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Holocene vegetational history of the central Arctic Foothills, northern Alaska: pollen representation of tundra and edaphic controls on the response of tundra to climate change

William Wyatt Oswald

A dissertation submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

University of Washington
2002

Program Authorized to Offer Degree: College of Forest Resources

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Abstract

Holocene vegetational history of the central Arctic Foothills, northern Alaska: pollen representation of tundra and edaphic controls on the response of tundra to climate change

William Wyatt Oswald

Chair of the Supervisory Committee:

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As arctic tundra responds to climate change, does its response vary spatially because of small-scale edaphic heterogeneity? This research addresses this question by reconstructing the past vegetational response to climate change of ecosystems on adjacent, but contrasting, glaciated surfaces in the central Arctic Foothills of northern Alaska. Vegetation history is inferred from pollen records from lakes on the Sagavanirktok surface (glaciated >125,000 BP), which has smooth topography and fine-textured soils, and the Itkillik II surface (glaciated 24,000 to 11,500 BP), which has irregular topography and coarse-textured soils. Modern pollen-vegetation relationships are examined using regional- and landscape-scale data sets. These studies (1) improve our understanding of how pollen represents tundra vegetation, (2) refine multivariate methods for comparing entire pollen assemblages, and (3) explore the ability of pollen data to distinguish between the dwarf-shrub tundra (DST) and prostrate-shrub tundra (PST) communities that dominate the Sagavanirktok and Itkillik II surfaces, respectively. Consistent with the tundra community composition of DST and PST, Sagavanirktok samples had relatively high percentages of *Rubus chamaemorus* and Ericales, and Itkillik II samples had relatively high percentages of *Equisetum* and *Thalictrum*. The findings of these pollen-vegetation calibration studies were then applied to Holocene records from Upper Capsule Lake (Sagavanirktok surface) and Red Green Lake (Itkillik II surface). During the early Holocene (11,300 to 10,000 cal BP) the vegetation of the Sagavanirktok surface resembled modern PST. It is likely that as effective moisture increased between 10,000 and 7000 cal BP, soil moisture increased on the Sagavanirktok surface, leading to higher vegetation cover, permafrost aggradation, increased soil acidity and anoxia, and slower decomposition. By 7000 cal BP Sagavanirktok vegetation was similar to modern DST. In contrast, the vegetation of the Itkillik II surface did not experience major vegetational changes between the early and middle Holocene. Because their coarse texture results in inherently low water-holding capacity, Itkillik II soils likely support relatively xeric tundra like PST regardless of climate. The critical role of substrate in the Holocene vegetational history of the central Arctic Foothills suggests that edaphic variability may impart strong spatial heterogeneity on the response of tundra ecosystems to future climate change.

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Acknowledgements

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CHAPTER 1: Overview

INTRODUCTION

Arctic tundra is spatially heterogeneous, with variations in ecosystem processes and plant community composition occurring at many spatial scales (e.g., Walker 2000). At the scale of the entire circumarctic region, the primary variations in vegetation result from the latitudinal climatic gradient. With increasing latitude comes shorter and cooler growing seasons, resulting in a transition from relatively productive, diverse tundra near treeline to barren, low-diversity polar deserts in the coldest parts of the tundra region (e.g., Young 1971; Alexandrova 1980; Yurtsev 1994). An important component of this vegetational gradient is the decreasing abundance and height of woody plants from south to north. From treeline northward, there is a gradual transition in plant stature from low shrubs, to dwarf shrubs, to prostrate shrubs, and finally to herbaceous tundra in which woody plants are absent (e.g., Edlund and Alt 1989). Along the climatic gradient there is also a major change in soils, with high amounts of organic carbon near treeline and lower carbon storage in the far north (Walker 2000).

