

Pollen-vegetation calibration for tundra communities in the Arctic Foothills, northern Alaska

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Summary

1 Palynology has been portrayed as a ‘blunt’ tool for reconstructing variations in arctic tundra vegetation. We tested this characterization in the Arctic Foothills of northern Alaska by analysing 56 modern pollen assemblages from lakes on contrasting glaciated surfaces. The two surfaces, which date to the Sagavanirktok (> 125 000 years BP) and Itkillik II (c. 11 500 years BP) ice advances from the Brooks Range, have considerably different geomorphology, soil characteristics and plant communities. Sagavanirktok surfaces are dominated by dwarf-shrub tundra (DST), and Itkillik II surfaces by prostrate-shrub tundra (PST).

2 We used two multivariate approaches, dissimilarity metrics (squared chord distance and Canberra metric distance) and discriminant analysis, to assess the ability of the pollen data to distinguish between the Sagavanirktok and Itkillik II landscapes, and to identify the taxa most strongly associated with one surface or the other. Receiver operating characteristic (ROC) analysis was used to evaluate the performance of the dissimilarity metrics and to determine their ‘critical values’ for distinguishing between assemblages from like and unlike plant communities.

3 According to the discriminant analysis, taxa indicative of the Sagavanirktok surface include *Rubus chamaemorus*, *Sphagnum* and Ericales, whereas *Equisetum*, *Thalictrum* and Polypodiaceae were faithful to the Itkillik II surface. These differences between the pollen assemblages make it possible to differentiate between the two landscapes using Canberra metric distance comparisons. The ROC analysis demonstrated that the Canberra metric distance is more effective than squared chord distance for distinguishing between the two surfaces. This study illustrates that palynology can be used to explore questions regarding the landscape-scale heterogeneity of past tundra vegetation.

Key-words: Alaska, modern pollen, North Slope, palaeoecology, palynology

Journal of Ecology (2003) **91**, 1022–1033

Introduction

Plant community composition and ecosystem properties of arctic tundra are spatially heterogeneous, varying in response to changes in climate, substrate and topography at circumarctic, regional and landscape scales (e.g. Walker 2000). It is likely that past vegetation in the Arctic also varied spatially due to climatic and edaphic heterogeneity (e.g. Schweger 1982; Anderson

1985; Guthrie 2001), but reconstructing that variability with fossil pollen records has proven challenging. Late Quaternary pollen data from the Arctic are notoriously difficult to interpret because of the over- and under-representation of key taxa, the inability to differentiate pollen types within many genera or families and the unclear spatial resolution of the data (e.g. Anderson *et al.* 1994; Gajewski *et al.* 1995).

Studies of the modern relationship between vegetation and pollen in sediments can inform interpretations of past vegetation (e.g. Webb 1974), and pollen-vegetation calibration research in the Arctic has shown that pollen data represent regional-scale changes in tundra vegetation (e.g. Ritchie 1974). For example, modern pollen

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spectra from northern Alaska correspond to the regional gradient of climate and vegetation: coastal sites are characterized by high percentages of Poaceae and Cyperaceae pollen, whereas inland sites have higher percentages of *Betula* and *Alnus* pollen (Anderson & Brubaker 1986; Oswald *et al.* 2003). These regional calibration studies provide some indication that pollen assemblages are also influenced by smaller-scale changes in vegetation related to edaphic variability, but the ability of pollen data to reflect the landscape-scale heterogeneity of tundra has not been assessed thoroughly. An examination of this topic is desirable because both palaeo- and modern ecologists are interested in landscape-scale (1–100 km) substrate controls on tundra plant communities (e.g. Schweger 1982; Jorgenson 1984; Walker *et al.* 1994; Oswald *et al.* 1999; Hobbie & Gough 2002).

To test the correspondence between tundra vegetation and pollen at the landscape scale, we analysed pollen in the modern sediments of 56 small lakes from the central Arctic Foothills of northern Alaska. The study sites represent two plant communities (dwarf-shrub tundra and prostrate-shrub tundra) that occur on adjacent glaciated surfaces (Sagavanirktok and Itkillik II) with contrasting landforms and soil textures (Walker *et al.* 1994, 1995). We employed two multivariate approaches, discriminant analysis and dissimilarity

metrics (squared chord distance and Canberra metric distance; Overpeck *et al.* 1985), to examine the differences in pollen assemblages between the two glaciated surfaces. The discriminant analysis loadings of the taxa illustrate which pollen and spore types are most strongly associated with one surface or the other, and we compared the patterns of those taxa with the community composition of dwarf-shrub tundra and prostrate-shrub tundra. In addition, we used receiver operating characteristic (ROC; Metz 1978) analysis to evaluate the performance of the dissimilarity metrics, as well as to determine dissimilarity metric 'critical values' (dissimilarity values indicating that pollen samples represent the same type of vegetation). Overall, this study tests the ability of pollen data to reflect landscape-scale patterns of tundra vegetation, and thus helps to define the spatial resolution that is achievable by palaeoecological studies in the Arctic.

Study area

The sampled sites are located in the central Arctic Foothills, an area of rolling uplands north of the Brooks Range (Fig. 1). The study area is characterized by 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

