

## Representation of tundra vegetation by pollen in lake sediments of northern Alaska

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### Abstract

**Aim** To understand better the representation of arctic tundra vegetation by pollen data, we analysed pollen assemblages and pollen accumulation rates (PARs) in the surface sediments of lakes.

**Location** Modern sediment samples were collected from seventy-eight lakes located in the Arctic Foothills and Arctic Coastal Plain regions of northern Alaska.

**Methods** For seventy of the lakes, we analysed pollen and spores in the upper 2 cm of the sediment and calculated the relative abundance of each taxon (pollen percentages). For eleven of the lakes, we used <sup>210</sup>Pb analysis to determine sediment accumulation rates, and analysed pollen in the upper 10–15 cm of the sediment to estimate modern PARs. Using a detailed land-cover map of northern Alaska, we assigned each study site to one of five tundra types: moist dwarf-shrub tussock-graminoid tundra (DST), moist graminoid prostrate-shrub tundra (PST) (coastal and inland types), low-shrub tundra (LST) and wet graminoid tundra (WGT).

**Results** Mapped pollen percentages and multivariate comparison of the pollen data using discriminant analysis show that pollen assemblages vary along the main north–south vegetational and climatic gradients. On the Arctic Coastal Plain where climate is cold and dry, graminoid-dominated PST and WGT sites were characterized by high percentages of Cyperaceae and Poaceae pollen. In the Arctic Foothills where climate is warmer and wetter, shrub-dominated DST, PST and LST were characterized by high percentages of *Alnus* and *Betula* pollen. Small-scale variations in tundra vegetation related to edaphic variability are also represented by the pollen data. Discriminant analysis demonstrated that DST sites could be distinguished from foothills PST sites based on their higher percentages of Ericales and *Rubus chamaemorus* pollen, and coastal PST sites could be distinguished from WGT sites based on their higher percentages of *Artemisia*. PARs appear to reflect variations in overall vegetation cover, although the small number of samples limits our understanding of these patterns. For coastal sites, PARs were higher for PST than WGT, whereas in the Arctic Foothills, PARs were highest in LST, intermediate in DST, and lowest in PST.

**Main conclusion** Modern pollen data from northern Alaska reflect patterns of tundra vegetation related to both regional-scale climatic gradients and landscape-scale edaphic heterogeneity.

### Keywords

Alaska, Arctic Coastal Plain, Arctic Foothills, modern pollen, North Slope, palynology, paleoecology, pollen accumulation rates, tundra.

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## INTRODUCTION

Understanding the history of the tundra biome has long been an important objective in paleoecology (Iversen, 1952; Livingstone, 1955; Colinvaux, 1964; Ritchie, 1984). During past glacial intervals, tundra was extensive not only in the Arctic, but also in lower latitude areas of North America and Eurasia that are currently forested (e.g. Jackson *et al.*, 2000; Prentice & Jolly, 2000). Knowledge of the nature of the vegetation during those times is relevant to a variety of research areas, including the modern floristic geography of the Arctic, human migration and settlement patterns, and the ecology of Pleistocene fauna (e.g. Fernald, 1925; Hultén, 1937; Hopkins *et al.*, 1981; Guthrie, 1990). Furthermore, studies of past changes in tundra ecosystems help us to understand how tundra responds to environmental change, a topic that has become prevalent as evidence builds that the Arctic will be especially sensitive to future changes in climate (e.g. Overpeck *et al.*, 1997; Serreze *et al.*, 2000).

There is particular interest in understanding the small-scale (1–100 km) heterogeneity of past tundra ecosystems. Studies of modern arctic tundra show that ecosystem processes and plant community composition are spatially heterogeneous in response to both regional-scale (100–1000 km) climatic gradients and landscape-scale edaphic variability (e.g. Walker, 2000), and many authors have hypothesized that past tundra also varied according to local variations in topography or substrate. For example, conflicting interpretations of the full-glacial vegetation of the Bering Strait region (e.g. Cwynar, 1982; Guthrie, 1985) were reconciled by the notion that the vegetation was a mosaic of different vegetation types (Schweger, 1982; Anderson, 1985; Eisner & Colinvaux, 1992). Valley bottoms and lowlands would have supported continuous, mesic tundra communities, while uplands featured xeric, sparsely vegetated tundra. Additionally, there is growing evidence that edaphic variability is likely to influence the response of tundra ecosystems to future climate change (e.g. Hobbie & Gough, 2002), and paleoecological studies may provide insights to this question (Oswald, 2002).

Reconstructing the subregional heterogeneity of past tundra vegetation, however, has proven difficult. Palynology, the method most commonly used in Quaternary paleoecology, is viewed as a 'blunt instrument' for reconstructing small-scale patterns of tundra (Colinvaux, 1967). Pollen assemblages (as represented by percentage data) are difficult to interpret because key species are over- or under-represented, pollen types cannot be differentiated within many genera or families, and the spatial resolution of the data is unclear (Nichols, 1974; Anderson *et al.*, 1994; Gajewski *et al.*, 1995). Pollen accumulation rates (PARs) (number of pollen grains  $\text{cm}^{-2} \text{year}^{-1}$ ) were explored as a possible metric of past variations in vegetation cover (e.g. Cwynar, 1982), but their utility has been disputed (e.g. Guthrie, 1985, 1990). Modern calibration studies have shown that pollen percentage data reflect the major, regional-scale variations in tundra (Ritchie, 1974; Anderson & Brubaker, 1986; Short *et al.*, 1986; Brubaker *et al.*,

1998), but the ability of pollen to represent the landscape-scale heterogeneity related to edaphic variability has not been tested.

The tundra region of northern Alaska is well suited for a study of the modern relationship between pollen data and patterns of vegetation. The distribution of different tundra types is influenced regionally by climatic gradients and at the landscape scale by variation in substrate (Muller *et al.*, 1999). In general, shrub-dominated tundra prevails in the relatively warm and wet Arctic Foothills in the southern portion of this region, whereas graminoid species dominate the Arctic Coastal Plain in the north where climate is colder and drier (Walker *et al.*, 1998; Muller *et al.*, 1999). The composition of the vegetation also varies at smaller spatial scales, primarily in response to heterogeneous soil drainage (Walker *et al.*, 1994, 1995; Walker, 2000). For example, shrubs occur on the coastal plain in areas where slightly higher topography affords drier soils (Walker & Everett, 1991; Muller *et al.*, 1999), and the coarse-textured soils of recently glaciated areas of the Arctic Foothills are occupied by different plant communities than the surrounding landscape (e.g. Jorgenson, 1984).

Based on pollen percentages in surface sediments of twenty-seven lakes in this region, Anderson & Brubaker (1986) showed that the primary gradient of vegetation and climate is represented by variation in the percentages of the major taxa. Coastal sites were characterized by high percentages of Cyperaceae and Poaceae pollen, whereas inland sites were characterized by high percentages of *Betula* and *Alnus* pollen. This study improves upon the previous work in two ways. First, we added forty-three pollen sites to that data set, thus enabling us to better define regional-scale patterns, as well as to explore variability within the major tundra zones. In addition, we used a recently created land-cover map of northern Alaska (Muller *et al.*, 1999) to classify each pollen site as one of five tundra types. Because the map presents the regional vegetation in more detail than was previously available (100-m pixel size), it allowed us to examine the variability in pollen assemblages within the broad coastal and inland vegetation zones and to assess whether that variability is related to the small-scale patterns of plant communities. We used discriminant analysis to define trends in the pollen data, and we compared those trends with climate and vegetation data to explore how the pollen data represent vegetational patterns associated with both climatic forcing and edaphic controls. Secondly, we analysed pollen in surface cores dated with  $^{210}\text{Pb}$  to estimate PARs for eleven sites representing the five tundra types. These analyses show that modern pollen assemblages reflect variations in tundra associated with the latitudinal gradient, and indicate that the landscape-scale variations in tundra related to edaphic heterogeneity also are recorded by pollen data.

