



ELSEVIER

Review of Palaeobotany and Palynology 96 (1997) 241–254

REVIEW
OF
PALAEOBOTANY
AND
PALYNOLOGY

Late Quaternary paleoecology of *Thuja* and *Juniperus* (Cupressaceae) at Crawford Lake, Ontario, Canada: pollen, stomata and macrofossils

Zicheng Yu^{a,b,*}

^a Department of Botany, University of Toronto, 25 Willcocks Street, Toronto, Ont. M5S 3B2, Canada

^b Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ont. M5S 2C6, Canada

Received 22 March 1996; accepted 5 September 1996

Abstract

In northeastern North America, paleoecological records of *Thuja* and *Juniperus* are problematic due to their indistinguishable and poorly preserved fossil pollen grains. However, macrofossils and stomata of *Thuja* and *Juniperus* are distinctive. Difficulties with macrofossil data are that the analysis is time-consuming, and macrofossils are usually scarce in lake sediments. Using stomata as a proxy of macrofossils has two advantages: (1) stomata are more abundant than macrofossils; and (2) they can be counted from pollen preparations. Crawford Lake has 5–15% *Thuja*–*Juniperus* (Cupressaceae) pollen through most of the past 13,000 yr except for a dearth during the *Pinus* pollen zone at ca. 10,000–7500 ¹⁴C yr BP. Macrofossil, stomatal and pollen results showed the late glacial (ca. 13,000–10,000 ¹⁴C yr BP) pollen mostly was derived from *Juniperus* (likely *J. communis*) indicated by smaller pollen, a few *Juniperus* stomata, and absence of *Thuja* stomata and macrofossils, whereas pollen at 7500–0 ¹⁴C yr BP was from *Thuja occidentalis* indicated by larger pollen, and abundant *Thuja* stomata and macrofossils. This bimodal stratigraphic pattern of Cupressaceae pollen appears at other sites in southern Ontario, which suggests the possibility of separating these taxa to an earlier *Juniperus* and later *Thuja* at these sites. The late glacial *Thuja* macrofossils reported in previous studies may indicate early immigration of a small population via favourable habitats along Ontario's Niagara Escarpment. Alternatively, these *Thuja* macrofossils may be derived from younger sediments, as suggested by the questionable stratigraphies and puzzling ¹⁴C dates. The separation of two genera would provide valuable information in paleoecological interpretation of pollen data because the taxa occupy different habitats.

Keywords: *Thuja occidentalis*; *Juniperus*; Stomata; Plant macrofossils; Fossil pollen; Paleoecology; Late quaternary

1. Introduction

In northeastern North America, the Cupressaceae pollen type mainly includes two genera, *Thuja* and *Juniperus*. The separation of *Thuja* and *Juniperus* fossils is important for paleo-

ecologic and paleoclimatic interpretations. *Thuja* is a northern temperate tree that grows on organic soils in lowlands and calcareous mineral soils on uplands (Johnston, 1990), whereas *Juniperus*, most commonly *J. communis*, is a widely distributed, heliophytic shrub of open ground, especially on

* Correspondence address: Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ont. M5S 2C6, Canada. Tel.: +1 416 586-5609. Fax: +1 416 586-5516. E-mail: yuzi@utcc.utoronto.ca

dry rocky soils in the subarctic and arctic. The pollen of these two genera cannot be separated with confidence by palynologists under the light microscope in routine pollen analysis (e.g. McAndrews et al., 1973; Moore et al., 1991), although *Juniperus* occasionally has a pore (monoporate) and *Thuja* has no aperture (inaperturate) (Adams and Morton, 1972, but see SEM micrographs in Bortenschlager, 1990). *Thuja* pollen tends to be about 20% larger than *Juniperus* on slides mounted with either glycerin jelly (Richard, 1970; Parent and Richard, 1990) or silicone oil (personal observation). Due to their lack of distinctive features the pollen grains may be confused with some algal and bryophyte spores (Moore, 1980). Thus, paleoecological records of *Thuja* and *Juniperus* are problematic.

Recently, Parent and Richard (1990) provide an identification key to separate *Thuja* and *Juniperus* pollen among other taxa in Cupressaceae family, but their key is difficult to use because the surface features such as gemmae are rarely preserved in fossil grains that are often angularly broken (McAndrews et al., 1973). Poor preservation may be responsible for the low abundance of Cupressaceae pollen in lake sediments and wetland peat because Cupressaceae has relatively high percentages (9%) in the modern pollen rain of southern Ontario using pollen trap methods (Cambon, 1994). The only criterion provided by Richard (1970) and Parent and Richard (1990) that might be useful to differentiate these two taxa in fossil records is the size measurement of the pollen grains, if a large number of grains are available. As classified by Parent and Richard (1990), there are five forms of Cupressaceae pollen grains: whole, slightly split, opened in a “V” shape, spindle-like, or split in halves, and the absence or presence of these shapes cannot be used as an identification criterion. The presence of intermediate forms makes size measurement difficult to apply, which is presumably the reason that Parent and Richard (1990) only measured whole and half grains and only used sizes of half grains in their key.

Fossil leaves and seeds of *Thuja occidentalis* are distinctive, and reports of *Thuja* macrofossils in late Quaternary sediments of northeastern North

America include McAndrews (1972, 1981), Watts (1979), Anderson (1982), Warner (1982), Warner et al. (1984), Liu (1990) and Yu et al. (1996). However, due to the highly time-consuming nature of macrofossil analysis and scarcity of macrofossils in most pollen cores, only a few pollen analysis investigations are accompanied by macrofossil studies.

Conifer-stomatal analysis of late Quaternary sediments as a paleoecological tool (e.g. Hansen, 1995) holds promise for separating *Thuja* and *Juniperus* and also confirming their local presence in the catchment. Conifer stomata resist decay, are usually well preserved and are identifiable to genus or even species level (Florin, 1951). Stomata of *Thuja* and *Juniperus* have distinctive and identifiable features. For stomatal analysis, pollen analysis slides are used and thus it requires little extra time in a paleoecological study. Analysis of conifer stomata has been used in paleoecology for reconstructing tree-line in the Alps (e.g. Ammann and Wick, 1993; Wick, 1994), for confirming local arrival of conifer trees in the Hudson Bay Lowlands (Hansen, 1995), and for identifying the tundra-forest border in central Canada (Hansen et al., 1996).

The objectives of this study are to combine pollen, stomatal, and macrofossil analyses to separate *Thuja* and *Juniperus* in a late Quaternary sediment record from Crawford Lake, Ontario, and to compare the record with those of other sites in southern Ontario, especially along the Niagara Escarpment. In this paper, I describe the differences between *Thuja* and *Juniperus* stomata from herbarium/fresh specimens and use the criteria to identify fossils from lake sediments. I use the detailed results from pollen, stomatal and macrofossil analyses at Crawford Lake to discuss the late Quaternary history of *Thuja* and *Juniperus* in southern Ontario and to summarize the advantages and disadvantages of these three paleoecological methods.