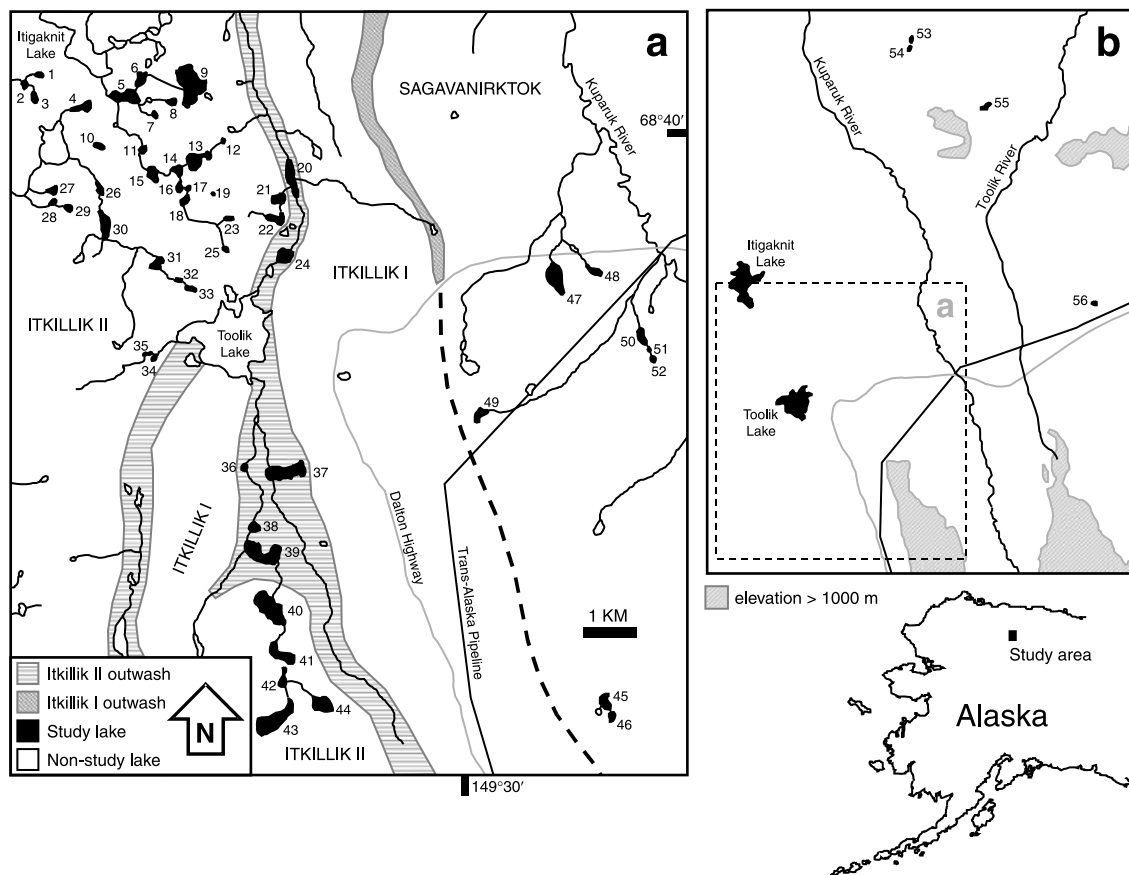


Fig. 1 Map of the study area indicating study sites for pollen-vegetation calibration research. Glacial geology redrawn from Hamilton (1978) and Walker *et al.* (1995). Lakes 53–56 are located on Sagavanirktok deposits. The Itkillik I outwash and dashed line define the boundary between the Sagavanirktok and Itkillik I surfaces.

occurs during summer (Zhang *et al.* 1996). Permafrost is continuous throughout the area (Hamilton 1978).

There is geomorphic evidence of three major Pleistocene glacial advances in the study area (Hamilton 1994). The Sagavanirktok River glaciation (> 125 000 years BP) extended northward from the Brooks Range and covered the entire study area. Two late Pleistocene glacial advances were largely restricted to the Brooks Range proper, but ice did reach the study area via the Atigun and Itkillik valleys (Hamilton 1978). The Itkillik I glaciation (> 60 000 years BP) terminated 15 km north of the study area, whereas a tongue of the Itkillik II (or Walker Lake) glacial advance (24 000–11 500 years BP) flowed across the western half of the study area, ending 10 km to the north-west (Hamilton 1978, 1994).

Sagavanirktok and Itkillik I landscapes have been greatly modified by long periods of weathering, mass wastage and eolian deposition (Hamilton 1994). These surfaces have gentle topography, clayey-to-silty soil textures and shallow active layers, resulting in poor drainage and large areas of acidic, waterlogged soils (Walker *et al.* 1989, 1994). Itkillik II surfaces have steeper, better drained and more irregular terrain, with coarser, higher pH soils, thinner organic horizons and deeper thaw layers (Hamilton 1994; Bockheim *et al.* 1998; Munroe & Bockheim 2001).

Spatial patterns of plant communities in the Arctic Foothills are strongly controlled by topography and substrate characteristics (Walker *et al.* 1994; Walker & Walker 1996). Sagavanirktok surfaces are dominated by moist dwarf-shrub tussock-graminoid tundra (DST, also called moist acidic tundra; Walker *et al.* 1995), the typical tussock tundra found throughout the Arctic in areas that were not glaciated during the late Pleistocene (Alexandrova 1980; Bliss & Matveyeva 1992; Muller *et al.* 1999). Dominant plants include *Eriophorum vaginatum*, *Sphagnum* species, *Betula nana*, *Ledum palustre* ssp. *palustre*, *Vaccinium vitis-idaea* and *V. uliginosum* (Table 1; Walker *et al.* 1994, 1995, 2001).

Table 1 Common and characteristic species of dwarf-shrub and prostrate-shrub tundra communities (Walker *et al.* 1994, 1995, 2001)

Dwarf-shrub tundra	Prostrate-shrub tundra
<i>Betula nana</i>	<i>Carex bigelowii</i>
<i>Salix planifolia</i> ssp. <i>pulchra</i>	<i>Eriophorum triste</i>
<i>Ledum palustre</i> ssp. <i>decumbens</i>	<i>Dryas integrifolia</i>
<i>Vaccinium uliginosum</i>	<i>Salix arctica</i>
<i>Cassiope tetragona</i>	<i>Salix reticulata</i>
<i>Empetrum hermaphroditum</i>	<i>Arctostaphylos rubra</i>
<i>Rubus chamaemorus</i>	<i>Rhododendron lapponicum</i>
<i>Polygonum bistorta</i>	<i>Senecio resedifolius</i>
<i>Petasites frigidus</i>	<i>Anemone parviflora</i>
<i>Eriophorum vaginatum</i>	<i>Equisetum arvense</i>
<i>Sphagnum angustifolium</i>	<i>Equisetum scirpoides</i>
<i>Sphagnum balticum</i>	<i>Tomentypnum nitens</i>
<i>Sphagnum girgensohnii</i>	<i>Aulacomnium turgidum</i>
<i>Sphagnum rubellum</i>	<i>Meesia uliginosa</i>

Vegetation cover is nearly continuous (< 1% bare soil), with a relatively tall plant canopy (*c.* 6.5 cm) (Walker *et al.* 2001). Higher-stature shrub communities dominated by *Salix* species are also common on the Sagavanirktok landscape, particularly in riparian areas (Walker *et al.* 1994; Muller *et al.* 1999).