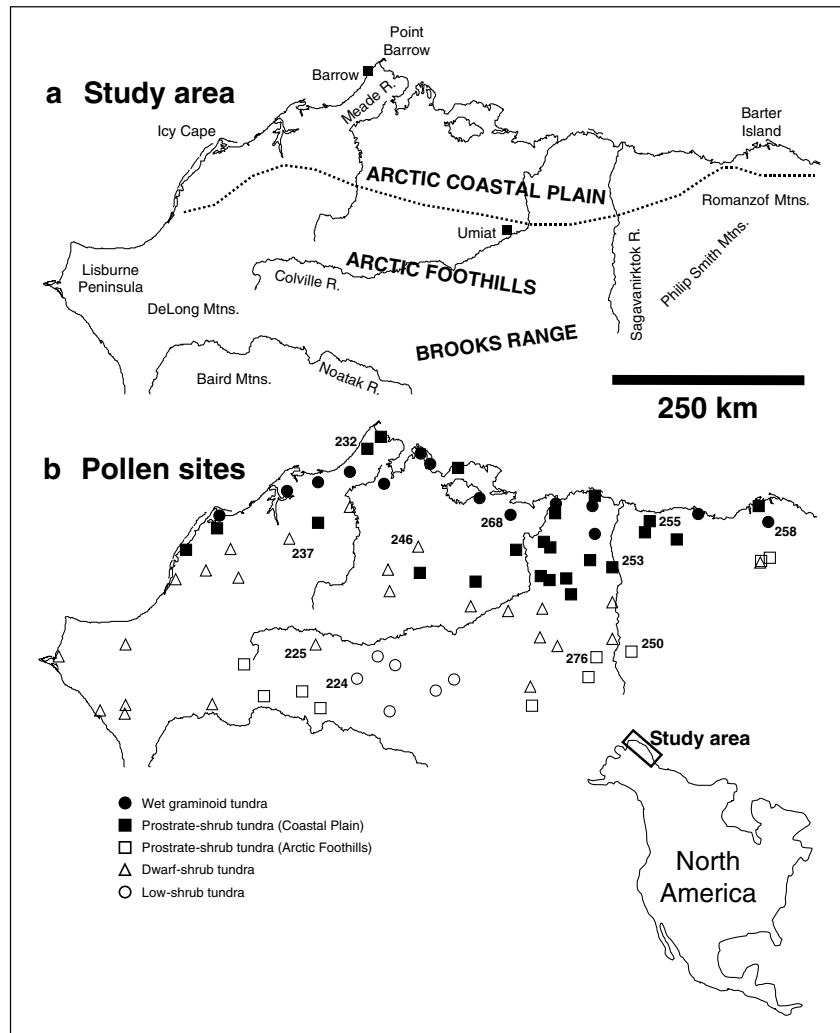
## STUDY AREA

There are two major physiographical zones in Alaska north of the Brooks Range (Wahrhaftig, 1965; Gallant *et al.*,

1995). The Arctic Foothills are rolling uplands located north of the mountains, and the Arctic Coastal Plain is a flat, lowland area that extends north from the foothills to the Arctic Ocean (Fig. 1a). The climate of this region is severe, with air temperatures remaining below 0 °C for 9 months of the year (Zhang *et al.*, 1996). However, climatic conditions vary with elevation and distance from the Arctic Ocean. Coastal areas have cool summers and relatively warm winters (mean July and January temperatures for Barrow are 4.5 and -25.5 °C, respectively), and low mean annual precipitation (Barrow = 113 mm). In contrast, the Arctic Foothills experience colder winters, warmer summers (mean July and January temperatures for Umiat are 12.2 and -29.3 °C, respectively), and higher mean annual precipitation (Umiat = 229 mm) (Zhang *et al.*, 1996), most of which occurs during summer months.

Edaphic variability in the Arctic Foothills is largely related to the history of glacial advances from the Brooks Range (Detterman *et al.*, 1958; Hamilton & Porter, 1975; Hamilton, 1994). Landscapes of Anaktuvuk (early

Pleistocene), Sagavanirktok (>125,000 yr BP), and Itkillik I (>60,000 yr BP) age have been subjected to long periods of weathering and eolian deposition, and thus are characterized by gentle topography and fine-textured soils (Hamilton, 1994). Summer thaw layers are shallow on these older surfaces, resulting in poor drainage and large areas of waterlogged soils (Walker *et al.*, 1989, 1994). Landscapes dating to the Itkillik II glacial advance (24,000 to 11,500 yr BP) have more irregular terrain and coarse-textured, drier soils (Hamilton, 1994). The Arctic Coastal Plain was never glaciated. Its surface materials are primarily unconsolidated marine and alluvial sediments highly modified by periglacial processes (Hamilton, 1986), including a vast (7000 km<sup>2</sup>) late Pleistocene, stabilized dune field in the central coastal plain (Carter, 1981). Wet soil conditions are typical, but drier soils occur in areas of slightly higher relief, including river banks, coastal bluffs and pingos (Walker & Everett, 1991; Walker *et al.*, 1991). Much of the Arctic Coastal Plain is covered with thermokarst lakes (Muller *et al.*, 1999).



**Figure 1** (a) Map of northern Alaska showing the major physiographical regions and locations mentioned in the text. Dotted line indicates the approximate boundary between the Arctic Coastal Plain and Arctic Foothills regions. (b) Locations of study sites. Symbols indicate the dominant vegetation type within a 2-km radius of the lake (Muller *et al.*, 1999). Site numbers are shown for sites used in the PAR calibration study.

The most recent land-cover map for the region (Muller *et al.*, 1999) designates six major vegetation types, two of which are most prevalent. The largest area is occupied by moist dwarf-shrub tussock-graminoid tundra (also called moist acidic tundra; Walker *et al.*, 1995), the typical tussock tundra found in much of the low Arctic (Hanson, 1953; Alexandrova, 1980; Bliss & Matveyeva, 1992). We refer to this vegetation as dwarf-shrub tundra (DST). DST is widespread in the Arctic Foothills (particularly on the older glaciated surfaces), and occurs elsewhere on moist hillslopes and moderately drained terrain where  $\text{pH} < 5.5$  (Walker *et al.*, 1994; Muller *et al.*, 1999). Dominant taxa include *B. nana* ssp. *exilis* (Sukatsch.) Hult., *Ledum palustre* ssp. *decumbens* (Ait.) Hult., *Vaccinium vitis-idaea* L., *V. uliginosum* L., *Eriophorum vaginatum* L. and *Sphagnum* species (Walker *et al.*, 1994).

In many other settings, including cryoturbated substrates, river terraces, moderately drained terrain where  $\text{pH} > 5.5$ , and recent glacial deposits, the dominant vegetation is moist graminoid prostrate-shrub tundra (also called moist non-acidic tundra; Walker *et al.*, 1995). We refer to this vegetation as prostrate-shrub tundra (PST). PST features prostrate shrubs [e.g. *Salix arctica* Pall. and *Arctostaphylos rubra* (Rehd. & Wilson) Fern.]; non-tussock-forming Cyperaceae (e.g. *Carex bigelowii* Torr.); non-*Sphagnum* mosses [e.g. *Tomentypnum nitens* (Hedw.) Loeske, *Aulacomnium turgidum* (Wahlenb.) Schwägr. and *Hypnum bambergeri* Schimp.]; and *Dryas integrifolia* M. Vahl. (Walker & Everett, 1991; Walker *et al.*, 1994, 1998).

Other vegetation types are common, but are less extensive than DST and PST. Moist tussock-graminoid dwarf-shrub tundra occurs on the coastal plain on the moist, sandy soils of the Pleistocene sand sea (Carter, 1981). This vegetation type is compositionally similar to DST, but has smaller *Eriophorum vaginatum* tussocks, fewer dwarf shrubs, and a less-developed moss understory (Muller *et al.*, 1999). Wet graminoid tundra (WGT) occurs in the thaw-lake region of the coastal plain and other wetland areas (Muller *et al.*, 1999). The most common species are *C. aquatilis* Wahlenb., *Eriophorum angustifolium* Honck., *Dupontia fischeri* R. Br., *Alopecurus alpinus* Sm. and *Arctophila fulva* Trin. Anderss. (Walker & Everett, 1991). Low-shrub tundra (LST) occurs in a variety of other situations, including riparian areas, south-facing slopes, and gently rolling uplands, with highest abundance in the relatively warm and wet south-central portion of the Arctic Foothills (Muller *et al.*, 1999). The dominant species in LST communities are *S. alaxensis* (Anderss.) Cov., *S. lanata* L. ssp. *richarsonii* (Hook.) A. Skvortz, *S. pulchra* Cham., *S. glauca* L. and *A. crispa* (Ait.) Pursh (Walker *et al.*, 1994). Finally, alpine tundra occurs in the Brooks Range, but was not sampled in this study.

