

Holocene pollen records from the central Arctic Foothills, northern Alaska: testing the role of substrate in the response of tundra to climate change

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Summary

1 To explore the role of edaphic controls in the response of arctic tundra to climate change, we analysed Holocene pollen records from lakes in northern Alaska located on glaciated surfaces with contrasting soil texture, topography and tundra communities. Using indicator taxa, pollen accumulation rates (PARs) and multivariate comparison of fossil and modern pollen assemblages, we reconstructed the vegetational changes at Upper Capsule Lake (Sagavanirktok surface) and Red Green Lake (Itkillik II surface) in response to increased effective moisture between the early and middle Holocene.

2 In the Red Green record, low PARs and the continuous presence of taxa indicative of prostrate-shrub tundra (PST; *Equisetum*, Polypodiaceae, *Thalictrum* and Rosaceae) indicate that the vegetation resembled PST throughout the Holocene. During the warm, dry early Holocene (11 300–10 000 cal years BP), PST also occurred on Sagavanirktok surfaces, as evidenced by PST indicators (Bryidae, Polypodiaceae, *Equisetum* and Rosaceae) in this interval of the Upper Capsule record. However, PARs increased, suggesting increased vegetation cover, PST taxa declined and taxa indicative of dwarf-shrub tundra (DST; *Rubus chamaemorus* and *Lycopodium annotinum*) increased between 10 000 and 7500 cal years BP.

3 We hypothesize that between the early and middle Holocene the fine-textured soils and smooth topography of Sagavanirktok surfaces led to increased soil moisture, greater vegetation cover, permafrost aggradation, anoxic and acidic soil conditions, slower decomposition and the development of a thick organic layer. In contrast, soil moisture remained low on the better-drained Itkillik II surface, and vegetational changes were minor.

4 Landscape-scale substrate variations have an effect on how tundra responds to climate change, suggesting that the response of arctic ecosystems to future variability may be spatially heterogeneous.

Key-words: Alaska, North Slope, palaeoecology, palynology, Toolik Lake

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Introduction

Arctic tundra is spatially heterogeneous, with variations in ecosystem processes and plant community composition occurring at a variety of spatial scales (e.g.

Walker 2000). At the scale of the entire circumarctic region, the primary variations in vegetation result from the latitudinal climatic gradient. Growing seasons are shorter and colder at higher latitudes and, as a result, there is a northward decrease in primary productivity, diversity, biomass, plant stature and carbon storage (e.g. Young 1971; Yurtsev 1994; Walker 2000). Tundra ecosystems also vary at smaller spatial scales (1–100 km), typically in response to edaphic heterogeneity caused by variations in parent material, eolian deposition

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or glacial history (e.g. Elvebakk 1994; Walker 2000). The resulting variations in geomorphology, soil pH or soil texture within a latitudinal climatic zone can strongly influence ecosystem processes and plant community membership, especially via effects on soil moisture (Walker *et al.* 1994; Muller *et al.* 1999).

The effects of both climate and substrate are evident in the vegetational patterns of northern Alaska (Muller *et al.* 1999; Walker 1999, 2000). Climate is largely responsible for the main north–south vegetational gradient between the Brooks Range and the Arctic Ocean. On the Arctic Coastal Plain, cold, windy conditions and a thin snowpack result in shallow depth to permafrost, poor soil drainage and thus extensive waterlogged areas dominated by wet graminoid tundra (Walker & Everett 1991; Muller *et al.* 1999). Further south, in the Arctic Foothills, annual precipitation and summer temperatures are higher than along the coast, and erect dwarf shrubs dominate the vegetation (Walker *et al.* 1994; Muller *et al.* 1999). Superimposed on the latitudinal gradient are smaller-scale variations in ecosystems within the coastal plain and foothills vegetational zones, mainly in response to edaphic variability. For example, slightly higher topography in some areas along the coast affords drier soils, resulting in higher abundance of prostrate shrubs (Walker & Everett 1991; Walker *et al.* 1998). Similarly, dwarf-shrub tundra, widespread in areas of the Arctic Foothills that were unglaciated during the last part of the Pleistocene, is interrupted by prostrate-shrub tundra in areas where late Pleistocene valley glaciers left behind coarse-textured deposits (Walker *et al.* 1994, 1995). In addition to the difference in shrub stature between the ecosystems of these contrasting substrates, there are also differences in soil pH, nutrient cycling, permafrost depth, soil moisture, carbon storage, plant community diversity and biomass (e.g. Walker *et al.* 1995; Gough *et al.* 2000; Munroe & Bockheim 2001).

Given that ecosystem processes and plant community composition of tundra vegetation in northern Alaska and elsewhere in the Arctic are strongly controlled by climate, we might expect current and future climate changes to have considerable effects on tundra. Many studies have documented recent environmental changes in the northern high-latitudes (e.g. Morison *et al.* 2000; Serreze *et al.* 2000), and observed changes in tundra community composition, carbon dynamics and shrub abundance have been attributed to climatic warming (Chapin *et al.* 1995; Oechel *et al.* 2000; Sturm *et al.* 2001). However, despite anticipation that northern ecosystems will continue to change as climate warms in the future (e.g. McGuire *et al.* 2000), and the growing understanding of edaphic controls on tundra, little attention has been placed on the effect of substrate heterogeneity on the response of tundra to climate change.

In this paper, we use a palaeoecological approach to examine substrate controls on tundra ecosystem response to climate change. By reconstructing the vegetation history of sites that differ in landform and soil characteristics, we examined how substrate influenced

ecological changes induced by past climate change. The study was conducted in the central Arctic Foothills of northern Alaska, an ideal setting for this research due to its Pleistocene glacial history and resultant edaphic variability. We analysed pollen records from lakes on contrasting glaciated surfaces, one with flat topography and fine-textured soils, the other with greater relief and coarse-textured soils. The sites are only 11 km apart, ensuring that they experienced the same climatic changes during the Holocene (i.e. the past 10 000 ¹⁴C years or 11 500 calibrated ¹⁴C years). Specifically, we examine the response of these sites to the onset of cool, moist climatic conditions between the early and middle Holocene, using knowledge of the modern pollen–vegetation relationships for this area (Oswald *et al.* 2003b) to achieve a detailed interpretation of the vegetational history.

Study area

The Arctic Foothills is an upland area north of the Brooks Range. This area has cold winters (mean January temperature of –22 °C) and cool summers (mean July temperature of 11 °C), with 325 mm mean annual precipitation, most of which falls during summer (Zhang *et al.* 1996). Permafrost is continuous throughout the area (Hamilton 1978).

The central Arctic Foothills have been glaciated repeatedly, and evidence of three major Pleistocene glacial advances exists in the study area (Fig. 1 and Oswald *et al.* 2003b). Landscapes of Sagavanirktok age (> 125 000 years BP) have been subjected to long periods of mass wasting, weathering and loess deposition and, as a result, have gently rolling topography and fine-textured soils. These surfaces are dominated by dwarf-shrub tundra (DST) communities, which have nearly continuous vegetation cover, a relatively tall plant canopy, and feature dwarf shrubs (e.g. *Betula nana*), the tussock-forming sedge *Eriophorum vaginatum* and a thick layer of *Sphagnum* mosses (Walker *et al.* 1994). In contrast, areas glaciated by the Itkillik II ice advance (24 000–11 500 years BP) have irregular topography and coarser, better-drained soils (Hamilton 1978, 1994; Bockheim *et al.* 1998; Munroe & Bockheim 2001). These surfaces are dominated by prostrate-shrub tundra (PST), which has a sparser, shorter canopy and features non-tussock sedges, prostrate shrubs and non-*Sphagnum* mosses (Walker *et al.* 1994, 2001).

