Postglacial vegetation history of oak savanna in southern Ontario

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Sizable areas of oak savanna were present in southern Ontario when the region was first settled by Europeans. The objective of this study was to reconstruct the vegetation history of oak savanna at a site in Ontario and to test the hypothesis that the savanna was created by Indian burning. The fossil pollen, plant macrofossil, and fossil charcoal records of the sediments of a small lake were used to reconstruct postglacial vegetation development in an area formerly occupied by oak savanna. The fossil record from the site extends from approximately 11 800 BP to the present. The initial vegetation around the lake was an open *Picea* woodland similar to that reported from other late glacial sites in southern Ontario. *Pinus banksiana* forest dominated the vegetation of the site between about 10 000 and 9000 BP. *Pinus strobus* replaced *Pinus banksiana* and remained the dominant tree species in the area until approximately 6000 BP. The persistence of *Pinus strobus* as the dominant tree species until 6000 BP is unique in southern Ontario. Between 6000 and 4000 BP the *Pinus strobus* forest was replaced by oak savanna. Oak savanna occupied the area until land clearance by Europeans at approximately A.D. 1850. The early date at which oak savanna developed makes it unlikely that Indian burning was the cause of savanna formation. Determining the cause of the late persistence of *Pinus strobus*-dominated vegetation and its replacement by oak savanna is difficult. It is possible that the late persistence of *Pinus strobus* in the study area is related to dry climatic conditions during the mid-Holocene (~8000 to 6000 BP). The establishment of oak savanna may have been caused by the transition to moister climatic conditions in the later half of the Holocene. The particularly dry and well-drained substrates associated with oak savanna may have restricted occupation of these regions by more mesic tree species and maintained herb and graminoid dominated openings by promoting natural fires.

Key words: Palaeoecology, fossil pollen, Holocene, oak savanna, southern Ontario.

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Dès l'établissement des nouveaux colons européens, il existait déjà de bonnes surfaces de savanne à chêne, dans le sud de l'Ontario. Les auteurs se sont donné comme objectif de reconstruire l'histoire de la végétation de la savanne à chêne sur un site de l'Ontario et de vérifier l'hypothèse que cette savanne aurait été créée par le feu, sous l'influence des indiens. Les données du pollen, des macrorestes et des charbons fossiles provenant des sédiments d'un petit lac sont utilisés pour reconstruire le développement de la végétation post glaciaire, sur un site occupé par une savanne à chêne. Les restes fossiles du site remontent depuis 11 800 BP. La végétation de départ autour du lac était constituée par une forêt à *Picea* semblable à celle rapportée pour d'autres sites de la fin de l'époque glaciaire du sud de l'Ontario. Des forêts de pin gris ont dominé la végétation du site entre 10 000 et 9000 BP. Le *Pinus strobus* a remplacé le *Pinus banksiana* et est demeuré l'espèce dominante dans la région jusqu'à 6000 BP. La persistance du *Pinus strobus* comme espèce arborescente dominante jusqu'à 6000 BP est unique pour le sud de l'Ontario. Entre 6000 et 4000 BP la forêt de *Pinus strobus* a été remplacée par la savanne à chêne. La savanne à chêne a occupé la région jusqu'à ce que les européens défrichent les terres, vers 1850 A.D. La venue très hâtive de la savanne à chêne rend peu probable que les feux des indiens puissent avoir causé la formation de la savanne. Il est difficile de déterminer la cause exacte du maintien tardif d'une végétation dominée par le *Pinus strobus* et son remplacement par la savanne à chêne. Il est possible que la persistance tardive du *Pinus strobus*, dans la région étudiée, soit reliée aux conditions climatiques sèches pendant le milieu de l'Holocène (8000 à 6000 BP). L'établissement de la savanne à chêne pourrait avoir été causé par la transition vers des conditions climatiques plus humides dans la deuxième moitié de l'Holocène. Les substrats particulièrement secs et bien drainés associés avec la savanne à chêne pourraient avoir restreint l'occupation de ces régions par des espèces arborescentes plus mésiques en maintenant des ouvertures dominées par des herbes et des espèces graminoïdes tout en favorisant les feux naturels.

Mots clés : paléoécologie, Holocène, savanne à chêne, sud de l'Ontario.

[Traduit par la rédaction]

Introduction

Quercus-dominated woodland is widespread in the midwestern United States where it forms an ecotone between prairie and deciduous forest (Cottam 1949; Curtis 1959; McAndrews 1966; Grimm 1984). Oak savanna was also found at scattered locations in southern Ontario when the region was first settled by Europeans (Wood 1961; Maycock 1963; Chanasyk 1972; Reznicek and Maycock 1983; Bakowsky 1988). Most of the savanna in Ontario has since been cleared for settlement and agriculture.

Studies of fossil pollen have shed considerable light on the postglacial history of oak savannas in the American midwest (e.g., McAndrews 1966; Grimm 1983). In addition, fossil pollen records from the prairie – oak savanna – deciduous forest ecotone have been used to reconstruct Holocene climate change (e.g., Webb and Bryson 1972; Bartlein *et al.* 1984). The most striking feature of the postglacial climate history of the midwest appears to be a period of pronounced aridity extending from 8000 to 4000 BP. Despite continued interest in the oak savanna of Ontario (Ball 1981; MacDonald 1987; Bakowsky 1988), no specific study to resolve its origin or history has been made. It has been suggested that repeated burning by native peoples to clear land for agriculture and hunting may have led to destruction of the original forests and their replacement by open, fire-tolerant vegetation (J. D. Wood 1961;

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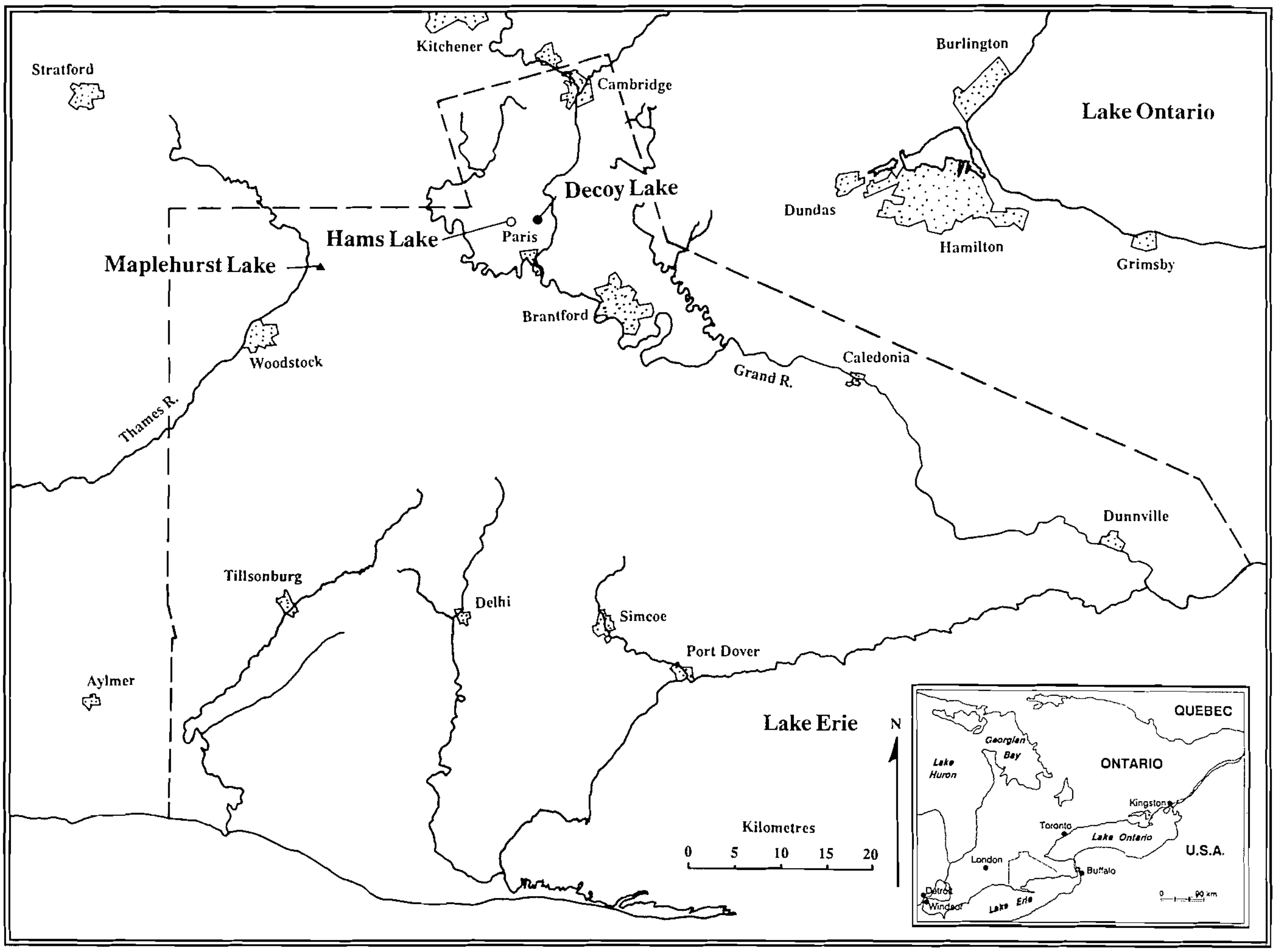


FIG. 1. Location of the study area in southern Ontario and the sites discussed in text.