Tundra ecosystems also vary at smaller spatial scales, usually in response to edaphic heterogeneity. Variations in geomorphology, soil pH, or soil texture within a latitudinal climatic zone can strongly influence ecosystem processes and plant community membership, especially via effects on soil moisture (Walker et al. 1994; Muller et al. 1999; Walker 2000). For example, in the Queen Elizabeth Islands in the Canadian Archipelago, alkaline limestone and dolomite deposits feature sparse tundra with *Dryas integrifolia*, *Salix arctica*, and *Saxifraga oppositifolia*, whereas acidic substrates are dominated by *Luzula confusa* (Edlund and Alt 1989). Similarly, the community composition of tundra on western Spitsbergen in Svalbard is also strongly controlled by substrate pH (Elvebakk 1982).

The effects of both climate and substrate are evident in the vegetational patterns of the tundra region of northern Alaska (Muller et al. 1999; Walker 1999, 2000). Climate appears responsible for a major north-south vegetational gradient between the Arctic Ocean and the Brooks Range (Fig. 1.1). In the northern portion of this region, along the Arctic Coastal Plain, cold, windy conditions and a thin snowpack result in shallow permafrost thaw, poor soil drainage, and thus large waterlogged areas dominated by wet graminoid tundra (WGT). South of the Arctic Coastal Plain, in the Arctic Foothills, annual precipitation and summer temperatures are higher than along the coast, and moist dwarf-shrub tussock-graminoid tundra (dwarf-shrub tundra; DST) is the dominant vegetation. However, at landscape-scales (1-100 km), there are ecosystem variations within the coastal plain and foothills vegetational zones, mainly in response to edaphic variability. For example, in coastal areas where slightly higher topography affords drier soils, the cold climate fosters chronic cryoturbation (Walker and Everett 1991; Bockheim et al. 1998; Walker et al. 1998), resulting in dominance by moist graminoid prostrate-shrub tundra (prostrate-shrub tundra; PST). Similarly, the DST vegetation of the Arctic Foothills, which is prevalent in areas of fine-textured soils that were unglaciated during the last part of the Pleistocene, is interrupted by PST in areas where late Pleistocene valley glaciers left behind coarse-textured deposits (Walker et al. 1994, 1995) (Fig. 1.2).

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

This dissertation examines the effect of substrate on tundra ecosystem response to climate change using a paleoecological approach. By using pollen records to reconstruct the vegetational history of two sites that differ in terms of landform and soil characteristics, it is possible to see how substrate influenced the ecological changes brought about by past climate change. The study was conducted in the central Arctic Foothills, which is an ideal setting for this type of research owing to its Pleistocene glacial history. To test the role of substrate, sediment cores were collected from lakes on adjacent, but contrasting glaciated surfaces, one with flat topography and fine-textured soils, the other with greater topographic relief and coarse-textured soils. The proximity of the sites (only 11 km) controls for geographic variation in climate, and thus ensures that they experienced the same climatic changes during the Holocene (i.e., the past 10,000 ^{14}C years or 11,500 calibrated ^{14}C years). Specifically, the pollen records from Upper Capsule Lake (Sagavanirktok surface) and Red Green Lake (Itkillik II surface) are used to reconstruct the vegetational response at these sites to the onset of cool, moist climatic conditions between the early and middle Holocene.