## METHODS

We collected surface sediments from seventy-eight lakes across the Arctic Foothills and Arctic Coastal Plain (Fig. 1b); twenty-seven of these have been previously described (Anderson & Brubaker, 1986). Sites were selected to achieve

an even geographical coverage and to represent an array of tundra types. Lake size varied considerably (0.2–28.8 km<sup>2</sup>), but the majority were between 1 and 4 km<sup>2</sup> in area (Table 1). Undisturbed sediment–water interface cores were obtained near the centre of each lake using either a 2.5-cm diameter gravity corer or a 5-cm diameter plastic tube fitted with a piston. Gravity cores were extruded vertically in 2-cm intervals; piston cores were extruded vertically in 0.5-cm intervals between 0 and 10 cm and in 1-cm intervals between 10 and 20 cm.

For seventy of the sites, subsamples (1–2 cm<sup>3</sup>) of the surface interval (0–2 cm) were prepared for pollen analysis following standard procedures for organic-poor sediments (Cwynar *et al.*, 1979; PALE, 1994). Pollen residues were stained with safranin, mounted in silicone oil, and microscopically examined using 40 and 100× objectives (12× eyepieces). At least 300 pollen grains of terrestrial plant taxa were counted for each sample. Pollen and spore abundances were expressed as a percentage of the sum of identified and unidentified pollen grains.

Pollen accumulation rates were calculated for the eleven sites where sediment was sampled with the piston corer. <sup>210</sup>Pb activity was measured by alpha spectrometry (Eakins & Morrison, 1978) at 0.5- or 1-cm increments in the upper 10–15 cm of each core, and sediment accumulation rates were estimated via constant flux : constant supply (cf : cs) modelling (Oldfield & Appleby, 1984). For the lakes in the Arctic Foothills, we also calculated PARs using sediment accumulation rates that were corrected for sediment focusing based on the atmospheric <sup>210</sup>Pb flux for the Toolik Lake area (site 276) (Fitzgerald & Engstrom, unpubl. data). For each core, a sediment subsample was removed from each level in the interval represented by the sediment accumulation rate (c. 1850 to present). Subsamples (0.5 cm<sup>3</sup>) were taken from the 0.5-cm thick levels, and 1-cm<sup>3</sup> subsamples were taken from the 1-cm thick levels. Those subsamples were combined and homogenized, and a 2-cm<sup>3</sup> sample of the combined sediment was removed for pollen analysis. These samples were prepared as described above, with the exception that tablets containing *Lycopodium clavatum* spores were added to allow estimation of pollen concentrations and PARs (Stockmarr, 1971).

Each site was assigned to one of the five vegetation categories using the land-cover map of Muller *et al.* (1999). We used ArcView 3.2 (ESRI, 1996) to determine the area of each cover type in a 2-km radius circular plot centred on each lake, as preliminary analyses showed that pollen and vegetation abundances were most strongly related at this distance (Oswald, 2002). The use of this plot size is generally consistent with the findings of empirical and simulation studies of pollen transport and deposition (e.g. Bradshaw & Webb, 1985; Jackson, 1990; Sugita, 1994; Sugita *et al.*, 1999), which suggest that pollen spectra from lakes of this size reflect vegetation patterns within c. 100 m to 4.5 km. The sites were assigned to the land-cover type that occupied the largest area (excluding water) within 2 km, and for 80% of the sites the assigned vegetation type covered >50% of the plot. The two lakes classified as moist tussock-graminoid

**Table 1** Vegetation type, location, elevation, lake size, and discriminant analysis scores for modern pollen sites. Sites lacking discriminant analysis scores were analysed only for the pollen accumulation rate study

| Vegetation    | Site   | Longitude<br>(° W) | Latitude<br>(° N) | Elevation<br>(m) | Lake size<br>(km <sup>2</sup> ) | Discriminant analysis |        |
|---------------|--------|--------------------|-------------------|------------------|---------------------------------|-----------------------|--------|
|               |        |                    |                   |                  |                                 | Axis 1                | Axis 2 |
| Wet graminoid | 258    | 143.55             | 69.86             | 113              | 1.3                             | 0.13                  | -0.82  |
|               | 256    | 145.77             | 70.09             | 9                | 1.8                             | -1.43                 | -0.26  |
|               | 63     | 149.23             | 70.33             | 1                | 0.5                             | -1.49                 | -1.37  |
|               | 254    | 149.26             | 70.02             | 40               | 2.2                             | -1.39                 | 0.12   |
|               | 64     | 150.45             | 70.40             | 2                | 1.7                             | -2.38                 | -1.15  |
|               | 268    | 152.00             | 70.19             | 18               | 5.7                             | -                     | -      |
|               | 269    | 153.00             | 70.51             | 2                | 3.1                             | -1.90                 | -2.88  |
|               | 95     | 154.67             | 70.93             | 3                | 2.0                             | -2.45                 | -2.98  |
|               | 231    | 154.98             | 71.04             | 2                | 2.5                             | -2.03                 | -2.03  |
|               | 230    | 156.27             | 70.70             | 5                | 3.8                             | -1.01                 | -0.66  |
|               | 233    | 157.41             | 70.83             | 19               | 3.3                             | -2.01                 | -1.74  |
|               | 234    | 158.49             | 70.69             | 18               | 8.3                             | -0.63                 | 0.17   |
|               | 235    | 159.55             | 70.58             | 17               | 6.5                             | -1.35                 | -1.90  |
|               | 91     | 161.45             | 70.15             | 13               | 28.8                            | -0.49                 | -2.82  |
| Coastal PST   | 257    | 143.75             | 70.06             | 8                | 2.2                             | -1.52                 | 1.25   |
|               | 259    | 146.61             | 69.84             | 140              | 1.5                             | -1.37                 | 0.78   |
|               | 255    | 147.40             | 70.08             | 13               | 2.6                             | -0.46                 | 0.38   |
|               | 260    | 147.59             | 69.97             | 46               | 2.8                             | -1.51                 | 0.80   |
|               | 253    | 148.49             | 69.37             | 122              | 2.3                             | -                     | -      |
|               | 266    | 149.11             | 70.44             | 5                | 3.3                             | 0.87                  | 0.94   |
|               | 62     | 149.50             | 69.73             | 119              | 2.0                             | -1.69                 | 0.81   |
|               | 61     | 150.23             | 69.37             | 213              | 1.2                             | -1.85                 | 0.20   |
|               | 261    | 150.33             | 69.55             | 122              | 3.1                             | -0.89                 | -0.52  |
|               | 267    | 150.51             | 70.30             | 6                | 6.6                             | -1.45                 | -0.11  |
|               | 66     | 150.77             | 69.92             | 29               | 2.8                             | -0.58                 | 0.84   |
|               | 67     | 150.88             | 69.55             | 76               | 2.5                             | -1.09                 | -0.14  |
|               | 65     | 150.97             | 69.98             | 15               | 1.3                             | -0.94                 | -0.99  |
|               | 262    | 151.16             | 69.60             | 74               | 4.0                             | -0.23                 | -0.67  |
|               | 263    | 151.89             | 69.92             | 57               | 6.6                             | 0.38                  | -0.03  |
|               | 101    | 153.25             | 69.58             | 152              | 2.6                             | -0.81                 | 2.65   |
|               | 270    | 153.72             | 70.87             | 3                | 1.5                             | -1.41                 | 0.80   |
|               | 227    | 155.05             | 69.70             | 64               | 2.2                             | -1.20                 | 0.83   |
|               | 93     | 156.37             | 71.23             | 3                | 0.5                             | -2.27                 | 0.72   |
|               | 232    | 156.50             | 71.60             | 12               | 5.3                             | -                     | -      |
| 236           | 158.43 | 70.26              | 24                | 3.8              | 0.24                            | -0.64                 |        |
| 238           | 161.80 | 70.11              | 14                | 10.0             | -0.98                           | 0.29                  |        |
| 240           | 162.72 | 69.81              | 15                | 6.2              | -1.30                           | 1.16                  |        |
| Foothills PST | 147    | 143.74             | 69.46             | 518              | 0.2                             | -0.97                 | -0.93  |
|               | 149    | 144.03             | 69.44             | 579              | 0.2                             | 1.67                  | -0.23  |
|               | 250    | 148.52             | 68.66             | 524              | 3.4                             | 3.05                  | -0.55  |
|               | 276    | 149.37             | 68.38             | 719              | 1.9                             | -                     | -      |
|               | 109    | 149.92             | 68.41             | 716              | 5.9                             | 2.84                  | -0.85  |
|               | 70     | 151.70             | 68.15             | 616              | 0.3                             | 0.56                  | -1.65  |
|               | 226    | 158.13             | 68.14             | 335              | 1.5                             | 1.19                  | 0.34   |
|               | 125    | 158.72             | 68.33             | 396              | 9.0                             | 3.14                  | 0.27   |
|               | 126    | 159.86             | 68.25             | 244              | 0.7                             | 3.77                  | -1.03  |
|               | 94     | 160.53             | 68.60             | 853              | 0.2                             | 3.24                  | 0.20   |
|               | 148    | 144.05             | 69.41             | 597              | 0.5                             | 0.38                  | 1.79   |
| Dwarf-shrub   | 252    | 148.95             | 69.24             | 213              | 1.5                             | 0.74                  | 0.83   |
|               | 251    | 149.06             | 68.82             | 518              | 0.8                             | 3.07                  | 0.27   |
|               | 272    | 150.79             | 68.80             | 427              | 0.9                             | 0.47                  | 1.67   |
|               | 68     | 151.15             | 69.23             | 162              | 1.6                             | 0.99                  | 1.98   |
|               | 69     | 151.32             | 68.92             | 329              | 4.5                             | 1.06                  | 2.07   |
|               | 274    | 151.71             | 68.36             | 762              | 1.1                             | 2.24                  | -1.15  |
|               | 265    | 152.27             | 69.23             | 198              | 1.9                             | 0.64                  | 2.08   |