Moist graminoid prostrate-shrub tundra (PST, also called moist non-acidic tundra; Walker *et al.* 1995) is the dominant vegetation of the drier hill crests, moraines and gravelly slopes that are typical of the Itkillik II surface (Walker *et al.* 1994; Muller *et al.* 1999). PST is dominated by prostrate shrubs (e.g. *Salix arctica*, *S. reticulata* and *Arctostaphylos rubra*), non-tussock-forming Cyperaceae (e.g. *Carex bigelowii*), non-*Sphagnum* mosses (e.g. *Tomentypnum nitens*, *Aulacomnium turgidum* and *Meesia uliginosa*), and *Dryas integrifolia* (Table 1; Walker *et al.* 1994, 1995, 2001). Vegetation cover is discontinuous (*c.* 8% bare soil), with a shorter plant canopy than DST (*c.* 3.9 cm). PST also differs from DST in plant diversity, wildlife habitat, carbon storage and fluxes of energy and trace gases (Walker *et al.* 1994; Michaelson *et al.* 1996; Nelson *et al.* 1997; Bockheim *et al.* 1998; Gough *et al.* 2000). The Itkillik II and Sagavanirktok surfaces have different spectral reflectance (NDVI) values (Walker *et al.* 1995), related to lower above-ground biomass for PST (*c.* 480 g m⁻²) than for DST (*c.* 610 g m⁻²) (Walker *et al.* 2001).

Methods

FIELD AND LABORATORY WORK

We obtained undisturbed sediment–water interface samples from 56 small lakes (< 25 ha). Samples were collected from near the centre of each basin using either a gravity corer or a piston surface-sediment sampler, and the uppermost 1–2 cm of sediment was used for pollen analysis. Twelve of the lakes are on the Sagavanirktok surface and 44 are on Itkillik II deposits (Table 2): the intermediate-aged Itkillik I surface was not sampled. The unequal sample size for the two surfaces reflects differences in the density of lakes. Most of the lakes are located within a 200-km² area centred on Toolik Lake (Fig. 1a), but four additional Sagavanirktok samples were collected from lakes as far as 19 km north-east of Toolik Lake (Fig. 1b).

Samples of 2 cm³ of sediment were prepared for pollen analysis following standard procedures for organic-poor sediments (Cwynar *et al.* 1979). 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). At least 350 pollen grains of terrestrial plant taxa were counted for each sample.

Pollen and spore abundances were expressed as a percentage of the sum of all identified and unidentified terrestrial pollen grains. We were also able to use the

Table 2 Locations, number of pollen grains counted and discriminant function scores for the 56 modern pollen sites. Lakes 1–44 are on the Itkillik II glaciated surface; 45–56 are on the Sagavanirktok surface

Lake number	Latitude	Longitude	Pollen grains counted	Discriminant function score
1	68°40.6' N	149°41.7' W	433	-2.26
2	68°40.5' N	149°42.1' W	549	-1.53
3	68°40.3' N	149°41.8' W	466	-2.01
4	68°40.3' N	149°40.7' W	509	-1.52
5	68°40.4' N	149°39.1' W	554	-1.23
6	68°40.6' N	149°38.8' W	387	-1.55
7	68°40.1' N	149°38.5' W	494	-2.02
8	68°40.3' N	149°38.1' W	501	-1.90
9	68°40.5' N	149°37.6' W	505	-0.79
10	68°39.9' N	149°40.2' W	456	-0.12
11	68°39.8' N	149°38.9' W	416	-0.84
12	68°39.9' N	149°36.6' W	422	-1.01
13	68°39.7' N	149°37.6' W	419	-0.49
14	68°39.7' N	149°37.8' W	379	-2.34
15	68°39.6' N	149°38.6' W	376	-1.27
16	68°39.5' N	149°37.8' W	461	-1.46
17	68°39.5' N	149°37.6' W	550	-2.64
18	68°39.3' N	149°37.7' W	557	-2.14
19	68°39.4' N	149°36.8' W	447	-0.30
20	68°39.5' N	149°34.7' W	436	-2.02
21	68°39.3' N	149°35.2' W	425	0.21
22	68°39.2' N	149°35.4' W	363	-2.08
23	68°39.2' N	149°36.5' W	396	-0.76
24	68°38.8' N	149°35.1' W	360	-1.24
25	68°38.8' N	149°36.6' W	432	-3.38
26	68°39.5' N	149°40.0' W	506	-0.82
27	68°39.4' N	149°41.3' W	466	-0.43
28	68°39.3' N	149°41.3' W	709	-2.91
29	68°39.2' N	149°40.9' W	393	-2.16
30	68°39.2' N	149°39.9' W	552	-1.77
31	68°38.7' N	149°38.5' W	375	-1.53
32	68°38.5' N	149°38.0' W	471	-3.23
33	68°38.4' N	149°37.7' W	642	-0.05
34	68°38.0' N	149°39.0' W	401	-1.64
35	68°38.0' N	149°39.0' W	402	-0.41
36	68°36.7' N	149°36.1' W	448	-1.87
37	68°36.6' N	149°35.0' W	428	-1.11
38	68°36.0' N	149°35.8' W	435	-1.15
39	68°35.7' N	149°35.6' W	519	-2.83
40	68°35.3' N	149°35.5' W	412	-0.89
41	68°34.8' N	149°35.3' W	370	-1.32
42	68°34.5' N	149°36.0' W	601	-1.41
43	68°34.2' N	149°34.9' W	455	-0.48
44	68°34.3' N	149°34.0' W	405	-1.72
45	68°37.2' N	149°29.2' W	641	4.66
46	68°34.4' N	149°26.0' W	1002	5.43
47	68°38.5' N	149°27.2' W	444	3.94
48	68°38.6' N	149°26.3' W	784	6.15
49	68°37.2' N	149°29.2' W	695	4.76
50	68°38.0' N	149°25.0' W	1202	4.21
51	68°37.9' N	149°24.8' W	862	6.78
52	68°37.8' N	149°24.6' W	1298	7.39
53	68°48.0' N	149°27.3' W	592	4.50
54	68°47.7' N	149°27.3' W	490	4.71
55	68°46.1' N	149°22.2' W	661	6.84
56	68°40.6' N	149°13.2' W	711	3.36

presence of two extra-local pollen types to estimate the absolute amount of local pollen deposited in these sediments (e.g. Maher 1972). *Picea glauca* and *P. mariana* reach their northern range limits in the southern foothills of the Brooks Range, whereas *Alnus crispa* occurs

north of the Brooks Range but is not found in the study area (Viereck & Little 1972). Nevertheless, *Alnus* and *Picea* pollen grains were encountered in all of the samples, and by assuming that their pollen rain is distributed homogeneously, the abundances of the major taxa