2. Study site

Crawford Lake (43°28'N, 79°57'W) is located about 60 km southwest of Toronto atop the

Niagara Escarpment at 279 m above sea level (Fig. 1). The lake has a surface area of 2.4 ha (250 × 150 m) and a maximum depth of 24 m. The lake is meromictic and has partially well-preserved laminated (varved) sediments in the deep north basin. The top varved sediments spanning the past 2000 yr have been studied for fossil pollen at 5-, 10- or 25-yr intervals (McAndrews and Boyko-Diakonow, 1989), and for microscopic charcoal (Clark and Royall, 1995). The lake is partly surrounded by dolomite cliffs of up to 6 m above the lake surface, which are mostly covered with eastern white cedar (*Thuja occidentalis*). A lakeside cedar swamp is present on the southeastern side of the

lake. Forests around the lake mainly consist of *Acer saccharum*, *Betula lutea*, *B. papyrifera*, *Carya cordiformis*, *Fagus grandifolia*, *Fraxinus americana*, *Ostrya virginiana*, *Pinus strobus*, *Quercus rubra*, *Thuja occidentalis*, *Tilia americana*, *Tsuga canadensis* and *Ulmus americana*. Soils are generally shallow with abundant rocks. The old-growth cedar forests on the cliff faces of the Niagara Escarpment have been intensively studied by Larson and his colleagues on community organization (Larson et al., 1989), distribution (Larson and Kelly, 1991), dendrochronology and dendroecology (Kelly et al., 1992, 1994).

3. Materials and methods

3.1. Stomatal reference preparation

The reference materials for conifer-stomatal analysis were collected from herbarium specimens (TRT, Royal Ontario Museum Vascular Plant Herbarium) except for a *Thuja* leaf sample collected from Crawford Lake (Table 1). The leaves from different parts of branches were mixed and ground. The samples were treated with hot 10% KOH, acetolysed, stained with safranin and mounted in silicone oil. Seven morphological characters (Fig. 2) were measured to the nearest 0.5 μm for the first ten entire stomata in surface view encountered on each slide at ×100 objective (×1000 magnification) using a NIKON microscope equipped with an ocular micrometer.

3.2. Fossil pollen and stomatal analysis

A sediment core of 5 cm in diameter was taken from the lake under 22.2 m water on 15 March 1994 with a modified Livingstone piston sampler (Wright, 1967), and a plastic tube sampler with a piston was used for taking the top 70 cm soft sediments. Core segments were wrapped in plastic wrap and aluminum foil in the field. Pollen samples were 0.8 ml (or 1.6 ml for basal clay samples). Pollen preparations followed standard procedure (Fægri and Iversen, 1989), with fine-sieving to remove clay-sized particles (Cwynar et al., 1979). The concentrate was stained with safranin and

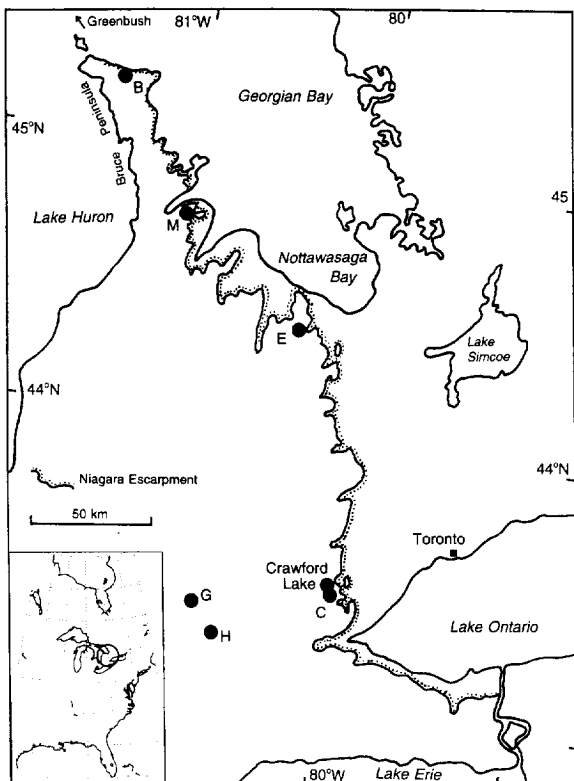


Fig. 1. Map showing location of Crawford Lake and other southern Ontario sites discussed in the text. H=Hams Lake (Bennett, 1987); C=Crawford Bog (J.H. McAndrews, in Karrow, 1987); G=Gage Street site (Anderson, 1982; Schwert et al., 1985); E=Edward Lake (McAndrews, 1981); M=Mary Lake (Bennett, 1992); B=Bartley Lake (Bennett, 1992) and Greenbush Swamp (Warner, 1982; Warner et al., 1984). Inset shows the study area (circle) in eastern North America.

Table 1
Measurements of *Thuja* and *Juniperus* stomata (in μm)

Taxon	Overall length (mean range)	Overall width (mean range)	Width of guard cell (mean range)	Width of pore (mean range)	Height of polar lamellae (mean range)	Width of polar lamellae (mean range)	Thickness of ventral wall (mean range)	N
<i>Thuja occidentalis</i> L. (TRT 16165, Ottawa, ON)	22.4 (20–25)	19.7 (17–22)	8.3 (6.5–9)	3.2 (2.5–5)	7.9 (6–9)	2.3 (1.5–3.5)	1.0 (<1–1.5)	10
<i>Thuja occidentalis</i> L. (ZY, Crawford Lake, ON; 95-01-28)	25.6 (22–29)	20.4 (16–24)	9.6 (8–12)	2.5 (2–3)	8.5 (7–11)	2.0 (1.5–2.5)	1.0 (<1–1.5)	10
<i>Juniperus communis</i> var. <i>depressa</i> Pursh. (TRT 111620, Hudson Bay, ON; 53-07-19)	29.3 (27–32)	21 (17–26)	8.2 (6–11)	5 (3–6)	10.2 (9–11.5)	3.9 (3–4.5)	2.0 (1.5–2.5)	10
<i>Juniperus communis</i> var. <i>depressa</i> Pursh (TRT 69181, Bruce Co., ON)	27.9 (25–30)	19.3 (16–24)	8.5 (7–11)	5 (4–6)	9.4 (7–10.5)	4.3 (3.5–5.5)	1.7 (1–2.5)	10
<i>Juniperus communis</i> var. <i>depressa</i> Pursh (TRT 151742, Macon Co., NC; 66-08-22)	27.1 (23–31)	19.9 (17–22)	8.4 (7–10)	3.2 (2.5–4)	10.6 (8–13)	3.7 (3–4)	1.7 (1.5–2.0)	10
<i>Juniperus virginiana</i> L. (TRT 35918, ON)	24.6 (22.5–27)	20.3 (17–25)	8.6 (7.5–10)	3.5 (2.5–4)	9.6 (9–10)	4.4 (3.5–6)	1.2 (1–1.5)	10
<i>Juniperus horizontalis</i> Moench (TRT 207551, Kenora, ON)	29.2 (24–33)	23.3 (20–26)	10 (9–12)	4.2 (3–6)	10.8 (10–12)	3.4 (2.5–4)	1.0	10