**Table 1** *continued*

| Vegetation | Site | Longitude<br>(° W) | Latitude<br>(° N) | Elevation<br>(m) | Lake size<br>(km <sup>2</sup> ) | Discriminant analysis |        |
|------------|------|--------------------|-------------------|------------------|---------------------------------|-----------------------|--------|
|            |      |                    |                   |                  |                                 | Axis 1                | Axis 2 |
|            | 248  | 153.45             | 69.31             | 229              | 1.3                             | -0.03                 | 1.76   |
|            | 246  | 155.60             | 69.60             | 49               | 2.2                             | -                     | -      |
|            | 96   | 156.05             | 69.48             | 91               | 0.3                             | 0.85                  | 0.16   |
|            | 244  | 156.11             | 69.74             | 91               | 2.0                             | -0.72                 | -0.91  |
|            | 89   | 157.40             | 70.43             | 20               | 2.6                             | -0.74                 | 2.22   |
|            | 225  | 158.21             | 68.52             | 518              | 7.5                             | -                     | -      |
|            | 237  | 159.23             | 70.30             | 274              | 1.3                             | -                     | -      |
|            | 243  | 160.91             | 69.56             | 107              | 5.0                             | -0.91                 | 0.53   |
|            | 239  | 161.27             | 69.88             | 55               | 6.8                             | -0.58                 | 0.19   |
|            | 98   | 161.42             | 68.12             | 190              | 2.3                             | 1.94                  | 0.56   |
|            | 242  | 162.03             | 69.62             | 36               | 2.8                             | -0.43                 | 2.14   |
|            | 241  | 162.96             | 69.48             | 23               | 1.9                             | -0.77                 | 1.74   |
|            | 40   | 164.00             | 67.90             | 73               | 1.1                             | 0.87                  | 1.58   |
|            | 39   | 164.02             | 68.00             | 104              | 0.4                             | 1.03                  | 2.61   |
|            | 38   | 164.27             | 68.68             | 216              | 3.0                             | 0.18                  | -0.70  |
|            | 36   | 164.73             | 67.90             | 6                | 0.6                             | 0.46                  | 1.81   |
|            | 37   | 166.25             | 68.43             | 30               | 0.3                             | -0.50                 | -0.34  |
| Low-shrub  | 220  | 154.06             | 68.48             | 518              | 3.0                             | 1.90                  | -3.53  |
|            | 221  | 154.64             | 68.36             | 914              | 4.5                             | 2.24                  | -2.72  |
|            | 222  | 155.86             | 68.66             | 396              | 0.9                             | 2.65                  | -0.72  |
|            | 104  | 156.03             | 68.13             | 632              | 8.1                             | 2.62                  | -1.77  |
|            | 223  | 156.42             | 68.75             | 335              | 2.0                             | 0.35                  | -0.76  |
|            | 224  | 157.20             | 68.30             | 518              | 3.8                             | -                     | -      |

PST, prostrate-shrub tundra.

dwarf-shrub tundra (sites 89 and 237) were grouped with the DST sites based on the compositional similarity of these vegetation types (Muller *et al.*, 1999). In addition, based on differences in community composition (Walker & Everett, 1991; Walker *et al.*, 1994) and pollen spectra, sites assigned to the PST vegetation type were split into two categories: Arctic Foothills type (ten sites) and Arctic Coastal Plain type (twenty-one sites).

We used discriminant analysis (DA) to test whether the five remaining tundra types (foothills PST, coastal PST, DST, LST and WGT) could be differentiated based on their pollen assemblages. DA (SPSS, 1999) creates a linear combination of variables, in this case pollen percentages, that maximizes the separation of samples assigned to different groups. The success of the analysis is assessed by how well the pollen samples are re-classified into their pre-determined vegetation groups (Prentice, 1980; Liu & Lam, 1985; Lynch, 1996). DA loadings were examined to determine which taxa were most important for distinguishing between different tundra types. The analysis was performed using the twenty-three taxa that occurred in at least fifteen of the seventy samples, as this combination of taxa provided better overall discrimination than other subsets of taxa that were considered during preliminary analyses.

To examine the correspondence between trends in the pollen data set and regional climatic gradients, we estimated several climate variables for each modern pollen site. Mean

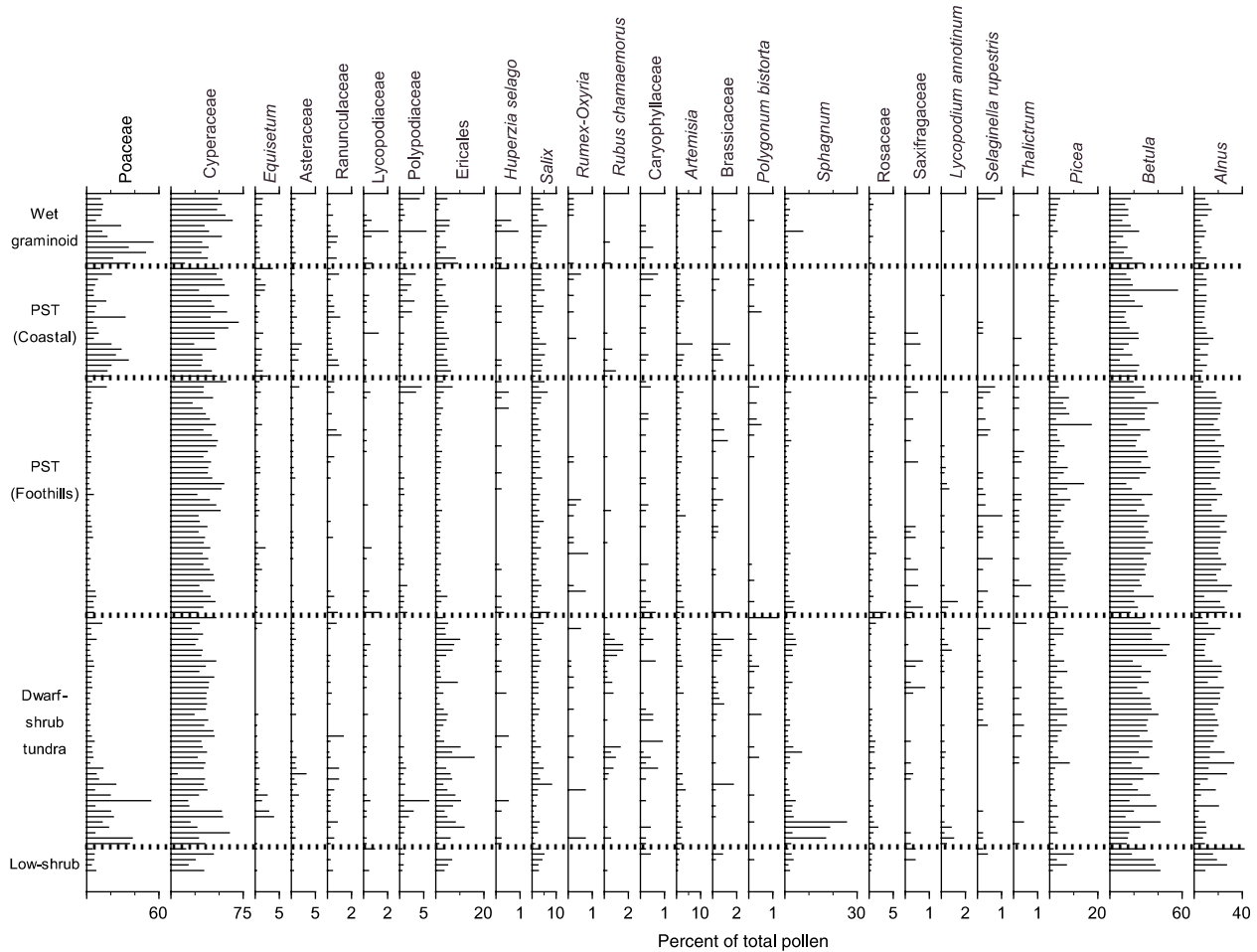
values of annual and monthly temperature and precipitation were obtained by interpolating within a  $0.5^\circ \times 0.5^\circ$  global climate data set (New *et al.*, 1999), with locally weighted lapse rates used to adjust for elevation during the interpolation (P. Bartlein, pers. comm.). DA scores for each site were compared with climate variables by Pearson product-moment correlation.

