

Rapid response of treeline vegetation and lakes to past climate warming

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FUTURE greenhouse warming is expected to be particularly pronounced in boreal regions¹, and consequent changes in vegetation in these regions may in turn affect global climate²⁻⁴. It is therefore important to establish how boreal ecosystems might respond to rapid changes in climate. Here we present palaeoecological evidence for changes in terrestrial vegetation and lake characteristics during an episode of climate warming that occurred between 5,000 and 4,000 years ago at the boreal treeline in central Canada. The initial transformation — from tundra to forest-tundra on land,

which coincided with increases in lake productivity, pH and ratio of inflow to evaporation — took only 150 years, which is roughly equivalent to the time period often used in modelling the response of boreal forests to climate warming^{5,6}. The timing of the treeline advance did not coincide with the maximum in high-latitude summer insolation predicted by Milankovitch theory⁷, suggesting that northern Canada experienced regionally asynchronous middle-to-late Holocene shifts in the summer position of the Arctic front. Such Holocene climate events may provide a better analogue for the impact of future global change on northern ecosystems than the transition from glacial to nonglacial conditions.

We obtained a 110-cm-long sediment core from Queen's Lake⁸ (unofficial name) and analysed it for fossil pollen, diatoms and sediment geochemistry in order to reconstruct and compare the changes in terrestrial and lake ecosystems that accompanied past climate warming at treeline (Fig. 1a-c). The lake is located at 64° 07' N, 110° 34' W, at an elevation of 480 m (Fig. 2). The surface area is ~50 ha and the maximum depth is 3.5 m. The region is rolling rockland composed of metamorphosed volcanics and intrusive granites. Cryic regosols and organic soils are found on discontinuous glacial overburden underlain by permafrost. Deglaciation commenced between 10,000 and 9,000 yr before present (BP)⁹. The lake is ~25 km north of the mapped limit of forest-tundra and lies on the boundary between the high subarctic and low arctic ecoclimatic regions¹⁰. The dominant vegetation is *Betula glandulosa* tundra. A few *Picea mariana* krummholz occur in the vicinity.