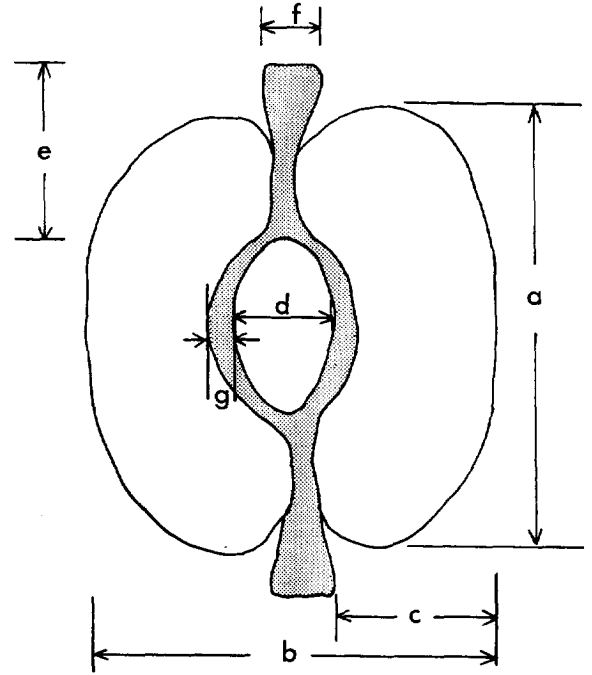


Fig. 2. Outline drawing of a conifer stoma (surface view) showing seven morphological characters measured: a =overall length; b =overall width; c =width of guard cell; d =width of pore; e =height of polar lamellae; f =width of polar lamellae; and g =thickness of ventral wall.

mounted in silicone oil. Pollen was identified by comparison with a reference collection aided by the illustrated key of McAndrews et al. (1973). Conifer-pollen percentages presented in this study were calculated on the sum of at least 300 terrestrial pollen. The conifer-stomatal identification was determined from pollen preparations by comparison with a reference collection aided by the key and drawings in Hansen (1995). The pollen and stomatal concentrations were estimated by addition of exotic *Lycopodium* spores (batch# 710961, mean = $13,911 \pm 306$ spores per tablet) as marker particles (Benninghoff, 1962; Maher, 1981). Size measurements of half grains of *Thuja*–*Juniperus* pollen were determined with a $\times 40$ objective for 7–10 half grains at selected levels.

3.3. 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 non-horizontally oriented macrofossils on or near the sediment surface were also removed for the same purpose (cf. 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 through 500 μm mesh to concentrate macrofossils. Identifiable materials were picked under a stereomicroscope at $\times 8$ magnification. Seeds and leaves were identified by comparison with a modern reference collection at the ROM.

4. Results

4.1. Reference stomata

In the reference materials (Table 1), *Juniperus communis* and *J. horizontalis* stomata are larger with a longer (9.4–10.8 μm) and wider (3.4–4.3 μm) polar lamellae, and thicker ventral wall (1.7–2 μm) compared to *Thuja occidentalis* stomata. Also *Juniperus* stomata tend to be oval or rectangular in shape with length-to-width ratio of about 1.36–1.45 (see p. 107 in Van Geel et al., 1989, for pictures of *Juniperus* stomata), whereas for *Thuja* the ratio is only 1.14–1.25 (see p. 247 in Hansen, 1995, for a picture of a *Thuja* stoma). For *Thuja* stomata, the Florin ring (subsidiary cells) and other epidermal cells are usually well preserved both in reference and in fossil materials, but they are seldom found in *Juniperus* even in reference materials. The most useful features for separating *Juniperus* and *Thuja* stomata are their shape, polar lamellae, ventral wall, overall size and Florin rings.

4.2. Fossil pollen, stomatal and macrofossil stratigraphy

The 430 cm long core presented in this study from Crawford Lake probably spans the past 13,000 ^{14}C yr, the time since local deglaciation history (Dyke and Prest, 1987). The chronology is based on four radiocarbon dates from the core and regional pollen correlation with nearby dated pollen sequences (e.g. McAndrews, 1981; Bennett, 1987). The combined conifer-pollen percentage

and conifer-stomatal percentage diagram is shown in Fig. 3. A herb/shrub-dominated tundra-like vegetation zone was recorded at the base of this core, lasting for several hundred years after deglaciation. During this interval neither stomata nor conifer macrofossils were found (Figs. 3, 4), and *Thuja-Juniperus* pollen was small in size (about 26 μm ; Table 2; Fig. 5). The spruce (*Picea*) pollen zone (ca. 12,000–10,000 ^{14}C yr BP) followed with abundant *Picea* stomata and a few *Juniperus* stomata; *Thuja-Juniperus* pollen was still small in size during the spruce zone. During the pine (*Pinus*) zone (ca. 10,000–7500 ^{14}C yr BP), percentages of *Thuja-Juniperus* pollen were very low with abundant *Pinus* stomata, and a few *Abies* and *Larix* stomata at the base of this zone. Starting from 260 cm depth (since ca. 7500 ^{14}C yr BP), the pollen record indicates a mixed forest dominated by *Fagus*, *Acer*, *Quercus*, *Ulmus*, *Tsuga* and *Thuja-Juniperus*. This zone was characterized by abundant *Thuja* stomata with a few *Tsuga* and *Pinus* stomata. The *Thuja-Juniperus* pollen size increased to about 30 μm (Table 2; Fig. 5). Fig. 4 shows the concentrations of pollen, stomata and macrofossils of all the conifers. *Thuja* macrofossils had similar abundance and pattern with its pollen and stomatal records. *Picea*, *Pinus* and *Juniperus* macrofossils were much scarcer than their stomata, and *Larix* and *Tsuga* macrofossils were more abundant than their stomata. Fig. 5 shows the summary diagram of *Thuja* and *Juniperus* pollen, stomata and macrofossils.