However, before undertaking the reconstruction of vegetational history at these sites, it is necessary to gain an improved understanding of how pollen represents tundra vegetation, particularly the landscape-scale vegetational patterns that arise due to edaphic variability. The ability of pollen data to reflect variation in tundra is a critical issue in arctic paleoecology, and thus was a major emphasis in this research. The need for better pollen-vegetation calibration arises because Quaternary pollen analysis in the Arctic is hindered by a number of problems that pose fewer challenges at lower latitudes. First, pollen assemblages from arctic tundra, especially those from glacial intervals, are dominated by taxa that are difficult to interpret. For example, full- and late-glacial pollen assemblages from Alaska have high percentages of Cyperaceae, Poaceae, *Artemisia*, and *Salix* pollen (e.g., Anderson and Brubaker 1994; Anderson et al. 1994; Oswald et al. 1999). Unfortunately, the pollen of individual species cannot be distinguished within these types, and thus these broad taxa potentially represent a wide range of ecological and environmental conditions. A number of approaches have been employed in attempts to overcome this problem, including calculating pollen accumulation rates (PARs) to approximate overall vegetation cover, comparing fossil and modern pollen assemblages using dissimilarity metrics, and basing interpretations on rare, but ecologically specific "indicator taxa" (Cwynar 1982; Anderson et al. 1994). However, each of these approaches has limitations. PARs are influenced by many factors besides vegetation cover (e.g., Davis and Ford 1982), and their application to questions about past arctic tundra has been strongly questioned (e.g., Guthrie 1985, 1990). The comparison of whole assemblages, or "modern analog" approach, may fail when past plant communities, and thus fossil pollen assemblages, have no equivalent vegetation under modern conditions (e.g., Anderson et al. 1994). The use of indicator taxa raises questions about the sample size required to reliably encounter rare types, as well as the true ecological specificity of these species (e.g., Cwynar 1982; Anderson et al. 1994). Second, because arctic pollen assemblages include both wind- and insect-dispersed pollen and spore types, species (or genera or families) may be greatly over- or under-represented. These factors have resulted in unanswered questions about past tundra community composition, as well as uncertainty about the spatial resolution of pollen data from the Arctic. In general, palynology is considered a "blunt instrument" for reconstructing arctic tundra, particularly for understanding small-scale vegetational patterns (Colinvaux 1967; Ritchie 1995; Birks and Birks 2000).

CALIBRATION STUDIES

The following sections briefly describe component studies of this dissertation that were conducted to improve our understanding of pollen-vegetation relationships.

Pollen representation of regional and subregional patterns of tundra

Previous studies of modern pollen assemblages from northern Alaska have shown that pollen data reflected the main north-south vegetational gradient. Climatically cold and dry coastal sites, dominated by graminoid species, are characterized by high percentages of Cyperaceae and Poaceae pollen, whereas warmer, wetter inland sites dominated by shrubs are characterized by high percentages of *Betula* and *Alnus* pollen (Anderson and Brubaker 1986; Short et al. 1986). The study presented in Chapter 2 improves upon the previous work in two ways. First, the density and geographic coverage of modern pollen sites was increased, thus enabling me to better define the region-scale patterns, and to explore variability within the major tundra zones. In addition, a recently created land-cover map of northern Alaska (Muller et al. 1999) was used 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, it allowed me 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 smaller-scale patterns of plant communities. I used discriminant analysis to define trends in the pollen data, and compared those trends with climate and vegetation data to show how the pollen data represent vegetational patterns associated with both climatic forcing and edaphic controls. Second, I analyzed pollen in surface cores dated with ^{210}Pb to estimate modern PARs for eleven sites representing the five tundra types.

These analyses clearly demonstrate that modern pollen assemblages reflect the variations in tundra associated with the latitudinal climatic gradient (Fig. 1.1). Arctic Foothills tundra types, DST, inland PST, and low-shrub tundra (LST), can be distinguished from the coastal vegetation types, coastal PST and WGT, based on differences in the percentages of major taxa (*Betula*, *Alnus*, Poaceae, and Cyperaceae) as well as minor taxa (e.g., *Lycopodium annotinum*). Moreover, these analyses suggest that landscape-scale variations in vegetation related to edaphic heterogeneity (Fig. 1.2) are recorded by pollen data. For example, in the Arctic Foothills, DST sites can be differentiated from PST sites by higher percentages of *Rubus chamaemorus* and Ericales pollen, as well as by higher total PARs. These differences correctly reflect the higher overall vegetation cover and greater abundance of *Rubus chamaemorus* and Ericaceae species in DST than in PST. These findings show that pollen percentage data can be used to examine the subregional heterogeneity of past tundra, and also give a strong indication that PARs provide information about past vegetation cover in tundra.

