka)	Description
CL-1a: <i>Alnus-Picea-Pinus</i> <i>Cyperaceae-Salix</i>	430–410	13–12.5	This basal subzone was dominated by the shrubs <i>Alnus</i> , <i>Salix</i> and <i>Thuja/Juniperus</i> (collectively c. 25%), and the herbs <i>Cyperaceae</i> , <i>Poaceae</i> and <i>Ambrosia</i> (collectively 20–25%). <i>Populus</i> (c. 5%) and possibly <i>Picea</i> (up to 30%) might be locally or regionally present but other tree pollen types such as <i>Pinus</i> , <i>Ulmus</i> and <i>Fraxinus</i> are attributed to long-distance transport of pollen grains from the south and west. Total pollen concentration was low at 10 000–15 000 grains ml ⁻¹ .
CL-1b: <i>Salix-Cyperaceae-Thuja/Juniperus-Artemisia</i>	410–387	12.5–12	<i>Alnus</i> decreased gradually, and <i>Salix</i> replaced <i>Alnus</i> as the predominant shrub in the upper part, together with the appearance of <i>Shepherdia canadensis</i> . <i>Cyperaceae</i> increased sharply and remained the dominant herb together with <i>Poaceae</i> ; <i>Artemisia</i> had a low peak near the top and <i>Tubuliflorae</i> is continuous in this subzone. Pollen concentration slightly increased to 16 000–40 000 grains ml ⁻¹ .
CL-2a: <i>Picea-Thuja/Juniperus</i>	387–360	12–10	This subzone was dominated by <i>Picea</i> pollen (up to 58%) with some <i>Thuja/Juniperus</i> and <i>Populus</i> . <i>Pinus</i> increased gradually from 2 to 25% at the top of this subzone. Herb and shrub (<i>Cyperaceae</i> , <i>Poaceae</i> , <i>Salix</i> and <i>Alnus</i>) pollen showed a gradual, significant decline. Pollen concentration increased to 50 000–60 000 grains ml ⁻¹ .
CL-2b: <i>Pinus-Picea-Thuja/Juniperus-Salix</i>	360–346	10–9.6	In the lower part of this subzone <i>Pinus</i> increased to 30% accompanied by an increase of deciduous tree pollen types such as <i>Betula</i> , <i>Fraxinus</i> , <i>Quercus</i> , <i>Ulmus</i> , <i>Ostrya/Carpinus</i> and <i>Acer</i> , whereas <i>Picea</i> , <i>Alnus</i> , <i>Salix</i> , <i>Cyperaceae</i> and <i>Artemisia</i> showed corresponding declines. Pollen concentration showed a steep increase up to 160 000 grains ml ⁻¹ . In the upper part of this subzone, <i>Picea</i> returned to become dominant (up to 38%) with corresponding declines of <i>Pinus</i> and most deciduous tree taxa. The upper part also showed a relative increase of shrub and herb pollen percentages and decreased pollen concentration (down to 60 000 grains ml ⁻¹).
CL-3: <i>Pinus-Quercus-Betula-Ostrya/Carpinus-Ulmus</i>	346–255	9.6–7.5	In this zone <i>Pinus</i> became dominant (up to 78%) with increases of most deciduous trees such as <i>Betula</i> (12–25%), <i>Quercus</i> (10%), <i>Ostrya/Carpinus</i> (up to 10%), <i>Ulmus</i> (up to 8%), <i>Fraxinus</i> and <i>Acer</i> , whereas <i>Picea</i> , <i>Thuja/Juniperus</i> , <i>Populus</i> , shrubs and herbs showed corresponding declines to negligible levels. A brief peak of <i>Betula</i> at the beginning of this zone is noticeable. Pollen concentration increased to 560 000 grains ml ⁻¹ .
CL-4a: <i>Fagus-Tsuga-Ulmus-Thuja/Juniperus-Acer</i>	255–175	7.5–4.8	In this subzone <i>Fagus</i> (25–30%) and other deciduous taxa such as <i>Ulmus</i> (12%) and <i>Acer</i> (8%) became dominant, together with <i>Tsuga</i> (8–15%) and <i>Thuja/Juniperus</i> (10%). Pollen concentration is at 350 000–500 000 grains ml ⁻¹ .
CL-4b: <i>Fagus-Ulmus-Thuja/Juniperus-Betula</i>	175–65	4.8–0.6	This subzone showed a decline of <i>Tsuga</i> (to ≤5%) and a slight increase of <i>Betula</i> (to 10%), <i>Pinus</i> (4%) and <i>Carya</i> . Other taxa are like the previous subzone CL-4a. Pollen concentration decreased to 250 000 grains ml ⁻¹ .
CL-5: <i>Quercus-Pinus-Betula-Ostrya/Carpinus</i>	65–25	0.6–0.1	In this zone <i>Fagus</i> (5%) declined and <i>Quercus</i> (up to 30%) and <i>Pinus</i> (20%) increased. Herbs increased slightly, especially <i>Poaceae</i> . Pollen concentration further declined to about 150 000 grains ml ⁻¹ .
CL-6: <i>Ambrosia-Poaceae-Betula</i>	25–0	0.1–0	This zone was dominated by herbs (collectively up to 35%), especially <i>Ambrosia</i> and <i>Poaceae</i> . This zone corresponded with European settlement. Pollen concentration declined to 80 000 grains ml ⁻¹ .

(a) Twiss Marl Pond: Percentages of trees and shrubs

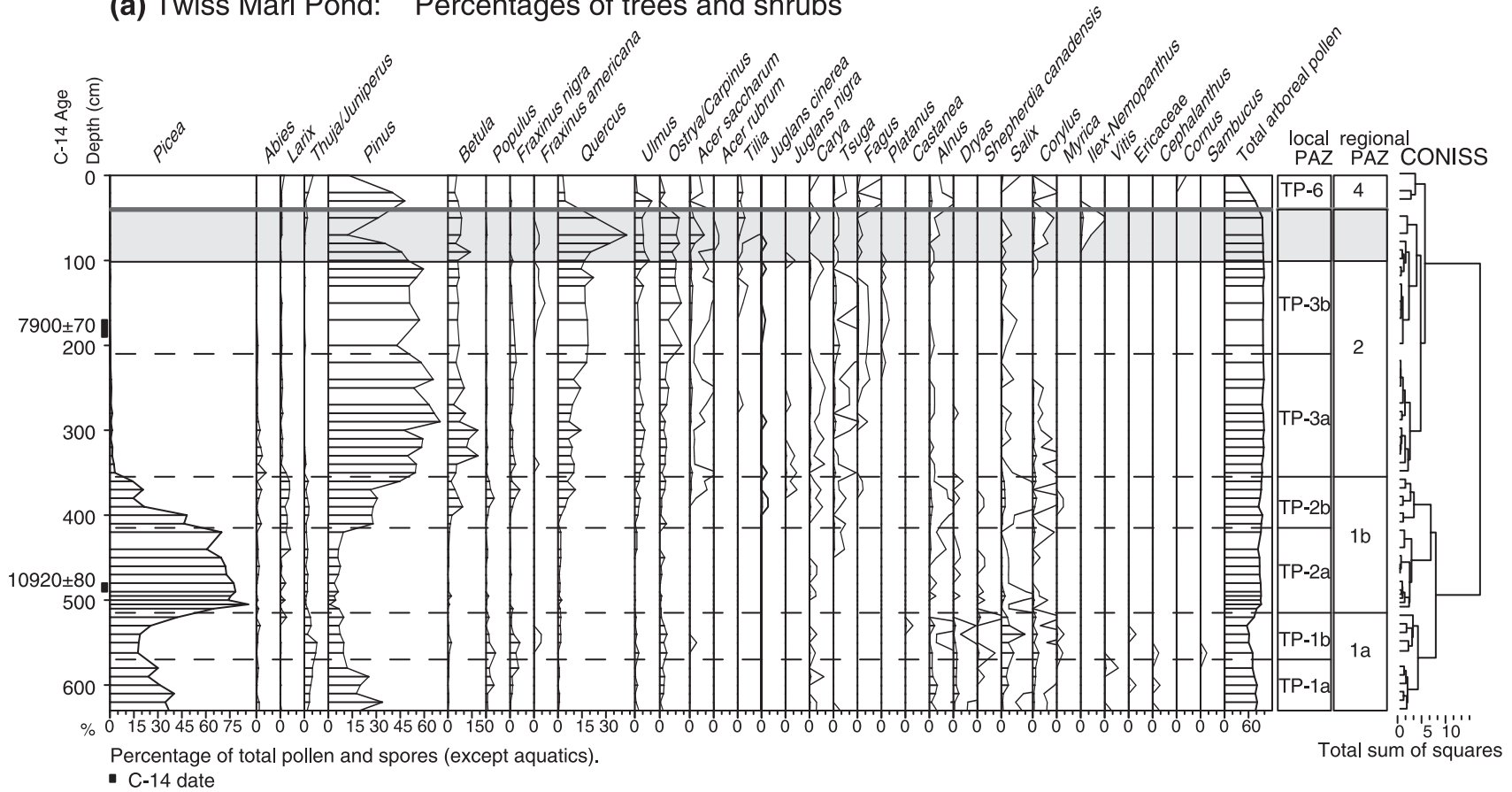


Fig. 6 Percentage pollen diagrams of Twiss Marl Pond. (a) Trees and shrubs; and (b) Herbs, ferns and stomata. Open curves for some pollen types are 10x magnification. Shaded band shows the hardened sediment immediately below the hiatus at 35 cm, which has distorted pollen assemblages. Regional pollen zones followed McAndrews (1981, 1994a).