Oswald *et al.* (2003b) showed that lakes on Itkillik II and Sagavanirktok surfaces could be differentiated based on their modern pollen assemblages, and that the modern pollen spectra of Itkillik II and Sagavanirktok samples realistically reflected their PST and DST communities, respectively. Sagavanirktok samples therefore have relatively high pollen or spore percentages of many taxa that are either prevalent in or restricted to DST, including *Rubus chamaemorus*, *Sphagnum*, Ericales, *Lycopodium annotinum*, *Betula* and *Polygonum bistorta*, whereas Itkillik II samples have lower percentages

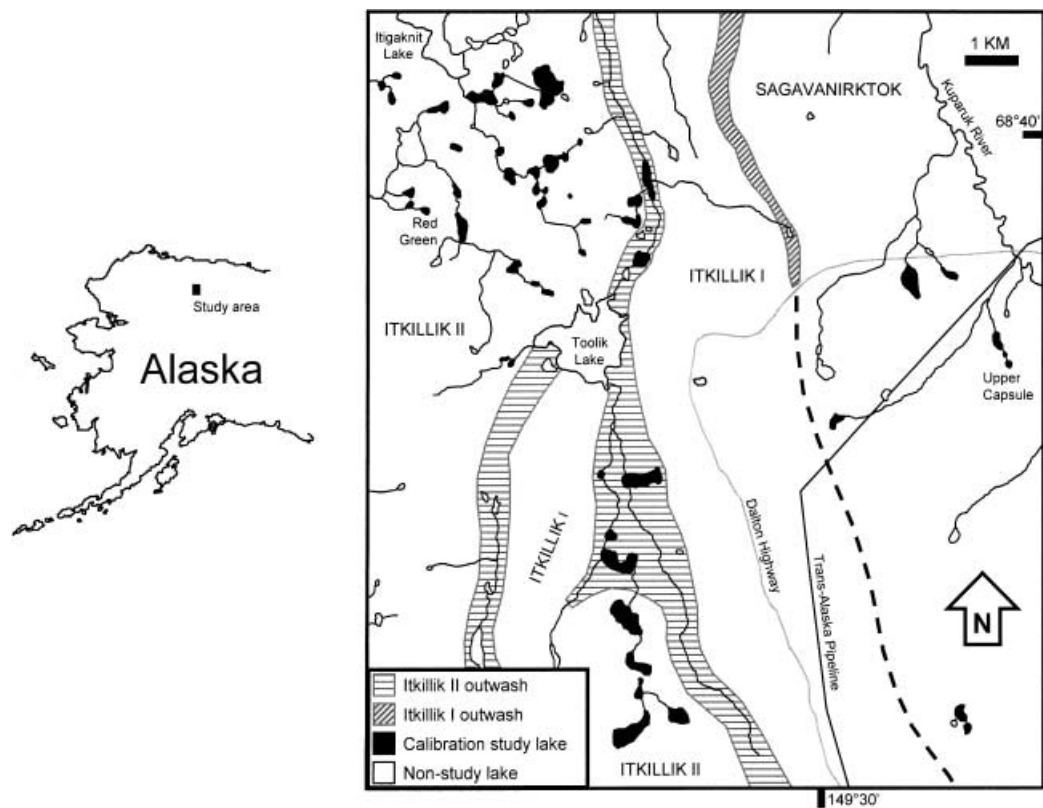


Fig. 1 Map of the study area with locations of Red Green Lake and Upper Capsule Lake. Glacial geology is redrawn from Hamilton (1978) and Walker *et al.* (1995). The Itkillik I outwash and dashed line define the boundary between the Sagavanirktok and Itkillik I surfaces. Lakes drawn in black were sampled for pollen-vegetation calibration study (Oswald *et al.* 2003b). Four additional pollen-vegetation calibration lakes are located as far as 19 km north-east of this study area (beyond map boundary).

of the DST indicator taxa, and higher percentages of taxa associated with PST, including *Equisetum*, *Thalictrum*, Rosaceae and Polypodiaceae (Table 1).

We selected two study sites with plant communities representing these vegetation types. Red Green Lake (68°39.2' N, 149°40.9' W) is located on the Itkillik II surface about 3 km north-west of Toolik Lake, the

location of the Arctic Long-Term Ecological Research site (Fig. 1). The c. 2-ha lake (3.2 m maximum depth) is located in a c. 50-ha watershed dominated by PST. It has a single outlet stream that flows west into the Itkillik River. Upper Capsule Lake (68°37.8' N, 149°24.6' N) sits on the Sagavanirktok surface about 7 km east of Toolik Lake. It is c. 1 ha in area (5.7 m maximum depth), and is located in a c. 350-ha watershed dominated by DST and shrub communities. A single outlet stream flows northward through two other small lakes before reaching the Kuparuk River.

Table 1 Taxa indicative of the vegetation of the Itkillik II surface (PST) and the Sagavanirktok surface (DST) according to modern pollen-vegetation calibration study (Oswald *et al.* 2003b). *Encalypta* is considered a PST indicator following Brubaker *et al.* (1998)

DST indicators	PST indicators
<i>Rubus chamaemorus</i>	<i>Equisetum</i>
<i>Sphagnum</i>	Polypodiaceae
Ericales	<i>Thalictrum</i>
Poaceae	Rosaceae
Brassicaceae	<i>Encalypta</i>
<i>Lycopodium annotinum</i>	Bryidae (excluding <i>Encalypta</i>)
Saxifragaceae	<i>Selaginella rupestris</i>
Asteraceae (excluding <i>Artemisia</i>)	
Lycopodiaceae (excluding <i>L. annotinum</i> and <i>H. selago</i>)	
<i>Betula</i>	
<i>Polygonum bistorta</i>	

Holocene climate history

Knowledge of the Holocene climate history of northern Alaska is based on various types of palaeoclimatic evidence, including fossil pollen data, plant and insect macrofossils, lake-sediment geochemistry from sites in northern and interior Alaska, lake-level reconstructions from interior Alaska and General Circulation Model (GCM) predictions. Our understanding of the mechanisms and patterns of Holocene climate change remains uncertain, but some general aspects are agreed upon. For example, climate became warmer and wetter during the late glacial period (15 000–11 500 cal years BP) as summer insolation increased, the Bering land bridge began to flood, and the influence of the Laurentide ice

sheet on large-scale circulation patterns began to diminish (Bartlein *et al.* 1992). Lake levels in interior Alaska rose rapidly during this interval (Abbott *et al.* 2000; Edwards *et al.* 2001) and shrub *Betula* expanded throughout northern Alaska (e.g. Anderson & Brubaker 1994).

By the early Holocene (11 500–8500 cal years BP), the Laurentide ice sheet exerted little influence on circulation patterns in Alaska and summer insolation reached a relative maximum (Bartlein *et al.* 1992). Lake-level data from interior Alaska indicate that precipitation was probably still lower than present, whereas temperatures were relatively warm (Abbott *et al.* 2000; Edwards *et al.* 2001). In northern Alaska, several types of palaeoclimatic evidence suggest that summer temperatures may have even been warmer than present. For example, few glaciers in the central Brooks Range persisted during this interval (Ellis & Calkin 1979), and early Holocene fluvial deposits from the northern Arctic Foothills contain insects indicative of well-drained substrates and summer temperatures 2–3 °C warmer than present (Nelson & Carter 1987). Furthermore, *Populus* wood dated to this interval occurs at sites beyond its modern range (Detterman 1970; Hopkins *et al.* 1981; Nelson & Carter 1987), and *Populus* pollen occurs in lake sediments at sites north of the modern limit of *Populus* (Oswald *et al.* 1999; Mann *et al.* 2002b). The early Holocene expansion of *Populus* is not fully understood (e.g. Bartlein *et al.* 1995; Hu *et al.* 1998), but the positive correlation between *Populus balsamifera* radial growth and summer temperature (Edwards & Dunwiddie 1985) indicates that it may have been a response to warm conditions. Alternatively, recent analyses of *Populus* macrofossils and fluvial deposits in northern Alaska suggest that the northward expansion of *Populus* may have been associated with periods of stream aggradation during which *Populus* established on newly deposited gravel bars (Mann *et al.* 2002b).

Summer insolation decreased after 8500 cal years BP (Bartlein *et al.* 1992), and effective moisture increased in response to either cooler temperatures, increased precipitation or both (Hu *et al.* 1998; Anderson *et al.* 2001; Edwards *et al.* 2001). Between 8500 and 6500 cal years BP, the increase in effective moisture crossed a threshold that permitted the expansion of *Alnus* throughout Alaska (e.g. Anderson & Brubaker 1994; Brubaker *et al.* 2001), including the region north of the Brooks Range (e.g. Eisner 1991; Oswald *et al.* 1999). The boundary conditions that control large-scale climatic variability reach their modern levels after 6500 cal years BP (Bartlein *et al.* 1992), and pollen and lake-level records from interior and northern Alaska give no indication of major climatic variations during this interval (e.g. Anderson & Brubaker 1994; Abbott *et al.* 2000). However, century-scale climatic variations are indicated by other evidence, including Brooks Range glacial advances, beach ridge dynamics along the north-west coast, dune activity in the Kobuk Valley and lake-sediment geochemistry (e.g. Ellis & Calkin 1984; Calkin 1988; Mason & Jordan 1993; Anderson

et al. 2001; Mann *et al.* 2002a). There is particularly strong evidence for warm, dry conditions during the Medieval Warm Period, c. 1100–600 cal years BP, and cool, wet conditions during the Little Ice Age, c. 600–200 cal years BP (Hu *et al.* 2001; Mann *et al.* 2002a).