Pollen representation of landscape-scale patterns of tundra

To further refine our understanding of how pollen data reflect landscape-scale tundra vegetational patterns, I conducted another calibration study focused on even smaller-scale variations in plant communities. Chapter 3 presents analyses of modern pollen data from 56 small lakes in the central Arctic Foothills. The lakes are located on two adjacent glaciated surfaces that have different landforms, soil textures, and tundra plant communities. The Sagavanirktok surface (glaciated >125,000 years BP) has smooth topography, fine-textured soils, and DST vegetation, whereas the Itkillik II surface (glaciated 24,000-11,500 years BP) has uneven topography, coarse-textured soils, and PST vegetation (Figs. 1.3 and 1.4). I compared the pollen assemblages to the community composition of their respective surfaces, and used two multivariate approaches, discriminant analysis and dissimilarity metrics (squared chord distance and Canberra metric), to assess the ability of pollen data to distinguish between the Sagavanirktok and Itkillik II surfaces. Receiver operating characteristic (ROC) analysis, a method borrowed from health science (e.g., Metz 1978), 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.

Similar to the study in Chapter 2, the modern pollen data in this study reflect small-scale differences in tundra communities between the Sagavanirktok and Itkillik II surfaces. Sagavanirktok surface assemblages had relatively high percentages of *Rubus chamaemorus*, *Sphagnum*, Ericales, Poaceae, Brassicaceae, *Lycopodium annotinum*, Saxifragaceae, Asteraceae, Lycopodiaceae, *Betula*, and *Bistorta plumosa*. Itkillik II surface assemblages had relatively high percentages of *Alnus*, *Equisetum*, *Picea*, Polypodiaceae, *Thalictrum*, and Rosaceae. These differences made it possible to differentiate quantitatively between the two landscapes using discriminant analysis and the Canberra metric. The ROC analysis showed that squared chord distance, the dissimilarity metric most commonly used in modern analog analysis of pollen data, was less effective than the Canberra metric for distinguishing between the two surfaces. The relatively high percentages of *Alnus* and *Picea* pollen in Itkillik II samples are notable, because *Alnus* and *Picea* species are not present in the study area, and thus their pollen rain should be homogeneous across the region. I attribute this pattern to higher pollen productivity for the Sagavanirktok surface, which is consistent with the finding in Chapter 2 that PARs were higher for DST than PST. Higher pollen productivity would dilute the extra-local pollen rain, thus resulting in lower percentages of *Alnus* and *Picea* in Sagavanirktok samples. This study provides additional evidence that palynology can be used to explore questions regarding the landscape-scale heterogeneity of past tundra vegetation.

SUPPLEMENTARY STUDIES

In a related study (Appendix 1), the pollen assemblages from the central Arctic Foothills calibration study (Chapter 3) were compared to vegetation data from the Muller et al. (1999) land-cover map (Figs. 1.1 and 1.2) to examine the spatial scale of the vegetation represented by the pollen data. I used ArcView 3.2 software (ESRI 1996) to determine the percent cover of several tundra types within concentric circular plots extending to 5000 m from the center of each lake. I then identified the plot radius at which different pollen and spore taxa were best correlated to the vegetation data, which is an approximation of the "relevant pollen source area" (Sugita 1994) for these lakes. In most cases the best pollen-vegetation correlation occurred at plot radii <2 km, which is consistent with the finding in Chapter 3 that pollen data reflect landscape-scale patterns of tundra vegetation. However, I also observed that the size and arrangement of patches of different tundra types were largely responsible for the patterns of correlation, which would suggest that this was not an entirely appropriate vegetation data set for assessing the spatial scale recorded by the pollen data.