(b) Twiss Marl Pond: Percentages of herbs and ferns

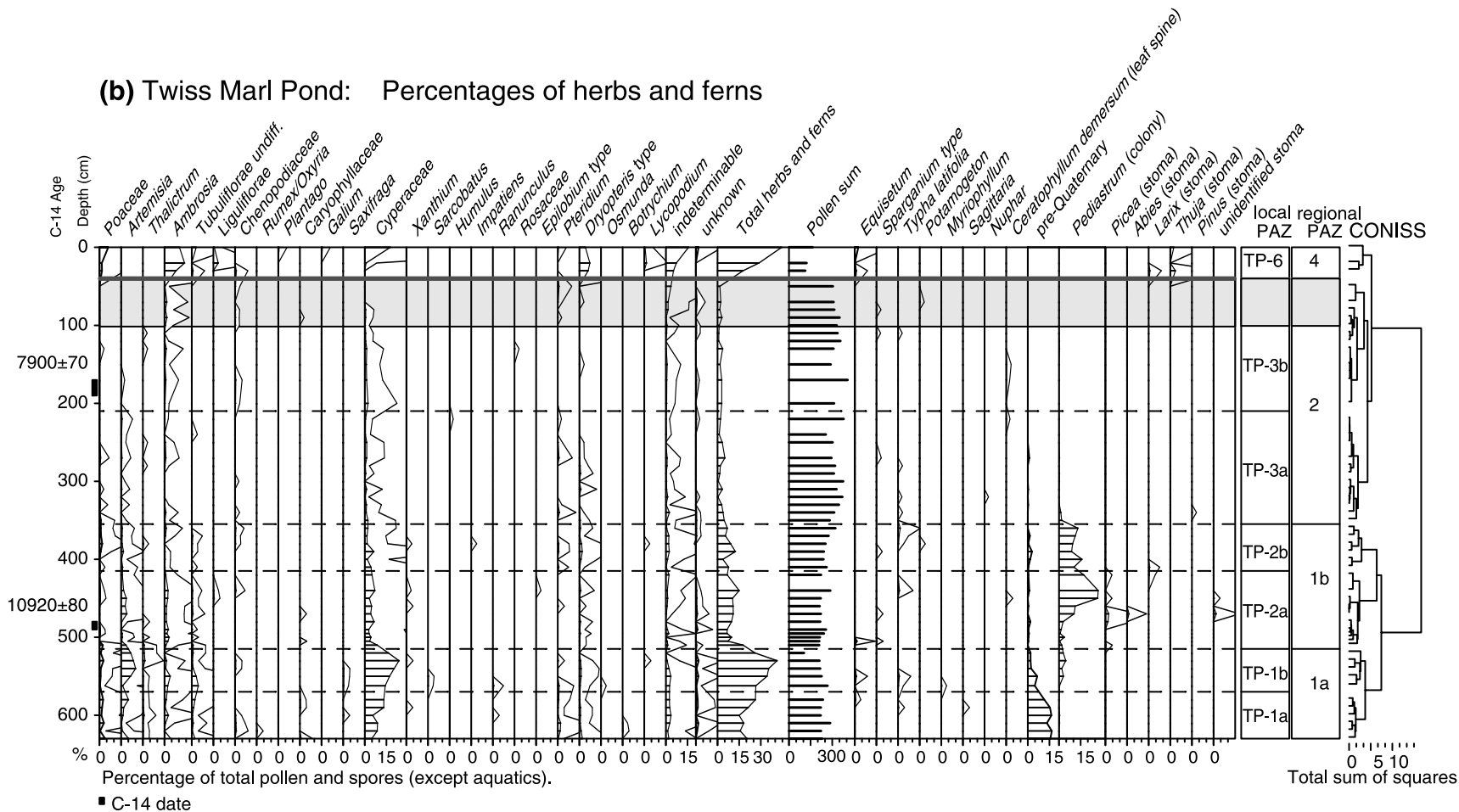


Fig. 6 Continued.

Table 4 Pollen assemblage zones at Twiss Marl Pond, Ontario, Canada

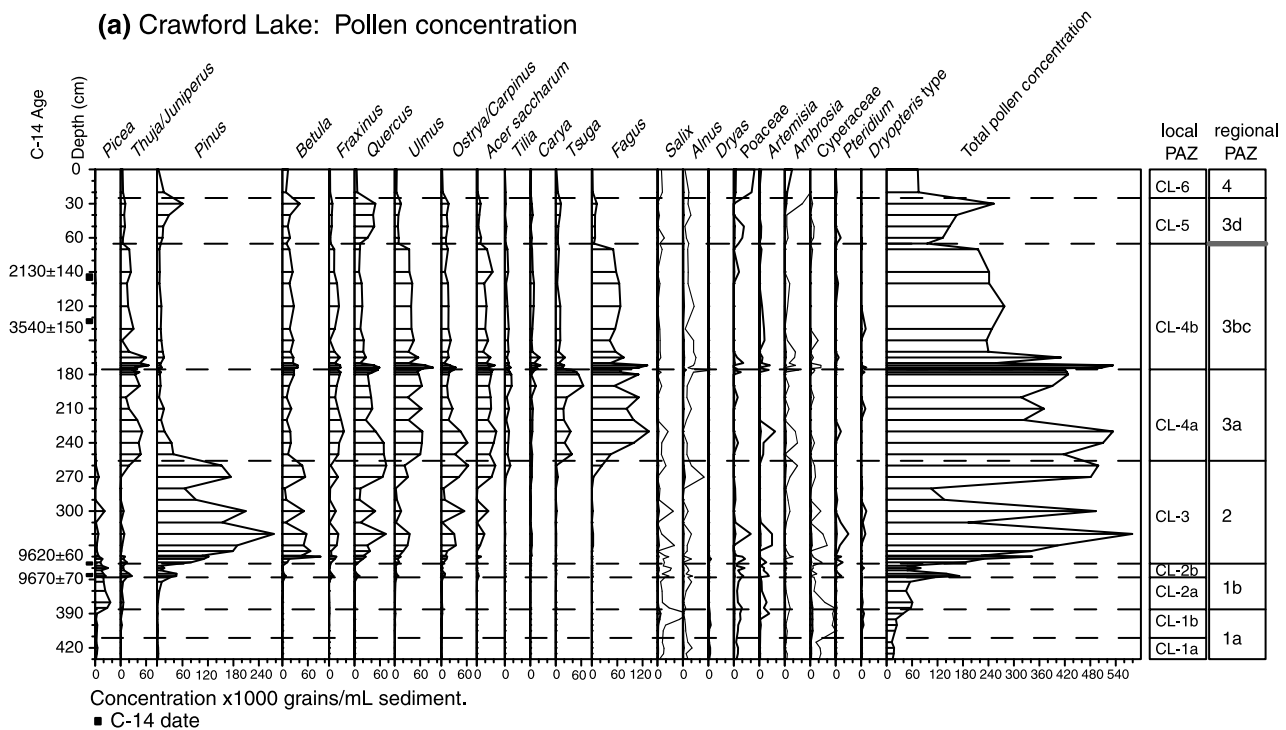
Zone/Subzone	Depth (cm)	Age (¹⁴ C ka)	Description
TP-1a: <i>Picea-Pinus-Cyperaceae</i> <i>Alnus-Dryas</i>	630–570	13–12.5	This basal subzone was dominated by trees <i>Picea</i> (30%) and <i>Pinus</i> (20%), shrubs <i>Alnus</i> , <i>Salix</i> , <i>Thuja/Juniperus</i> (likely <i>Juniperus</i>) and <i>Dryas</i> (collectively 10–12%) and <i>Cyperaceae</i> (10%) and other herbs (collectively 20%). <i>Populus</i> (up to 5%) and possibly <i>Picea</i> might be locally or regionally present but other tree pollen types such as <i>Pinus</i> , <i>Ulmus</i> , <i>Ostrya/Carpinus</i> and <i>Fraxinus</i> were probably derived from long-distance transport from the south and west. Pollen concentration was low at 5000–10 000 grains ml ⁻¹ .
TP-1b: <i>Salix-Cyperaceae-Artemisia-Thuja/Juniperus-Picea</i>	570–515	12.5–12	In this subzone <i>Alnus</i> decreased gradually, and <i>Salix</i> replaced <i>Alnus</i> as the predominant shrub. <i>Thuja/Juniperus</i> increased to maximum (8%), together with more frequent occurrence of <i>Shepherdia canadensis</i> . <i>Cyperaceae</i> and <i>Artemisia</i> increased sharply and remained the dominant herbs together with <i>Tubuliflorae</i> (undiff.) near the bottom. Pollen concentration slightly increased to 10 000–15 000 grains ml ⁻¹ .
TP-2a: <i>Picea-Cyperaceae</i>	515–415	12–10	This subzone was dominated by <i>Picea</i> (up to 78%) with some <i>Larix</i> , <i>Thuja/Juniperus</i> and <i>Cyperaceae</i> . Herbs and shrubs (<i>Cyperaceae</i> , <i>Poaceae</i> , <i>Artemisia</i> , <i>Salix</i> and <i>Alnus</i>) all declined. The top of this subzone showed an abrupt increase in green algae <i>Pediastrum</i> colonies (up to 25%). Pollen concentration increased to 15 000–30 000 grains ml ⁻¹ .
TP-2b: <i>Picea-Pinus-Larix-Salix</i>	415–355	10–9.6	In this subzone <i>Picea</i> decreased from 50% to 5% and <i>Pinus</i> increased to 40% accompanied by increased deciduous tree pollen types such as <i>Betula</i> , <i>Fraxinus</i> , <i>Quercus</i> , <i>Ulmus</i> and <i>Ostrya/Carpinus</i> , whereas <i>Cyperaceae</i> , <i>Artemisia</i> and <i>Ambrosia</i> declined. A distinct feature of this transitional zone is the return of <i>Populus</i> and the shrubs <i>Alnus</i> , <i>Salix</i> and <i>Corylus</i> and the persistence of <i>Larix</i> . <i>Pediastrum</i> persisted at 10%. Pollen concentration decreased slightly to 20 000 grains ml ⁻¹ .
TP-3: <i>Pinus-Quercus-Ostrya/Carpinus-Betula</i>	355–100	9.6–7.5	<i>Pinus</i> became predominant (up to 70%) with increases in most deciduous tree pollen types <i>Betula</i> , <i>Quercus</i> , <i>Ulmus</i> and <i>Ostrya/Carpinus</i> . Virtually all shrubs including <i>Thuja/Juniperus</i> , herbs and <i>Pediastrum</i> disappeared. Subzone TP-3a had more <i>Betula</i> and <i>Fraxinus nigra</i> , whereas subzone TP-3b had more <i>Quercus</i> , <i>Ostrya/Carpinus</i> and <i>Tsuga</i> . This zone also showed a sharp increase of pollen concentration to about 60 000–59 000 grains ml ⁻¹ . The interval from 100 to 35 cm is a hardened, dry sediment linked to the hiatus at 35 cm; this interval has poorly-preserved pollen, abnormally-low pollen concentration and, presumably, distorted pollen assemblages.
TP-6: <i>Ambrosia-Poaceae-Cyperaceae-Dryopteris</i> type	35–0	0.1–0	This zone was dominated by herb pollen (up to 45%) and corresponded with European settlement in this area. Pollen concentration was very low at 15 000 grains ml ⁻¹ .