5. Discussion

5.1. Stomatal analysis in the context of other paleoecological tools

Because stomata are probably one of the most important features of leaf cuticles, they have long been studied by paleobotanists. Florin (1951) found that the stomata are a striking feature for differentiating conifer leaves. Boulter (1971) used SEM techniques to examine the fine details of conifer leaf cuticles, especially stomata, and

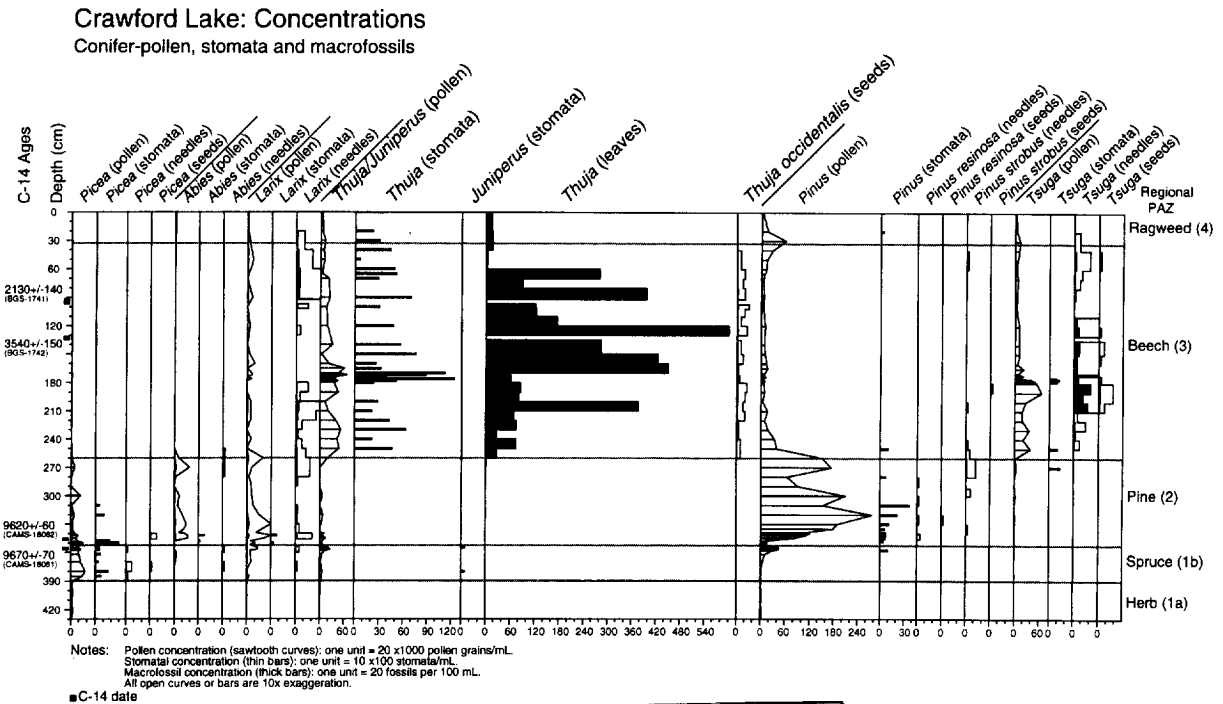


Fig. 4. Concentration diagram of conifer pollen (sawtooth curves), stomata (thin bars) and macrofossils (thick bars) at Crawford Lake. One unit = 20 × 1000 pollen grains/mL, 10 × 100 stomata/mL and 20 macrofossils per 100 mL, respectively. All open curves or bars are × 10 exaggeration.

south of Crawford Lake) rapid sediment accumulation rates (4 m of marl deposited in 4500 yr from ca. 12,500 to 8500 ^{14}C yr BP) allowed excellent preservation of pollen and macrofossils, but stomata were rare. Their scarcity is attributed to the low release rates of stomata from well-preserved needles or a dilution effect of rapidly accumulated sediments (Z. Yu, unpublished data).

A general term for the studies of non-palynomorph remains in palynological preparations is palynodebris analysis (cf. Boulter, 1994), which includes examination of leaf cuticles and well-preserved wood (tracheids and rays). Paleoecologists have emphasized different aspects of palynodebris. For example, the inability to identify grass pollen grains in grassy environments of tropical Africa and the presence of abundant cuticular fragments (on the order of 100/mL) led Palmer (1976) to undertake a systematic study of grass epidermis. Palmer found that epidermal features are useful in identifying members of the

family Gramineae (=Poaceae) and concluded that cuticular analysis supplements interpretations based on pollen analysis. In paleoecological studies of soil samples, opal phytolith analysis (based on shape of dispersed silica bodies) has been used to provide paleoenvironmental information in cases where pollen was poorly preserved or absent (e.g. Rovner, 1971; Fredlund and Tieszen, 1994).

5.2. *Paleoecological records of Thuja and Juniperus in southern Ontario*

Pollen, stomatal and macrofossil records from Crawford Lake help to clarify the history of *Thuja* and *Juniperus* in southern Ontario. *Thuja occidentalis* has been an important component of the mixed hardwood forest since ca. 7500 ^{14}C yr BP. No macrofossils and stomata of this species were found in older sediments. The smaller pollen and the occurrence of a few *Juniperus* stomata indicated that the late glacial (ca. 13,000–10,000 ^{14}C yr BP)

Table 2
Size measurement of *Thuja–Juniperus* (Cupressaceae) pollen from Crawford Lake

Level (cm)	Half grain		V shape		Whole grain	
	Mean and range (μm)	<i>N</i>	Mean and range (μm)	<i>N</i>	Mean and range (μm)	<i>N</i>
0	31 (28–38)	7	31 (30–31)	3	24 (23–25)	4
30	33 (29–35)	7	25 (23–28)	2	23 (21–25)	4
50	31 (26–33)	7	28 (28–29)	2	26 (21–30)	2
70	32 (30–35)	7	24 (23–25)	2	30	1
100	29 (24–34)	7	25 (24–25)	3	24	2
120	29 (24–33)	7	30	1	23 (19–25)	3
140	27 (24–33)	7	25 (20–29)	5		
170	28 (26–32)	7	30	2	23	2
200	29 (24–38)	7	28	1	23	2
220	30 (28–33)	8	22 (21–23)	2		
240	30 (28–33)	9	21	1	22	1
250	29 (23–33)	10				
348	26 (23–29)	7	26 (25–28)	3	19	1
352	25 (21–31)	10				
358	25 (23–28)	9	25	1		
370	24 (23–26)	7	24 (23–26)	3		
380	27 (24–35)	7	22 (20–24)	3		
395	25 (21–29)	7	22 (21–24)	3	20	1
415	26 (23–30)	7	24 (23–28)	4		
425	26 (20–29)	7	23	2	23	1

peak of Cupressaceae pollen likely came from *Juniperus* cf. *communis*. The occurrence of *Juniperus* needles from other late glacial sites in northeastern North America also confirms its presence at that time (e.g. Karrow et al., 1975; Miller and Thompson, 1979; Jackson, 1989; Mayle and Cwynar, 1995). Abundant *Juniperus* stomata were also recorded during the *Picea* pollen zone at a forest hollow site near Crawford Lake, although no *Juniperus* macrofossils were found (Z. Yu, unpublished data). The low percentage of Cupressaceae pollen during the *Pinus* pollen zone suggests that competitive exclusion may have reduced the role of *Thuja* and *Juniperus* in the vegetation.