Table 3 Discriminant analysis loadings for each taxon

Pollen or spore type	Discriminant analysis loading
<i>Rubus chamaemorus</i>	0.36
<i>Sphagnum</i>	0.24
Ericales	0.23
Poaceae	0.16
Brassicaceae	0.12
<i>Lycopodium annotinum</i>	0.12
Saxifragaceae	0.12
Asteraceae (excluding <i>Artemisia</i>)	0.11
Lycopodiaceae (excluding <i>L. annotinum</i> and <i>H. selago</i>)	0.10
<i>Betula</i>	0.09
<i>Polygonum bistorta</i>	0.09
<i>Huperzia selago</i>	0.08
<i>Artemisia</i>	0.07
<i>Salix</i>	0.06
<i>Encalypta</i>	0.01
Caryophyllaceae	0.01
<i>Rumex-Oxyria</i>	-0.02
Bryidae (excluding <i>Encalypta</i>)	-0.02
Ranunculaceae (excluding <i>Thalictrum</i>)	-0.03
<i>Selaginella rupestris</i>	-0.04
Cyperaceae	-0.07
<i>Selaginella selaginoides</i>	-0.07
Rosaceae	-0.09
<i>Thalictrum</i>	-0.09
Polypodiaceae	-0.11
<i>Picea</i>	-0.12
<i>Equisetum</i>	-0.15
<i>Alnus</i>	-0.16

should reflect differences in local pollen productivity when expressed as a ratio to the sum of *Alnus* and *Picea*.

DATA ANALYSIS

Discriminant analysis was used to determine which taxa were most useful for discriminating between the Sagavanirktok and Itkillik II surfaces (e.g. Lynch 1996), whereas dissimilarity metrics were used to determine whether samples from the different surfaces could be differentiated based on their pollen spectra, and to create a framework for comparing this modern pollen data set with fossil pollen assemblages (e.g. Overpeck *et al.* 1985). The analyses were performed using the 28 pollen and spore types that were found in at least eight samples (Table 3), as this combination of taxa provided the best overall discrimination.

In discriminant analysis (SPSS 1999), all samples are analysed simultaneously to create a linear combination of variables, in this case the percentages of pollen and spore taxa, that maximizes the separation of samples assigned to different groups. The success of the analysis is measured by re-classification of the samples to see how many are correctly assigned to their predetermined group. We also performed a 'leave-one-out' cross-validation analysis to test whether the classification results were sensitive to small changes in the data

set. We were particularly interested in the discriminant analysis loading for each taxon (the correlation of pollen percentages with discriminant function scores), which reflect its usefulness (Liu & Lam 1985; Lynch 1996).

In contrast, dissimilarity metrics measure the multivariate dissimilarity between a pair of samples. When applied to modern pollen data, this type of analysis can be used to compare the overall dissimilarity of paired samples from within vs. between vegetation groups (e.g. Overpeck *et al.* 1985; Anderson *et al.* 1989). We made pairwise comparisons of all samples using two dissimilarity metrics that differ in their weighting of rare taxa. Squared chord distance (SCD), a 'signal-to-noise' distance measurement, is the most commonly used metric for analysis of pollen percentage data (Overpeck *et al.* 1985). It lowers the weight of abundant taxa relative to less abundant taxa, although major taxa are still weighted more heavily than minor ones. Canberra metric distance (CMD) is an 'equal weight' metric that scales the taxa so that each has an equal effect on the distance value (Prentice 1980).

Next, we used receiver operating characteristic (ROC, e.g. Metz 1978) analysis to determine the SCD and CMD values that best separate samples from like and unlike vegetation types (critical values), and to compare the relative effectiveness of SCD and CMD for this task. ROC analysis is commonly used as a diagnostic tool in medicine to determine the test result that best indicates the presence of a disease, and to assess the ability of different tests to differentiate between diseased and non-diseased conditions (Metz 1978; Zwiig & Campbell 1993). Wahl (in press) and Gavin *et al.* (2003) provide a general framework for applying ROC methods to Quaternary pollen analysis.

Each SCD and CMD measurement between paired pollen samples can be classified as either within (e.g. Sagavanirktok to Sagavanirktok) or between surfaces. If the metric were able to differentiate perfectly between pollen samples from the two glaciated surfaces, then the dissimilarity values for within-surface paired-sample comparisons would always be smaller than the between-surface values, and histograms of within- and between-surface comparisons would not overlap. In this case, the critical value used to judge whether samples come from like or unlike vegetation types would fall between the within- and between-surface histograms (Fig. 2a). However, when the pollen spectra for the two surfaces are not completely dissimilar, the within- and between-surface histograms overlap to some extent and the critical value is less obvious (Fig. 2b). In this scenario, ROC analysis can be used to determine the 'critical' SCD or CMD value that provides the best separation of the within- and between-surface histograms, and thus best differentiates between assemblages from like and unlike vegetation types. In ROC analysis, each SCD or CMD value has a corresponding true positive fraction (TPF, also known as sensitivity) and true negative fraction (TNF, also

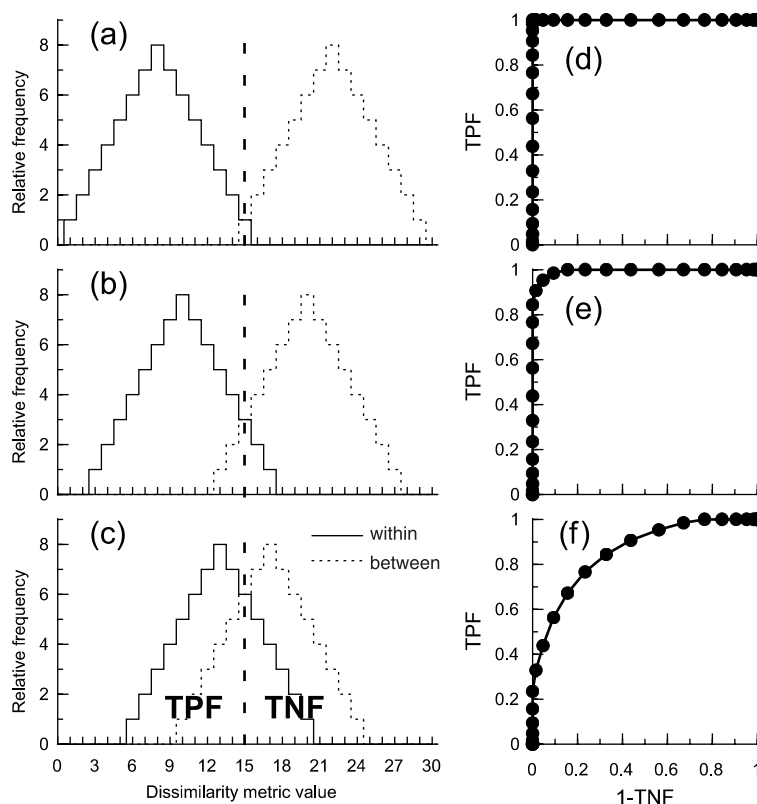


Fig. 2 Idealized histograms of within- and between-surface dissimilarity metric comparisons (a, b, c) and corresponding receiver operating characteristic (ROC) plots (d, e, f). The first scenario (a, d) has perfect discrimination between like and unlike vegetation types, the second scenario (b, e) is intermediate, and the third scenario (c, f) has considerable overlap. Vertical lines indicate the critical value (15 in each case). In c, the true positive fraction (TPF) is the portion of the within-surface histogram that occurs below a given dissimilarity metric value (in this case 15) and the true negative fraction (TNF) is the portion of the between-surface histogram that occurs above that value.