Larix) and mid-Holocene (*Fagus*, *Acer*, *Tsuga*) from late Holocene taxa (*Quercus*, *Betula*).

In the ordination of pollen samples of Crawford Lake (Fig. 12a), the first and second axes account for 59.9% and 17.9% of variance in pollen data, respectively. The first two principal components together captured about 80% of variance, so variation in their sample scores represents shifts in vegetation. The DCA results essentially show similar patterns (not shown here). Sample groupings in the ordination

space as represented by the first two axes are associated with the local pollen assemblage zones. The first axis separates late-glacial tundra (zone 1) and *Picea* woodland (zone 2) from mid- and late Holocene assemblages (zones 4, 5 and 6). The second axis separates early Holocene *Pinus* forest samples (zone 3) on the positive end from all other samples. Samples of sparse and dense tundra (subzones 1a and 1b) are tightly clustered, whereas late-glacial *Picea* woodland samples spread along the second axis from tundra to *Pinus*

(a) Crawford Lake: Pollen concentration



(b) Twiss Marl Pond: Pollen concentration

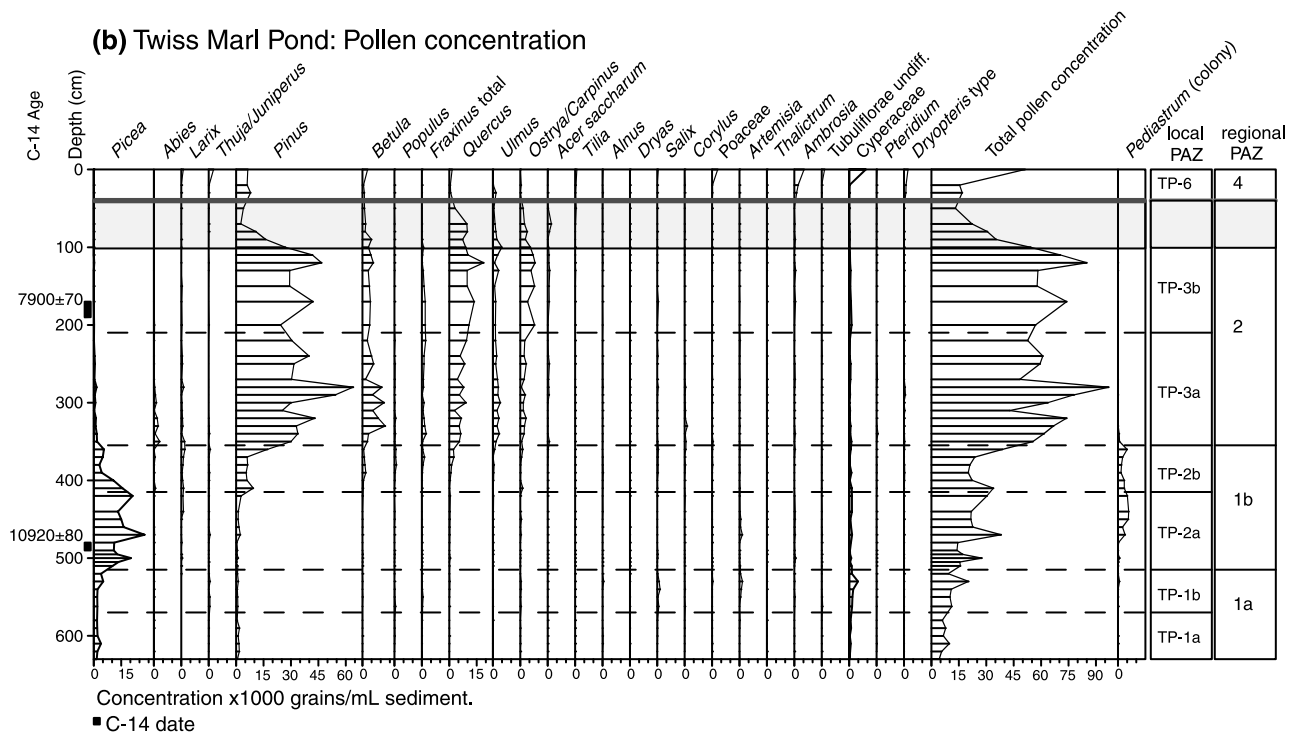


Fig. 7 Pollen concentration diagrams of selected pollen types from (a) Crawford Lake, and (b) Twiss Marl Pond. Open curves for some pollen types are 10x magnification.

forest groupings. The samples around the *Picea* recurrence in the early Holocene (subzone 2b) show shifting back and forth between *Picea* woodland (subzone 2a) and *Pinus* forest (zone 3). The *Fagus-Tsuga* mixed forest (Zone 4)

samples are tightly clustered. The *Quercus-Pinus* forest (zone 5) samples in the late Holocene revert toward early Holocene *Pinus* forest (zone 3) from mid-Holocene mixed forest (zone 4).

Crawford Lake, Ontario, Canada
Late-Glacial and Early Holocene Summary Pollen Diagram

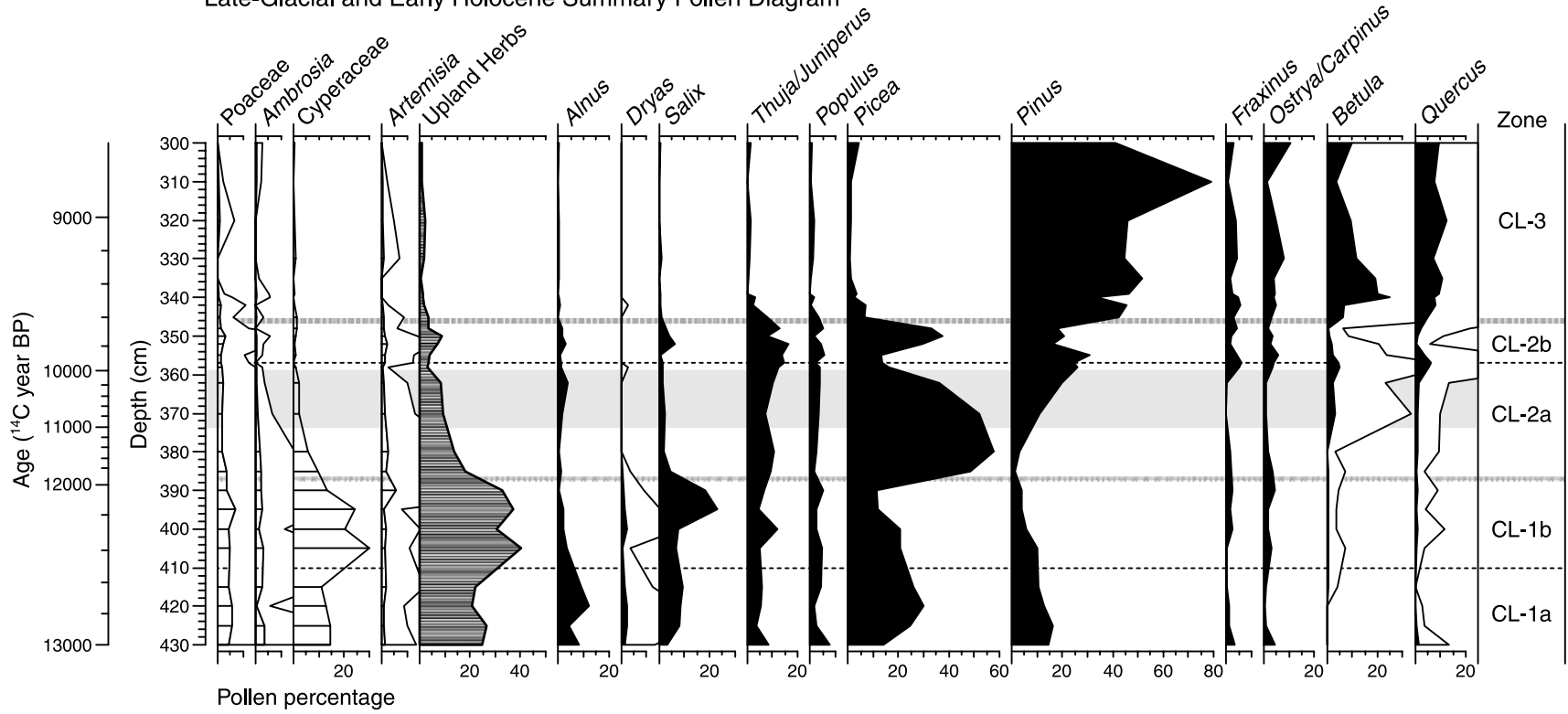


Fig. 8 Summary pollen percentage diagram of late-glacial and early Holocene period at Crawford Lake also shown on age scale. Shaded band indicates the Younger Dryas chronozone from 11 000 to 10 000 ¹⁴C BP.