A similar stratigraphic pattern of Cupressaceae pollen is present at other sites in southern Ontario, especially along the Niagara Escarpment (Fig. 1, Fig. 6). At Hams Lake (Fig. 6a; Bennett, 1987), Cupressaceae pollen percentages are low with one peak in the late glacial during the *Picea* zone (2–3%), and another peak spanning the past 8000 ^{14}C yr (1–2%). Low percentages of Cupressaceae pollen (<1%) occur during the *Pinus* zone. The

generally low percentages at Hams Lake may be due to its more southern and distant location from the Escarpment (see Fig. 1). At Crawford Bog (by J.H. McAndrews, in Karrow, 1987), a similar pattern can be found with much higher percentages of Cupressaceae pollen (4–15%). Two peaks with values of 2–8% Cupressaceae pollen occur at Edward Lake (Fig. 6b; McAndrews, 1981). At Mary Lake (Fig. 6c; Bennett, 1992), a similar pattern is evident, with two Cupressaceae peaks of 5–10%. At Bartley Lake (Fig. 6d; Bennett, 1992), two Cupressaceae pollen peaks occur but the Holocene peak begins in the middle of the *Pinus* zone. In northern Ontario, Cupressaceae pollen usually shows a proliferation in the mid-Holocene (e.g. Richard, 1980; McAndrews, 1981; Bennett, 1987; Liu, 1990). For these sites, the late glacial Cupressaceae pollen in tundra or open spruce forest zones was likely derived from *Juniperus* cf. *communis*, whereas the Holocene peak was likely from *Thuja occidentalis*, although almost no macrofossil and stomatal results are available from these sites.

In southern Ontario, Warner (1982) and

Crawford Lake: *Thuja* and *Juniperus*

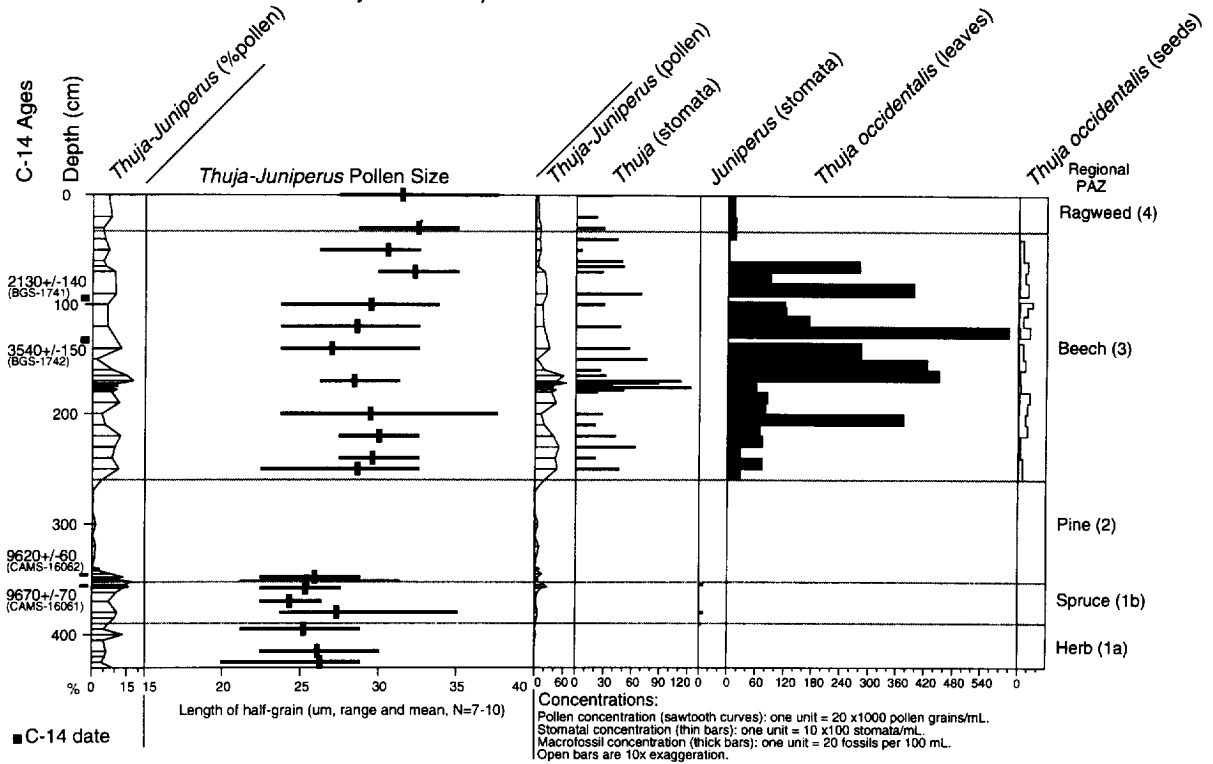


Fig. 5. Summary diagram of *Thuja* and *Juniperus* pollen, stomata and macrofossils at Crawford Lake.

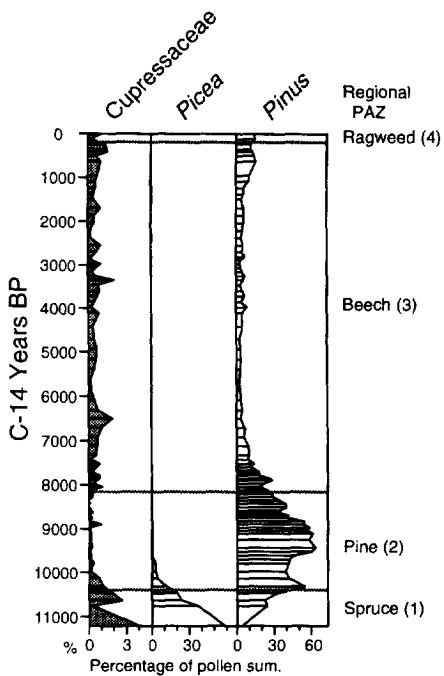
Table 3
 Comparison of pollen, stomata, and macrofossils from Crawford Lake

	Pollen	Stomata	Macrofossils
Concentration (No./ml)	$\times 10^5$	$\times 10^3$	$\times 10^0$
Spatial resolution	low, mostly regional source	high, local source	high, local source
Taxon resolution	genus or family, rarely species	genus or species	usually species
Usefulness	regional vegetation	local occurrence of the taxon	local flora and vegetation
Factors affecting abundance	production, vegetation cover, preservation, transport ability	balance between preservation and decay of needles, proximity to coring site	preservation, proximity to coring site, basin characters