known as specificity). TPF is the fraction of within-surface comparisons that occurs below a given SCD or CMD value, whereas TNF is the fraction of between-surface comparisons that occurs above that value. TPF and TNF are inversely related to each other such that large SCD and CMD values have high TPF and low TNF. Thus, a trade off between TPF and TNF is implicit in the choice of a dissimilarity metric critical value. There are a variety of methods used to choose critical values (e.g. Metz 1978), but we simply select the SCD or CMD value that maximizes the sum of TPF and TNF.

We also used ROC analysis to compare how well the dissimilarity metrics distinguished between samples from the Sagavanirktok and Itkillik II surfaces. Because SCD and CMD weight major and minor taxa differently, any two given pollen samples will appear more or less similar depending upon which metric is used, and thus histograms of within- and between-surface comparisons will have different degrees of overlap. We can evaluate the relative diagnostic accuracy of SCD and CMD by calculating TPF and TNF over the range of SCD and CMD values. A plot (the ROC curve) of TPF vs. 1-TNF (also known as false positive fraction) can be used to describe the overall performance of the dissimilarity metrics (Fig. 2). The area

under the ROC curve is a measure of how well a given metric differentiates between the within- and between-surface comparisons, with possible values varying from 0.5 (pollen spectra indistinguishable) to 1.0 (perfect differentiation of like and unlike vegetation samples). For this study, the dissimilarity metric with the greater area under the curve is judged to be better at discriminating between pollen samples from like and unlike vegetation. There are several methods available to estimate the area under the ROC curve (e.g. Centor & Schwartz 1985). We used the sum of rectangles under the curve (Zweig & Campbell 1993).

Results

Discriminant analysis (values in Table 2) effectively distinguished between samples from the different glaciated surfaces. All 56 samples were correctly classified (Table 4), with the 44 Itkillik II samples occurring below a discriminant function score of 1, and the 12 Sagavanirktok samples with scores greater than 3 (Table 2). In the cross-validation tests, only a small percentage (6.8%) of the samples were incorrectly classified (in each case Itkillik II as Sagavanirktok), indicating that the discriminant analysis results are robust.

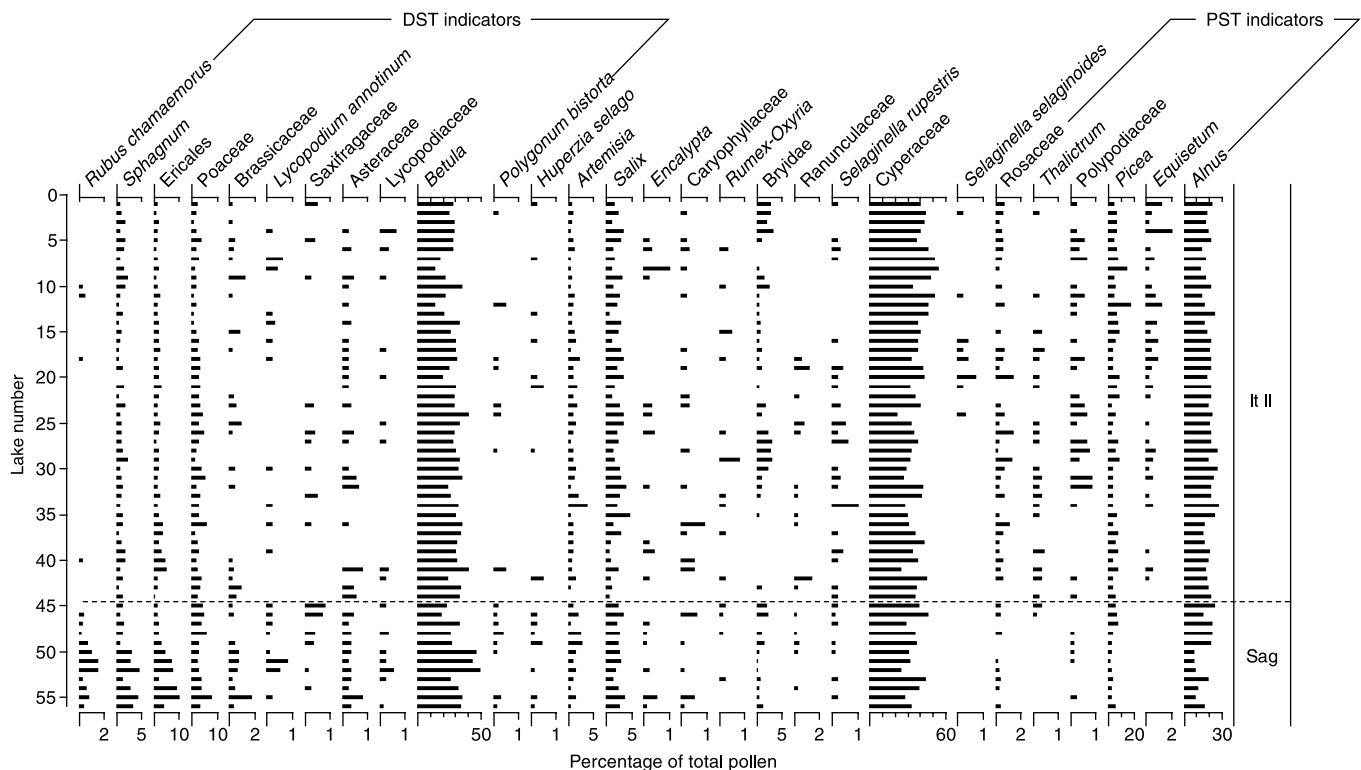


Fig. 3 Pollen and spore percentage diagram for modern lake-sediment samples from the central Arctic Foothills, northern Alaska (analysis by W.W. Oswald). The pollen and spore taxa are ordered according to their discriminant analysis loadings (Table 3). Scales of x axes vary.