Crawford Lake: Plant macrofossils

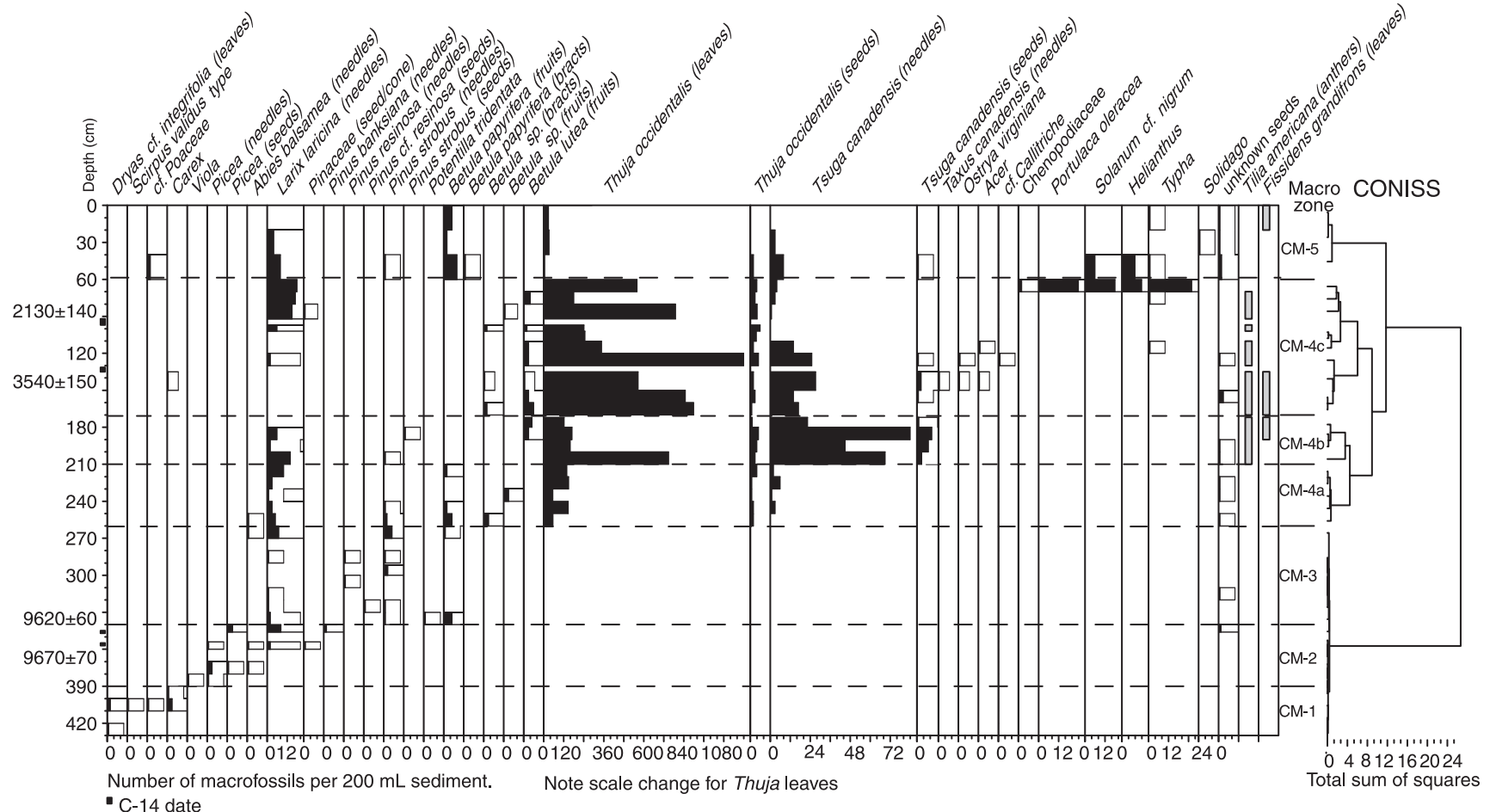


Fig. 9 Plant-macrofossil concentration diagram of Crawford Lake. Seeds or fruits unless indicated otherwise. The samples at 92–97, 130–135, 170–172, 270–280, 290–292, 346–347 and 353–354 cm were not analyzed for macrofossils. Open bars are 10x magnification. Note scale change for *Thuja occidentalis* leaves (at 1/10).

Table 5 Plant-macrofossil assemblage zones at Crawford Lake, Ontario, Canada

Zone/Subzone	Depth (cm)	Age (^{14}C ka)	Description
CM-1: <i>Dryas-Carex</i>	430–390	13–12	Only a few fossil <i>Dryas</i> leaves, <i>Carex</i> seeds, <i>Scirpus validus</i> type seeds and a cf. Poaceae seed.
CM-2: <i>Picea-Abies</i>	390–340	12–9.5	<i>Picea</i> appeared, together with <i>Abies</i> and <i>Larix</i> . A <i>Pinus banksiana</i> needle occurs at the top of this zone.
CM-3: <i>Pinus-Larix</i>	340–260	9.5–7.5	<i>Pinus resinosa</i> and <i>P. strobus</i> , together with <i>Betula papyrifera</i> fruits.
CM-4a: <i>Thuja-Larix-Tsuga</i>	260–210	7.5–5.8	<i>Thuja</i> , <i>Tsuga</i> appeared.
CM-4b: <i>Tsuga-Thuja-Larix</i>	210–170	5.8–4.8	Abrupt increase of <i>Tsuga</i> needles and the appearance of <i>Tsuga</i> seeds and <i>Tilia</i> anthers. <i>Betula lutea</i> (= <i>B. alleghaniensis</i>) appeared too.
CM-4c: <i>Thuja-Tsuga-Betula lutea</i>	170–60	4.8–0.6	A sharp increase of <i>Thuja</i> leaves, a decline of <i>Tsuga</i> fossils and continuous appearance of <i>Betula lutea</i> and other fossils such as <i>Acer</i> , <i>Ostrya virginina</i> and <i>Taxus canadensis</i> .
CM-5: <i>Betula papyrifera-Tsuga-Thuja</i>	60–0	0.6–0	Abundant weed fossils of <i>Portulaca oleracea</i> , Chenopodiaceae and <i>Typha</i> at the transition, together with Indian-utilized plants such as sunflower (<i>Helianthus</i>) and black nightshade (<i>Solanum</i> cf. <i>nigrum</i>) (Fig. 11a).

Table 6 Plant-macrofossil assemblage zones at Twiss Marl Pond, Ontario, Canada

Zone/Subzone	Depth (cm)	Age (^{14}C ka)	Description
TM-1: <i>Dryas-Salix-Potamogeton</i>	630–540	13–12.2	Dominated by <i>Dryas integrifolia</i> leaves and <i>Salix herbacea</i> leaves, together with their receptacles, seeds and buds (Fig. 11); aquatics including <i>Potamogeton</i> , <i>Carex</i> , <i>Nitella</i> (lower) and <i>Chara</i> (upper); many unknown fossils in this zone; a <i>Picea</i> seed in this zone is a broken seed (?) fragment, appearing to be a <i>Picea</i> seed but not being identified with confidence.
TM-2: <i>Picea</i>	540–410	12.2–10	Abundant <i>Picea</i> needles and seeds, together with some <i>Carex</i> and Ericaceae leaves; one <i>Larix</i> needle at the base of this zone possibly being displaced from younger sediments, as suggested by a too young AMS ^{14}C date with this fossil (see note in Table 1).
TM-3a: <i>Larix-Picea</i>	410–330	10–9.4	Increased <i>Larix</i> and declined <i>Picea</i> ; <i>Betula papyrifera</i> appeared; <i>Najas flexilis</i> increased
TM-3b: <i>Larix-Najas-Betula</i>	330–190	9.4–8?	<i>Betula</i> and <i>Najas</i> increased to peak values, whereas <i>Larix</i> declined slightly; a few <i>Pinus resinosa</i> and <i>P. strobus</i> needles.
TM-3c: <i>Pinus-Larix</i>	190–20	8?–7.5	Abundant <i>Pinus strobus</i> needles; a slight increase of <i>Larix</i> needles; no fossils preserved in the upper part, probably due to oxidation of exposed top marl below the hiatus.
TM-4: <i>Thuja-Carex</i>	20–0	0.1–0	Post-settlement macrofossil assemblage dominated by <i>Thuja</i> and <i>Carex</i> , with diverse wetland taxa, including <i>Lycopus americanus</i> , <i>Leersia</i> , <i>Rubus</i> , <i>Eleocharis ovata</i> type and <i>Mentha arvensis</i> ; <i>Betula papyrifera</i> (fruits and bracts) reappeared.