Lumsden 1966; C. J. B. Wood 1966; Bakowsky 1988). Alternatively, it has been proposed that a combination of local climatic and edaphic factors may have resulted in the development of the oak savanna, perhaps through an alteration of natural fire regimes (C. J. B. Wood 1966; Bakowsky 1988).

The objective of this research was to determine the timing and assess potential causal factors relating to the origin of oak savanna in southern Ontario. The study is composed of two parts: (*i*) an examination of the presettlement distribution of oak savanna in southern Ontario and an assessment of physical environmental factors that may have controlled the distribution of oak savanna, and (*ii*) the palaeoecological analysis of a sediment core from a lake that lies within the presettlement oak savanna.

Oak savanna in southern Ontario

Physiognomy and floristics

The oak savanna in southern Ontario, as described in accounts by early settlers (J. D. Wood 1961; C. J. B. Wood 1966; Chanasyk 1972), was typified by well-spaced *Quercus* trees, with an understorey of herbs and shrubs. *Carya, Castanea*, and *Populus* trees were also common. In some areas, however, oaks and other trees occurred as scrubby thickets rather than individual trees. An early traveller described the savanna south of Cambridge as ". . .an extensive range of open, grove-like woodland, principally oak, and the trees so dispersed as to not interfere materially with the plough" (Fergusson in Ball 1981). In this paper the term oak savanna is used to describe a vegetation consisting of an admixture of oak and grassy-herbaceous openings. The precise physiognomy of the vegetation likely ranged from thickets of oak dominated woods with grassy openings to areas of widely spaced oaks with an open understorey.

In a recent study, Bakowsky (1988) examined the floristics and phytosociology of 52 savanna stands throughout southern Ontario. The sites cover a soil moisture spectrum from very dry to wet-mesic. *Juniperus virginiana* dominated on very dry soils, but all remaining stands were dominated by *Quercus* species and had averages of 33 to 55% canopy cover. The species composition (botanical nomenclature follows Gleason 1952) of oak savanna stands varied depending on soil moisture conditions, but *Quercus velutina* and *Quercus alba* were the strongest dominants. Also important were *Prunus serotina, Quercus macrocarpa, Quercus palustris, Quercus rubra, Populus deltoides*, and *Carya ovata*. The understorey was dominated by sedge and grass genera such as *Carex, Andropogon*, and *Poa*. Other common herbs included *Aster umbellatus, Geranium maculatum, Helianthus divaricatus*, and *Solidago altissima*. Important shrubs included *Vitis riparia* and *Cornus racemosa*.

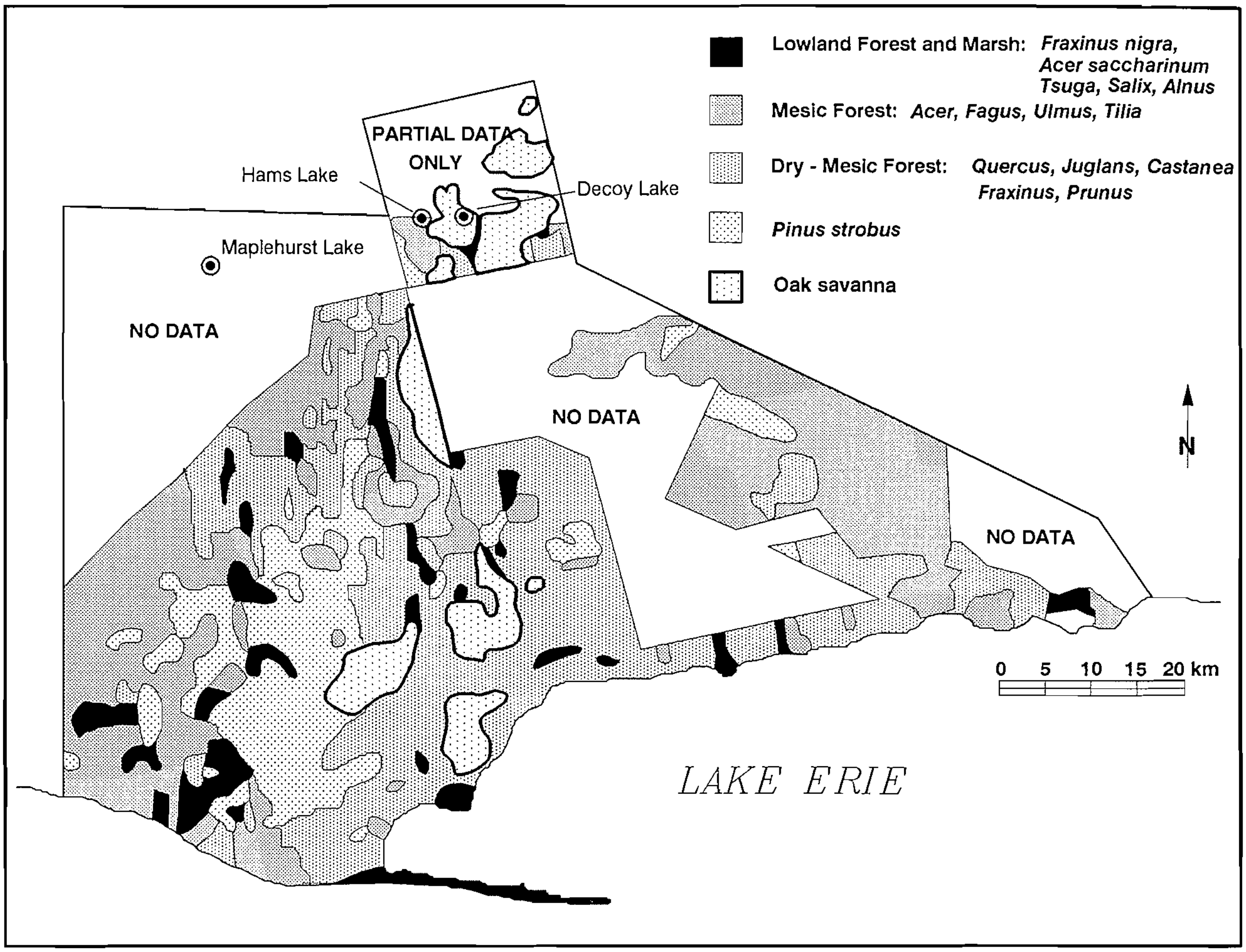


FIG. 2. Presettlement vegetation of the study area, reconstructed from 19th century survey data (based on J. D. Wood 1961; C. J. B. Wood 1966; Chanasyk 1972).