## RESULTS AND DISCUSSION

### Pollen percentages and vegetation patterns

#### *Mapped pollen percentages*

The variability of the major taxa in modern sediments generally reflects the regional-scale patterns of vegetation (Figs 2 & 3). Cyperaceae pollen percentages were high throughout the region, reflecting the importance of Cyperaceae species in all of the vegetation types of northern Alaska. In the Arctic Foothills, where Cyperaceae pollen percentages were generally 30–45%, *C. bigelowii* is important in PST and *Eriophorum vaginatum* is abundant in DST and LST communities (Walker *et al.*, 1994). However, Cyperaceae percentages were highest in Arctic Coastal Plain sites, reaching > 45% in the Icy Cape area and the eastern coastal plain between the Colville River and the Barter Island area. These high values reflect the dominance of WGT and especially coastal PST

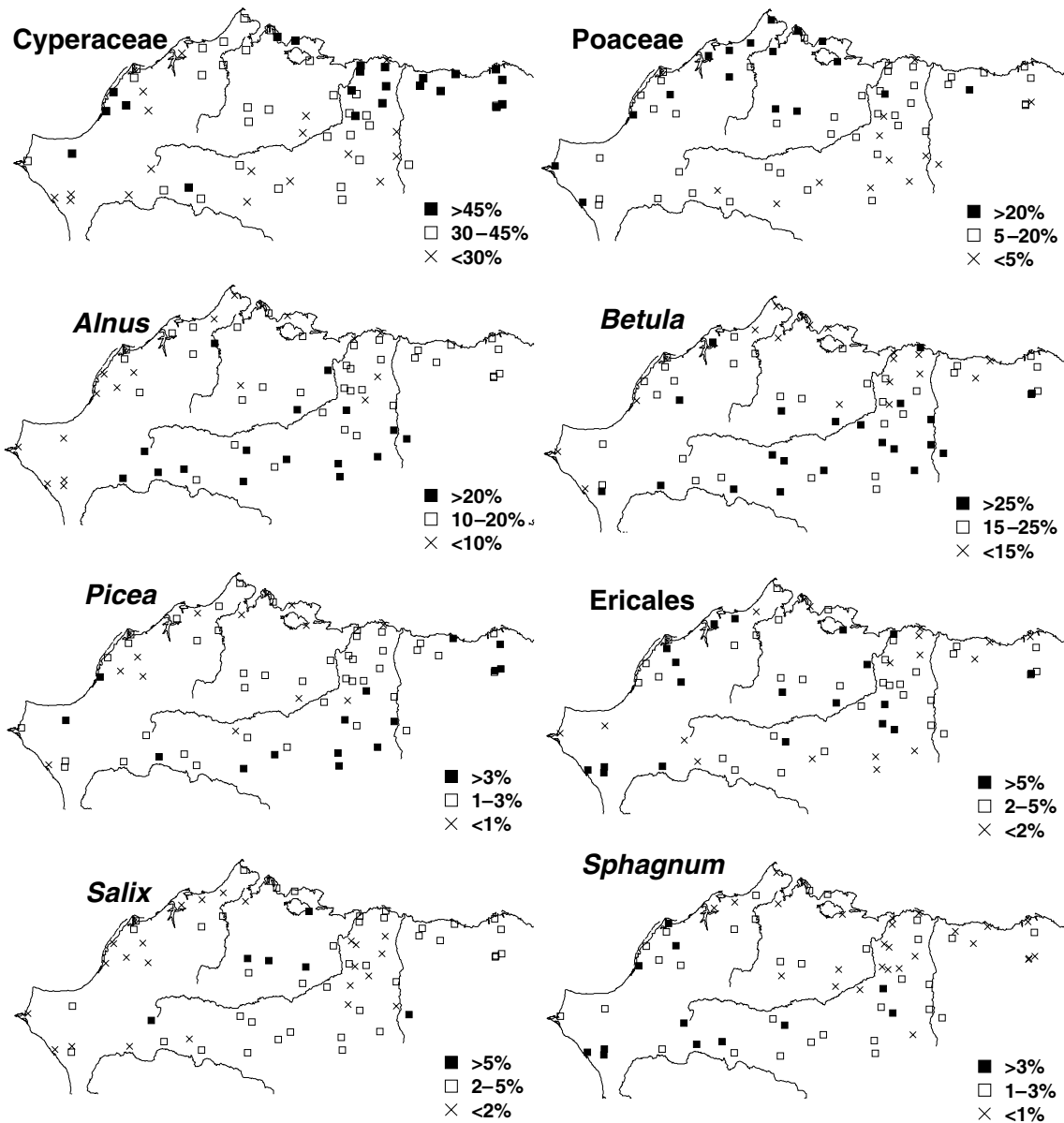


**Figure 2** Percentage diagram for modern pollen assemblages from northern Alaska. Within each vegetation type, sites are ordered from east to west. Taxa are ordered by their loadings for the first discriminant axis.

communities by *C. aquatilis* and *Eriophorum angustifolium* (Walker & Everett, 1991). Poaceae pollen percentages were also high on the Arctic Coastal Plain, particularly along the northwest coast from the Lisburne Peninsula to Point Barrow where they reach 20–50%. This pattern reflects the dominance of Poaceae species (e.g. *Dupontia Fischeri*, *Alopecurus alpinus*, and *Arctophila fulva*) in the coastal vegetation types. In contrast, *Alnus* and *Betula* pollen percentages were highest in the southern portion of the study area. *Betula nana* is largely restricted to the Arctic Foothills, where it is an important species in DST and LST (Viereck & Little, 1972; Walker *et al.*, 1994). This distribution generally corresponds to *Betula* pollen percentages >25%, although a few foothill sites had somewhat lower percentages and a few coastal sites have percentages >25%. *Alnus* species (*A. crispa* and *A. tenuifolia* Nutt.) are widespread in the boreal forest region, but north of the mountains *A. tenuifolia* does not occur and *A. crispa* is mainly restricted to thickets along rivers in the foothills, especially along the Colville River above Umiat (Viereck & Little, 1972). The high percentages of

*Alnus* pollen at sites in the Arctic Foothills (>20%) reflects the abundance of *A. crispa* in that area, but those lakes probably also receive *Alnus* pollen transported by wind from south of the Brooks Range.