At Twiss Marl Pond, the first axis separates herb- and *Picea*-dominated samples of zones 1 and 2 from the rest (zones 3 and 6), while the second axis further separates each of these two groups (Fig. 13a). The first and second axes account for 59.3% and 8.4% of variance in pollen data, respectively.

Discussion

Pioneer treeless vegetation

Initially after the retreat of the ice sheets, pollen records from the two sites show a vegetation succession from

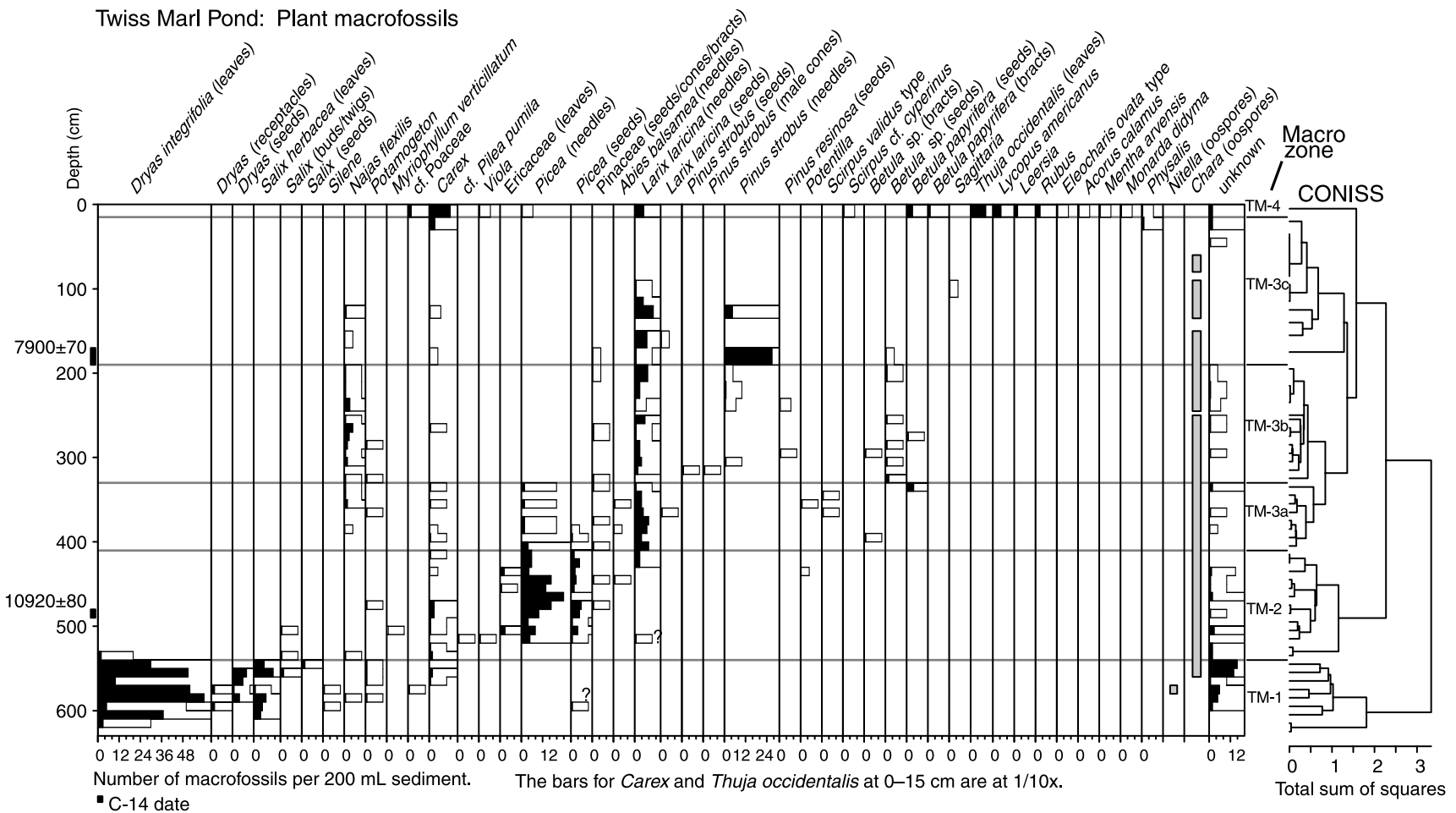


Fig. 10 Plant-macrofossil concentration diagram of Twiss Marl Pond. Seeds or fruits unless indicated otherwise. The samples at 30–40, 80–90, 135–150 and 245–250 cm were not analyzed for macrofossils. Open bars are 10x magnification. Note scale changes for *Carex* and *Thuja occidentalis* leaves at 0–15 cm (at 1/10).

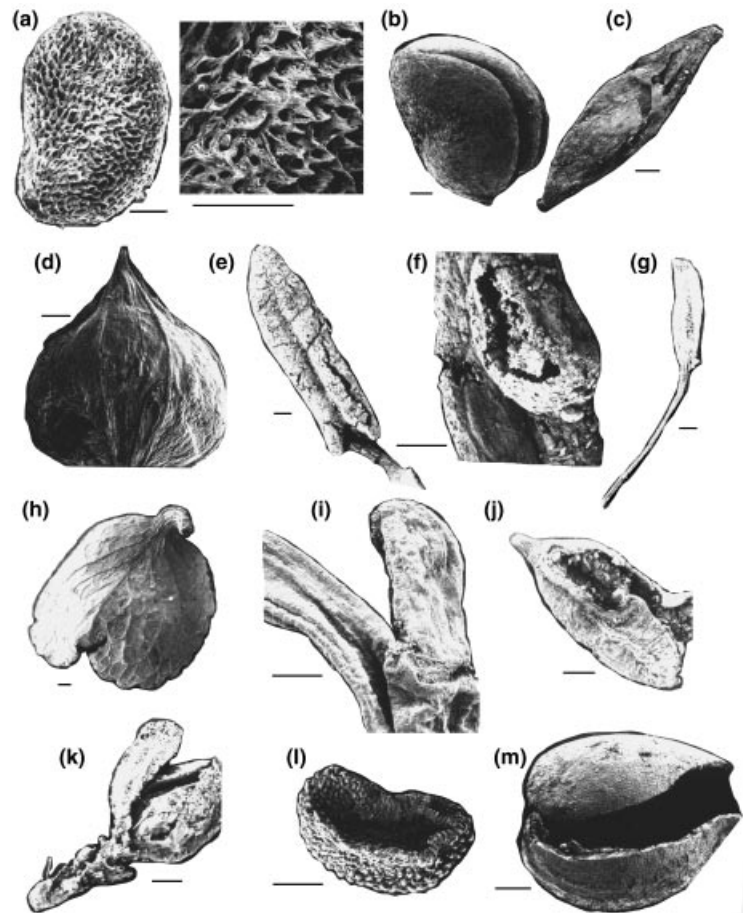


Fig. 11 Scanning electron microscopy (SEM) micrographs of selected plant macrofossils. Crawford Lake: (a) *Solanum* cf. *nigrum* at 135–150 cm; and Twiss Marl Pond: (b) *Potamogeton* fruitstone at 580–590 cm; (c) *Najas flexilis* seed (inner wall) at 530–540 cm; (d) *Carex* achene at 590–600 cm; (e) *Dryas integrifolia* leaf at 580–590 cm; (f) *Dryas integrifolia* leaf with gall at 570–580 cm; (g) *Dryas* seed at 570–580 cm; (h) *Salix herbacea* leaf at 550–560 cm; (i) *Salix* twig with bud at 550–560 cm; (j) *Salix herbacea* seed at 560–570 cm; (k) *Salix* bud (?) at 550–560 cm; (l) *Silene* cf. *acaulis* seed at 590–600 cm; and (m) *Viola* seed at 510–520 cm. Scale bars are 200 μ m.

Alnus-Dryas-Cyperaceae sparse tundra (subzone 1a) to *Salix-Juniperus-Cyperaceae-Artemisia* dense tundra (subzone 1b). *Alnus*-dominated tundra had sparse plant cover (perhaps a barren periglacial desert), as suggested by low pollen concentrations and, presumably, low accumulation rates, and high percentages of long-distance transported pollen. Although I have not systematically distinguished pollen grains of *Alnus* to species, most pollen in this zone is attributed to *A. crispa* based on its small size, unclear arcs and delicate appearance (Richard, 1970). *A. crispa* is a low shrub, usually occurring in tundra as a pioneer species (Matthews, 1992, pp. 273–276). *A. crispa* pollen has been recorded during the early postglacial at other sites in southern Ontario (Bennett, 1987). The sparse tundra also had some pollen of the shrubs *Dryas* and *Salix* and pollen of the herbs Poaceae, *Thalictrum*, *Urtica*, *Pteridium* and Caryophyllaceae. Plant macrofossils recorded several arctic-alpine plants that grew at or around the sites, including abundant *Dryas integrifolia* (a species of calcareous and neutral soils) leaves and seeds, *Salix herbacea* (a snowbed species) leaves and seeds and *Silene* cf. *acaulis* (a cushion plant) seeds. These plants grow in a treeless landscape, which is also supported by the absence of tree macrofossils such as *Picea*

that were abundant in succeeding woodland/forest stages. *A. crispa* and *Dryas integrifolia* are nitrogen-fixers and thus adapted to raw soils. Recent ecological studies show that nitrogen-fixers are not necessary in the early stages of glacier foreland succession (Chapin *et al.*, 1994; Fastie, 1995), but in bedrock settings and very shallow soils around these sites they might be essential for plants to colonize and establish.