In another related study (Appendix 2), a series of ^{14}C dating experiments were conducted to improve our understanding of the chronology of lake sediments. This topic is crucial because to reconstruct the response of ecosystems to past climate change, the timing of stratigraphic changes in pollen records must be accurately defined. Late Quaternary lake sediments normally are dated with ^{14}C analysis, but in the northern high-latitudes the determination of sediment age may be complicated by the paucity of datable organic material, as well as the re-deposition of old organic material from terrestrial soils into lake sediments (e.g., Nelson et al. 1988). Accelerator mass spectrometry (AMS) ^{14}C dating helps to overcome those problems, as AMS allows the analysis of very small organic materials. However, in many AMS-dated records there are problems with age reversals: dates that are anomalously old or young compared with the age-depth relationship for the majority of dates from a core. To test the hypotheses that age reversals result from either the size or type of material dated, I conducted a series of experiments using plant macrofossils from sediment cores from Alaska and Siberia. In the size experiments, I obtained ^{14}C dates for several different-sized pieces of a single woody macrofossil, and found that ages were reliable for samples as small as 0.05 mg C. In the type experiments, I obtained ^{14}C dates for several types of plant material (e.g., mosses, wood, seeds) from a single depth in the core. In those experiments, wood was older than the other materials, in some cases by more than 500 years. This result is alarming because woody macrofossils are often preferentially selected for ^{14}C dating, and because many paleoecological studies are striving to understand century-scale ecosystem changes, which requires more secure chronology than this type of error would allow. I attribute the age differences between woody and non-woody macrofossils to the slower decomposition and longer terrestrial residence time of woody materials in northern environments (e.g., Hobbie 1996), and perhaps to the "inbuilt age" effect that may occur in ecosystems with long-lived plants (e.g., Gavin 2001). These experiments helped me understand several age reversals in the Red Green and Upper Capsule records, and provided justification for the removal of those dates from the age-depth models (Chapter 4).

VEGETATION HISTORY

The pollen-vegetation calibration studies (Chapters 1 and 2) provide the basis for a detailed interpretation of the Holocene vegetational history of Sagavanirktok and Itkillik II glaciated surfaces in the central Arctic Foothills (Chapter 4). In the Upper Capsule pollen record, early Holocene (11,300-10,000 cal years BP) assemblages had relatively high percentages of taxa indicative of modern PST, including *Equisetum*, Polypodiaceae, *Thalictrum*, and Rosaceae. Canberra metric distance (CMD) comparisons between the fossil and modern assemblages also suggest similarity to the modern vegetation of the Itkillik II surface (CMD <13). I interpret this vegetation as relatively dry tundra dominated by Cyperaceae species and prostrate shrubs (*Salix* and Ericaceae), not unlike modern PST. Between 10,000 and 7000 cal years BP, the vegetation of the Sagavanirktok surface underwent a transition. Pollen assemblages in this interval of the Upper Capsule record featured both PST and DST indicator taxa, and comparison with the modern pollen assemblages suggests that the vegetation was not analogous to either PST or DST (CMD >13). After 7000 cal years BP, pollen and spore types indicative of PST were virtually absent, *Betula* PARs increased, and DST indicator taxa were prevalent (e.g., *Lycopodium annotinum*, *Rubus chamaemorus*, and *Polygonum bistorta*). These changes suggest greater vegetation cover, increased soil moisture, and plant community composition similar to the DST that occurs at Upper Capsule Lake at present.

In contrast to the major vegetational changes in the Upper Capsule record during the early and middle Holocene, there were only minor changes in the Red Green record. The Red Green sediment core begins around 8500 cal years BP, and for the entire record its pollen assemblages were similar to modern samples from the Itkillik II surface (CMD <13). DST taxa were rare in Red Green assemblages, PARs are low, and PST taxa (e.g., Bryidae and *Equisetum*) had relatively high percentages throughout the record. These findings suggest that the vegetation of the Itkillik II surface has resembled PST since the early Holocene, although high percentages of *Encalypta* spores early in the record indicate that the vegetation may have been drier and more open than modern PST prior to *ca*. 8000 cal years BP.