Mapped patterns of pollen taxa with intermediate abundance (i.e. reaching 5–20%) are also related to vegetation. *Picea* percentages reached >3% only at sites near the mountains, indicating that pollen grains produced by *Picea glauca* (Moench) Voss and *P. mariana* (Mill.) Britt., Sterns & Pogg. in the boreal forest region south of the Brooks Range are not transported in relatively large numbers beyond the Arctic Foothills. Percentages of *Ericales* and *Salix* pollen were not consistently higher in either the foothills or the coastal plain. *Ericales* pollen percentages were highest (>5%) in the central part of the study area, along the northwest coast, and south of the Lisburne Peninsula, whereas *Salix* pollen percentages were relatively high (>2%) throughout the study area. These patterns are consistent with the nearly universal occurrence of these taxa in tundra communities in northern Alaska. *Ericaceae* and *Salix* species are common both in the Arctic Foothills (e.g. *Ledum*



**Figure 3** Maps of pollen percentage data for the main taxa.

*palustre* and *S. lanata*) and on the coastal plain (e.g. *Vaccinium vitis-idaea* and *S. reticulata* L.) (Hultén, 1968; Walker & Everett, 1991; Walker *et al.*, 1994). Percentages of *Sphagnum* spores were relatively high (>2%) in the southern and western portions of the study area, reflecting the prevalence of *Sphagnum* species in foothills tundra (particularly DST) and along the western coast of Alaska (Walker *et al.*, 1994; Brubaker *et al.*, 1998).

#### Discriminant analysis

In the discriminant analysis, 75.7% of samples were correctly classified into their assigned vegetation groups, including perfect classification of the LST sites (Table 2). DST had

the largest number of incorrectly assigned samples, with 4.6% of those sites classified as foothills PST, 18.2% classified as coastal PST, 4.6% classified as LST and 4.6% classified as WGT. Also problematic were the incorrect classifications of WGT sites as coastal PST (15.4%) and foothills PST as DST (14.3%).

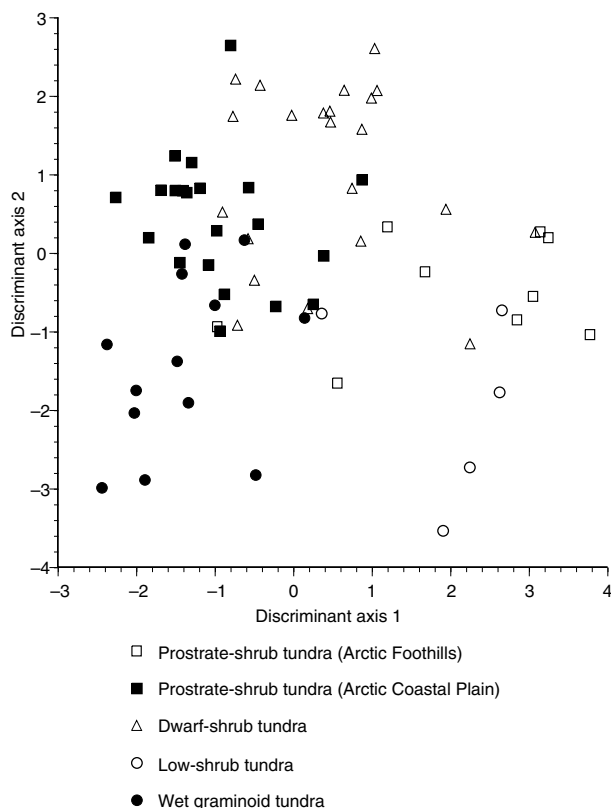
The primary trend in the mapped pollen percentage data, high Poaceae and Cyperaceae percentages along the coast and high *Alnus* and *Betula* percentages in the foothills, is also apparent in the discriminant analysis (Fig. 4). The first DA axis represents changes in pollen assemblages along the latitudinal gradient, as inland vegetation types (DST, foothills PST and LST) have positive axis 1 values and coastal



**Table 2** Classification results for discriminant analysis of modern pollen samples

| Actual group  | Predicted group |             |     |           |               |
|---------------|-----------------|-------------|-----|-----------|---------------|
|               | Foothills PST   | Coastal PST | DST | Low-shrub | Wet graminoid |
| Foothills PST | 6               | 1           | 1   | 0         | 1             |
| Coastal PST   | 0               | 16          | 3   | 0         | 2             |
| DST           | 1               | 4           | 15  | 1         | 1             |
| Low-shrub     | 0               | 0           | 0   | 5         | 0             |
| Wet graminoid | 0               | 2           | 0   | 0         | 11            |

PST, prostrate-shrub tundra; DST, dwarf-shrub tundra.

**Figure 4** Discriminant analysis axis 1 and 2 scores for modern pollen sites from northern Alaska.

vegetation types (coastal PST and WGT) have negative values. DA axis 1 loadings show that these same four taxa are largely responsible for the discrimination of sites along this gradient (Table 3). *Alnus* and *Betula* had the strongest positive loadings, and *Poaceae* and *Cyperaceae* had the strongest negative loadings. Several other taxa had strong positive DA axis 1 loadings (e.g. *Saxifragaceae*, *Lycopodium annotinum*, *Picea* and *Selaginella rupestris*), reflecting higher percentages in the foothills than on the coastal plain. In general, this pattern of percentages accurately depicts the greater abundance of these taxa in the vegetation of the foothills than on the coast. *Lycopodium annotinum* L. is common in DST, *Selaginella rupestris* f. *siberica* Milde. occurs in PST in the Arctic Foothills, and a greater number

**Table 3** Loadings for each taxon for discriminant analysis axes 1 and 2

| Taxon   | Axis 1 | Axis 2 |
|---|--------|--------|
| <i>Poaceae</i>  | -0.336 | -0.038 |
| <i>Cyperaceae</i>   | -0.311 | -0.027 |
| <i>Equisetum</i>  | -0.217 | 0.177  |
| <i>Asteraceae</i>   | -0.110 | 0.204  |
| <i>Ranunculaceae</i> (excl. <i>Thalictrum</i> )                           | -0.066 | 0.102  |
| <i>Huperzia selago</i>  | -0.051 | -0.130 |
| <i>Rubus chamaemorus</i>  | -0.009 | 0.224  |
| <i>Lycopodiaceae</i><br>(excl. <i>L. annotinum</i> and <i>H. selago</i> ) | -0.008 | -0.256 |
| <i>Rumex-Oxyria</i>   | 0.004  | 0.074  |
| <i>Brassicaceae</i>   | 0.006  | 0.000  |
| <i>Polypodiaceae</i>  | 0.013  | -0.031 |
| <i>Ericales</i>   | 0.021  | 0.278  |
| <i>Salix</i>  | 0.061  | -0.157 |
| <i>Artemisia</i>  | 0.080  | 0.236  |
| <i>Caryophyllaceae</i>  | 0.131  | 0.068  |
| <i>Sphagnum</i>   | 0.143  | 0.203  |
| <i>Rosaceae</i> (excl. <i>R. chamaemorus</i> )                            | 0.152  | 0.195  |
| <i>Selaginella rupestris</i>  | 0.257  | -0.150 |
| <i>Lycopodium annotinum</i>   | 0.314  | 0.170  |
| <i>Picea</i>  | 0.356  | -0.217 |
| <i>Saxifragaceae</i>  | 0.361  | -0.069 |
| <i>Betula</i>   | 0.391  | 0.140  |
| <i>Alnus</i>  | 0.491  | -0.164 |

of *Saxifragaceae* species occur in the foothills than on the coast (Hultén, 1968; Walker *et al.*, 1994). However, as is evident in the mapped percentages, the association of *Picea* with the Arctic Foothills reflects the proximity of that region to the boreal forest south of the Brooks Range.