Methods

Red Green Lake was cored through 2 m of ice in May 1997, and Upper Capsule Lake was cored from a raft in July 1997. Uppermost sediments, including an undisturbed mud–water interface, were collected using a piston surface-sediment sampler and extruded vertically in 0.5-cm segments. Lower sediments were retrieved using a 4.5-cm diameter square-rod piston sampler (Wright *et al.* 1984) and extruded in 1-m drive lengths.

Sediment subsamples (1 cm³) were dried at 90 °C and ashed at 550 °C to calculate loss-on-ignition (LOI). Subsamples of 2 or 3 cm³ were prepared for pollen analysis following standard procedures for organic-poor sediments (Cwynar *et al.* 1979). Tablets containing *Lycopodium clavatum* spores were added to the subsamples to allow estimation of pollen concentrations and pollen accumulation rates (Stockmarr 1971). Pollen residues were stained with safranin, mounted in silicone oil and examined microscopically using 40 and 100× objectives (12× eyepieces). Non-*Sphagnum* moss (Bryidae) spores were classified according to Brubaker *et al.* (1998) and ascomycete spores were identified following van Geel (1972, 1978; van Geel *et al.* 1982). At least 300 pollen grains of terrestrial plant taxa were counted for each sample, and all pollen and spore abundances are expressed as a percentage of the sum of identified and unidentified terrestrial pollen grains.

To interpret the fossil pollen assemblages, we relied upon previous studies of the modern relationships between pollen data and patterns of different tundra communities in northern Alaska (Oswald *et al.* 2003a), in particular the landscape-scale patterns of PST and DST on the Itkillik II and Sagavanirktok surfaces (Oswald *et al.* 2003b). Our interpretation involved several approaches, including analysis of indicator taxa, multivariate comparison of pollen assemblages, and calculation of pollen accumulation rates (PARs). First, we examined patterns of individual pollen and spore types that are known to be indicative of modern plant communities or specific environmental conditions (indicator taxa, e.g. Cwynar 1982). Taxa were classified as indicators (Table 1) based on their association with DST or PST in a modern pollen-calibration study for this area (Oswald *et al.* 2003b), as well as other calibration studies for northern Alaska (Brubaker *et al.* 1998; Oswald *et al.* 2003a). Secondly, we compared entire pollen assemblages between fossil and modern samples using a multivariate dissimilarity metric (modern analogue method, e.g. Overpeck *et al.* 1985). For each record, we calculated the Canberra metric distance (CMD) between each fossil pollen assemblage and each of the modern pollen assemblages from the Itkillik II and

Sagavanirktok surfaces. CMD is a dissimilarity metric in which the distance between multivariate samples is strongly influenced by minor taxa, and it was shown to be more effective than the widely applied squared chord distance for distinguishing between the Itkillik II and Sagavanirktok modern pollen assemblages (Oswald *et al.* 2003b). As an index of the similarity of each fossil sample to modern PST and DST plant communities, we calculated its average CMD to the Itkillik II ($n = 44$) and Sagavanirktok ($n = 12$) modern samples. Analyses of the modern pollen data set identified a CMD of 13 as the 'critical value' for distinguishing between like and unlike plant communities. Lastly, to approximate the overall vegetation cover of past plant communities, fossil PARs (number of grains $\text{cm}^{-2} \text{year}^{-1}$) were compared with modern PARs from northern Alaska. The link between PARs and tundra vegetation cover has been disputed (e.g. Guthrie 1985), but Oswald *et al.* (2003a) found that patterns of vegetation cover were broadly reflected by modern PARs in the Arctic Foothills.

Results

CORE STRATIGRAPHY AND CHRONOLOGY

The Red Green Lake sediment core (Fig. 2) consists of coarse sand (285–239 cm) overlain by inorganic, irregularly banded, grey-brown silt (239–209 cm) and dark

organic silt (209–0 cm). Mollusc shells are abundant between 200 and 160 cm. LOI is low (< 10%) below 200 cm, and higher (30–50%) above 200 cm. Pollen was not analysed below 240 cm due to very low pollen concentrations. The base of the Upper Capsule Lake core is inorganic silt (328–327 cm) overlain by peaty organic sediment (327–310 cm) with high LOI (50–60%). Between 310 and 273 cm, the sediment is grey-brown silt with diffuse bands, and the upper 273 cm of the core is dark organic silt. LOI values decrease above 310 cm (12–32%).

For both records, dating control is provided by accelerator mass spectrometry (AMS) ^{14}C analyses of plant fragments sieved (> 500 μm) from the sediment (Fig. 2, Table 2). Seven ages were obtained for the Red Green core, one of which (202–203 cm) is the average of three ^{14}C dates for different plant materials from the same depth (Oswald 2002). The dates were converted to calibrated ages with the CALIB 4.1 program (Stuiver & Reimer 1993). The age of the 16–21 cm sample was rejected because it was anomalously old relative to the age–depth relationship for the other dates from the core (Fig. 2). The age–depth model used to calculate PARs and to assign sample ages is based on linear interpolation between the six remaining calibrated ^{14}C ages.

We obtained nine ages for the Upper Capsule record, two of which (155–157 and 310–311 cm) are the average age of multiple ^{14}C dates for different plant materials from the same depth (Oswald 2002). These dates

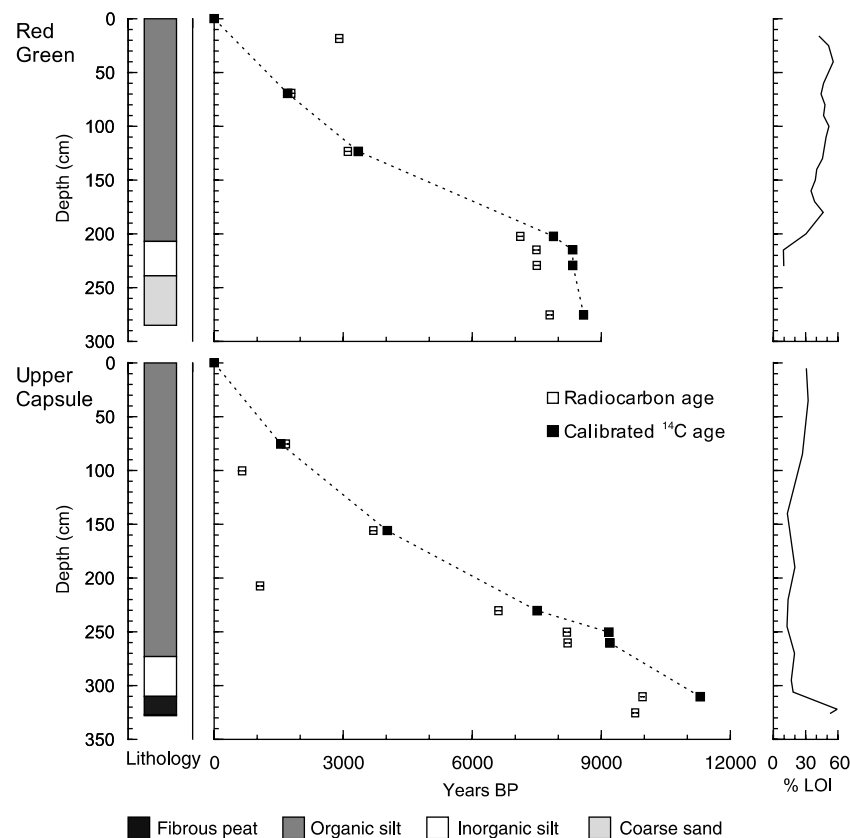


Fig. 2 Lithology, chronology and percentage weight loss-on-ignition (% LOI) for sediment cores from Red Green Lake and Upper Capsule Lake. The age–depth plots show radiocarbon ages (with ± 1 SE indicated by horizontal line within each symbol) and calibrated ^{14}C ages for those dates included in the age–depth model.