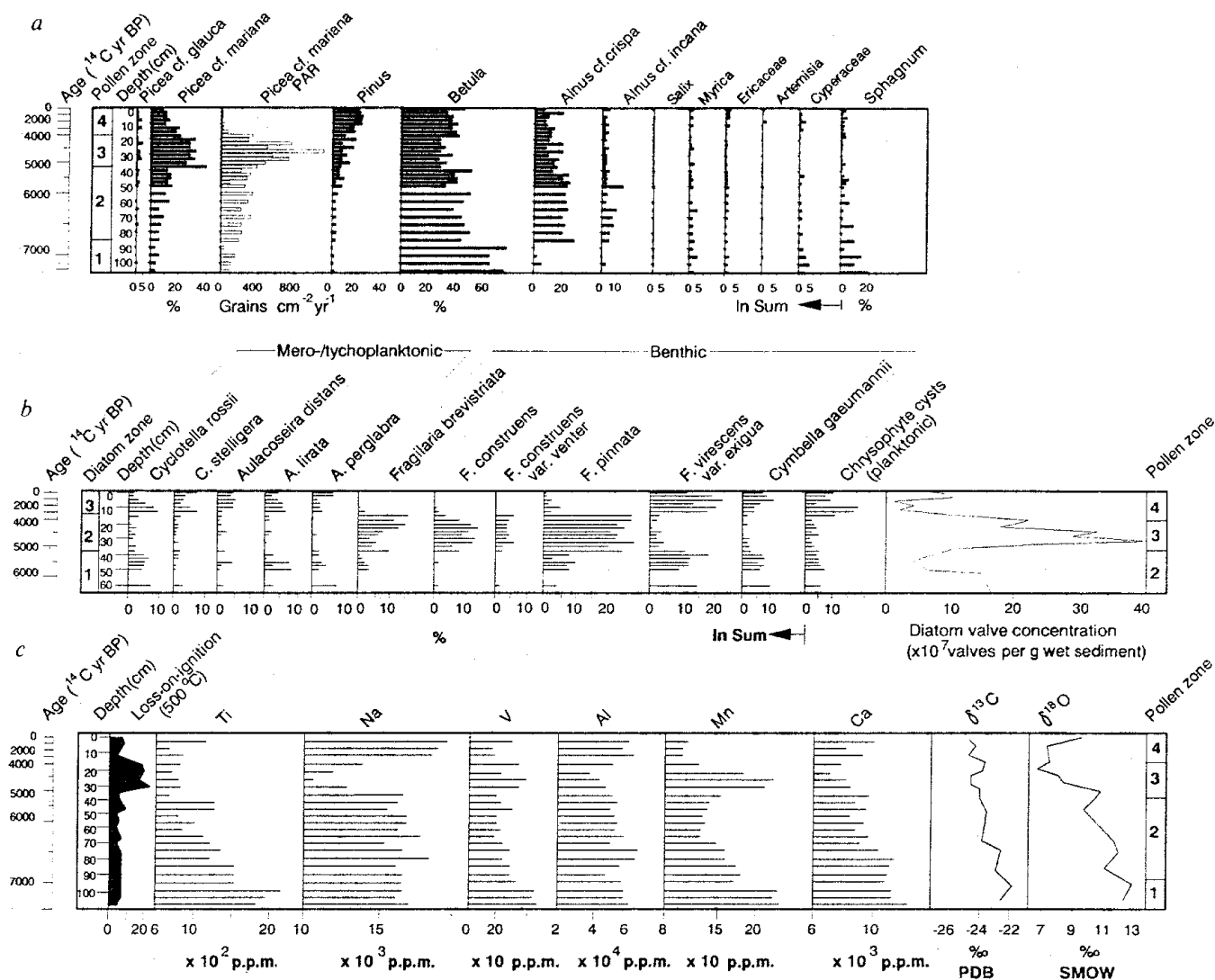


FIG. 1 Fossil pollen (a), diatom (b) and geochemical (c) stratigraphy of the Queen's Lake core. The entire core was sampled at 5-cm intervals for pollen and geochemical analyses. The upper portion was sampled at 2.5-cm intervals for pollen and diatom analyses. Sampling intervals were dictated by the quantity of sediment required and available for each technique and radiocarbon dating. Chronological control was provided by straight-line extrapolation between five radiocarbon dates (Table 1). The dates are internally consistent, have low standard errors and provide similar estimates of rates of sediment deposition and the timing of major vegetation changes as radiocarbon dates obtained from other lakes in the region (Table 1). Fossil pollen, diatoms and chrysophyte cysts were extracted and analysed using standard techniques²⁵⁻²⁷. The relative abundance of organic matter

was examined using loss-on-ignition (LOI)²⁸. The elemental geochemistry was determined using instrumental neutron activation analysis of bulk sediment^{29,30}. Carbon and oxygen isotope analyses were undertaken on cellulose extracted from the <143 μm fraction of the sediments to estimate changes in the δ¹³C of dissolved inorganic carbon (DIC) and the δ¹⁸O of the lake water^{31,32}. Cellulose from such finely divided limnic organics appears to originate primarily from aquatic plants and algae, possibly reflecting the burial and preservation of zooplankton faecal pellets^{31,33}. Isotope ratios are expressed in conventional δ notation as deviations in parts per mil from the PDB and SMOW standards. Analytical uncertainties of ±0.4‰ apply for δ values.

At ~5,000 yr BP, there was a sharp increase in both the percentages and pollen accumulation rates (PARs) of *Picea cf. maritima* (Fig. 1a), suggesting a rapid increase in the density of trees. There was also a rapid decrease in pollen percentages of *Betula* at this time. However, the continued high abundance of *Betula* and *Alnus* pollen suggests that the site was occupied by forest-tundra rather than closed forest. A decrease in *Picea cf. maritima* pollen and an increase in *Betula* signals a return to tundra vegetation following 4,000 yr BP. The increasing abundance of *Pinus* pollen from 6,000 yr BP to the present represents the growth populations of *Pinus banksiana* located more than 100 km to the south⁸.