Table 4 Re-classification and cross-validation results for the discriminant analysis of the modern pollen samples

<i>Re-classification</i>		<i>Predicted surface</i>	
<i>Actual surface</i>	Itkillik II	Sagavanirktok	
Itkillik II	44	0	
Sagavanirktok	0	12	
<i>Cross-validation</i>		<i>Predicted surface</i>	
<i>Actual surface</i>	Itkillik II	Sagavanirktok	
Itkillik II	41	3	
Sagavanirktok	0	12	

Several taxa had higher percentages in samples from one surface or the other (Fig. 3). Taxa associated with the Itkillik II surface (discriminant analysis loading ≤ -0.09) included *Alnus*, *Equisetum*, *Picea*, *Polypodiaceae*, *Thalictrum* and *Rosaceae*. On the other hand, taxa associated with the Sagavanirktok surface (discriminant analysis loading ≥ 0.09) included *Rubus chamaemorus*, *Sphagnum*, *Ericales*, *Poaceae*, *Brassicaceae*, *Lycopodium annotinum*, *Saxifragaceae*, *Asteraceae*, *Lycopodiaceae*, *Betula* and *Polygonum bistorta* (Table 3). The discriminant analysis loading for one of the major taxa (Cyperaceae, -0.07) was ambiguous, but the ratios of Cyperaceae pollen to extra-local pollen were generally higher for Sagavanirktok samples than for Itkillik II samples (Fig. 4). The ratios of the other dominant pollen type (*Betula*) to extra-local pollen (*Alnus* + *Picea*) were substantially higher for the Sagavanirktok surface. *Huperzia selago*, *Artemisia*, *Salix*, *Encalypta*, *Caryophyllaceae*, *Rumex-Oxyria*, *Bryidae*, *Ranunculaceae*,

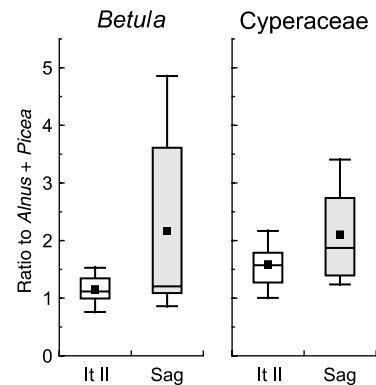


Fig. 4 Ratios of the major taxa (*Betula* and *Cyperaceae*) to the sum of *Alnus* and *Picea* pollen. White and grey boxes are Itkillik II and Sagavanirktok samples, respectively. The box represents the 25th and 50th percentiles, the whiskers indicate the 10th and 90th percentiles, the horizontal line shows the median, and the mean is represented by the square.

Selaginella rupestris and *Selaginella selaginoides* had similar abundance patterns for both surfaces.

The critical values for CMD and SCD were 13 and 0.075, respectively (Fig. 5). However, CMD was more effective than SCD for differentiating between the Sagavanirktok and Itkillik II surfaces. For CMD, within- and between-surface comparisons generally had values < 13 and > 13 , respectively, whereas SCD had more overlap. This observation was confirmed by the ROC analysis (Fig. 6), as the area under the ROC curve was higher for CMD (0.88) than for SCD (0.78).

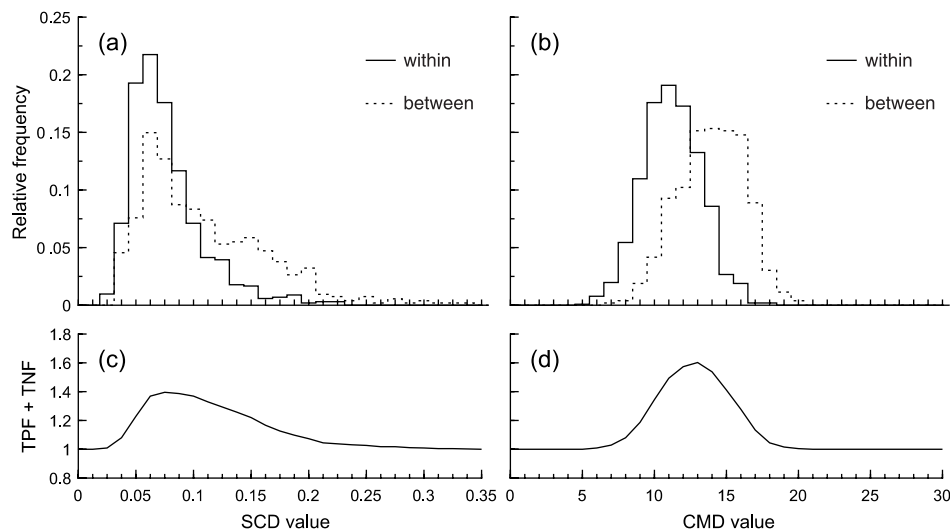


Fig. 5 Histogram of squared chord distance (A) and Canberra metric distance (B) values for all within- and between-surface comparisons of Sagavanirktok and Itkillik II samples. The maximum TPF + TNF value indicates the critical value for square chord distance (C) and Canberra metric distance (D).

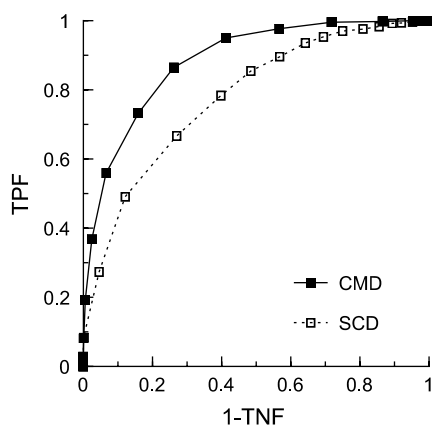


Fig. 6 Receiver operating characteristic (ROC) plots for squared chord distance (SCD) and Canberra metric distance (CMD) dissimilarity metrics.