Geographic Distribution

Evidence of presettlement oak savanna has been reported from a number of sites in southern Ontario. Early accounts describe it as occurring south of Windsor, on the south and east shores of Lake St. Clair, along the lower Thames River in Kent County, west of London, north of Turkey Point on Lake Erie, and around Brantford (J. D. Wood 1961; C. J. B. Wood 1966; Chanasyk 1972; Bakowsky 1988). A small number of undisturbed oak savanna stands remain in the region. The stands investigated by Bakowsky (1988) were located around Windsor, on Walpole Island north of Lake St. Clair, at Sarnia, Long Point, and Brantford, on Pelee Island, and at Grand Bend on the southern shore of Lake Huron. Reznicek and Maycock (1983) describe a small prairie surrounded by about 11 ha of *Quercus rubra – Pinus strobus* savanna on the south shore of Lake Simcoe. The presence of a small, scattered population of *Quercus ellipsoidalis* north of Brantford is noted by Ball (1981). The species reaches its maximum importance on oak savanna in the midwestern U.S., and this population is 200 km east of the nearest localities in Michigan.

An area including Haldimand-Norfolk, Brant, Elgin, and Waterloo counties was selected for detailed examination of the geographic distribution of oak savanna (Fig. 1). The presettlement vegetation of this region (Fig. 2) was reconstructed using a combination of early survey data (J. D. Wood 1961; C. J. B. Wood 1966; Chanasyk 1972) and more recent phytosociological research (Maycock 1963). Dry soils were dominated by *Quercus rubra, Quercus velutina, Quercus alba, Carya ovata, Ostrya virginiana, Castanea dentata, Fraxinus americana, Juglans nigra, Prunus serotina,* and *Pinus strobus*. Mesic forest, dominated by *Acer saccharum* and *Fagus grandifolia*, was the most common association in southern Ontario (Maycock 1963). Within the study area, however, it was restricted to the eastern and western margins. *Tilia americana, Acer nigrum, Acer rubrum, Ulmus americana,* and *Carya cordiformis* were important subdominants on mesic sites. Moist lowlands supported *Ulmus americana* and *Acer saccharinum*, with lesser amounts of *Quercus palustris, Platanus occidentalis, Tilia americana, Fraxinus nigra*, and *Tsuga canadensis*.

Physical setting

The study area is underlain by Devonian and Silurian rocks composed mainly of limestone and dolomite. The bedrock is blanketed by tills, glaciolacustrine and glaciofluvial sediments (Fig. 3). Ice-retreat from the region occurred between 13 000 and 12 000 BP (Chapman and Putnam 1984; Karrow 1987; Karrow and Warner 1988). The clayey silty Port Stanley Till and the silty Zorro Till along the western edge of the region comprise the oldest surficial deposits (Cowan 1972; Chapman

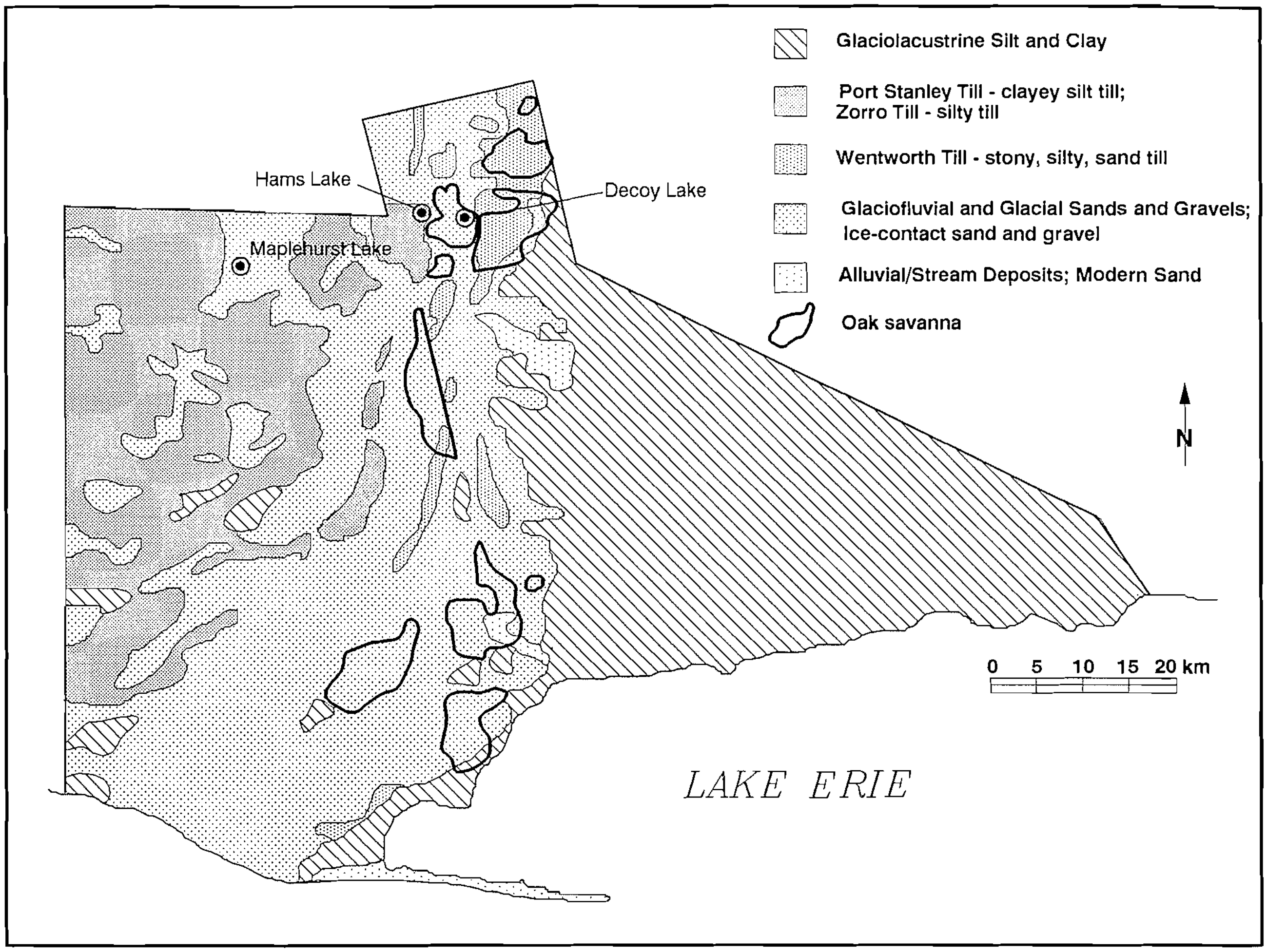


FIG. 3. Surficial geology of the study area and distribution of oak savanna (based on Chansyk 1972, Cowan 1972, Chapman and Putnam 1984, and Karrow 1987).

and Putnam 1984). The more recent Paris and Galt Moraines in the centre of the study area are composed of coarse-grained deposits of Wentworth Till (Karrow 1987; Karrow and Warner 1988). These sediments were laid down during the Port Huron advance (14 000 to 13 000 BP) (Chapman and Putnam 1984; Karrow 1987; Karrow and Warner 1988). Fluvial and deltaic sands and gravels were deposited throughout the central part of the region by meltwaters running in a spillway between the ice front and exposed land to the west. The deposits of sand to the south of Brantford are up to 20 m deep and have partially buried portions of the Galt and Paris Moraines. Fine silts and clays that settled on the bed of proglacial Lake Warren form the Haldimand Clay Plains in the eastern half of the study area.

Soils in the study area are primarily Grey-Brown Luvisols (Bentley 1978). Soil drainage classes correlate closely with the texture of the Quaternary deposits (Presant and Wicklund 1971; Ontario Institute of Pedology 1988). Coarse, well-drained soils overlie most of the Wentworth Till and sandy outwash and deltaic deposits but are far less common on the Haldimand Clay Plains or Port Stanley Till.

The climate of the study area (Fig. 4) is continental, but modified by the proximity of the Great Lakes (Hare and Thomas 1979). Mean daily temperatures in July average about 20°C and in January average −5°C. Mean daily winter temperatures decrease along a southeast to northwest gradient within the study area, while summer temperatures and the mean number of degree-days >5°C show little regional variation (Fig. 4). Annual precipitation varies from over 950 mm in the southwest to less than 850 mm in the north.

The distribution of presettlement vegetation is strongly correlated with the surficial deposits of the study area (Figs. 2 and 3). Oak savanna was found exclusively on coarse soils developed on outwash sands and gravels or Wentworth Till. Mesic *Fagus-Acer* forests were most common on Port Stanley Till or glaciolacustrine silts and clays. The distribution of the presettlement vegetation does not appear to correspond with regional variation in precipitation or temperatures (Figs. 2 and 4).