Table 2 Radiocarbon dates from Red Green and Upper Capsule Lakes. Calibrated ages in bold were used in age–depth model. See Oswald (2002) for discussion of average ages from multiple dates

Depth (cm)	¹⁴ C years BP	CAMS number	Material	Mass (mg C)	+1 SE [Calibrated ¹⁴ C age(s) BP] –1 SE
Red Green					
16–21	2910 ± 100	69 507	Plant and insect fragments	0.06	3 236 [3061, 3046, 3037, 3007, 3003] 2886
69–70	1790 ± 50	54 625	Terrestrial moss fragments	0.16	1 816 [1710] 1627
123–124	3110 ± 60	54 626	Moss fragments and stems	0.47	3 382 [3350] 3265
202–203	7116 ± 73	–	Average age for three dates*	–	8 001 [7940, 7885 , 7882] 7859
214–216	7490 ± 100	64 011	Moss and semi-woody pieces	0.09	8 389 [8335] 8180
229–230	7500 ± 70	54 627	Wood and moss fragments	0.17	8 385 [8341] 8195
275–276	7800 ± 140	64 012	Semi-woody fragment	0.06	8 928 [8590] 8413
Upper Capsule					
75–76	1670 ± 50	66 740	Moss fragments	1.37	1 687 [1553] 1524
100–101	650 ± 80	54 634	<i>Betula</i> and other leaf fragments	0.08	668 [649, 578, 572] 549
155–157	3705 ± 67	–	Average age for two of three dates†	–	4 148 [4081, 4030 , 3993] 3929
207–208	1070 ± 50	64 013	Terrestrial moss fragments	0.51	1 051 [966] 932
230–231	6610 ± 60	54 635	Woody and semi-woody pieces	0.41	7 569 [7551, 7542, 7505 , 7499, 7484] 7431
250–251	8200 ± 50	66 744	Terrestrial moss fragments‡	1.08	9 268 [9238, 9220, 9187, 9178 , 9130, 9095, 9093] 9030
260–261	8220 ± 50	54 636	Leaf, terrestrial moss, and graminoid pieces	0.47	9 395 [9248, 9216, 9208, 9198 , 9192, 9172, 9133] 9033
310–311	9957 ± 32	–	Average age for six of seven dates§	–	11 545 [11 333, 11 321, 11 298 , 11 270, 11 262] 11 257
325–326	9790 ± 50	54 637	Plant and woody fragments	0.71	11 226 [11 196] 11 172

*Average of CAMS 66 737, 66 738 and 66 739.

†Average of CAMS 66 741 and 66 743; 66 742 not used.

‡Second sample from this level (CAMS 66 745) not used.

§Average of CAMS 66 734, 66 735, 66 736, 66 746, 66 748 and 66 749; 66 747 not used.

were also converted to calibrated ages using CALIB. We reject the dates for 100–101 and 207–208 cm, which are younger than would be expected based on the age–depth relationship for the other dates (Fig. 2). The ages of the lowest samples (310–311 and 325–326 cm) are statistically the same, indicating that the organic peat at the base of the core was deposited rapidly, and thus the age from 325 cm to 326 cm is not included in the age–depth model. PAR calculations and age assignments are based on linear interpolation between the six remaining calibrated ¹⁴C ages.

EARLY HOLOCENE (ZONE 1: 11 300–10 000 CAL YEARS BP)

The records from the two lakes begin at different times, and only the Upper Capsule record covers the early Holocene interval (Fig. 3). The Sagavanirktok surface was not glaciated during the late Pleistocene (Hamilton 1978), but the Upper Capsule basin appears to have been dry during the Itkillik II glaciation, perhaps due to low precipitation. The peaty basal sediments of the Upper Capsule core suggest that the basin first contained a bog or wetland, but the statistically identical ¹⁴C dates at the bottom and top of the peat indicate that the conditions favouring the accumulation of organic sediments were short-lived. The change from peat to silty sediment indicates that the lake began to fill around 11 300 cal years BP. In contrast, the lack of record from Red Green Lake (Fig. 4) during this part of the Holocene may indicate that Itkillik II landscapes were unstable due to recent glacial retreat, the

continued presence of stagnant ice and low vegetation cover.

Zone 1 pollen assemblages for Upper Capsule (UC-1, Fig. 3) are dominated by Cyperaceae (*c.* 50%), *Betula* (*c.* 35%), Ericales (5–20%), *Salix* (*c.* 5%) and *Sphagnum* (*c.* 5%), with minor taxa indicative of the modern vegetation of the Itkillik II surface, including *Thalictrum*, Polypodiaceae, *Equisetum*, *Encalypta*, Bryidae and *Selaginella rupestris* (Oswald *et al.* 2003b). These assemblages reflect tundra dominated by Cyperaceae species and prostrate shrubs (*Salix* and Ericaceae), probably not unlike modern PST. Indeed, comparison of UC-1 assemblages with modern pollen spectra (Fig. 5) suggests that the early Holocene vegetation near Upper Capsule was compositionally similar to the current tundra of the Itkillik II surface (CMD < 13). Taxa indicative of mesic tundra (*Betula* and *Sphagnum*) are present in UC-1, but the similarity of their percentages with modern pollen spectra of the Itkillik II surface suggests that they were uncommon. For example, *Betula* and *Sphagnum* percentages in UC-1 are comparable with those in modern lake sediments from the Itkillik II surface (*c.* 35% and 2%, respectively), where *Betula nana* and *Sphagnum* species are rare at present (Walker *et al.* 1994). PAR values in UC-1 (*c.* 2000 grains cm⁻² year⁻¹) are higher than modern PARs for PST (*c.* 300 grains cm⁻² year⁻¹; Oswald *et al.* 2003a), perhaps reflecting somewhat higher vegetation cover than that of the Itkillik II surface at present. Alternatively, the difference in PARs may reflect greater allochthonous input for Upper Capsule than Red Green, which is likely given its larger watershed.

Upper Capsule Lake

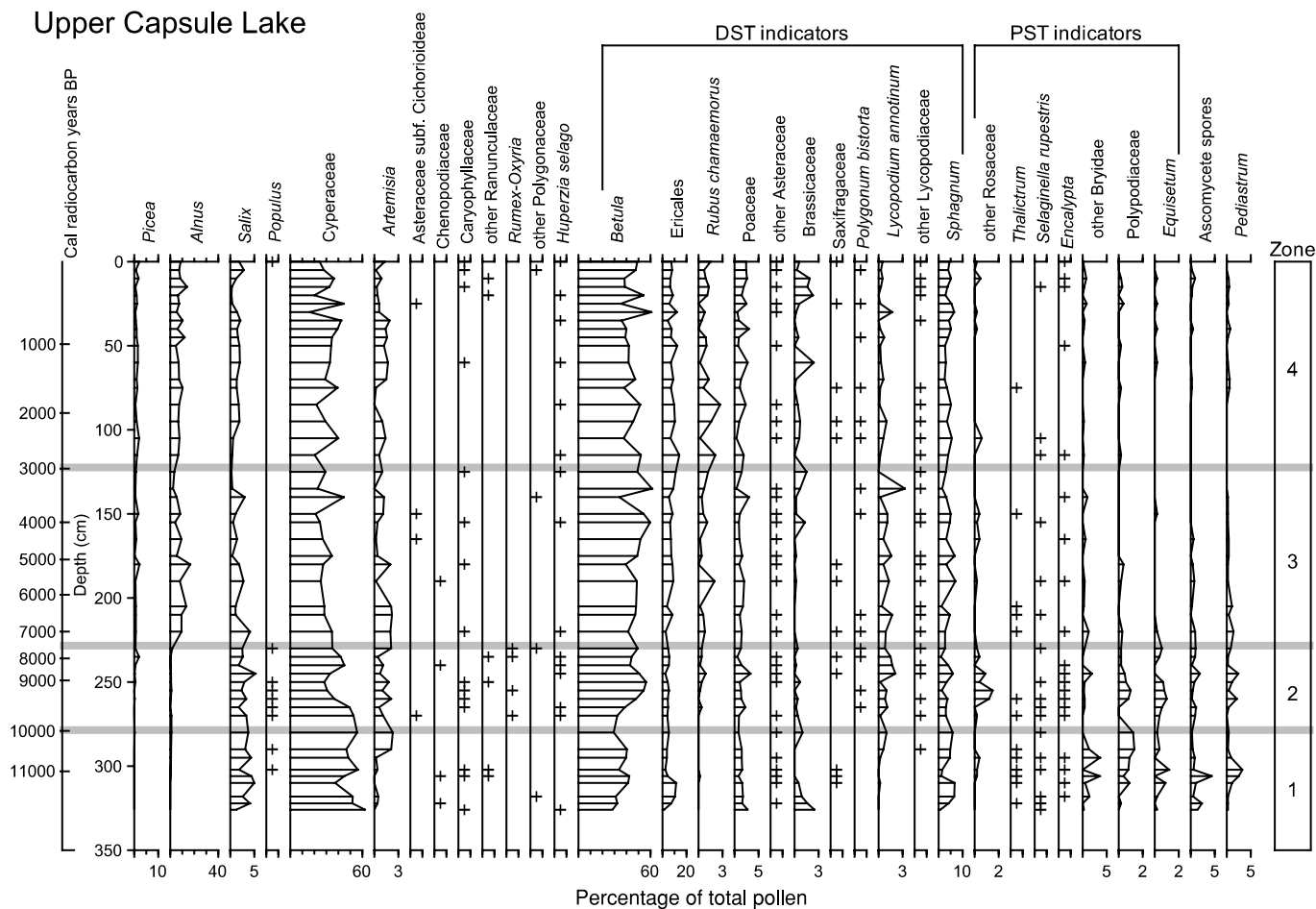


Fig. 3 Pollen and spore percentage diagram for Upper Capsule Lake (analysis by W.W. Oswald). Pollen, spores and *Pediastrum* are expressed as a percentage of the total pollen sum. Scales of the *x* axes vary. Taxa are classified as indicators of DST or PST vegetation based on their patterns in modern pollen assemblages (Table 1). Symbols (+) indicate < 2%.