Before forest-tundra expansion at 5,000 yr BP, the diatom record was dominated by pennate benthic taxa such as *Fragilaria*

pinnata, *Fragilaria virescens* var. *exigua* and *Cymbella gaeumannii* (Fig. 1b). The latter two species are associated with slightly acidic waters. The most abundant centric diatoms are mero-tychoplanktonic species of the genera *Cyclotella* and *Aulacoseira*. The low diatom concentrations and dominance of acidophilous species indicate low lake productivity and pH. A sharp change in the lake at 5,000 yr BP is indicated by an abrupt increase in small benthic *Fragilaria* species, replacing the acidophilous benthic and mero-tychoplanktonic species as the most abundant forms. The cysts of planktonic chrysophytes declined in relative abundance, and total diatom concentrations reached a maximum. The high concentrations of diatoms coupled with the declines in acidophilous species indicate an increase in lake productivity during the forest-tundra period.

Invasion by spruce might promote lake acidification because surface water running through coniferous needle litter would be acidified¹¹. However, the results from Queen's Lake and studies of modern lakes¹² suggest that this is not always the case. Following 4,000 yr BP, the diatom record is marked by a return to conditions similar to those before 5,000 yr BP.

The loss-on-ignition (LOI) stratigraphy indicates a rapid increase in organic content at 5,000 yr BP and a decline following 4,000 yr BP (Fig. 1c). The abundance of crustal elements such as Ti, Na, Al and Ca declined between 5,000 and 4,000 yr BP (Fig. 1c). These results suggest increased lake productivity and/or decreased clastic erosion during the period of forest-tundra dominance. The increase in Mn between 5,000 and 4,000 yr BP is consistent with decreased lake water acidity and increased productivity¹³. It is not clear what might have caused the increase in V during this time.

The cellulose $\delta^{13}\text{C}$ in the sediments shifts from about -22% at the base of the core to -25% at the top (Fig. 1c). This decline probably reflects the increasing contribution of ^{13}C -deficient DIC, released by oxidation of organic matter accumulating in bottom sediments. A subdued excursion to higher $\delta^{13}\text{C}$ between $\sim 4,500$ and $3,500$ yr BP suggests a productivity-driven enrichment in DIC $\delta^{13}\text{C}$ consistent with the diatom, LOI and geochemical evidence for increased lake productivity during the forest-tundra period.

Lake water $\delta^{18}\text{O}$ values declined substantially during the shift from tundra to forest-tundra at 5,000 yr BP and then returned to intermediate values following 4,000 yr BP (Fig. 1c). This pattern probably reflects changes in the ratio of inflow to evaporation of the lake. By analogy with the interpretation of isotopes from lake carbonate¹⁴, covariance between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in the lower portion of the core suggests that the lake was initially a hydrologically closed basin. The decoupling of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ following 6,000 yr BP suggests an opening of hydrological conditions because of increasing water inflow. The apparent acceleration of increase in the inflow:evaporation ratio at 5,000 yr BP probably reflects higher runoff and lower evaporation rates. This interpretation is consistent with data from modern lakes which indicate that water balance (inflow:evaporation ratio), rather than temperature-dependent variations in the $\delta^{18}\text{O}$ of local precipitation, determines the isotopic composition of lake waters in this region¹⁵. The interpretation is also supported by data indicating that tundra watersheds in central Canada experience higher evaporation rates than nearby forest-tundra sites¹⁶.