The dense tundra (1b) dominated by *Salix*, *Juniperus*, *Cyperaceae* and *Artemisia* is suggested by increased pollen concentration and, presumably, accumulation rates, and also decreased percentages of exotic long-distance pollen input. The synchronous decline of *Picea* and *Pinus* indicates decreased importance of long-distance or extra regional pollen contribution to the local and regional pollen rains. This is mainly because of increased local pollen production and contribution with increased plant covers, despite closer proximity of these boreal taxa in subsequent migration northward. McAndrews & Jackson (1988) found a similar decline of *Picea* and *Pinus* pollen percentages during this period (their zone 1a) at the Rostock site in southern Ontario (see Fig. 1a for location), when pollen percentages are calculated without presumed local *Cyperaceae* pollen in the pollen sum

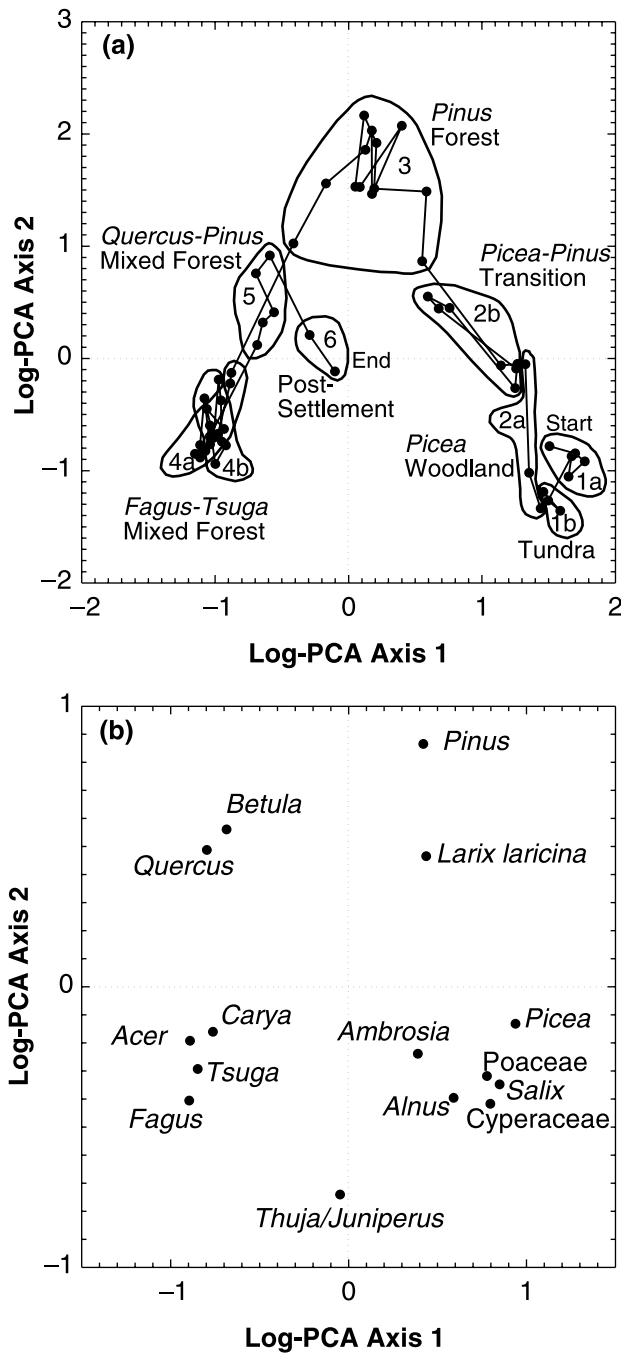


Fig. 12 Log-contrast PCA ordinations of the Crawford Lake pollen data. (a) The ordination of pollen samples along the first two axes showing groupings of pollen assemblages from zones 1–6. (b) The ordination of pollen types along the first two axes. Only shown selected 15 major pollen types of 27 types used. The first and second axes account for 59.9% and 17.9% of variance in pollen data, respectively. Considering both sample and pollen type plots together visualizes the pollen/vegetation changes as related to dominant pollen taxa. Three end-member assemblages, tundra (zone 1), *Pinus* forest (zone 3), and *Fagus-Tsuga* forest (zone 4), are located at three points of the triangle-shaped sample configuration, with other assemblages being admixture of these end-member components.

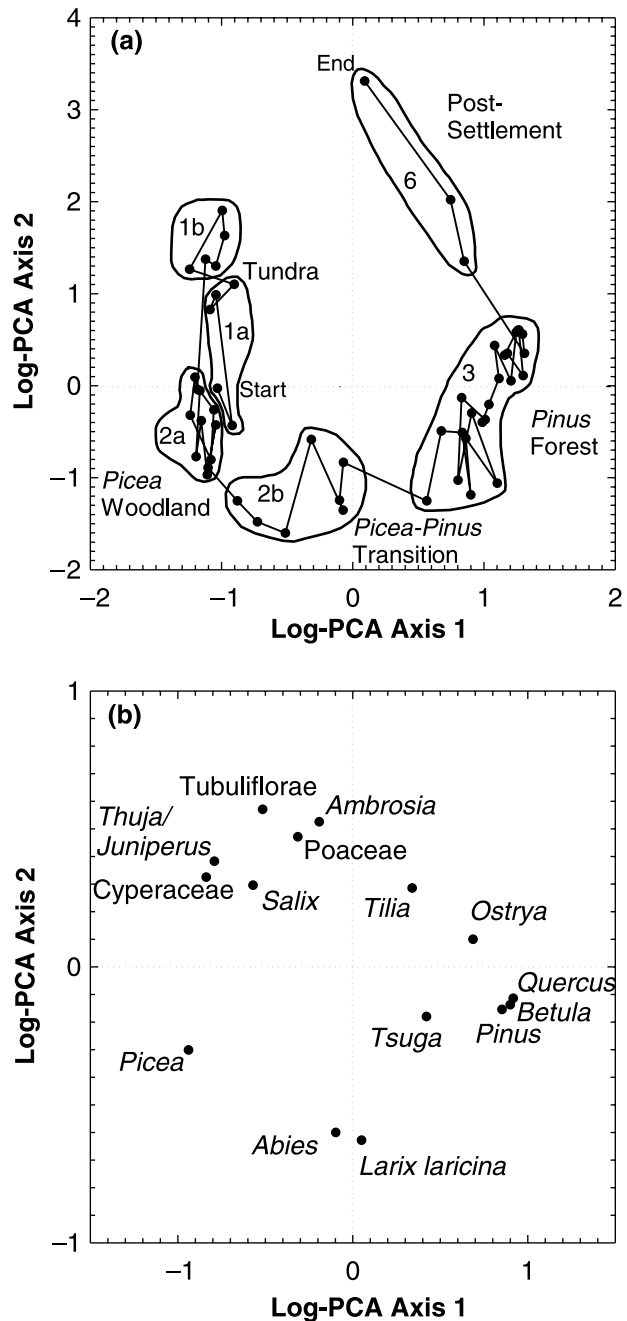


Fig. 13 Log-contrast PCA ordinations of the Twiss Marl Pond pollen data. (a) The ordination of pollen samples along the first two axes showing groupings of pollen assemblages from zones 1–6, with missing zones 4 and 5. (b) The ordination of pollen types along the first two axes. Only 15 selected major pollen types of the 22 types used are shown. The first and second axes account for 59.3% and 8.4% of variance in pollen data, respectively.

(McAndrews, 1994a). Abundant *Dryas* and *Salix* macrofossils, together with some *Carex*, *Scirpus* and cf. *Poaceae* macrofossils, at the two sites supported the interpretation of increased local vegetation cover and perhaps wetter conditions. *Thuja*

Juniperus pollen shows an increase, which most likely reflects open-ground shrub *Juniperus communis* (Yu, 1997b). *Shepherdia canadensis* occurred more frequently in the dense tundra stage; it is an entomophilous shrub of open, unstable sites and contains nitrogen-fixing symbiotic bacteria (Stewart, 1967). Areas of open, well-drained gravel and sand habitats might have persisted locally, especially at Twiss Marl Pond, as suggested by high *Artemisia* and *Ambrosia* pollen (Birks, 1976). During the tundra period, there was severe soil erosion in the watersheds as indicated by pre-Quaternary palynomorphs and minerogenic clay sediments and high erosion-derived elements (Yu & Eicher, 1998). The reworked palynomorphs from bedrock are not very high, especially at Crawford Lake, due to consolidated dolomite bedrock around the sites, which is unlike some arctic regions with exposed unconsolidated Cretaceous and Tertiary bedrock (Gajewski *et al.*, 1995).

The treeless boreal vegetation from *c.* 13 000–12 000 ¹⁴C BP may have only occurred locally in the Crawford Lake and Twiss Marl Pond watersheds. At the Brampton site, only 30 km north-east of my sites but below the Niagara Escarpment (Fig. 1a), *Picea glauca* cones were found and dated to 12 320 BP ± 360 BP (BGS-551; Terasmae & Matthews, 1980). This implies that factors such as very shallow glacial deposits and strong winds atop the Escarpment might have restricted tree growth and delayed successful establishment around my two sites, although trees such as *Picea* already migrated into southern Ontario by that time. To confirm the importance of local site-specific conditions in determining tree establishment and persistence of tundra vegetation, more data at other similar locations are required.