The presence of *Populus* pollen in UC-1 corroborates other evidence that *Populus balsamifera* occurred north of the Brooks Range during the early Holocene (Detterman 1970; Hopkins *et al.* 1981; Oswald *et al.* 1999).

The source of the ascomycete spores in UC-1 assemblages is uncertain. If the spores were derived from soil ascomycetes, their abundance may reflect moderate soil moisture conditions, as most tundra fungi are negatively affected by excessively wet or dry soils (e.g. Dowding & Widden 1974). Alternatively, the spores may reflect past lichen cover, as ascomycetes are the fungal partner for the overwhelming majority of lichens (Hale 1983), and fruticose lichens are presently widespread in northern Alaska (Thomson 1979), particularly in relatively xeric tundra like PST (Evans *et al.* 1989; Walker *et al.* 1994). However, the production of spores by lichenized ascomycetes is relatively low compared with other ascomycetes (J. Ammirati, personal communication), so this explanation is less likely. In either case the presence of ascomycete spores in UC-1 is consistent with our characterization of the early Holocene vegetation of the Sagavanirktok surface as similar to modern PST, as this type of tundra has both moderately drained soils and high lichen cover.

EARLY TO MIDDLE HOLOCENE TRANSITION (ZONE 2: 10 000–7 500 CAL YEARS BP)

In UC-2, *Cyperaceae* percentages decrease to 25–40%, *Betula* percentages increase to 40–50%, and minor taxa are indicative of both PST and DST. Taxa associated with modern PST are still present (*Selaginella rupestris*, *Encalypta*, Polypodiaceae and *Equisetum*), and percentages of Rosaceae, another PST indicator, are even higher than in UC-1. However, Bryidae percentages are lower than in UC-1 and taxa indicative of modern DST (*Rubus chamaemorus*, *Polygonum bistorta*, *Lycopodium annotinum* and Lycopodiaceae) are regularly encountered. The presence of both PST and DST indicators in UC-2 spectra is manifest in the multivariate analyses (Fig. 5), which indicate that the fossil assemblages are not analogous to modern vegetation of either the Itkillik II or the Sagavanirktok surface (CMD > 13). Overall, these palynological changes suggest that both PST and DST species occurred on the Sagavanirktok surface during this transitional period. PST species were probably still present in the steeper, better-drained portions of the landscape, but *Betula nana* and other DST species were able to establish in mesic sites.

Red Green Lake

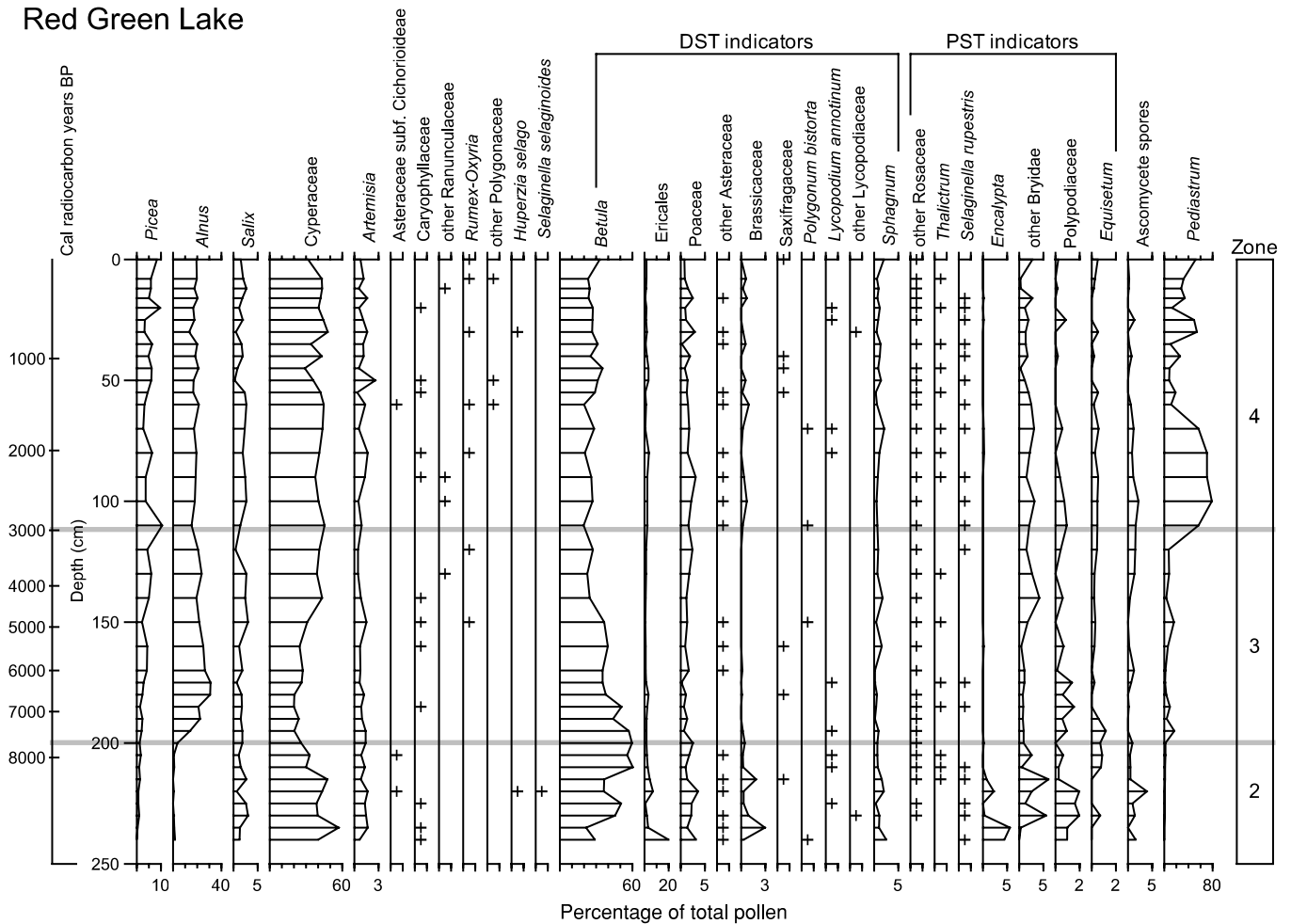


Fig. 4 Pollen and spore percentage diagram for Red Green Lake (analysis by W.W. Oswald). Pollen, spores and *Pediastrum* are expressed as a percentage of the total pollen sum. Scales of the x axes vary. Taxa are classified as indicators of DST or PST vegetation based on their patterns in modern pollen assemblages (Table 1). Symbols (+) indicate < 2%.

The Red Green Lake record (Fig. 4) begins at 8400 cal years BP, in the middle of zone 2. The lake probably started to fill at this time as a result of the regional increase in effective moisture (Edwards *et al.* 2001). Total PARs are low (< 700 grains cm⁻² year⁻¹) throughout RG-2, suggesting sparse overall vegetation cover (Fig. 6). *Betula* pollen increases from 30 to 60% and Cyperaceae percentages decrease from 60 to 25%. However, the low PARs for these taxa indicate that *Betula nana* and Cyperaceae species were not abundant. The minor taxa (Rosaceae, *Selaginella rupestris*, Bryidae, Polypodiaceae and *Equisetum*) are indicative of PST, and ascomycete spores are also present. Comparison with the modern spectra suggests that the vegetation of RG-2 was similar to the current tundra of the Itkillik II surface (CMD < 13), especially during the upper portion of this zone. The relatively high percentages of *Encalypta*, Bryidae and Polypodiaceae spores in the lower portion of RG-2 indicate that the vegetation near Red Green was actually drier and more open than modern PST tundra prior to around 8000 cal years BP.