Discussion

POLLEN DATA AND PLANT COMMUNITY COMPOSITION

The landscape-scale mosaic of tundra plant communities in this area of the central Arctic Foothills was reflected accurately in the modern lake-sediment samples by variations in the percentages of key pollen and spore types. Sagavanirktok samples were characterized by pollen from a number of taxa that either dominate (e.g. *Betula nana*; Walker *et al.* 1994) or are generally restricted to DST communities (*Rubus chamaemorus*, *Lycopodium annotinum* and *Polygonum bistorta*; Hultén 1968; Vitt *et al.* 1988; Walker *et al.* 1994). Similarly, the pattern of *Sphagnum* spores agrees with observations that *Sphagnum* species, including *S. angustifolium*, *S. balticum*, *S. girgensohnii* and *S. rubellum*, are widespread on the Sagavanirktok surface and uncommon in the PST of the Itkillik II surface (Walker

et al. 1994). High percentages of Ericales pollen in Sagavanirktok lakes reflect the prevalence of species such as *Cassiope tetragona*, *Ledum palustre* ssp. *palustre*, *Vaccinium uliginosum* and *V. vitis-idaea* in DST, compared with the less frequent occurrence of *Arctostaphylos rubra* and *Rhododendron lapponicum* in PST (Walker *et al.* 1994). Spores assigned to Lycopodiaceae were often degraded and could not be identified to species, but they may represent *Lycopodium annotinum*, *L. alpinum* or *L. clavatum*, all of which prefer acidic soils like those of the Sagavanirktok surface (Hultén 1968). Although Cyperaceae pollen percentages were high in all samples, reflecting the importance of Cyperaceae species in both PST (e.g. *Eriophorum triste* and many *Carex* species) and DST, the overall cover of Cyperaceae is higher in DST, mainly due to the dominance of *Eriophorum vaginatum*, a tussock-forming sedge (Walker *et al.* 1994). The higher ratios of Cyperaceae pollen to extra-local pollen for Sagavanirktok samples indicate that the absolute deposition of Cyperaceae pollen was higher on that surface.

The associations of other pollen types with the Sagavanirktok surface are less intuitive because each represents a diverse array of species. However, in each case some of the species can be linked to Sagavanirktok landscapes. For example, Saxifragaceae pollen was likely derived from *Saxifraga punctuata* and *S. nelsoniana*, both of which are characteristic of DST. Many Poaceae species, including *Phippsia algida*, *Arctagrostis latifolia*, *Calamagrostis canadensis*, *Arctophila fulva* and *Dupontia fisheri*, favour the boggy, acidic conditions of DST (Hultén 1968; Walker *et al.* 1994), although other Poaceae occur on the Itkillik II surface (e.g. *Poa glauca*). Similarly, some Brassicaceae species are present in PST (e.g. *Eutrema edwardsii*), but *Cardamine pratensis*, *Parrya nudicaulis* and *Smelowskia calycina* occur on acidic, moist substrates on older glaciated landscapes (Hultén 1968; Walker *et al.* 1994).

Asteraceae species occur in both PST (e.g. *Senecio resedifolius*) and DST, but the relatively high percentages of Asteraceae pollen in Sagavanirktok samples may be derived from *Petasites frigidus*, a common species in DST (Walker *et al.* 1994).

Itkillik II samples are characterized by higher percentages of taxa associated with PST, and by lower percentages of the Sagavanirktok indicators. For example, the occurrence of *Equisetum* spores in Itkillik II samples reflects the presence of *Equisetum scirpoides*, *E. variegatum* and *E. arvense* in PST communities (Walker *et al.* 1994). Although Polypodiaceae species are rare in the central Arctic Foothills, *Cystopteris fragilis*, *Woodsia alpina*, *W. glabella* and *Dryopteris fragans* do occur in dry, rocky or calcareous soils (Hultén 1968). Consistent with this substrate preference, spores of Polypodiaceae are more common in Itkillik II than Sagavanirktok samples. *Thalictrum* pollen probably indicates the presence of *Thalictrum alpinum*, which is usually found on rocky slopes (Hultén 1968), and Rosaceae pollen is likely from species that occur in the drier, rocky, calcareous soils typical of PST and the Itkillik II surface, including *Dryas integrifolia*, *Geum rossii*, *G. glaciale*, *Spirea beauverdiana* and numerous *Potentilla* species (Hultén 1968; Walker *et al.* 1994). Although we encountered *Selaginella selaginoides* only occasionally and thus its discriminant analysis loading is not strong, it is notable that its spores occur only in Itkillik II samples, as this species prefers calcareous substrates (Hultén 1968).

Several other taxa are of interest because the absence of strong patterns in the modern pollen assemblages is unexpected given the distribution of the plants themselves. For example, we might have expected Ranunculaceae to be associated with the Sagavanirktok surface, as many species within this family (e.g. *Anemone richardsonii*) prefer the boggy conditions that typify Sagavanirktok-aged landscapes. However, some Ranunculaceae species, such as *Anemone parviflora* and *Ranunculus pedatifidus*, are found in xeric sites and PST communities (Hultén 1968; Walker *et al.* 1994). Bryidae spore percentages were noticeably higher only in Itkillik II lakes from the north-western portion of the study area, even though Bryidae species, such as *Aulacomnium acuminatum*, *A. turgidum*, *Meesia uliginosa*, *Tomentypnum nitens* and *Dicranum angustum*, occur in all PST communities (Walker *et al.* 1994). This pattern may reflect more abundant moss cover near the lakes concerned, but we are unable to address adequately any smaller-scale variability within the Itkillik II landscape. We also expected *Selaginella rupestris* to be an Itkillik II indicator, as this species typically occurs on dry, rocky substrates (Hultén 1968). Although it did not vary between the two surfaces according to the discriminant analysis, *Selaginella rupestris* spores were encountered at higher percentages in Itkillik II samples (frequently 0.4–1.0%) than in Sagavanirktok samples (always < 0.2%). We suspect that this minor difference might prove to be significant with

a larger sample (either more lakes or higher pollen sums), and therefore we consider *Selaginella rupestris* to be a marginal indicator of the Itkillik II landscape.

PATTERNS OF POLLEN PRODUCTIVITY

Because the amount of extra-local *Alnus* and *Picea* pollen serves as a benchmark for approximating the absolute amount of pollen in these sediments, the ratios of *Betula* and Cyperaceae to the sum of *Alnus* and *Picea* pollen show that pollen productivity is higher on Sagavanirktok surfaces (Fig. 4). The pollen percentages of *Alnus* and *Picea* also reflect local pollen productivity, as high local productivity would dilute the extra-local pollen rain, resulting in lower *Alnus* and *Picea* percentages, as in the Sagavanirktok samples (Fig. 3). DST thus has higher pollen productivity than PST, mainly due to higher amounts of *Betula* pollen, presumably resulting from the greater abundance of *Betula nana* and higher overall plant cover on the Sagavanirktok surface (Walker *et al.* 1994, 1995, 2001). The link between vegetation and absolute pollen abundance has been debated (Lehman 1975; Cwynar 1982; Davis & Ford 1982; Guthrie 1985; Hicks 2001), but the consistent patterns of extra-local pollen percentages and ratios in this data set suggest that this relationship deserves further consideration.