Evidence for tundra in paleoecological records

Studies in arctic paleoecology together with modern pollen spectra provide important baseline data for interpretation of late-glacial herb/shrub pollen assemblages (Ritchie & Lichti-Federovich, 1967; Birks, 1973; Gajewski, 1995). Recently, Gajewski *et al.* (1995) reviewed the problems associated with arctic paleoecology. In summary, there is a low density of arctic plants on the landscape, and many tundra plants are nonanemophilous with low pollen production; thus local plants have low pollen dispersal and representation. The long-distance transported pollen such as *Pinus*, and *Betula* contributes up to 50% of pollen in modern pollen spectra (Ritchie & Lichti-Federovich, 1967; Birks, 1973; Webb & McAndrews, 1976; Gajewski, 1995). In the late glacial period, long-distance transported pollen could contribute a higher proportion to pollen assemblages than the present tundra due to a narrower tundra vegetation belt at that time and the proximity of boreal taxa southward. Thus, combining plant-macrofossil data is essential in studying the earliest vegetation history (Watts, 1967).

In southern Ontario, there are few pollen records showing substages of succession in initial tundra or forest-tundra

vegetation. Kettle-hole lakes are the more common types of sites for paleoecological studies in the Great Lakes region. Since the classic diatom work by Florin & Wright (1969), several studies have explicitly documented the problem with this type of site due to delayed formation of lakes, which were unable to record the contemporary pollen assemblages of the time. These studies show that the delay might last for several thousand years after ice retreat before the lake sediments were deposited (e.g. at nearby Georgetown site; Warner *et al.*, 1991). The two sites in this study are situated in bedrock basins, and there are almost no or very thin glacial deposits around the sites and beneath the lacustrine sediments, so they did not likely suffer the delay problem and did not record the reworked pollen from glacial deposits. Unlike the present extensive tundra belt in the arctic region, tundra in the Great Lakes region usually diminished in importance during the late glacial, which probably reflects the steep south-north temperature gradients at the margins of the continental ice sheet (Webb *et al.*, 1993a,b; Brubaker *et al.*, 1995; Levesque *et al.*, 1997). Therefore, a narrow band of tundra or forest-tundra ecotone may have fringed the southern edge of ice sheets in most of North America and Europe (Huntley & Birks, 1983; Webb *et al.*, 1993a), which implies that only carefully selected sites could record this earliest stage of vegetation changes.

Several paleoecological studies in southern Ontario record tundra plants. At the Gage Street site (Fig. 1a), pollen and plant macrofossils display a tundra flora before the *Picea* zone, likely representing forest tundra (Anderson, 1982; Schwert *et al.*, 1985). The fossil insects were dominantly boreal forest inhabitants, and no obligate tundra or tree line insects were found (Schwert *et al.*, 1985). However, contamination of organic debris, including macrofossils, may cause mixed macrofossil assemblages. A detailed multidisciplinary investigation using pollen, insect and stable isotope records from the Gage Street site has failed to provide evidence for climate changes during the late glacial, even no climatic signal for the Pleistocene–Holocene transition (Fritz *et al.*, 1987; Yu, 2000). At the Rostock site, above the redeposited basal pollen assemblages that have abundant pre-Quaternary palynomorphs and *Pinus* and *Picea* pollen (their subzone 1p), McAndrews & Jackson (1988) found a period (their subzone 1a) dominated by Cyperaceae (up to 70%) and *Salix* (up to 10%) before the *Picea* peak. This pollen assemblage is interpreted as representing a tundra woodland, based on the occurrence of *Picea*, *Larix*, *Salix*, *Betula glandulosa* and *Dryas integrifolia* macrofossils and/or pollen (McAndrews & Jackson, 1988). The high Cyperaceae pollen abundance at Rostock site is attributed to local aquatic source (McAndrews, 1994a) rather than from upland tundra, suggested by high pollen of other aquatic plants. The fossil insect records from the tundra woodland zone at Rostock site also implied tree-line conditions, as indicated by typical insect species of northern boreal forest and of open, barren ground (Pilny *et al.*, 1987).

Many sites record initial treeless tundra vegetation east of the Great Lakes region in southern Québec and New England, the southern Great Lakes region, and westward in Minnesota. In southern Québec, the initial nonarctic pollen sequence from several sites shows structurally different tundra substages from 12 000 to 10 000 ^{14}C BP, suggesting progressive succession from a barren-rock tundra, through a herb-rich tundra, to a shrub tundra (Richard, 1994). This nonarctic pollen sequence, together with macrofossils of arctic-alpine plants, represents not only a physiognomic tundra (regional absence of trees), but a genuine floristic tundra (Richard, 1994). In northern New England, the basal herb zone spanning from 14 000 to 10 000 ^{14}C BP is interpreted as tundra (Davis & Jacobson, 1985), but this long-lasting period rarely shows succession change and represents a structurally undifferentiated pollen zone. In southern New England the classic basal herb (T) zone as defined by Deevey (1951) was difficult to interpret due to high percentages of *Picea* and *Pinus*, and other hardwood pollen that co-occurred within this nonarctic zone (Davis, 1969). The controversy regarding the interpretation of these pollen as long-distance transported vs local signals has lasted for many years (Gaudreau & Webb, 1985). In central Appalachia, Watts (1979) showed pollen and macrofossil evidence of grass-dominated tundra with dwarf shrubs in unglaciated regions of eastern Pennsylvania and sedge-dominated tundra in glaciated terrains of north-eastern Pennsylvania and in the higher mountains of central Appalachia. South of the Great Lakes region, most sites show an absence of a herb pollen zone before the *Picea* peak (Calkin & McAndrews, 1980; Fritz *et al.*, 1987; Shane, 1987), with the exceptions of Allenberg Bog – Section C (Miller, 1973) and Belmont Bog (Spear & Miller, 1976), which show an undifferentiated basal herb zone. In the western Great Lakes region, however, a clear successional change from a herb tundra to a shrub-dominated tundra has been documented at several sites (Cushing, 1967; Watts, 1967; Wright & Watts, 1969; Birks, 1976). Detailed pollen and macrofossil records at Wolf Creek indicated a floristically diverse, treeless, predominantly herbaceous vegetation between 20 500 and 14 700 ^{14}C BP (Birks, 1976). However, Birks (1976) stated that ‘although much of the vegetation near Wolf Creek may have resembled tundra in physiognomy, the term tundra is potentially misleading, as it implies a vegetation that is treeless because the climate is too cold for tree growth’ (p. 414). He suggested that factors such as wind might have been more effective than low temperature in restricting tree growth, which may have resulted in general soil instability. This view regarding the late glacial treeless vegetation is also applicable to my two sites as discussed above.

Vegetation responses to climate oscillations

Vegetation shifts as summarized by log-contrast PCA (Figs 12a & 14b,c) correspond with major pollen zone boundaries