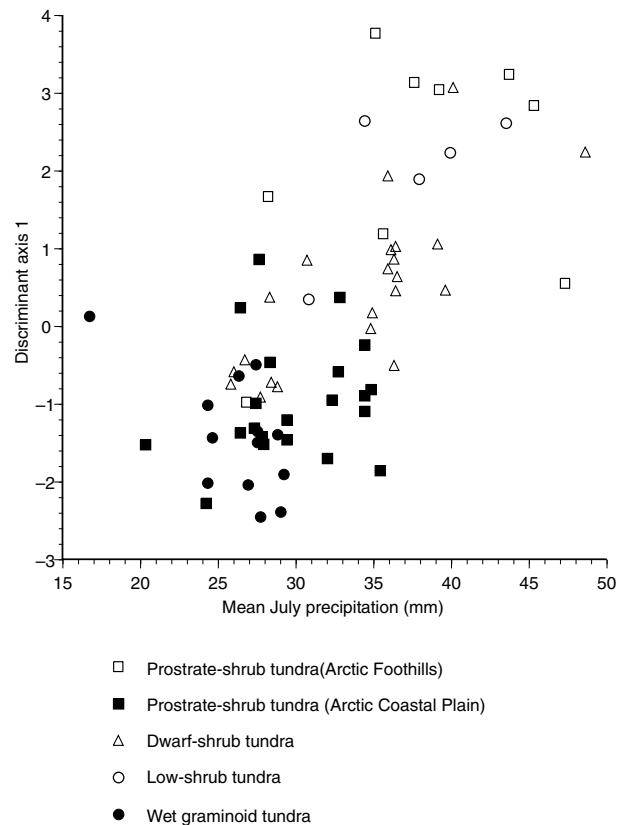
The tundra types within the foothills and coastal tundra zones are separated along DA axis 2. The coastal types, PST and WGT, in general had positive and negative values along axis 2, respectively. For foothills types, DST sites had positive axis 2 values, whereas values for PST and LST sites were negative. This pattern of discrimination of pollen assemblages along the second axis suggests that the pollen data reflect not only the variations in tundra community composition associated with the north-south climatic gradient, but also vegetational variability within the Arctic Foothills and Arctic Coastal Plain. Because the lakes were assigned to tundra types based on the vegetation within

**Table 4** Correlations between discriminant analysis axes 1 and 2 and climatic variables

|                       | Axis 1 | Axis 2 |
|-----------------------|--------|--------|
| Annual temperature    | 0.34   | -0.21  |
| Annual precipitation  | 0.53   | -0.13  |
| January temperature   | -0.28  | -0.27  |
| January precipitation | 0.15   | -0.25  |
| April temperature     | 0.32   | 0.02   |
| April precipitation   | 0.28   | -0.21  |
| July temperature      | 0.23   | -0.03  |
| July precipitation    | 0.71   | 0.08   |
| October temperature   | 0.09   | -0.28  |
| October precipitation | -0.26  | -0.29  |

2 km, this secondary trend presumably represents the small-scale heterogeneity within the broader foothills and coastal tundra zones that arises because of edaphic variability (e.g. Walker *et al.*, 1994, 1995). The loadings for individual taxa support this interpretation. Taxa with strong positive DA axis 2 loadings include Ericales, *Artemisia*, and *Rubus chamaemorus*, whereas taxa with strong negative loadings include Lycopodiaceae and *Picea*. These loadings represent higher percentages of *Picea* for foothills PST and LST than for DST. Likewise, there are higher percentages of *Artemisia* for coastal PST than for WGT, and higher percentages of Lycopodiaceae for WGT than for coastal PST. The ability to distinguish between DST and foothills PST sites by their Ericales percentages is consistent with the landscape-scale distribution of Ericaceae species in the Arctic Foothills. Although some members of this family occur on the coarse-textured deposits where PST is prevalent (e.g. *Arctostaphylos rubra* and *Rhododendron lapponicum* (L.) Wahlenb.), Ericaceae species are much more abundant on the fine-textured soils dominated by DST (e.g. *Ledum palustre*, *Vaccinium uliginosum* and *V. vitis-idaea*) (Walker *et al.*, 1994). *Rubus chamaemorus* L. has an even stronger edaphic preference, as it commonly occurs in mesic DST, but is absent from PST-dominated sites (Walker *et al.*, 1994). The association of Lycopodiaceae with WGT may be spurious, as the strong negative DA axis loading appears to result from a relatively high percentage value at a single site. However, the relatively high percentages of *Artemisia* pollen in coastal PST confirms that DA axis 2 represents substrate-controlled tundra patterns, as *Artemisia borealis* Pallas occurs on relatively dry sites within the Arctic Coastal Plain (Walker & Everett, 1991).

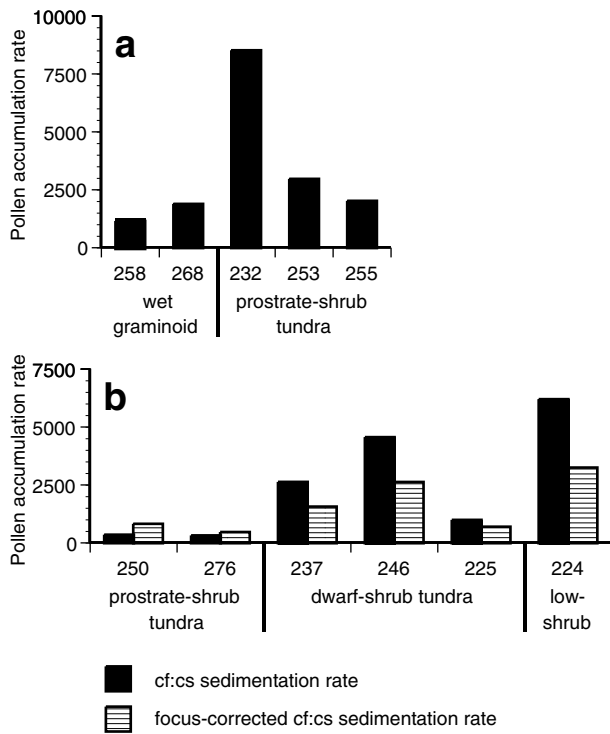
Comparison of DA values and climate variables helps to confirm our understanding of how the pollen data reflect the patterns of vegetation related to climatic forcing and edaphic controls (Table 4). DA axis 1 values were most strongly correlated to July precipitation ( $r = 0.71$ ) (Fig. 5). Sites with positive axis 1 values (mostly DST, foothills PST, and LST sites) generally have high mean July precipitation (30–50 mm), whereas sites with negative axis 1 values (mostly coastal PST and WGT sites) have low mean July precipitation (15–35 mm). In contrast, axis 2 values were

**Figure 5** Mean July precipitation versus discriminant analysis axis 1 values for modern pollen sites from northern Alaska.

not related to any of the climatic variables (Table 4). The absence of a relationship to climate implies that the secondary trend in the pollen data may reflect the vegetational response to landscape-scale edaphic variations.

#### Pollen accumulation rates

Uncorrected PARs were highest (*c.* 4500–8500 grains  $\text{cm}^{-2} \text{year}^{-1}$ ) at one of the coastal plain PST sites (232), the lone LST site (224), and one of the DST sites (246). WGT sites and the remaining DST and Arctic Coastal Plain PST sites had intermediate values (*c.* 1000–3000 grains  $\text{cm}^{-2} \text{year}^{-1}$ ), and the two foothills PST sites had the lowest values (*c.* 300 grains  $\text{cm}^{-2} \text{year}^{-1}$ ). When PARs were re-calculated for foothills sites using the focus-corrected sedimentation rates, the values were 50–140% higher for the PST sites, but 30–50% lower for the DST and LST sites. However, regardless of whether the correction was applied, the main trends in the PAR data are similar, including unexpectedly high PARs for coastal sites relative to those for foothills sites. Based on the premise that PARs are a metric of vegetation cover (e.g. Cwynar, 1982), we hypothesized that modern PARs would be lower for sites on the coastal plain than in the foothills. Tundra in the foothills generally has a closed canopy with 80–100% vegetation cover, whereas on the coastal plain the canopy is interrupted by



**Figure 6** Modern pollen accumulation rates (PARs) for lakes on the Arctic Coastal Plain (a) and in the Arctic Foothills (b). Focus-corrected PARs are shown for foothill sites.

patches of bare soil, and thus the overall vegetation cover is only 50–80% (Walker, 1999). These results suggest that PARs are not simply a reflection of overall vegetation cover.