Palaeoecological study site

Since the oak savanna occurred as relatively small and discontinuous units (Fig. 2), a small basin (0.42 ha) was selected for the palaeoecological study to maximize the pollen signal from local vegetation relative to the regional pollen rain (Jacobson and Bradshaw 1981). Decoy Lake (unofficial name) is situated at latitude 43°14′N, longitude 80°22′W, and an elevation of approximately 260 m asl (Fig. 1). The lake occupies a kettle formed in coarse outwash gravels deposited in a glacial spillway during the Port Huron Advance (Chapman and Putnam 1984). Decoy Lake is 60 m by 70 m and has

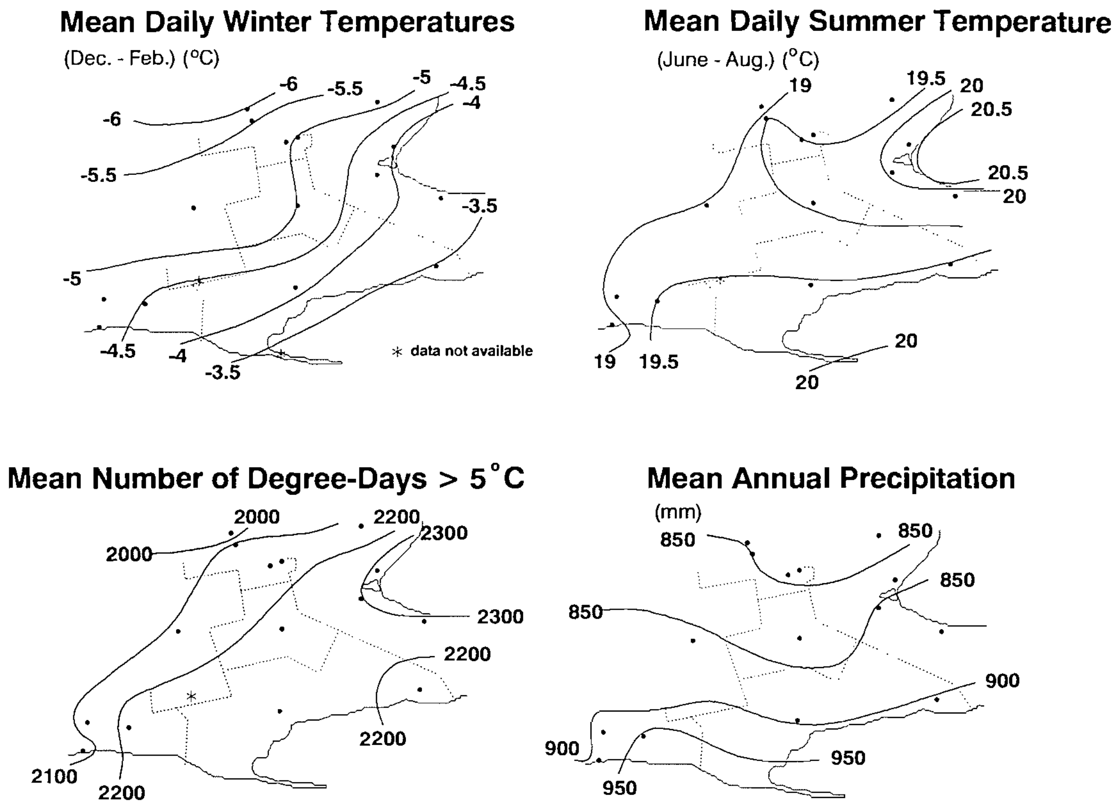


FIG. 4. Mean winter temperature, mean summer temperature, mean number of degree-days greater than 5°C and mean annual precipitation for the study area. Isolines are hand-drawn based on data from 16 climate recording stations (Environment Canada 1982*a*, 1982*b*, 1982*c*).

a maximum depth of 50 cm. The soils around the site are the well-drained Burford Loam series (Presant and Wicklund 1971; Ontario Institute of Pedology 1988). The lake is well within the limits of presettlement oak savanna (Fig. 2). Corn (*Zea mays*) fields now surround the site on all sides, though an area within 100 to 200 m of the lake has remained uncultivated (Table 1). The lake is ringed by shrubs (*Cornus stolonifera*, *Prunus serotina*, *Prunus virginiana*, *Salix* spp., *Vitis riparia*) and about 20 mature *Quercus alba* and *Quercus macrocarpa* trees. The unploughed slopes are occupied by a low cover of herbs and scattered *Populus tremuloides*, *Quercus macrocarpa*, *Quercus ellipsoidalis*, and *Ulmus americana* trees. It is notable that *Quercus ellipsoidalis*, rare in southern Ontario, reaches its maximum abundance in midwestern oak savanna (Ball 1981).

Methods

Field sampling

Decoy Lake was cored in 1987 using a modified Livingstone piston corer (Wright *et al.* 1984). Since the uppermost sediment was extremely unconsolidated, the top 23 cm was sampled using a plastic tube.

Laboratory analysis

Sediment samples were taken at 5-cm intervals and the organic carbon content of the sediment was examined by loss on ignition (LOI) as outlined by Dean (1974). Accelerator mass spectrometry (AMS) was used to obtain five radiocarbon dates for terrestrial plant macrofossils from the core. The AMS dating was carried out by the Isotrace Laboratory of the University of Toronto.

The core was subsampled for pollen analysis at 5-cm intervals. The samples were prepared following the procedures described by Cwynar *et al.* (1979) and MacDonald (1988). Samples with a high content of coarse organic matter were sieved with a 0.6-mm mesh screen. A known quantity of pretreated *Lycopodium* spores was added to each sample prior to processing to allow calculation of pollen accumulation rates (PAR) (Maher 1972). Between 290 and 480 grains of terrestrial pollen were counted at each level. Fossil pollen grains were identified using a modern reference collection and McAndrews *et al.* (1973). *Picea* grains were differentiated into *Picea* cf. *glauca* and *Picea* cf. *mariana* using the morphological characteristics detailed by Hansen and Engstrom (1985). The proportions of haploxylon (*Pinus strobus*) and diploxylon (*P. banksiana* and *P. resinosa*) pine pollen were estimated for selected samples. A minimum of 25 pine pollen grains were differentiated per sample. The microscopic charcoal content of the pollen slides was examined using digital image analysis (MacDonald *et al.* 1991). The abundance of charcoal was represented as the ratio of charcoal to terrestrial pollen (CHAR:PAR) and was calculated as μm^2 charcoal·/(cm^2·year) to pollen·/(cm^2·year). Theoretical and empirical studies suggest that variations in the abundance of microscopic charcoal fragments are representative of regional fire activity (Clark 1988; MacDonald *et al.* 1991).

Samples of 50 mL of sediment were taken from the core at 20-cm intervals. The samples were soaked in water and sieved through a 0.6-mm mesh screen to isolate plant macrofossils. The macrofossils were identified using a modern reference collection and Montgomery (1977).

Numerical analysis

Difference diagrams (Jacobson 1979) were constructed to compare the presettlement pollen stratigraphy of Decoy Lake with that of nearby sites that lie beyond the known limits of oak savanna. The closest pollen records to Decoy Lake come from Hams Lake (Bennett 1987), a 2.5-ha kettle lake located about 5 km W of Decoy Lake, and Maplehurst Lake (Mott and Farley-Gill 1978), a 6-ha lake located about 25 km WSW of Decoy Lake (Fig. 1). Both lakes are located in regions that are dominated at present by *Fagus grandifolia* – *Acer saccharum* forest. The diagrams were constructed by subtracting the pollen percentages of important taxa at one site from the percentages

TABLE 1. Floristic survey of the Decoy Lake site

Grassy slopes around pond	Ring of trees and (or) shrubs around pond	Edge of pond
Trees and shrubs	Canopy trees	*Carex mulenburghii*
Cornus stolonifera	*Quercus alba*	*Carex sychnocephala*
Populus tremuloides	*Quercus macrocarpa*	*Epilobium* sp.
Quercus ellipsoidalis		*Leersia oryzoides*
Quercus macrocarpa	Understorey	*Lycopus europaeus*
Ulmus americana	*Cornus stolonifera*	*Panicum* sp.
	Cornus racemosa	*Poa palustris*
Herbs	*Prunus serotina*	*Phalaris arundinacea*
Ambrosia artemisiifolia	*Prunus virginiana*	*Polygonum lapathifolium*
Arctium minus	*Prunus americana*	*Polygonum pensylvanicum*
Asclepias syriaca	*Rhamnus* sp.	*Scirpus atrovirens*
Aster ericoides	*Salix* sp.	
Bromus inermis	*Vitis riparia*	
Dipsacus sylvestris		
Lespedeza capitata		
Monarda fistulosa		
Oenothera biennis		
Poa pratensis		
Potentilla canadensis		
Rosa blanda		
Solidago canadensis		
Solidago nemoralis		
Trifolium dubium		
Verbascum thapsus		
Verbena hastata		

NOTE: Survey was compiled in August and October of 1988 with the assistance of W. Bakowsky, University of Toronto.