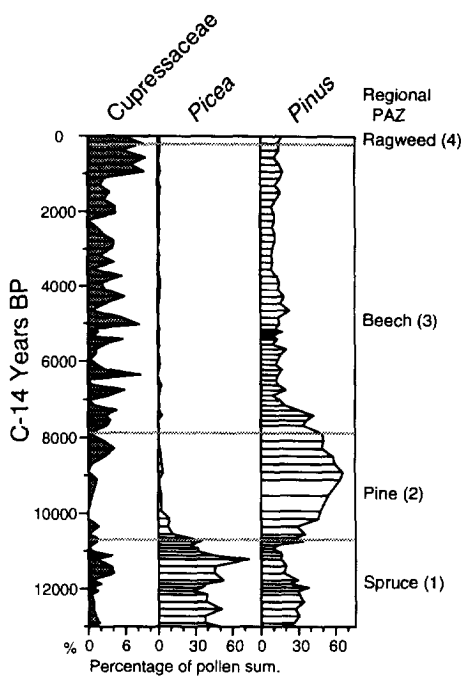
Anderson (1982) reported *Thuja occidentalis* macrofossils during the late glacial period. A well-preserved *Thuja* leaf twig fragment was found in clastic silty gravel sediments from the shallow basin at Greenbush Swamp on Manitoulin Island (see Fig. 1 for approximate location; Warner, 1982). The age of the clastic sediments was inferred to be ca. 10,000 ^{14}C yr BP by pollen correlation with a dated core from the deep basin (Warner

et al., 1984). This age assignment is questionable because the two cores may not be correlated correctly. It is possible that the clastic sediments in the shallow part of the basin were deposited after those in the centre of the basin. The age of this *Thuja* fossil will not be resolved until an AMS date is obtained on the twig directly. At the Gage Street site in Kitchener (see Fig. 1 for location; Anderson, 1982; Schwert et al., 1985), the puzzling

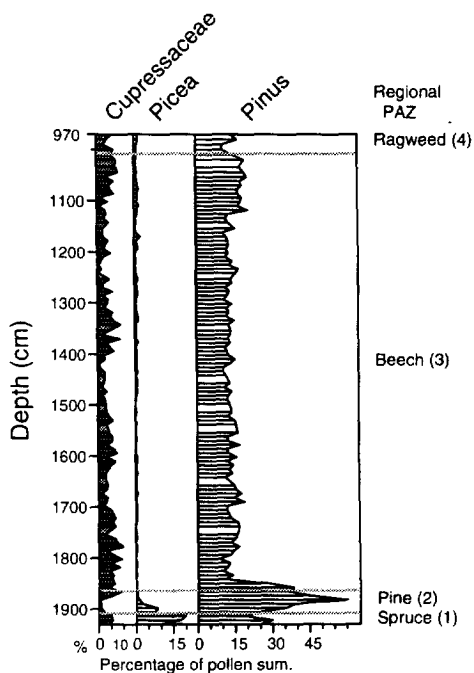
a. Hams Lake
(43 14'N; 80 25'W)



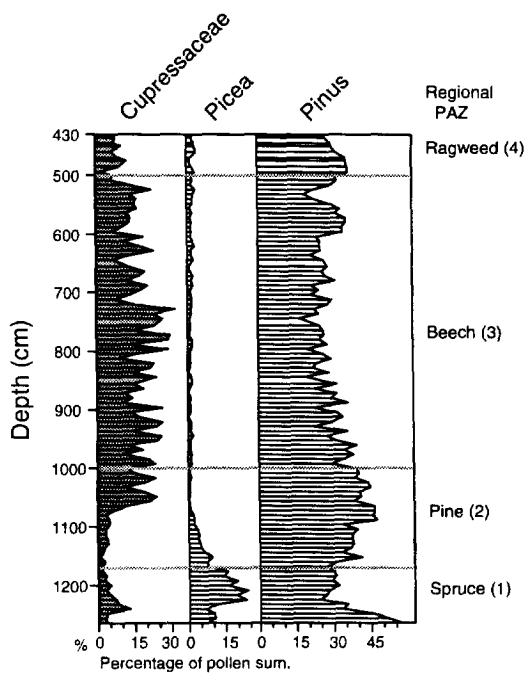
b. Edward Lake
(44 22'N; 80 15'W)



c. Mary Lake
(44 44'N; 81 00'W)



d. Bartley Lake
(45 13'N; 81 29'W)



radiocarbon dates from the late glacial are a clue for interpreting the occurrence of *Thuja* macrofossils. Two radiocarbon dates from the same level on plant detritus are significantly different (8600 ± 100 ^{14}C yr BP, BIRM-896; $10,700 \pm 900$ ^{14}C yr BP, WAT-157) and all are younger than the age based on regional pollen zonation (at least 12,000 ^{14}C yr BP). These young dates suggest that the plant detritus from this interval might derive from contaminant macrofossils.

McAndrews (1981) found that the *Thuja* leaves are confined to sediments younger than 8000 ^{14}C yr BP (mixed hardwood pollen zone). At Twiss Pond, *Thuja* leaves and seeds were not found during the *Picea* and *Pinus* zones, although Cupressaceae pollen had percentages of 2–8%. If *Thuja* were present during that time, it would have been more likely to be preserved as macrofossils than other upland conifer needles because of its proximity to the deposition site, either from upland cliffs or from lowland swamps. Larson and Kelly (1994) and Larson and Melville (1996) reported the radiocarbon dates from submerged cedar stumps in growth position and from wave-washed logs and wood fragments in emerged coastal caves along the Bruce Peninsula. The oldest dates are 7660 ± 50 ^{14}C yr BP (TO-4065) and 8200 ± 60 ^{14}C yr BP (Beta-81977), whereas the rest of over thirteen dates are mostly late Holocene in age. These oldest cedars may come from the earliest *Thuja* populations in the northern Escarpment, as suggested by pollen records at nearby Mary and Bartley lakes (see Fig. 6c, d). The possible time-transgressive trend for the initial expansion of Cupressaceae pollen in the Holocene as evident from pollen records in Fig. 6 suggests that *Thuja* could have migrated southward into southwestern Ontario along the Niagara Escarpment. In this case, the age estimate of the *Thuja* macrofossil on Manitoulin Island may not be much older than its true age. This southward migration hypothesis may be further tested by investigating more sites

with reliable dating along the northern Escarpment and in northern Ontario.

In northern Ontario and western Quebec, the high percentages of Cupressaceae pollen in the mid-Holocene from several sites have been attributed to *Juniperus* (Richard, 1980) and *Thuja* (Liu, 1990). Both are interpreted as evidence of warmer and drier climate than present but they imply different mechanisms. *Juniperus* expansion is thought to be caused by higher frequencies of fires which resulted in a more open forest canopy, whereas *Thuja* expansion is due to favourable condition in warm climate and expanded lowland habitats caused by lowered regional water tables. The rare occurrence of *Thuja* macrofossils during the mid-Holocene does not preclude the possibility of contributions by *Juniperus* pollen, because *Juniperus*, an upland shrub, would have been less likely to be represented in the macrofossil record than is *Thuja* (Liu, 1990). Conifer-stomatal analysis may help to differentiate *Thuja* and *Juniperus* fossil records and provide more reliable paleoecological interpretations. A detailed macrofossil study from a wetland site in southern Ontario also shows an increase of *Thuja* during the mid-Holocene dry/warm climate (Yu et al., 1996). At Crawford Lake, the proliferation of *Thuja* stomata and leaves starting at 170 cm (4800 ^{14}C yr BP inferred from *Tsuga* decline) might be caused by expanded favourable lowland habitats during the mid-Holocene dry/warm period, as indicated by low lake levels (Yu and McAndrews, 1995). The decrease in *Thuja*–*Juniperus* pollen size (Fig. 5) at this interval could be also related to habitat and/or climate changes, although present data are insufficient to determine the significance of this slight size change and we lack understanding of pollen size variations in ecological terms. The measurements of stomatal density of fossil *Thuja* leaves from Crawford Lake are in progress, which may provide another line of evidence for habitat and climate change, assuming that *Thuja* leaves