The changes in vegetation and lake characteristics at $\sim 5,000$ yr BP are not unique to Queen's Lake. We have obtained similar fossil pollen and LOI records from the three other treeline lakes that we have studied in central Canada (Fig. 2). The precise time when these records indicate maximum *Picea cf. mariana* pollen percentages and LOI values varies by several hundred years, and it is not possible to resolve whether these variations are real or simply noise associated with the radiocarbon dating of limnic sediments. These sites also record decreases in forest cover and lake productivity following 4,000 yr BP, although the rates and magnitudes of these decreases are more variable. The evidence of treeline advance at $\sim 5,000$ yr BP corresponds well with fossil pollen and palaeosol studies from more easterly sites in central Canada^{17,18}. In contrast, investigations in northwestern Canada indicate a northern extension of forest by 9,000 yr BP and forest decline at 5,000 yr BP^{7,19}. The mid- to late Holocene timing of treeline change in central Canada cannot be attributed to the Milankovitch summer insolation maximum that has been used to explain early Holocene treeline advance in northwestern Canada. It is possible that the environmental changes evident in central Canada reflect shifts in the summer position of the Arctic front caused by small changes in frontal wave characteristics^{18,19}. Such changes in geometry could cause treeline advance in central Canada with opposite or negligible impact in northwestern Canada¹⁹. A northward shift in central

TABLE 1 Radiocarbon dates (^{13}C -corrected) from lake sediment cores

Depth (cm)	Material	Age (yr BP $\pm 1\sigma$)	Laboratory number
<i>Queen's Lake</i>			
15-20	Organic sediment	3,820 \pm 60	WAT-1770
45-50	Organic sediment	5,600 \pm 60	WAT-1771
60-65	Organic sediment	6,150 \pm 60	WAT-1772
100-105	Organic sediment	7,150 \pm 70	WAT-1773
105	Twig	7,470 \pm 80	TO-827
<i>McMaster Lake</i>			
10-12	Organic sediment	3,690 \pm 50	TO-766
20-22	Organic sediment	3,680 \pm 60	TO-158
30-32	Organic sediment	5,120 \pm 60	TO-767
40-42	Organic sediment	5,360 \pm 60	TO-156
60-62	Organic sediment	6,180 \pm 60	TO-154
<i>Toronto Lake</i>			
35-40	Organic sediment	1,760 \pm 90	Beta-49705
80-85	Organic sediment and moss	4,200 \pm 80	Beta-53129
125-130	Organic sediment and moss	5,460 \pm 90	Beta-53130
155-160	Organic sediment	7,040 \pm 120	Beta-49708
<i>Waterloo Lake</i>			
28-31	Organic sediment	4,030 \pm 50	TO-3312
54-56	Organic sediment	4,640 \pm 50	TO-3311
61-63.5	Organic sediment	5,300 \pm 50	TO-3110
75-77	Moss	7,640 \pm 100	TO-3313

TO dates are based on accelerator mass spectrometry analysis and all others are conventional radiocarbon dates. Chronology for cores was derived using straight extrapolation between dates except at McMaster Lake where a line was fitted using the average extrapolated age provided by TO-766 and TO-158, and TO-767 and TO-156.