TABLE 2. Radiocarbon dates for Decoy Lake core

Depth (cm)	Material	Weight (mg)	Lab. No.	Age (BP ± 1σ)
94	Twig fragment	42	T0-1050	2 620 ± 40
135	Bark fragment	152	T0-1051	6 320 ± 60
250	Twig fragment	139	T0-1052	8 600 ± 80
418	Bark fragment	90	T0-1048	10 160 ± 80
497	Twig	449	T0-1049	11 770 ± 90

NOTE: All dates are $\delta^{13}C$ corrected.

of the same taxa at one of the other two sites. The diagrams present the difference between pollen samples at 500-year intervals. The pollen percentages from samples within 150 years of each 500-year interval were averaged to provide the values used in the calculation of the difference diagrams.

Results

Sediment stratigraphy and radiocarbon dates

From the base to 497 cm, the core is composed of inorganic clays and sands (Fig. 5). The core consists of gyttja between 497 and 445 cm in depth. The sediment then grades into peaty gyttja that continues to 30 cm in depth. The peaty gyttja contains numerous vascular plant remains and wood fragments. A 2-cm sand and clay lens is present at 286 cm depth. The top 30 cm of the core is composed of gyttja. The radiocarbon dates are internally consistent and indicate that the core spans the Holocene (Table 2). The sedimentation rate in the lake appears to have decreased as the Holocene progressed (Fig. 5).

Pollen, plant macrofossil, and charcoal stratigraphy

The pollen stratigraphy of Decoy Lake was divided into five zones by visual inspection of the pollen percentages (Fig. 6). The plant macrofossil and charcoal records (Figs. 6 and 7) are described in relationship to the pollen stratigraphy. To correlate the main core with the plastic-tube core, the rise in *Ambrosia* pollen was used as a marker horizon. Analysis of the annually laminated sediments of Crawford Lake, 40 km NW of Decoy Lake, show an abrupt rise in *Ambrosia* pollen at about A.D. 1850 (McAndrews 1988). The rise in *Ambrosia* occurs at a depth of 33 cm in the main core and 12 cm in the plastic-tube core. The discrepancy in the depth of the *Ambrosia* rise likely reflects a combination of settling of the highly unconsolidated sediment in the plastic tube following coring and the fact that first drive with the Livingstone corer began slightly above the actual sediment–water interface.

The rates of total pollen accumulation for Decoy Lake (Fig. 6) indicate that sediment focussing (Davis *et al.* 1984) occurred during the early to mid-Holocene. As a result, PARs for individual taxa are extremely difficult to interpret and are not presented here.

*Zone 1 (*Picea *zone): 495–415 cm (11 800–10 100 BP)*

High percentages (45–80%) of *Picea* pollen characterize this zone. *Picea* cf. *glauca* pollen is more abundant than that of *Picea* cf. *mariana*. The pollen of *Quercus, Ostrya/Carpinus*, and *Fraxinus* is moderately abundant (2–10%). *Betula* pollen rises to a peak of 13% near the top of the zone. The lower levels of the zone contain higher amounts of herb, Cyperaceae, *Quercus* and *Fraxinus* pollen, and lesser amounts of *Picea* pollen. *Picea* needle fragments are abundant at the base of the zone. Values of CHAR:PAR reach a maximum of over 2000 at the base of the core. The basal CHAR:PAR value is from extremely inorganic sediment and likely reflects the very low pollen accumulation rates in this portion of the core (Fig. 6) and the misclassification of reworked organic material and

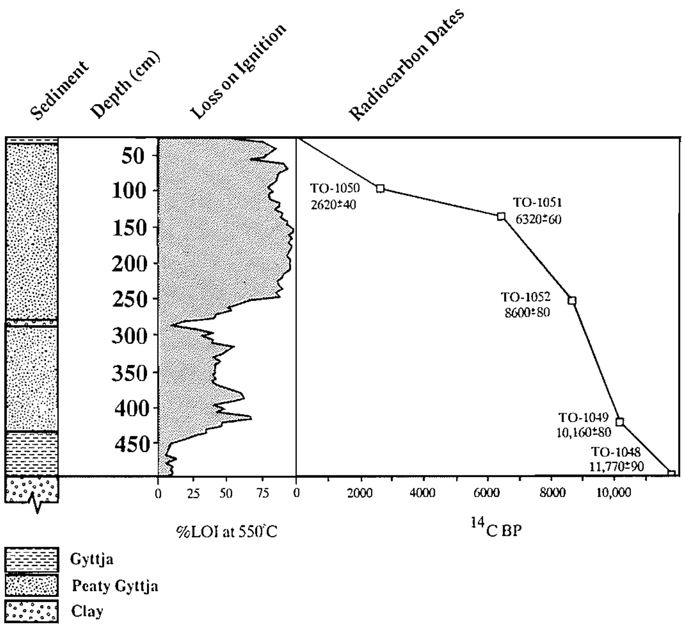


FIG. 5. Sediment and radiocarbon stratigraphy of Decoy Lake.

mineral matter as charcoal. Values of CHAR:PAR in the remainder of the zone range from about 600 to less than 100.

*Zone 2 (*Pinus *zone): 410–135 cm (10 100–6 300 BP)*

The second zone is characterized by very high frequencies of *Pinus* pollen (60–95%) and low percentages of nearly all other taxa. *Pinus banksiana*/*resinosa* pollen dominates in the lower portion of the zone, but is subsequently replaced by pollen from *Pinus strobus*. *Quercus* pollen occurs at frequencies of 8–12% throughout most of the zone. Herb pollen is poorly represented. Several *Pinus strobus* needle fragments, a *Pinus strobus* seed, and a *Pinus banksiana* needle were found in this section of the core. The values of CHAR:PAR are variable. However, on the average, the ratio of CHAR:PAR is lower in this zone than in other zones.

*Zone 3 (*Pinus–Quercus *zone): 130–115 cm (6300–4000 BP)*

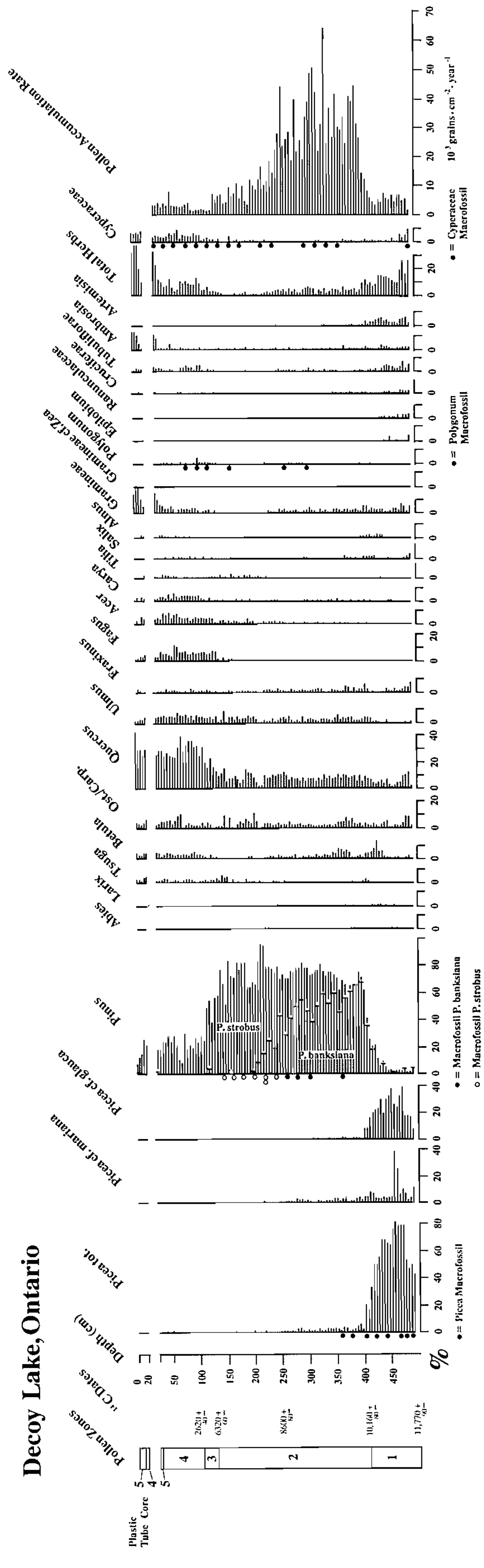
This zone represents a transition between the preceding *Pinus*-dominated assemblage and the following *Quercus*–*Pinus*-herb zone. *Pinus* pollen averages about 50%, while *Quercus* rises from about 12 to 20% from the base to the top of the zone. *Fagus* and *Acer saccharum* pollen rise to levels of 7 and 5%, respectively. The percentage of herb and grass pollen increases to values of 4–9%. The ratios of CHAR:PAR are variable, but generally high in this zone.