Fig. 6. Summary pollen diagrams showing Cupressaceae (*Thuja*–*Juniperus*) pollen from sites along Ontario's Niagara Escarpment: (a) Hams Lake (Bennett, 1987); (b) Edward Lake (McAndrews, 1981); (c) Mary Lake (Bennett, 1992); and (d) Bartley Lake (Bennett, 1992). Note the scales change for different pollen types. Pollen counts for these sites are available from the North American Pollen Database (NAPD) through NOAA/National Geophysical Data Center, Boulder, CO, USA.

from swamp and cliff habitats have different water use efficiency and thus different stomatal density.

6. Conclusions

The combined pollen, stomatal and macrofossil data from Crawford Lake refined the late Quaternary history of *Thuja* and *Juniperus* in southern Ontario, which indicate a bimodal temporal distribution pattern of *Juniperus* (likely *J. communis*) in the late glacial (~13,000–10,000 ¹⁴C yr BP) and *Thuja occidentalis* in the Holocene (7500–0 ¹⁴C yr BP). The separation of these taxa in fossil records is important for paleoecologic and paleoclimatic interpretations because the taxa occupy different habitats. Stomatal analysis is a promising paleoecological tool because stomata not only can be used as a proxy of macrofossils to confirm the local presence of conifer taxa, but also provide lower taxonomic identification of certain taxa than pollen.

Acknowledgements

This paper is dedicated to Dr. John (Jock) H. McAndrews, who introduced me to palynology and to Crawford Lake.

I thank Sharon Hick, Jock McAndrews and Will McKenna for assistance with field sediment coring, Darakhshan Siddiqi for help with macrofossil identification, Barbara Hansen for advice on stomatal analysis, Linda Shane and Bob Jefferies for help with two AMS radiocarbon dates, Keith Bennett for providing pollen counts from Mary and Bartley lakes, Jim Eckenwalder, Jock McAndrews, Cathy Whitlock and an anonymous reviewer for constructive reviews and helpful comments on the manuscript, and the Halton Region Conservation Authority for permission to sample at Crawford Lake. This work was in part supported by an Ontario Graduate Scholarship and a University of Toronto Open Fellowship to the author and a Natural Sciences and Engineering Research Council of Canada grant to J. McAndrews.

References

- Adams, R.J. and Morton, J.K., 1972. An atlas of pollen of the trees and shrubs of eastern Canada and the adjacent United States. Part 1. Univ. Waterloo, Dept. Biol., Waterloo, Ont., Biol. Ser. 8, 52 pp.
- Ammann, B. and Wick, L., 1993. Analysis of fossil stomata of conifers as indicators of the alpine tree line fluctuations during the Holocene. In: B. Frenzel (Editor), Oscillations of the alpine and polar tree limits in the Holocene. Paläoklimaforschung, 9: 175–185.
- Anderson, T.W., 1982. Pollen and plant macrofossil analyses on late Quaternary sediments at Kitchener, Ontario. Geol. Surv. Can. Pap., 82-1A: 131–136.
- Bennett, K.D., 1987. Holocene history of forest trees in southern Ontario. Can. J. Bot., 65: 1792–1801.
- Bennett, K.D., 1992. Holocene history of forest trees on the Bruce Peninsula, southern Ontario. Can. J. Bot., 70: 6–18.
- Benninghoff, W.S., 1962. Calculation of pollen and spore density in sediments by the addition of exotic pollen in known quantities. Pollen Spores, 4: 332–333.
- Bortenschlager, S., 1990. Aspects of pollen morphology in the Cupressaceae. Grana, 29: 129–137.
- Boulter, M.C., 1971. Fine details of some fossil and recent conifer leaf cuticles. In: V.H. Heywood (Editor), Scanning Electron Microscopy: systematic and evolutionary applications. Academic, Toronto, pp. 211–235.
- Boulter, M.C., 1994. An approach to a standard terminology for palynodebris. In: A. Traverse (Editor), Sedimentation of Organic Particles. Cambridge Univ. Press, Cambridge, pp. 199–216.
- Cambon, G., 1994. Modern pollen spectra and vegetation in southern Ontario, Canada. Rev. Palaeobot. Palynol., 82: 147–155.
- Clark, J.S. and Royall, P.D., 1995. Transformation of a northern hardwood forest by aboriginal (Iroquois) fire: charcoal evidence from Crawford Lake, Ontario, Canada. Holocene, 5: 1–9.
- Cwynar, L.C., Burden, E. and McAndrews, J.H., 1979. An inexpensive sieving method for concentrating pollen and spores from fine-grained sediments. Can. J. Earth Sci., 16: 1115–1120.
- Dyke, A.S. and Prest, V.K., 1987. Late Wisconsin and Holocene history of the Laurentide Ice Sheet. Géogr. Phys. Quat., 41: 237–263.
- Fægri, K. and Iversen, J., 1989. Textbook of Pollen Analysis. Wiley, London, 4th ed., 328 pp.
- Florin, R., 1951. Evolution in cordaites and conifers. Acta Horti Berg., 15: 285–388.
- Fredlund, G.G. and Tieszen, L.T., 1994. Modern phytolith assemblages from the North American Great Plains. J. Biogeogr., 21: 321–335.
- Hansen, B.C.S., 1995. Conifer stomate analysis as a paleoecological tool: an example from the Hudson Bay Lowlands. Can. J. Bot., 73: 244–252.
- Hansen, B.C.S., MacDonald, G.M. and Moser, K.A., 1996. Identifying the tundra–forest border in the stomate record:

- an analysis of lake surface samples from the Yellowknife area, Northwest Territories, Canada. *Can. J. Bot.*, 74: 796–800.
- Jackson, S.T., 1989. Postglacial vegetational changes along an elevational gradient in the Adirondack Mountains (New York): a study of plant macrofossils. *NY State Mus. Bull.* 465, 29 pp.
- Johnston, W.F., 1990. *Thuja occidentalis*. In: *Silvics of North America: 1. Conifers*. Agriculture Handbook 654. US Dep. Agric., Washington, DC, pp. 580–589.
- Karrow, P.F., 1987. Quaternary geology of the Hamilton–Cambridge area, southern Ontario. *Ont. Geol. Surv. Rep.* 255, 94 pp.
- Karrow, P.F., Anderson, T.W., Clarke, A.H., Delorme, L.D. and Sreenivasa, M.R., 1975. Stratigraphy, paleontology, and age of Lake Algonquin sediments in southwestern Ontario, Canada. *Quat. Res.*, 5: 49–87.
- Kelly, P.E., Cook, E.R. and Larson, D.W., 1992. Constrained growth, cambial mortality, and dendrochronology of ancient *Thuja occidentalis* on cliffs of the Niagara Escarpment: an eastern version of bristlecone pine? *Int. J. Plant Sci.*, 153: 117–127.
- Kelly, P.E., Cook, E.R. and Larson, D.W., 1994. A 1397-year tree-ring chronology of *Thuja occidentalis* from cliff faces of the Niagara Escarpment, southern Ontario, Canada. *Can. J. For. Res.*, 24: 1049–1057.
- Kerp, H., 1990. The study of fossil gymnosperms by means of cuticular analysis. *Palaios*, 5: 548–569.
- Larson, D.W. and Kelly, P.E., 1991. The extent of old-growth *Thuja occidentalis* on cliffs of the Niagara Escarpment. *Can. J. Bot.*, 69: 1628–1636.
- Larson, D.W. and Kelly, P.E., 1994. Holocene remnants of Niagara Escarpment *Thuja occidentalis* forests: ecological, hydrological and geological implications. *GAC/MAC Progr. Abstr.*, 19: A61.
- Larson, D.W. and Melville, L., 1996. Stability of wood anatomy of living and Holocene *Thuja occidentalis* L. derived from exposed and submerged portions of the Niagara Escarpment. *Quat. Res.*, 45: 210–215.
- Larson, D.W., Spring, S.H., Matthes-Sears, U. and Bartlett, R.M., 1989. Organization of the Niagara Escarpment cliff community. *Can. J. Bot.*, 67: 2731–2742.
- Liu, Kam-biu, 1990. Holocene paleoecology of the boreal forest and Great Lakes–St. Lawrence forest in northern Ontario. *Ecol. Monogr.*, 60: 179–212.
- Maher, L.J., 1981. Statistics for microfossil concentration measurements employing samples spiked with marker grains. *Rev. Palaeobot. Palynol.*, 32: 153–191.
- Mayle, F.E. and Cwynar, L.C., 1995. Impact of the Younger Dryas cooling event upon lowland vegetation of Maritime Canada. *Ecol. Monogr.*, 65: 129–154.
- McAndrews, J.H., 1972. Fossil pollen and plant macrofossils from the Fernbank site, New York. *Friends of the Pleistocene*, 35th Annu. Reunion Guideb., pp. 5–11.
- McAndrews, J.H., 1981. Late Quaternary climate of Ontario: temperature trends from the fossil pollen record. In: W.C. Mahaney (Editor), *Quaternary Paleoclimate*. GeoAbstracts, Norwich, pp. 319–333.
- McAndrews, J.H. and Boyko-Diakonow, M., 1989. Pollen analysis of varved sediment at Crawford Lake, Ontario: evidence of Indian and European farming. In: R.J. Fulton (Editor), *Quaternary Geology of Canada and Greenland*. (Geology of Canada, 1). *Geol. Surv. Can.*, pp. 528–530.
- McAndrews, J.H., Berti, A.A. and Norris, G., 1973. Key to the Quaternary pollen and spores of the Great Lakes region. *Life Sci. Misc. Publ., R. Ont. Mus.*, Toronto, Ont., 61 pp.
- Miller, N.G. and Thompson, G.G., 1979. Boreal and western North American plants in the late Pleistocene of Vermont. *J. Arnold Arbor.*, 60: 167–218.
- Moore, P.D., 1980. The reconstruction of the late glacial environment: some problems associated with the interpretation of pollen data. In: J.J. Lowe, J.M. Gray and J.E. Robinson (Editors), *Studies in the Late Glacial of Northwest Europe*. Pergamon, Oxford, pp. 151–155.
- Moore, P.D., Webb, J.A. and Collinson, M.E., 1991. *Pollen analysis*. Blackwell, Oxford, 2nd ed., 216 pp.
- Oladele, F.A., 1983. Scanning electron microscope study of stomatal-complex configuration in Cupressaceae. *Can. J. Bot.*, 61: 1232–1240.
- Palmer, P.G., 1976. Grass cuticles: a new paleoecological tool for East African lake sediments. *Can. J. Bot.*, 54: 1725–1734.
- Parent, J. and Richard, P.J.H., 1990. Morphologie pollinique des Cupressaceae de l'est du Canada et du nord-est des États-Unis appliquée à l'étude des sédiments quaternaires. *Can. J. Bot.*, 68: 79–89.
- Richard, P.J.H., 1970. Atlas pollinique des arbres et de quelques arbustes indigènes du Québec. I. Introduction générale, II. Gymnospermes. *Nat. Can.*, 97: 1–34.
- Richard, P.J.H., 1980. Histoire postglaciaire de la végétation au sud du lac Abitibi, Ontario et Québec. *Géogr. Phys. Quat.*, 34: 77–94.
- Rovner, I., 1971. Potential of opal phytoliths for use in paleoecological reconstruction. *Quat. Res.*, 1: 343–359.
- Schwert, D.P., Anderson, T.W., Morgan, A., Morgan, A.V. and Karrow, P.F., 1985. Changes in late Quaternary vegetation and insect communities in southwestern Ontario. *Quat. Res.*, 23: 205–226.
- Van Geel, B., Coope, G.R. and Van der Hammen, T., 1989. Palaeoecology and stratigraphy of the Lateglacial type section at Usselo (The Netherlands). *Rev. Palaeobot. Palynol.*, 60: 25–129.
- Warner, B.G., 1982. Late Glacial fossil leaves of *Thuja occidentalis* from Manitoulin Island, Ontario. *Can. J. Bot.*, 60: 1352–1356.
- Warner, B.G., Hebda, R.J. and Hann, B.J., 1984. Postglacial paleoecological history of a cedar swamp, Manitoulin Island, Ontario, Canada. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 45: 301–345.
- Watts, W.A., 1979. Late Quaternary vegetation of central Appalachia and the New Jersey coastal plain. *Ecol. Monogr.*, 49: 427–469.
- Wick, L., 1994. Early-Holocene reforestation and vegetation

- change at a lake near the Alpine forest limit: Lago Basso (2250 m asl), Northern Italy. *Diss. Bot.*, 234: 555–563.
- Willmer, C.M., 1983. *Stomata*. Longman, London, 166 pp.
- Wright Jr., H.E., 1967. A square rod piston sampler for lake sediments. *J. Sediment. Petrol.*, 37: 975–976.
- Yu, Zicheng and McAndrews, J.H., 1995. Postglacial paleohydrology at Crawford Lake, Ontario: Dry climate triggered mid-Holocene hemlock decline? *AASP Progr. Abstr.*, 28: A21–22.
- Yu, Zicheng, McAndrews, J.H. and Siddiqi, D., 1996. Influences of Holocene climate and water levels on vegetation dynamics of a lakeside wetland. *Can. J. Bot.*, 74: 1602–1615.