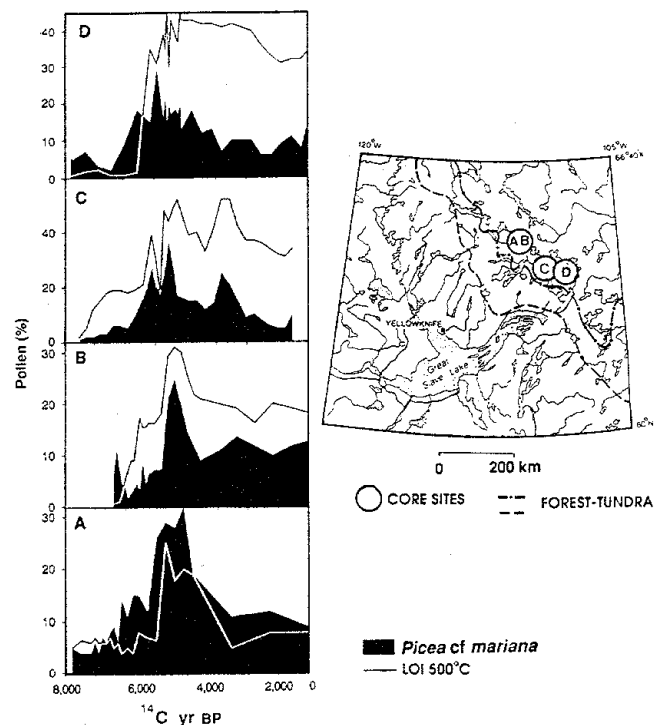


FIG. 2 Summary diagrams of *Picea cf. mariana* pollen percentages and LOI from the sediments of four small lakes located just north of the present forest-tundra in central Canada. A, Queen's Lake; B, McMaster Lake (unofficial name), 64° 08' N, 110° 35' W; C, Toronto Lake (unofficial name), 63° 43' N, 109° 09' W; D, Waterloo Lake (unofficial name), 63° 44' N, 108° 06' W. Radiocarbon dates used for chronological control are provided in Table 1.

Canada at 5,000 yr BP would produce warmer and moister summer conditions. A southward shift following 4,000 yr BP would cause a return to dominance by cool dry arctic air.

The earliest indications of the transition from tundra to forest-tundra vegetation and changes in lake characteristics are coincidental changes in the pollen and diatom percentages from the Queen's Lake core (Fig. 1). For the period 5,600–3,820 yr BP the time interval represented by 2.5 cm of deposition between each pollen and diatom sample is ~150 years. The shift in diatom flora from an acidophilous, low productivity assemblage to an assemblage reflecting higher pH and productivity occurs at exactly the same time as the shift in the pollen percentages. However, the shifts in total lake productivity as measured by diatom valve concentration, LOI and $\delta^{13}\text{C}$, and the geochemical and hydrological conditions of the lake as measured by elemental geochemistry and $\delta^{18}\text{O}$ were 150–300 years slower in registering a response to the shift from tundra to forest-tundra environmental conditions (Fig. 1). This suggests that the composition of the diatom flora adjusted quickly to temperature changes whereas adjustments of the total lake productivity and isotope balance took longer. Rapid change in small lakes, particularly in the composition of the diatom flora, is not surprising as short life cycles and widespread dispersal ability allow diatoms to respond quickly to changes in climate²⁰. Surprisingly, the record from Queen's Lake, and the information from the other sites, does not indicate a large time lag between changes in lake characteristics and changes in treeline vegetation (Figs 1 and 2). The rapid increase in *Picea mariana* at Queen's Lake may have been helped by its typical spatial distribution in central Canada, where scattered krummholz occur more than 100 km north of the mapped limits of forest-tundra. Intervals of mild climate as short as 10 years have been shown to initiate successful reproduction by treeline populations of *Picea* in eastern Canada²¹. Scattered trees that can rapidly produce viable seeds at the onset of climate warming provide ideal expansion foci which promote fast responses to favourable environmental changes²². The rapid changes in vegetation and lake characteristics at 5,000 yr BP may reflect rapid and synchronous climatic warming. It is also possible the nonlinear ecological responses caused by feedbacks between vegetation, permafrost, soils and boundary-layer climate could amplify rates of vegetation and lake ecosystem change once critical thresholds are crossed⁵.

Our evidence on the nature and rate of past environmental changes at treeline may help to predict the response of vegetation, hydrology and lake characteristics to future climate warming. These results show that for the central Canadian treeline, the 250-year time frame used in modelling the short-term response of northern boreal forests is reasonable^{5,6}. Palaeoecological investigations of *Pinus sylvestris* treeline in northern Scotland suggest similar rapid responses of vegetation and hydrology to shifts in the Azores high between 4,400 and 3,800 yr BP²³. The rapid change in the distribution of *Pinus sylvestris* may not have required the same spatial distribution of seed sources as we propose for *Picea mariana* in central Canada. Late Holocene episodes of climate change such as these in central Canada and Scotland may be better analogues for future global warming than is the change from glacial to nonglacial conditions, when the distribution of solar radiation and Earth boundary conditions were very different from today²⁴. It remains a concern that greenhouse warming may occur even faster than these Holocene events²³. □

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