Regional differences in the way that lakes form and collect sediment may obscure variation in PARs related to patterns of vegetation cover. Lakes on the Arctic Coastal Plain are nearly all thermokarst lakes, formed when surface permafrost thaws and creates a depression (Carson & Hussey, 1962). Most thermokarst lakes are less than 6 m deep (Black & Barksdale, 1949), so bottom sediments may be mixed by windstorms. More importantly, the shores of these lakes are unstable, and continued summer thawing can cause the banks to collapse, thus depositing large amounts of terrestrial sediment into the basin (e.g. Murton, 1996). Obviously, these depositional processes would affect the accumulation of pollen in the sediment. In contrast, lakes in the Arctic Foothills tend to occur in stable basins, often in glaciated terrain where depressions are created by moraines or the thawing of stagnant ice blocks (Hamilton & Porter, 1975). Sediment input to these lakes is likely to be less erratic than in thermokarst lakes, and thus PARs from the Arctic Foothill sites may be more reliable than from coastal plain sites. However,  $^{210}\text{Pb}$  profiles for these lakes indicate that the near-surface sediments are not severely disrupted, as the mixed depth is typically less than 2 cm and never greater than 4 cm (Brubaker & Engstrom, unpubl. data).

In contrast to the confounding relationship between PARs and tundra patterns at the regional scale, the variability of

PARs within the coastal plain and foothills regions is consistent with landscape-scale patterns of vegetation cover. For the coastal plain sites, we would expect PST sites to have higher PARs than WGT sites. Vegetation cover is relatively low in WGT (Walker & Everett, 1991), particularly in areas where thermokarst lakes predominate. In PST, vegetation cover is higher and there are fewer large areas of standing water (Walker & Everett, 1991), and thus there is more vegetation per unit area to contribute pollen to lakes. Similarly, the differences in PARs among the Arctic Foothills tundra types are consistent with patterns of vegetation cover. The high modern PAR value for lake 224 is reasonable as shrub communities have the highest primary production and vegetation cover of the inland tundra types (Shaver *et al.*, 1996; Walker, 1999; Williams & Rastetter, 1999). Furthermore, DST has more continuous vegetation cover than PST (Walker *et al.*, 1995), so higher PARs for DST than PST are consistent with their interpretation as a metric of plant cover.

The differences in PARs among the Arctic Foothills vegetation types help us better understand the patterns of *Alnus* and *Picea* percentages. *Alnus* percentages were generally higher at foothills PST sites than at DST sites, despite the fact that *A. crispa* is no more common in PST than DST (Walker *et al.*, 1994; Muller *et al.*, 1999). It is likely that some proportion of the *Alnus* pollen in PST and DST lakes arrives via long-distance transport from areas of shrub tundra where *A. crispa* is abundant, or from *A. crispa* and *A. tenuifolia* in the boreal forest of interior Alaska. Long-distance transport is obviously the case for *Picea* pollen, as *Picea glauca* and *P. mariana* reach their range limit in the southern foothills of the Brooks Range (Hultén, 1968). However, because PARs were higher in DST than in PST, presumably because of the higher vegetation cover, the extra-local *Alnus* and *Picea* pollen rain was diluted by locally produced pollen, resulting in lower percentages of *Alnus* and *Picea* in DST samples.

## IMPLICATIONS

Modern pollen assemblages from northern Alaska clearly reflect the north–south variation in tundra vegetation that arises from the influence of the regional climatic gradient. Along the coast where climate is cold and dry, the vegetation is dominated by graminoid species and modern pollen assemblages are characterized by higher percentages of Cyperaceae and Poaceae pollen. In contrast, warmer, wetter inland sites dominated by shrubs are characterized by high percentages of *Betula* and *Alnus* pollen. The strength of this relationship is illustrated by the successful multivariate differentiation of coastal and foothill sites in the discriminant analysis, and by the correlations between the main trend in the pollen data (DA axis 1) and the climatic variables (especially mean July precipitation). The correspondence between modern pollen data and tundra vegetation at this large spatial scale has been documented by previous studies (e.g. Ritchie, 1974; Ritchie *et al.*, 1987; Anderson *et al.*, 1991), including the research in northern Alaska that

precedes this study (Anderson & Brubaker, 1986; Short *et al.*, 1986). Knowledge of this regional-scale relationship between climate, vegetation and pollen spectra has proven useful for interpreting fossil pollen records. For example, the interpretation of increased *Betula* and *Alnus* percentages in the early to middle Holocene as the regional expansion of these taxa in response to warmer and wetter conditions (e.g. Anderson *et al.*, 1994; Edwards *et al.*, 2001) is consistent with the trends in the modern pollen, vegetation and climate data.

By increasing the density of modern pollen sites, comparing the pollen data with detailed vegetation data, and measuring modern PARs, we have also shown that pollen spectra from this tundra region reflect small-scale changes in vegetation. Although we did not directly measure substrate properties at the study sites, we know that landscape-scale vegetational heterogeneity in this region results primarily from substrate variability (e.g. Walker *et al.*, 1994; Walker, 2000). Thus, it is likely that the pollen data reflect changes in tundra related to edaphic controls. These small-scale vegetational patterns have a weaker influence on the variations in pollen assemblages than does the main north–south gradient, as evidenced by the secondary importance of this trend in the discriminant analysis. However, the consistency between patterns of pollen abundance and plant community composition, including the associations of Ericales and *R. chamaemorus* pollen with DST and *Artemisia* pollen with coastal PST, indicates that this variability in the pollen data reflects real landscape-scale variations in tundra. Moreover, because this pattern demonstrates that these taxa are locally dispersed, it suggests that their abundance in fossil pollen assemblages may be interpreted in terms of landscape-scale vegetational patterns. Thus, with carefully selected study sites and improved knowledge of how small-scale changes in tundra vegetation are reflected by the patterns of key taxa, it may be possible to reconstruct the heterogeneity of past tundra, including the ‘troublesome’ full-glacial vegetation of Beringia (Anderson *et al.*, 1994).

Variations in PARs may also reflect subregional changes in tundra vegetation, but given the small number of study sites and our concern that coastal plain and foothills lakes may not accumulate sediment and pollen in the same way, our understanding of these patterns is limited. Nonetheless, the similarity between the PARs observed in these near-surface sediments (300–8500 grains cm<sup>-2</sup> year<sup>-1</sup>) and the PARs in fossil pollen records from arctic and subarctic sites in northern Siberia, Alaska and northern Yukon is notable. For the Beringian region, pre-Holocene PARs are typically <1000 grains cm<sup>-2</sup> year<sup>-1</sup>, whereas Holocene PARs range from c. 500 to 25,000 grains cm<sup>-2</sup> year<sup>-1</sup> (Cwynar, 1982; Anderson, 1985, 1988; Edwards *et al.*, 1985; Anderson *et al.*, 1988; Hu *et al.*, 1993, 1995; Lozhkin *et al.*, 1993; Oswald *et al.*, 1999). The higher PARs in the Holocene have been interpreted as an increase in vegetation cover (e.g. Cwynar, 1982), although others dispute the link between fossil PARs and vegetation (e.g. Guthrie, 1985, 1990). Various studies have demonstrated that PARs are influenced by factors besides vegetation, including input of allochthonous

sediment, production of autochthonous sediment, sediment decomposition and sediment focusing (Davis *et al.*, 1971; Davis & Brubaker, 1973; Lehman, 1975; Bonny, 1978; Davis & Ford, 1982). However, several aspects of this data set suggest a link between vegetation and PARs, including the consistency of PARs within a vegetation type, the reasonable variability of PARs between vegetation types, the coherent geographical pattern of PARs and extra-local pollen percentages, and the similar ranges of modern and fossil PARs. The increase in PARs from 100 to 1000 grains cm<sup>-2</sup> year<sup>-1</sup> appears to reflect higher vegetation cover, suggesting that variations in fossil PARs of this order of magnitude may indicate similar changes in past vegetation.

Overall, this study indicates that palynology is more applicable to questions about the heterogeneity of past arctic ecosystems than previously assumed (e.g. Colinvaux, 1967; Birks & Birks, 2000). The modern pollen assemblages reflect the north–south variations in vegetation controlled by regional climate, as well as the landscape-scale vegetational variability related to edaphic heterogeneity. However, the landscape-scale relationship between pollen and tundra vegetation requires additional study. Future work should assess this relationship in other regions and with an even finer network of modern pollen sites so that we can define the smallest spatial scale at which pollen data reflect tundra vegetation.

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## BIOSKETCHES

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