*Zone 4 (*Quercus–Pinus–*herb zone): 110–35 cm (4000–100 BP)*

This zone is characterized by a dominance of *Quercus* pollen (30%). The frequency of *Pinus* pollen declines to values of 8–28%. Herb pollen increases to an average of 8–10%. Cyperaceae pollen percentages rise to levels of 4–6%. The values of CHAR:PAR are similar to the preceding zone.

*Zone 5 (*Ambrosia *zone): 30–25 cm main core, 10–0 cm upper core (100 BP to present)*

A marked increase in herb pollen delineates the beginning of this zone. *Ambrosia* rises from 4 to 12%, and Gramineae rises from less than 10% to nearly 20%. Several herb taxa that



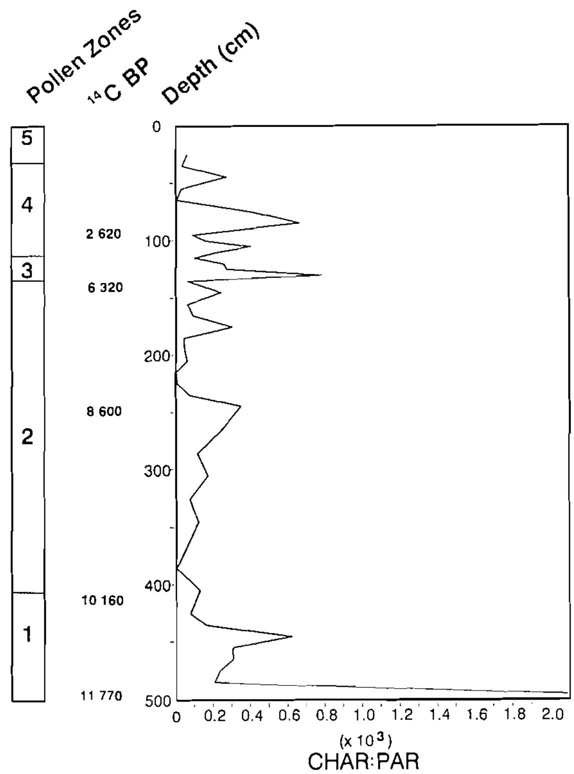


FIG. 7. CHAR:PAR ratio for Decoy Lake.

are good indicators of European settlement and clearance (McAndrews 1988) are found in this zone. These include *Zea mays, Rumex*, and *Plantago lanceolata*. Most arboreal taxa decrease in this zone, including *Pinus*, which drops from over 20% to less than 10%. The values of CHAR:PAR decline to values of less than 100.

Difference diagrams

Decoy Lake vs. Hams Lake

From 11 000 to 10 000 BP Hams Lake had higher percentages of *Pinus* and Cyperaceae pollen, while Decoy Lake had greater amounts of *Picea* and herb pollen (Fig. 8*a*). At 10 000 BP, the difference in *Picea* pollen percentages became negligible, whereas *Pinus* percentages at Decoy Lake increased to well above those at Hams Lake. The difference in the percentages of *Pinus* pollen at the two sites was greatest between 8000 and 4000 BP. *Quercus* and *Ostrya/Carpinus* were more abundant at Hams Lake in the early to mid-Holocene. *Fagus, Ulmus, Acer, Fraxinus*, and *Betula* pollen percentages at Hams Lake were greater than at Decoy Lake for most of the mid to late Holocene. The pollen percentages of *Quercus* at Decoy Lake were higher than those at Hams Lake from 4000 BP to approximately 500 BP. Pollen from Cyperaceae and herbs was more abundant at Decoy Lake from approximately 6000 BP to the present.

Decoy Lake vs. Maplehurst Lake

This diagram (Fig. 8*b*) is similar to the one comparing Decoy and Hams Lakes. The salient features are the greater abundance of *Pinus* pollen at Decoy Lake during the early to mid-Holocene and higher percentages of *Quercus* and herb pollen at Decoy Lake during the late Holocene. The pollen percentages of *Tsuga, Betula, Ulmus, Fraxinus, Fagus*, and *Acer* were much higher at Maplehurst lake than at Decoy Lake during the mid and late Holocene.

Hams Lake vs. Maplehurst Lake

The differences between these two sites (Fig. 8*c*) are relatively small. *Tsuga* pollen was more abundant at Maplehurst Lake than at Hams Lake. *Quercus* was generally more abundant at Hams Lake, particularly in the last 1000 years. *Fagus* had similar pollen percentages at the two lakes until 1000 BP, when its values declined at Hams Lake. *Carya* percentages were higher at Hams Lake following 6000 BP, while *Acer* was generally more abundant at Maplehurst Lake.

Postglacial vegetation development at Decoy Lake

Vegetation reconstruction

The abundance of wood fragments and *Picea* needles in the basal sediments indicates that Decoy Lake was formed following the collapse of an ice block that was overlain by glacial deposits that supported vegetation (Florin and Wright 1969). The radiocarbon date of 11 770 BP obtained on the largest of the wood fragments compares closely with dates of 11 900 and 12 000 BP obtained by Karrow and Warner (1988) on a *Picea* log found in a similar "trash zone" at the base of a peat and lake sediment sequence located approximately 20 km NW of Decoy Lake.

The earliest pollen assemblage recorded at Decoy Lake is indicative of *Picea*-dominated forest-tundra. High percentages of Gramineae, Tubuliflorae, Cruciferae, Cyperaceae, Ranunculaceae, and *Artemisia* pollen attest to the open nature of the vegetation. At 11 300 BP the frequency of *Picea* increases substantially at the expense of herbs, indicating the development of closed boreal forest. *Picea glauca* is likely to have dominated on the well-drained and mesic sites, while *Picea mariana* likely grew on moist soils adjacent to the lake. Also present were *Abies balsamea, Larix laricina*, and *Populus* spp. It is possible that populations of *Quercus, Fraxinus*, and *Ostrya* or *Carpinus* were also growing in the vicinity of the site. However, the presence of these taxa in the pollen record may reflect long distance transport from populations to the south, or the redeposition of pollen from melting glacial ice (McAndrews 1984). The relatively high ratios of CHAR:PAR suggest that fires did occur at this time.