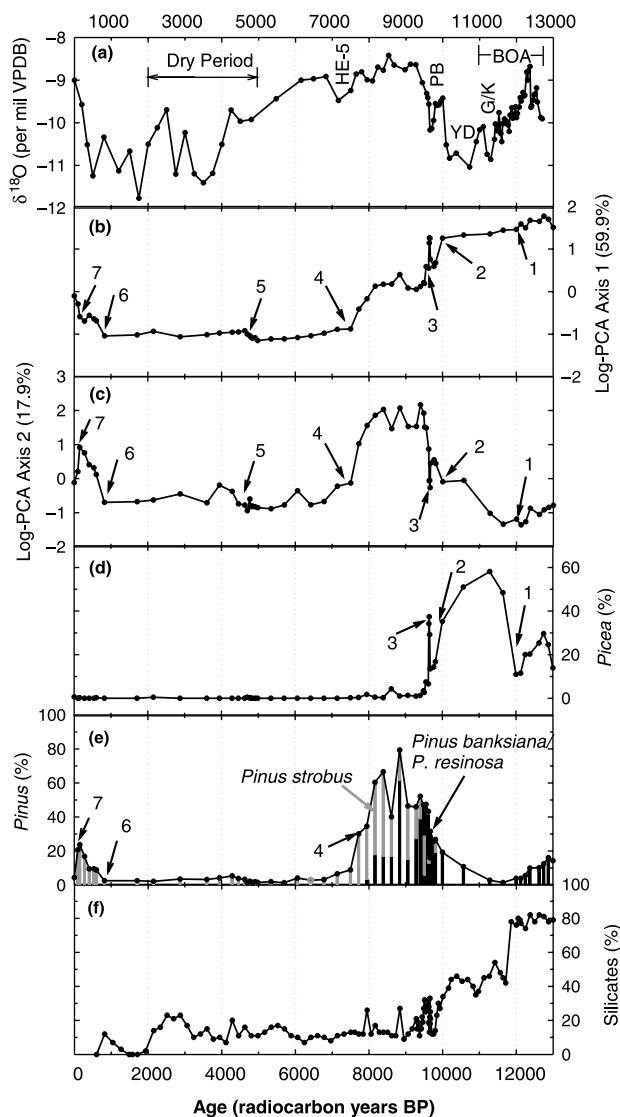


Fig. 14 Correlation of vegetation shifts as summarised by multivariate analysis and climate variation as inferred from independent stable isotope data. (a) Oxygen isotopes from carbonates of core SC at Crawford Lake (Yu *et al.*, 1997; Yu & Eicher, 1998, 2001). The major climatic variations that were shown include the Bølling-Allerød warming and warm period (BOA), Gerzensee/Killarney Oscillation (G/K), Younger Dryas (YD), Preboreal Oscillation (PB), Holocene Event 5 (HE5; 8200 cal year BP cooling event), and late mid-Holocene dry period. The ages of core SC were derived from pollen correlation with core DC, based on major pollen transitions (see Fig. 3 caption for dates used). The age uncertainty was estimated to be no more than 200 years at these anchoring points. (b) Samples scores of log-PCA Axis 1 of pollen data from core DC at Crawford Lake, which represents 59.9% of variance. (c) Sample scores of log-PCA Axis 2 of pollen data from core DC at Crawford Lake, which represents 17.9% of variance. Both axes together represent 77.8% of variance in pollen data and summarise the vegetation shifts/transitions: 1. Tundra – *Picea*; 2. *Picea* – *Pinus*; 3. *Picea* recurrence; 4. *Pinus* – *Fagus*/*Tsuga*; 5. *Tsuga* decline; 6. *Fagus*/*Acer* – *Quercus*/*Pinus*; and 7. *Ambrosia* increase. (d) *Picea* pollen percentage from core DC at Crawford Lake plotted against age. (e) *Pinus* pollen percentage from core DC at Crawford Lake plotted against age. Also shown are two differentiable pollen types within *Pinus* (*P. banksiana/resinosa*, and *P. strobus*). (f) Silicate percentage from core DC at Crawford Lake plotted against age.

as seen in the pollen diagram from Crawford Lake (Fig. 5) and were compared with climate variations as inferred from oxygen isotopes from another core at the same site (Fig. 14a; Yu *et al.*, 1997; Yu & Eicher, 1998, 2001). The correlation between isotopic profile from core SC and pollen PCA results from core DC was anchored by the same major pollen boundaries at the site. The ages for both cores were determined by radiocarbon dates and by correlation with regional dated pollen diagrams. Possible dating uncertainty will not affect the following discussion on vegetation response to climate variation because these pollen boundaries should be regarded as synchronous at the same site.

At Crawford Lake, the Bølling-Allerød warming started at *c.* 12 700 ¹⁴C BP as inferred from oxygen isotopes (Yu & Eicher, 1998), which is in the middle of tundra phase. Climate conditions at that time were probably similar to early Holocene climate and would have favored growth of trees climatically. However, *Picea* woodlands started to establish > 500 yr after this initial BOA warming (Figs 5, 9 and 14d). During this period the presence of herbs and shrubs might have been necessary to modify the local environment, especially soils, to facilitate invasion of *Picea* trees. Plants with associated nitrogen-fixing bacteria, such as *Alnus crispa* and *Shepherdia canadensis*, were important in enriching the soil with nitrogen. The Younger Dryas (YD) cold event and Gerzensee/Killarney (G/K) Oscillation occurred in the middle of *Picea* woodland phase and appear to have had no significant impact on upland vegetation (Fig. 14). This persistence of upland vegetation under shifting climate suggests possible biological inertia of this noncottonal forest to short-term climate fluctuations. However, forest understory composition and forest structure did respond to the YD cooling as indicated by slight increase in herbs pollen percentages, especially at Twiss Marl Pond (Fig. 6b), and slight decrease in pollen concentration (Fig. 7). The aquatic biota showed significant shifts at the onset of the YD as suggested by increase of green algae *Pediastrum* (Fig. 6b) and freshwater gastropods, and disappearance of warmth-loving aquatic plants (*Typha latifolia*, *Najas flexilis*) at Twiss Marl Pond (Yu & Eicher, 1998; Yu, 2000). This contrast response supports the notion that natural ecosystems respond differently to environmental changes (Wright, 1984) and that aquatics may respond more rapidly and sensitively (Iversen, 1954; Cwynar & Levesque, 1995). At sites close to, or downstream of, the North Atlantic in North America and Europe, however, late-glacial climate oscillations were registered in pollen records with time lags of often < 200 yr (Mayle & Cwynar, 1995; Birks & Ammann, 2000; Williams *et al.*, 2002). Clearly the YD climatic reversal itself and its ecological impact show significant regional variations as would be expected due to regional differences in climatic controls and in vegetation types (Yu & Wright, 2001; Shuman *et al.*, 2002b).

This vegetation and climate relation during the late glacial is in sharp contrast to what occurred in the early Holocene.

Around 10 000 ¹⁴C BP *Pinus*, initially *P. banksiana* or *P. resinosa* and later *P. strobus* (Fig. 14e), migrated northward and westward and reached the study area as *Picea* declined and retreated northward. At the onset of Holocene warming and end of the YD cold event this *Picea-Pinus* ecotonal forests responded rapidly with replacement of *Picea* by *Pinus* and deciduous trees (*Quercus*, *Ulmus*, *Frixinus*). This ecotonal forest even showed sensitive response to a brief cooling during the Preboreal Oscillation at 9600 ¹⁴C BP. The major vegetation shift at *c.* 7500 ¹⁴C BP from coniferous forest to mixed coniferous and deciduous forest corresponds to a major shift in climate regimes from deglacial to full postglacial climates (Stager & Mayewski, 1997; Shuman *et al.*, 2002a). This transition was marked by the final collapse of the Laurentide continental ice sheet (Barber *et al.*, 1999) and the corresponding widespread, prominent Holocene cooling about 8200 cal year BP (equivalent to *c.* 7500 ¹⁴C BP; e.g. Alley *et al.*, 1997, HE5 in Fig. 14a).

After the transition in climate regimes at 7500 ¹⁴C BP the climate – isotope relations also appear to change from strong isotope – temperature correlation to strong moisture sources and local hydrology influences on isotopes (Yu *et al.*, 1997; Yu, 1997a; Yu & Eicher, 1998). During the mid- and late Holocene, vegetation responded more directly to natural and anthropogenic disturbances, which may or may not be caused by climate shifts. At Crawford Lake, the declining oxygen isotope values after 6000 ¹⁴C BP were interpreted as caused by more frequent excursion of dry and isotopically depleted Pacific air mass, which was followed by a dry climate from 4800 to 2000 ¹⁴C BP as indicated by lowered lake levels (Yu *et al.*, 1997). The pathogen-induced *Tsuga* decline and subsequent forest response was the major forest shift during the mid-Holocene in eastern North America (Davis, 1981; Allison *et al.*, 1986; Foster & Zebryk, 1993; Fuller, 1998). Based on the close correspondence between *Tsuga* decline and a dry climate, Yu & McAndrew (1995) hypothesized that this drought initiated around 5000 ¹⁴C BP in eastern Midwest (Baker *et al.*, 1996) and southern Ontario (Yu *et al.*, 1997) might have triggered the pathogen outbreaks. Recent paleohydrological studies at other sites in eastern North America show a similar timing of dry climate around 5000 ¹⁴C BP (Lavoie & Richard, 2000; Almquist *et al.*, 2001; Shuman *et al.*, 2001), suggesting that dry conditions around the time of the hemlock decline were more widespread than previously thought. Clearly more multiple proxy investigations are needed to test this hypothesis. The isotopic fluctuations in the past 4000 yr were either caused by local hydrological change or perhaps an expression of Holocene millennial-scale climate cycles (Bond *et al.*, 1997). In any case, vegetation shifts in the late Holocene either responded to anthropogenic disturbance after aboriginal and EuroCanadian settlements (McAndrews, 1988; Clark & Royall, 1995) or showed a disequilibrium response triggered by the Little Ice Age 600 year BP (Campbell & McAndrews, 1993).

Conclusions

Detailed paleoecological studies from two sites at the edge of the southern Niagara Escarpment were used to reconstruct vegetation history since the last deglaciation (the past *c.* 13 000 ¹⁴C yr), and to discuss vegetation response to climate oscillations during different stages of vegetation development. Combined fossil-pollen and plant-macrofossil stratigraphic records document a treeless vegetation for several hundred years immediately following the retreating glacier ice. Pollen data indicated a distinct successional change from *Alnus*-Cyperaceae-*Dryas* sparse tundra or periglacial desert to *Salix-Juniperus*-Cyperaceae dense tundra. Plant-macrofossil data provided records of floristic composition of this earliest treeless vegetation, including arctic/alpine species *Dryas integrifolia*, *Salix herbacea* and *Silene cf. acaulis*.

Comparison of vegetation shifts, summarized by log-contrast principal component analysis of pollen record, and climate variations, inferred from oxygen isotopes, indicates lagged response of upland forests to deglacial climate warming. *Picea* woodlands became established *c.* 500 yr after the initial Bølling-Allerød warming, the apparent delay possibly due to very shallow soils around the sites. Plants with associated nitrogen-fixing bacteria, such as *Alnus crispa*, may have been important in enriching the bare shallow soil with nitrogen. The onset of the Younger Dryas cold event occurred in the middle of *Picea* woodland phase and did not cause a major forest transformation, suggesting biological inertia of non-ecotonal forests to abrupt climate shifts. However, this is in sharp contrast with the sensitive response of *Picea-Pinus* ecotonal forest to the onset of Holocene warming at *c.* 10 000 ¹⁴C BP and even to a brief Preboreal Oscillation as indicated by *Picea* recurrence at 9650 ¹⁴C BP. Vegetation during the mid- and late Holocene responded more directly to natural (drought-triggered pathogen-induced *Tsuga* decline) and human disturbances (aboriginal and EuroCanadian settlements). This study also demonstrated that bedrock basins most faithfully recorded the earliest vegetation change because they usually experienced short delay in lake formation after ice retreat.

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