INTERPRETATION OF ARCTIC POLLEN DATA

Because late Quaternary pollen assemblages from the Arctic are often dominated by Poaceae, Cyperaceae and *Artemisia*, which are difficult to interpret because of their broad ecological ranges (e.g. Anderson *et al.* 1994), palaeoenvironmental interpretations are often based on rare, but ecologically specific, indicator taxa (e.g. Cwynar 1982; Oswald *et al.* 1999). However, this is the first study to verify that the pollen or spores of such taxa are associated with the occurrence of specific tundra plant communities or environmental conditions near the lake. For example, *Rubus chamaemorus* and *Polygonum bistorta* are considered indicative of mesic soil conditions (e.g. Cwynar 1982; Anderson 1985; Anderson *et al.* 1994; Oswald *et al.* 1999), and pollen grains of these species occur reliably in samples from the wetter Sagavanirktok landscape. Likewise, *Thalictrum* and *Selaginella rupestris* are interpreted as indicators of rocky substrates and open or discontinuous vegetation (e.g. Cwynar 1982; Anderson 1985; Anderson *et al.* 1994; Oswald *et al.* 1999) and, in this study, were associated with the drier Itkillik II surface.

On the other hand, only two pollen and spores types (*Equisetum* and *Selaginella selaginoides*) were restricted to one surface or the other. The presence or absence of most individual taxa therefore was not an entirely faithful discriminator between these tundra types, and thus this data set suggests that palaeoecological interpretations should be based on coherent patterns of several indicator taxa, in conjunction with

multivariate analyses of the entire pollen assemblage (e.g. Anderson *et al.* 1994). However, the choice of a technique for analysing pollen assemblage data should be considered carefully if it is necessary to maximize the information contained in the patterns of rare taxa, as was the case in this study. CMD emphasizes the minor taxa, and therefore was better than SCD, the dissimilarity metric most commonly applied to pollen data (e.g. Overpeck *et al.* 1985; Anderson *et al.* 1994), at distinguishing between tundra types (Fig. 6). SCD has proven more useful for comparisons between biomes, where there are greater differences in the pollen spectra of the separate vegetation types. For example, SCD successfully differentiated modern pollen assemblages from boreal forest and tundra, with values for same-vegetation comparisons generally < 0.185 (Anderson *et al.* 1989). The finding that nearly all SCD values in this study (within- and between-surfaces; Fig. 5) were below that critical value is consistent with Anderson *et al.* (1989), as the comparison of samples from within the same biome (i.e. tundra) should yield relatively low dissimilarity values with SCD.

SPATIAL SCALE OF ARCTIC POLLEN DATA

The results of this study provide indirect information about the landscape area represented by pollen data from arctic tundra. The theoretical understanding of relevant pollen source area, the area producing that component of the pollen rain that varies in response to differences in vegetation from location to location, is based on a variety of empirical and modelling studies (e.g. Prentice 1985; Jackson 1990; Sugita 1993, 1994; Calcote 1995, 1998). However, all of those studies were focused on forested vegetation where pollen is dispersed mainly by wind. Relevant pollen source area may differ for tundra vegetation because many of the pollen types are insect-dispersed, and also because the smaller stature of the vegetation may result in different pollen dispersal patterns than in forests. However, the fact that it was possible to perceive differences in the pollen assemblages of sites that are separated by only a few kilometres suggests that the source area is quite small. Sugita (1994) found the relevant pollen source area for lakes of this size (< 25 ha) in forested vegetation to be 600–800 m, and the results of this study indicate that the relevant pollen source area for tundra vegetation is comparable.

IMPLICATIONS

This study provides insights into the pollen–vegetation relationship for tundra and, because the results indicate that pollen data reflect landscape-scale vegetational patterns, suggests that it may be possible to revisit controversial questions about the spatial variability of past ecosystems in the Arctic. For example, late Pleistocene pollen spectra from north-western Canada were interpreted as indicative of xeric, discon-

tinuous tundra (Cwynar & Ritchie 1980; Cwynar 1982). However, palaeontologists (e.g. Guthrie 1982) criticized this interpretation, asserting that the vertebrate fossil record suggests that landscapes in Alaska and the Yukon supported large numbers of megafauna (e.g. mammoths, giant bison and horses; Guthrie 1968). They contended that only a productive, well-vegetated ecosystem, such as a grassland or steppe-tundra, could have supported large grazers. To resolve these seemingly contradictory interpretations, Quaternary researchers invoked the notion of past tundra mosaics (Schweger 1982; Anderson 1985; Eisner & Colinvaux 1992), suggesting that a landscape-scale patchwork of vegetation types was present. Low-lying, productive, mesic portions of the landscape would have provided habitat for megafauna, whereas upland areas were sparsely vegetated. However, because palynology has been considered a ‘blunt instrument’ for reconstructing past tundra vegetation (e.g. Colinvaux 1967; Birks & Birks 2000), the hypotheses about past vegetation mosaics have not been investigated.

The finding that modern tundra plant communities in the central Arctic Foothills can be distinguished from each other by their pollen assemblages indicates that the perceived spatial uncertainty of arctic pollen records is unfounded. With guidance provided by modern pollen–vegetation calibration, palynology may yet prove useful for studying the landscape-scale heterogeneity of past tundra, including the controversial full-glacial vegetation. For example, taxa that occur in full-glacial pollen assemblages, such as *Thalictrum* and *Selaginella rupestris*, appear to be locally dispersed and thus reflective of landscape-scale patterns of tundra. By focusing on the variations in these and other indicator pollen and spore types, it will be possible to explore the landscape-scale variability of full-glacial vegetation and other past arctic plant communities.

Acknowledgements

We thank the Toolik Field Station for logistical support, the BLM Northern Field Office for assistance with research permits, and Torre and Janet Jorgenson for loaning field equipment. This study benefited from our interactions and conversations with many colleagues, including Randy Calcote, Lisa Carlson, Terry Chapin, Ed Cushing, Margaret Davis, Wendy Fujikawa, Laura Gough, Phil Higuera, Kristina Hill, Sarah Hobbie, Sara Hotchkiss, George Kling, Kendra McLauchlan, Tim Parshall, Shinya Sugita, Eugene Wahl, Marilyn Walker and Skip Walker. We are grateful to Pat Anderson, Shelley Crausbay, Charlie Halpern, Doug Sprugel, Darlene Zabowski, Lindsey Haddon and two anonymous referees for their thoughtful reviews of the manuscript. This research was funded by National Science Foundation grant OPP-9615947 and the Global Palaeorecords Research Training Group at the University of Minnesota. This is contribution 206 from the Palaeoenvironmental Arctic Science (PARCS) programme.

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Received 23 December 2002

revision accepted 22 July 2003