Towards the end of zone 1 the dominance of *Picea glauca* began to decrease rapidly. *Pinus banksiana/resinosa* very rapidly replaced *Picea* as the dominant tree at approximately 10 000 BP. *Pinus banksiana* likely dominated well-drained and perhaps mesic sites. The over-representation of *Pinus* pollen and the poor representation of some taxa in the pollen record makes accurate interpretation of the pollen assemblage difficult. However, *Abies balsamea, Larix laricina*, and *Populus* spp. probably remained common components of the vegetation. Also present, but less abundant, were *Tsuga canadensis, Betula, Quercus, Fraxinus, Ulmus*, and *Ostrya/Carpinus*. Between 10 000 and 9000 BP, *Pinus strobus* populations began to expand, until by 8000 BP the species had replaced *Pinus banksiana*. *Pinus strobus* was probably a dominant on both dry and mesic soils, though today in southern Ontario and the adjacent United States it is restricted primarily to well-drained soils (Fowells 1965; Lancaster and Leak 1978; Hibbs 1982). Small increases in the pollen percentages of *Tilia* and *Acer* indicate the development of a greater temperate, mixed-woods component in the *Pinus strobus* dominated forests following 8000 BP. The ratio of CHAR:PAR associated with the pine-

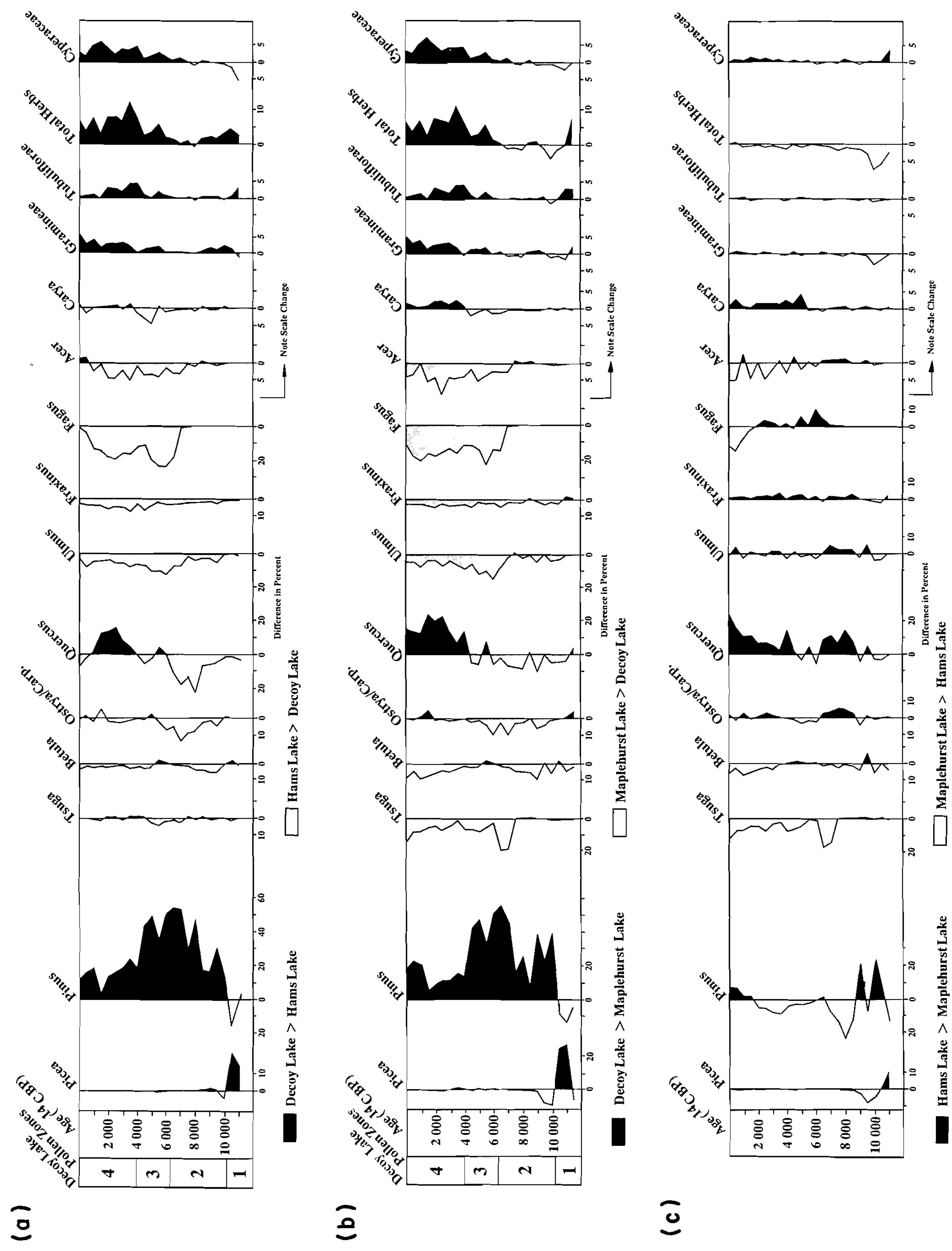


FIG. 8. Pollen percentage difference diagrams. (*a*) Decoy Lake – Hams Lake. (*b*) Decoy Lake – Maplehurst Lake. (*c*) Hams Lake – Maplehurst Lake.

dominated vegetation is generally low. It is possible that this indicates a decrease in fire activity. However, it is also possible that the ratio was depressed due to the high pollen productivity of pine.

Between 6300 and 4000 BP the vegetation around Decoy Lake changed markedly as the *Pinus strobus*-dominated forest was replaced by a mixture of hardwoods and herb-dominated openings. Rapid increases in *Fagus* and *Acer* pollen suggest the presence of *Fagus grandifolia–Acer saccharum* forests on nearby mesic sites. In the drier areas adjacent to the lake, it appears that *Pinus strobus* was replaced by a *Quercus* and herb–graminoid association. *Pinus strobus* was not eliminated completely in the vicinity of the site. Its pollen remains at an average of 20–25% for the majority of zone 4. Survey records indicate that *Pinus strobus* dominated stands grew within 10 km of Decoy Lake immediately prior to European land clearance (Fig. 2).

The poor PAR record and inability to distinguish many herb taxa beyond the family level prevent a detailed vegetation reconstruction of the *Quercus–Pinus*–herb zone. It is impossible to determine the exact physiognomy of the oak-dominated vegetation from the pollen record. However, the pollen assemblage at 4000 BP is nearly identical to that of immediate presettlement times, when oak savanna is known to have existed around Decoy Lake. Bakowsky (1988) showed that species of Gramineae, Cyperaceae, and Tubuliflorae comprised the dominant understorey components of oak savanna in southern Ontario. Thus the oak savanna as encountered by early settlers appears to have developed by about 4000 BP. If a nonsavanna *Quercus–Pinus*–herb association replaced *Pinus strobus*, its transition to oak savanna by historic times is not recorded in the pollen percentage record at Decoy Lake. The relatively high ratio of CHAR:PAR suggests that fire was an important component of the environment of the oak savanna.

Major vegetation changes did not occur again at Decoy Lake until about 100 BP when European land clearance commenced. Increases in the pollen of *Ambrosia* and Gramineae attest to the opening of the canopy. *Pinus strobus* also declined rapidly in the Decoy Lake area at this time. The original vegetation of oak savanna, *Pinus strobus* stands and mesic hardwood forests, was replaced by a mosaic of agricultural fields, pastureland, urban development, and a few forested areas.

Decoy Lake vegetation history in a regional context

Between 12 000 and 11 000 BP, *Picea*-dominated forest or forest-tundra was present throughout southwestern Ontario (Terasmae and Anderson 1970; Mott and Farley-Gill 1978; Terasmae and Matthews 1980; McAndrews 1981; Bennett 1987). Rapid expansion of *Pinus banksiana* between 11 000 and 10 000 BP and its subsequent replacement by *Pinus strobus* is evident at all sites in southwestern Ontario (Terasmae and Anderson 1970; Mott and Farley-Gill 1978; McAndrews 1981; Bennett 1987). Between 7500 and 8000 BP, *Pinus strobus* was replaced by more mesic taxa such as *Tsuga*, *Ostrya/Carpinus*, and *Quercus*. By 6500 BP, *Fagus* and *Acer* dominated southern Ontario forests, with lesser amounts of *Ulmus*, *Tsuga*, and *Quercus*. The composition of the forest remained fairly constant until about 500 to 1000 BP (Terasmae and Anderson 1970; Mott and Farley-Gill 1978; McAndrews 1981; Bennett 1987). At this time, some sites show decreases in *Acer* and *Fagus* and increases in *Quercus* and *Pinus*. This last change may be due to clearance by native agriculture or Little Ice Age cooling (McAndrews 1976; Ritchie 1987). Land clearance by European settlers substantially altered the vegetation of southern Ontario beginning 150 to 200 years ago.