MIDDLE HOLOCENE (ZONE 3: 7500–3000 CAL YEARS BP)

At both sites, increased percentages of *Picea* and *Alnus* c. 7500 cal years BP reflect the expansion of these taxa in the regional vegetation. Records from northern Alaska show that *Picea glauca* and *P. mariana* reach their modern range limits in the southern foothills of the central Brooks Range between 8000 and 7000 cal years BP (e.g. Anderson & Brubaker 1994). However, it is unlikely that either *Picea* species occurred in the Arctic Foothills during this interval, as *Picea* percentages in UC-3 and RG-3 do not exceed modern values. *Alnus crispa* occurs north of the Brooks Range (Viereck & Little 1972), but is not currently found in the study area. Percentages of *Alnus* are slightly higher than modern between 7500 and 5000 cal years BP, similar to other sites in the central and western Brooks Range (e.g. Anderson & Brubaker 1994), suggesting that *Alnus* species were more abundant in the regional vegetation than they are at present.

In UC-3, PST taxa decrease in abundance, DST taxa increase in abundance, and pollen assemblages become

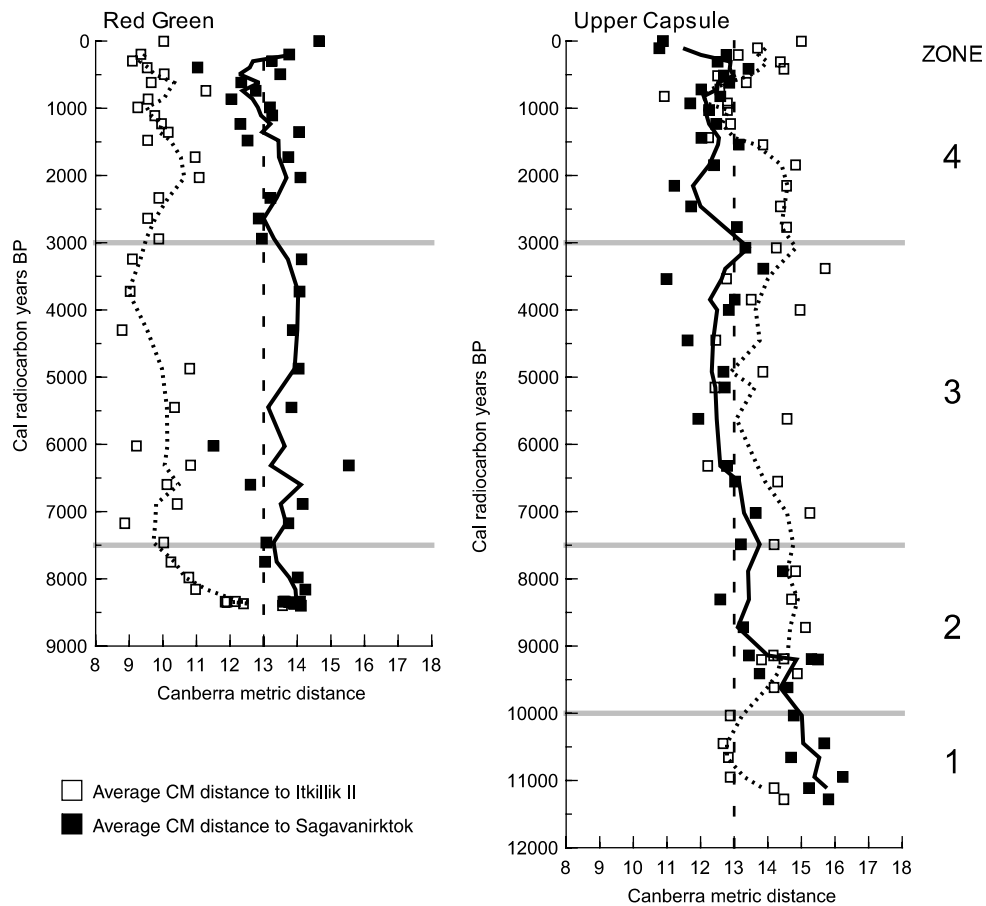


Fig. 5 Canberra metric distance (CMD) comparison of Red Green and Upper Capsule fossil pollen assemblages with modern pollen assemblages from the Itkillik II and Sagavanirktok surfaces. Each point is the average value of a fossil assemblage to the modern samples of either the Itkillik II or Sagavanirktok surface. Summary lines are three-point moving averages. The vertical lines show the CMD critical value separating samples from like (CMD < 13) and unlike (CMD > 13) vegetation types (Oswald *et al.* 2003b).

analogous to the modern spectra of the Sagavanirktok surface (CMD < 13). Specifically, *Salix* percentages decline slightly between UC-2 and UC-3, and most PST indicators (Rosaceae, Bryidae, Polypodiaceae and *Equisetum*) are either absent or very rare in UC-3. On the other hand, percentages of DST indicators, including Ericales, *Rubus chamaemorus*, *Lycopodium annotinum*, Lycopodiaceae and *Sphagnum*, either increase or remain relatively high. These changes mark the end of the transition from PST dominance in UC-1 to the DST ecosystem that exists today in the Upper Capsule watershed. By the start of UC-3 (7500 cal years BP), Upper Capsule pollen assemblages indicate that DST had come to dominate those portions of the landscape that were occupied by PST in the preceding zone, and the increase in PARs, particularly for *Betula*, suggests that vegetation cover was higher overall. A coincident decrease in ascomycete spore abundance may reflect an increase in soil moisture that was unfavourable to soil ascomycetes, or perhaps reduced lichen cover on the Sagavanirktok surface. The latter interpretation is consistent with the recent finding that the abundance of lichens decreases in response to increased vascular plant biomass (Cornelissen *et al.* 2001).

In contrast to the substantial changes in pollen and spore percentages in the Upper Capsule record, there are only minor changes in the Red Green record between zones 2 and 3. Percentages of Brassicaceae and *Equisetum* decrease slightly, but overall the pollen assemblages continue to exhibit similarity to the modern vegetation of the Itkillik II surface (CMD < 13). Percentages of the major taxa vary during this zone, with *Betula* decreasing from 60 to 25% and Cyperaceae increasing from 20 to 40%. However, as in RG-2, PARs for *Betula* and Cyperaceae are consistently low throughout RG-3, indicating that neither *Betula nana* nor Cyperaceae species were abundant.

LATE HOLOCENE (ZONE 4: 3000 CAL YEARS BP TO PRESENT)

Minor palynological changes occur between zones 3 and 4 at both sites. In the Red Green record, percentages of a number of minor taxa are higher in RG-4 than in RG-3, including both DST indicators (Ericales, Brassicaceae and *Lycopodium annotinum*) and PST indicators (*Thalictrum* and *Selaginella rupestris*). In the Upper Capsule record, spores of Polypodiaceae

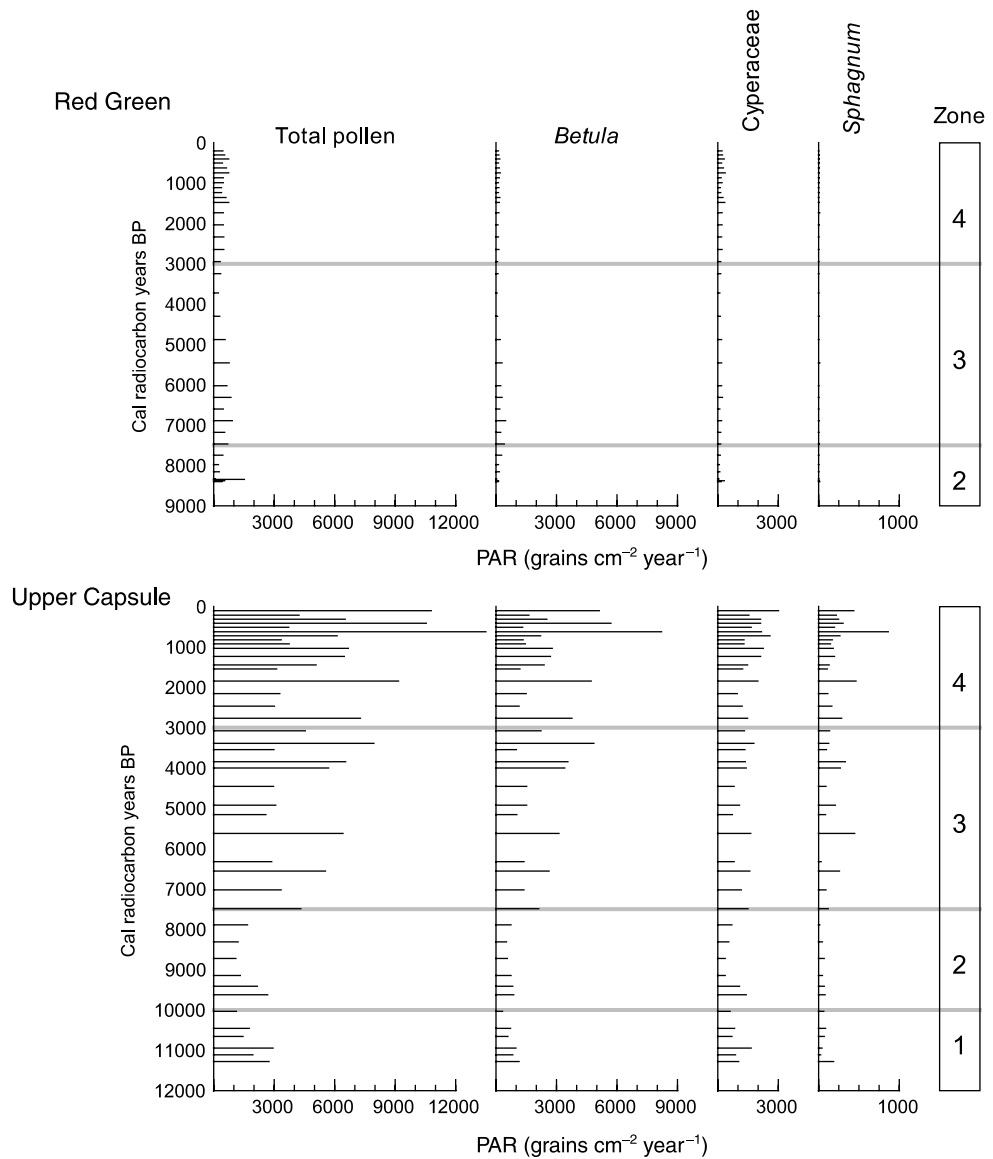


Fig. 6 Total pollen accumulation rates (PARs) and PARs for selected taxa in the pollen records from Red Green Lake (RG) and Upper Capsule Lake (UC). Five levels with artificially inflated PARs are not shown. Those levels include RG 220 cm = 4319 grains cm⁻² year⁻¹, RG 225 cm = 21 128 grains cm⁻² year⁻¹, RG 230 cm = 1511 grains cm⁻² year⁻¹, UC 255 cm = 54 571 grains cm⁻² year⁻¹, and UC 260 cm = 40 669 grains cm⁻² year⁻¹. Scale of *x* axis for *Sphagnum* differs from other taxa.

and *Huperzia selago* are encountered more frequently in UC-4 than in UC-3, and spores of *Lycopodium annotinum* are slightly less common. These changes are small relative to those observed during the early and middle Holocene, and their meaning is difficult to interpret as the PST and DST taxa do not vary consistently. Nevertheless, the contemporaneous changes in the abundance of several taxa at 3000 cal years BP indicate that the vegetation of both surfaces varied to some extent between the middle and late Holocene, perhaps in response to cooler or wetter climatic conditions during this interval (e.g. Hamilton 1986). The sharp rise in the percentages of *Pediastrum* algal cell nets in RG-4 are also notable, although their meaning is unclear given our uncertainty about the controls on *Pediastrum* abundance (e.g. Anderson & Brubaker 1986; Hu *et al.* 1995).

In addition, changes in pollen and *Pediastrum* percentages within zone 4 indicate further variations in climate and vegetation during the past two millennia. In the Red Green record, *Pediastrum* percentages decline between 1500 and 500 cal years BP, and pollen assemblages from this interval exhibit increased similarity to the modern assemblages of the Sagavanirktok surface (CMD < 13), although the palynological changes are minor. There is a more obvious change in the Upper Capsule record, as the similarity to Itkillik II modern pollen assemblages increases abruptly at 1500 cal years BP (CMD < 13). The changes in pollen percentages are subtle, but it appears that the increased similarity to Itkillik II modern vegetation results from slight decreases in the percentages of Lycopodiaceae, *Sphagnum*, Asteraceae and *Betula*. However, the Red Green and Upper Capsule fossil assemblages remain more

similar to the modern assemblages of their corresponding surface during this interval, and after 500 cal years BP they become less similar to the modern assemblages of the contrasting surface. Taken together, these changes may reflect the response of both terrestrial and aquatic ecosystems to the century-scale climatic variations that occurred during the late Holocene, including the Medieval Warm Period and the Little Ice Age (e.g. Calkin 1988; Hu *et al.* 2001; Mann *et al.* 2002a). However, the chronology and sampling frequency of these records are not adequate for a more detailed examination of the environmental and ecological changes of the late Holocene.

Discussion

EDAPHIC CONTROLS ON ECOSYSTEM RESPONSE TO CLIMATE CHANGE

The differences in geomorphology and soil texture between the Itkillik II and Sagavanirktok glaciated surfaces were probably responsible for the disparate vegetational responses at Red Green and Upper Capsule to the climatic changes of the early to middle Holocene. As effective moisture increased between 10 000 and 7500 cal years BP, we hypothesize that a more pronounced increase in soil moisture occurred on the Sagavanirktok surface because its fine-textured soils and flat landforms retained more water than the better-drained substrates of the Itkillik II surface (Fig. 7). Higher soil moisture fostered an increase in plant cover on Sagavanirktok landscapes, which initiated a series

of ecological and hydrological changes leading ultimately to the transition from PST to DST. Most important were the effects of the vegetation on the depth of the summer thaw layer. First, the increase in plant cover, in particular the upright, woody species, such as *Betula nana* and *Vaccinium uliginosum*, would have shaded the ground and thus reduced the amount of energy reaching the soil. Secondly, these woody, dwarf-shrub species, as well as mosses, contributed slowly decomposing litter to the soil (Hobbie 1996), thus helping to create a thicker organic layer. Thirdly, the deep layer of organic litter, mosses and sedge tussocks would have further reduced thermal conductance to the soil, and together these changes would have caused a major reduction in soil temperature and reduced soil thawing (Klinger 1996; Young *et al.* 1997). Shallower thawing impeded soil drainage, leading to anoxic and acidic soil conditions. The combination of cold soil temperatures, increased abundance of recalcitrant litter, and especially soil anoxia and acidity, would have greatly reduced decomposition rates (Hobbie 1996; Johnson *et al.* 1996). In turn, even thicker organic layers contributed further to permafrost aggradation (Van Cleve *et al.* 1991). The outcome of this transition can be seen today, as soils of DST have thicker organic horizons (c. 20 cm vs. c. 10 cm) and shallower active layers (thaw depth of c. 40 cm vs. c. 55 cm) than soils of PST (Bockheim *et al.* 1998; Walker *et al.* 2001).

The pollen records from Upper Capsule and Red Green lakes shed new light on the origin of the differences between DST and PST. The importance of the ecological and hydrological feedbacks in DST has been noted

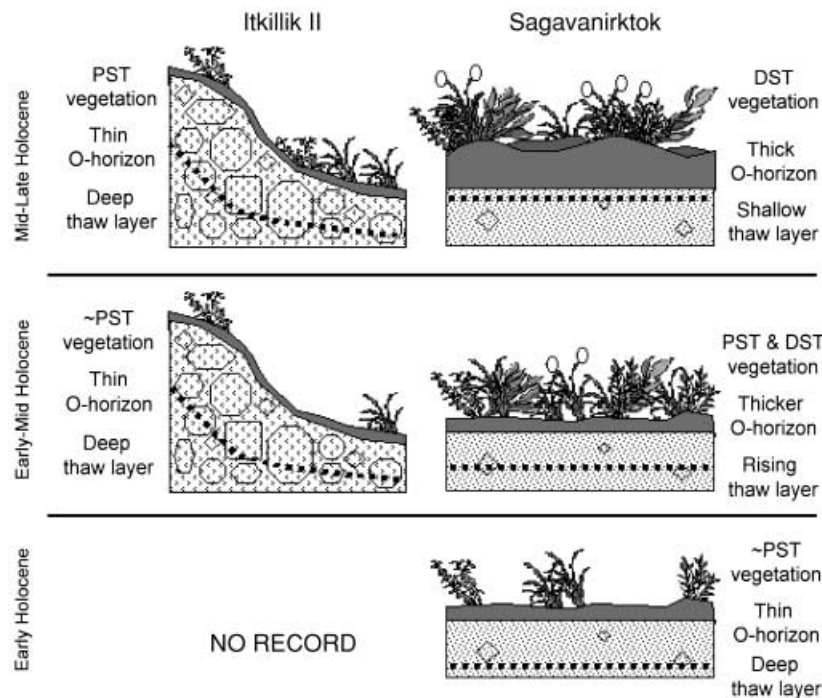


Fig. 7 Schematic diagram illustrating the vegetation and soil characteristics of Itkillik II and Sagavanirktok surface ecosystems before, during and after the early to middle Holocene increase in effective moisture, as inferred from the Red Green and Upper Capsule pollen records. Dashed lines indicate thaw depth.