Until about 8000 BP the vegetation around Decoy Lake was generally similar to other sites in southern Ontario. However, at Decoy Lake, *Pinus strobus* forest remained the dominant association for 2000 to 2500 years longer than at other sites in southwestern Ontario. *Pinus strobus* forest was not replaced by oak savanna until between 6300 and 4000 BP. The pollen assemblage produced by oak savanna at Decoy Lake is distinct from any assemblages yet reported from southern Ontario. It is also distinct from assemblages representing oak savanna in the midwestern United States. All of the American records have lower percentages of *Pinus* and much higher percentages of herbs, particularly Gramineae and *Artemisia* (McAndrews 1966; Jacobson 1979; Grimm 1983). These differences probably result from the greater spatial extent of midwestern oak savanna, its proximity to open prairie, and a warmer, drier climatic regime. The postsettlement pollen spectrum at Decoy Lake is similar to those throughout southwestern Ontario.

Discussion

The magnitude of native impact on the forests of northeastern North America continues to be a matter of debate. Day (1953) speculated that Indians had a large impact on the forests of northeastern North America, primarily by burning. Several palaeoecological studies in southern Ontario have shown that successional changes in local vegetation occurred following A.D. 1450 and were probably due to native land clearance for agriculture (Burden *et al.* 1986; McAndrews 1976). Dorney and Dorney (1989) demonstrated that native burning was the probable cause behind the development of an area of oak savanna in northeastern Wisconsin. However, the suggestion of widespread burning by natives, even during the late prehistoric period, has been questioned by Russell (1983). The extent of vegetation disturbance by native peoples would have depended upon the subsistence activities of the population. Groups of hunter-gatherers did not generally settle in permanent villages, but kept mobile to exploit changing resources. Fires set to drive game and for other purposes would likely not be concentrated in the same small area year after year, if they were set at all (Patterson and Sassaman 1988). Sedentary agricultural societies were more likely to employ fairly widespread burning to clear land for agriculture. The relatively high population density and permanent villages of these societies could lead to frequent burning and thus a successional change in forest composition to more fire- or disturbance-tolerant vegetation. Therefore, if native burning was responsible for the establishment and maintenance of the oak savanna, there should be a correlation between the establishment of the savanna and the timing of prehistoric agricultural settlement in the region.

Southern Ontario was inhabited by Laurentian Archaic peoples between 6300 and 3000 BP (Wright 1972; Spence and Fox 1983). It was during this time that oak savanna replaced *Pinus strobus* in the vicinity of Decoy Lake. The Laurentian Archaic was followed by the Early and Middle Woodland cultures (Wright 1972; Spence and Fox 1983). All three were hunter-gatherer cultures. Most of the Laurentian Archaic sites discovered so far have been concentrated on sand plains of the Deciduous Forest region (Spence and Fox 1983). A survey of archaeological finds within 7 km of Decoy Lake shows that 14 of 19 sites have Laurentian Archaic affinities (K. Dandy, personal communication). All of the 19 sites represent temporary camps. While this and other areas of sand plains appear to have been favoured hunting ground for these peoples, there is no evidence for any permanent or semipermanent settlements; the first structures are not seen in southern Ontario until 2500 BP (Dodd 1984). A hunting and gathering society such as the Laurentian Archaic or the subsequent Early and Middle Woodland culture is unlikely to have repeatedly burned the same area over a period of several thousand years for the purposes of improving browse and driving game. Agriculture was introduced into southern Ontario at the end of Middle Woodland period at about A.D. 500 (Fecteau 1985). There is no evidence of prehistoric agricultural settlement in the vicinity of Decoy Lake (K. Dandy, personal communication). It is therefore very unlikely that disturbance of the original *Pinus strobus*-dominated forests by the Laurentian Archaic and subsequent Woodland peoples initiated and sustained the oak savanna in the region of Decoy Lake for 4000–6000 years.

The alternative hypothesis to native burning as a cause for the development of oak savanna in southern Ontario is climate change. Continental scale climate models (Kutzbach and Guetter 1986; Webb *et al.* 1981; COHMAP 1988) and vegetation changes at a number of sites in the U.S. midwest (e.g., McAndrews 1966; Webb and Bryson 1972; Brubaker 1975; Jacobson 1979; Grimm 1983; Bartlein *et al.* 1984; Dean *et al.* 1984; Winkler *et al.* 1986), central and northern Ontario (Liu 1990), Quebec (Terasmae and Anderson 1970), and New Hampshire (Davis *et al.* 1980) indicate the prevalence of warm and dry conditions between about 8000 and 4000 BP. Paleoclimatic reconstructions based on the isotopic analysis of lake marls and wood cellulose at three sites in southern Ontario (Edwards and Fritz 1986, 1988) generally concur with these results. Following 6000 BP, the record of photosynthetic humidity indicates moisture increased above present levels to a maximum between 4000 and 3000 BP, gradually decreasing thereafter to modern levels. Mean annual temperatures were greater than present between about 7500 and 2000 BP. The period of *Pinus strobus* dominance at Decoy Lake (9000 to 6000 BP) was likely typified by high summer temperatures, low winter temperatures, and low precipitation (Edwards and Fritz 1986, 1988; Kutzbach and Guetter 1986). The period of transition from *Pinus strobus* dominance to oak savanna at Decoy Lake (6000 to 4000 BP) was characterized by decreasing summer temperatures, increasing winter temperatures, and increasing precipitation.

Ecological and forestry research on *Pinus strobus* in northeastern North America consistently equates dominance by the species with extremely well drained and dry substrates (Fowells 1965; Lancaster and Leak 1978; Scott 1983; Heckman *et al.* 1986). *Pinus strobus* appears only able to out-compete *Tsuga* and most hardwoods on very dry soils (Lancaster and Leak 1978; Scott 1983; Heckman *et al.* 1986). It is possible that the coarse soils of the Decoy Lake region, combined with the drier climate of the early to mid-Holocene, allowed *Pinus strobus* to continue to dominate the landscape of the study site between 8000 and 6000 BP when hardwoods were replacing it at other sites in the province.

Between 6000 and 3000 BP, available moisture began to increase in much of northeastern North America, including southern Ontario, owing to a combination of gradually decreasing summer temperatures and increasing precipitation (Edwards and Fritz 1986, 1988; Kutzbach and Guetter 1986). These climatic changes may have led to the replacement of *Pinus strobus* by oak savanna on the sand plains and coarse tills around Decoy Lake. A similar situation was noted in northern Michigan by Brubaker (1975). She concluded that following 5000 BP, increases in soil moisture enabled hardwood forests (*Acer, Quercus*) to invade *Pinus strobus* forests that had been maintained on sites with coarse soils. However, at Decoy Lake the magnitude of the climatic change appears to have been insufficient to allow the dominance of mesic trees such as *Fagus grandifolia* and *Acer* spp. on the sandy soils of the study area. The open areas of oak savanna may have been the result of fires associated with the dry vegetation substrates promoted by the extremely well drained sand and gravel soils. The fossil charcoal record indicates that fires have occurred throughout the period of oak savanna dominance. It is notable that all evidence points to fire as being an important factor in creating open sites and maintaining oak savanna in the midwest (Ellarson 1949; Curtis 1959; McAndrews 1966; Jacobson 1979; Grimm 1983, 1984).

An alternative climatic change hypothesis is that an increase in aridity led to the development of oak savanna in southern Ontario. Midwestern oak savannas generally occupy drier sites than *Pinus strobus* (Curtis 1959), and development of savanna in the midwest is associated with increasing aridity (McAndrews 1966; Jacobson 1979). *Tilia* is a mesic tree in Ontario (Maycock 1963), and so decreases in *Tilia* pollen percentages after 6000 BP at Decoy Lake could be interpreted as a result of increased aridity. However, this hypothesis is not supported by continental (Kutzbach and Guetter 1986) or regional (Edwards and Fritz 1986, 1988) climatic reconstructions for southern Ontario. Midwestern savannas are dominated by *Quercus macrocarpa*, whereas *Quercus velutina* and *Quercus alba* dominate in southern Ontairo (Bakowsky 1988). This and other floristic differences between midwestern and Ontario savannas may be a factor in the replacement of *Pinus strobus* by oak savanna around Decoy Lake during a period of increasing moisture.

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