previously (e.g. Walker *et al.* 1989, 1994), but the manner in which these differences arose is not clearly understood. Jorgenson (1984) made the insightful observation that different tundra ecosystems occupied the Sagavanirktok and Itkillik II glaciated surfaces, leading to the hypothesis that plant community succession occurred in response to long-term landscape evolution. This hypothesis suggested that as glacial deposits in the Arctic Foothills aged over millennia, they experienced mass wasting, slope reduction, eolian deposition, the development of a thick layer of organic matter and vegetation (especially *Sphagnum*), and ice aggradation (Jorgenson 1984; Walker *et al.* 1989, 1994). As these changes proceeded, there was a gradual succession from PST to DST. Because the changes in landform and soil characteristics were viewed as the primary drivers of ecosystem change, this hypothesis emphasized the importance of landscape evolution over climate change in the development of DST ecosystems. More recently, pollen records from northern Alaska have helped to clarify our understanding of the role of climate in ecosystem change (e.g. Walker *et al.* 1995), and the records from Red Green and Upper Capsule illustrate even more clearly that DST does not result solely from landscape evolution. The topography and soil texture of glaciated landscapes most likely were transformed over many thousands of years, but the ecological changes associated with the switch from PST to DST occurred more rapidly. At Upper Capsule, DST developed over a relatively short interval (*c.* 2500 years) when cool, moist climatic conditions acted upon the smooth topography and fine-textured soils of the Sagavanirktok surface.

COMPARISON WITH OTHER PALAEOECOLOGICAL EVIDENCE

The changes in the Red Green and Upper Capsule records are consistent with other palaeoecological records from the Arctic Foothills and elsewhere in northern Alaska, suggesting that edaphic controls on the vegetational response to Holocene climate change were important throughout the region. Nearby sites on the Sagavanirktok surface show a gradual change from PST to DST during the middle Holocene, similar to the transition at Upper Capsule. For example, at Oil Lake (2 km northwest of Upper Capsule), PST indicators (*Equisetum* and Polypodiaceae) have highest percentages *c.* 12 500–10 000 cal years BP, slightly lower percentages during the transition from 10 000 to 7500 cal years BP, and are nearly absent after 7500 cal years BP. On the other hand, DST indicators (*Lycopodium annotinum* and Ericales) are present in low percentages during the transitional period, but become more abundant (including *Rubus chamaemorus* and *Polygonum bistorta*) after 7500 cal years BP (Eisner & Colinvaux 1992; W. Oswald and L. Brubaker, unpublished data). Pollen records from a peat deposit at Imnavait Creek (10 km east of Upper Capsule) and Ahaliork Lake (60 km north-west of the study area, Anaktuvuk surface) lack the temporal

resolution to perceive the details of this transition, but in general their stratigraphy is consistent with the Upper Capsule record. The Imnavait Creek record has relatively high percentages of PST indicators (*Equisetum* and Rosaceae) during the early Holocene (Eisner 1991), whereas the Ahaliork record has higher percentages of Ericales pollen in the late Holocene than in the early Holocene (Eisner & Colinvaux 1990; P. Anderson and L. Brubaker, unpublished data).

Similar palynological changes are evident at sites in the western Brooks Range and Arctic Foothills that, like Upper Capsule, were not glaciated during the late Pleistocene. In pollen records from the Kobuk and Noatak drainages, percentages of Polypodiaceae and *Equisetum* are generally high during the early Holocene, and a transition occurs between the early and middle Holocene to assemblages featuring higher percentages of Ericales, *Sphagnum* and *Lycopodium* (Anderson 1985, 1988; Anderson *et al.* 1994). These sites differ from Red Green and Upper Capsule in that they have higher percentages of *Betula*, *Alnus* and *Sphagnum* and lower percentages of Cyperaceae during the Holocene. The pollen record from Tukuto Lake in the western Arctic Foothills shares many of the same stratigraphic patterns as the Upper Capsule record, including an interval when both PST and DST indicator taxa are present. During the beginning of the Holocene, Tukuto assemblages have relatively high percentages of Polypodiaceae and *Equisetum* spores. That zone is followed by the transitional period in which the PST indicators are present at low percentages and DST indicators (Ericales and *Rubus chamaemorus*) also occur. Lastly, there is a switch to DST *c.* 7500 cal years BP indicated by the near absence of PST taxa and increased percentages of Ericales (Oswald *et al.* 1999). A notable difference between this record and that of Upper Capsule is that *Lycopodium annotinum* percentages decrease after 7500 cal years BP at Tukuto but not at Upper Capsule. The pollen record from Lake of the Pleistocene, a late glacial to early Holocene deposit located near Tukuto Lake, shares some similarities with the Upper Capsule record, including the first occurrence of *Rubus chamaemorus* pollen *c.* 9500 cal years BP (Mann *et al.* 2002b). In addition, the record from Red Green Lake is similar to two pollen records from recently glaciated sites in the western Brooks Range. Etivlik Lake (Itkillik II surface) and Feniak Lake (Itkillik I surface) have relatively high percentages of *Equisetum* and Polypodiaceae spores in the early Holocene, but do not exhibit the change to DST in the middle Holocene that characterizes records from older glaciated surfaces (Eisner & Colinvaux 1992; Oswald *et al.* 1999).

The consistent patterns of indicator taxa in these records suggests that the early to middle Holocene changes in vegetation observed in the central Arctic Foothills occurred regionally, but with some variability related to geographical and edaphic factors. In both the central Arctic Foothills and the western Brooks Range, tundra apparently similar to modern PST was present

at the beginning of the Holocene. However, between *c.* 10 000 and 7500 cal years BP there was a transition from PST to DST on Sagavanirktok and other old surfaces, after which PST taxa were no longer abundant in the vegetation. In contrast, the pollen records from Red Green Lake and other sites on recently glaciated surfaces (Etivlik Lake and Feniak Lake) show that areas with coarse-textured substrates did not undergo this vegetational change. Instead, these surfaces have been occupied by tundra not unlike modern PST since at least 8500 cal years BP.

Related evidence for past tundra ecosystem dynamics in northern Alaska comes from ¹⁴C dates on basal organic deposits, which have been interpreted as representing the onset of paludification and organic peat accumulation (Mann *et al.* 2002b). A recent analysis of basal organic dates from relatively old surfaces (> 14 000 ¹⁴C years BP) across this region suggests that peat accumulation began *c.* 15 000 cal years BP in topographic low points, and by *c.* 9500 cal years BP occurred on most areas of the landscape (Mann *et al.* 2002b). The palynological evidence from Upper Capsule Lake and other sites on older glaciated surfaces is generally consistent with this interpretation of the history of paludification, although the pollen records suggest that organic soils did not achieve their current coverage until a somewhat later date. For example, *Sphagnum* spores were encountered throughout the Upper Capsule record and after 12 800 ¹⁴C years BP in the Tukuto Lake record (Oswald *et al.* 1999), indicating that some mesic substrates have been present in those watersheds since the late glacial interval. Likewise, the pattern of DST indicator taxa in the Upper Capsule record suggests that Sagavanirktok surface soils became wetter and more acidic beginning at 10 000 cal years BP. However, the stratigraphic pattern of taxa associated with PST indicates that some relatively xeric substrates were present until *c.* 7500 cal years BP, which is 2000 years later than the basal organic dates would suggest.

IMPLICATIONS

The finding that Sagavanirktok and other old surface ecosystems experienced a stronger vegetational response to Holocene climatic change than their recently glaciated counterparts suggests that old, weathered landscapes may be more susceptible to major environmental changes in the future. If, as in the early Holocene, future warming results in lower effective moisture in northern Alaska, we might expect the complex feedbacks of the DST ecosystems to be disrupted. For example, warmer conditions might reduce soil moisture and accelerate soil decomposition rates (e.g. Hobbie 1996), reducing vegetation cover and the depth of the organic layer, and thus leading to deeper permafrost thawing and even drier soils. In contrast, the vegetation of Itkillik II surface was relatively insensitive to past climate change, and therefore may not be as

strongly affected by future warming as the Sagavanirktok surface. Because their coarse-texture results in inherently low water-holding capacity, Itkillik II soils are likely to support relatively xeric, sparse tundra vegetation regardless of climate. The effect of substrate on ecosystem sensitivity to climate change may also be important at the circumarctic scale. Substrate varies greatly across the Arctic, with heterogeneity occurring at a variety of spatial scales, and resulting from many different factors (e.g. glacial history, parent material or eolian deposition; Walker *et al.* 1998; Walker 2000). The critical role of substrate in the Holocene ecosystem history of the central Arctic Foothills suggests that this edaphic variability may impart strong spatial heterogeneity on how arctic tundra ecosystems respond to future climate change.

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