The differences in geomorphology and soil texture between the Itkillik II and Sagavanirktok glaciated surfaces were probably responsible for the disparate vegetational responses at Red Green and Upper Capsule to the climatic changes of the early to middle Holocene. As climate became cooler and wetter between 10,000 and 7000 cal years BP, it is likely that a more pronounced increase in soil moisture occurred on the Sagavanirktok surface because its fine-textured soils and flat landforms retained more water than the better-drained substrates of the Itkillik II surface. Higher soil moisture fostered an increase in plant cover on Sagavanirktok landscapes, which initiated a series of ecological and hydrological changes leading ultimately to the transition from PST to DST. Most important were the effects of the vegetation on the depth of the summer permafrost thaw layer. First, the increase in plant cover, in particular the upright, woody species, would have shaded the ground and thus reduced the amount of energy reaching the soil. Second, these woody, dwarf-shrub species, as well as mosses, contributed slowly decomposing litter to the soil (Hobbie 1996), thus helping to create a thicker organic layer. Third, the deep layer of organic litter, mosses, and sedge tussocks would have further reduced thermal conductance to the soil, and together these changes would have caused a major reduction in soil temperature and reduced soil thawing (Benninghoff 1952; Klinger 1996; Young et al. 1997). Shallower permafrost thawing impeded soil drainage, leading to anoxic and acidic soil conditions. The combination of cold soil temperatures, increased abundance of recalcitrant litter, and especially soil anoxia and acidity, would have greatly reduced decomposition rates (Hobbie 1996; Johnson et al. 1996). In turn, even thicker organic layers would have contributed further to permafrost aggradation (Van Cleve et al. 1991) (Fig. 1.5).

IMPLICATIONS

This research provides a new perspective on the role of climate-substrate interactions on ecosystem change in the Arctic, and also contributes to an improved understanding of arctic palynology in general. The edaphic controls on Holocene vegetational change observed at Red Green and Upper Capsule are also evident in other pollen records from northern Alaska. Sites on Sagavanirktok and older surfaces in the Arctic Foothills and the western Brooks Range have a vegetational history similar to Upper Capsule (e.g., Anderson 1985, 1988; Eisner 1991; Anderson et al. 1994). Taxa associated with PST were prevalent in the early Holocene, and between the early and middle Holocene there was a transition from PST to DST. Fewer records are available from younger landscapes, but two records from recently glaciated surfaces resemble the Red Green record, with PST indicator taxa throughout the Holocene and no indication of a transition to mesic tundra between 10,000 and 7000 cal years BP (Eisner and Colinvaux 1992; Oswald et al. 1999). The finding that the vegetation of the Sagavanirktok surface and other sites with flat topography and fine-textured soils were more sensitive to Holocene climatic change than their recently glaciated counterparts suggests that these substrates may be more susceptible to major environmental changes in the future. If, as in the early Holocene, future warming results in lower effective moisture in northern Alaska, we might expect the complex feedbacks of the DST ecosystems to be disrupted. For example, warmer conditions might reduce soil moisture and accelerate soil decomposition rates (e.g., Hobbie 1996), reducing vegetation cover and the depth of the organic layer, and thus leading to deeper permafrost thawing and even drier soils. In contrast, the Itkillik II surface was relatively insensitive to past climate change, and therefore may not be as strongly effected by future warming as the Sagavanirktok surface. Because of their coarse-texture, the water holding capacity of Itkillik II soils is inherently low, resulting in relatively xeric, sparse tundra vegetation regardless of climate. The effect of substrate on ecosystem sensitivity to climate change may also be important at the circumarctic scale. Substrate varies greatly across the Arctic, with heterogeneity occurring at variety of spatial scales. For example, at both regional and landscape scales there are differences in glacial history, parent material, and current eolian deposition (Edlund and Alt 1989; Walker et al. 1998; Walker 2000). The critical role of substrate in the Holocene ecosystem history of the central Arctic Foothills suggests that this edaphic variability may impart strong spatial heterogeneity on how arctic tundra ecosystems respond to future climate change.

Lastly, the finding that present (Chapters 2 and 3) and past (Chapter 4) tundra communities in the central Arctic Foothills can be distinguished from each other based on relatively minor differences in pollen assemblages indicates that the perceived spatial uncertainty of arctic pollen records is unfounded under certain circumstances. 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 of Alaska. For example, taxa that occur in many 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 should be possible in future studies to explore the small-scale variability of full-glacial vegetation and other past arctic plant communities.

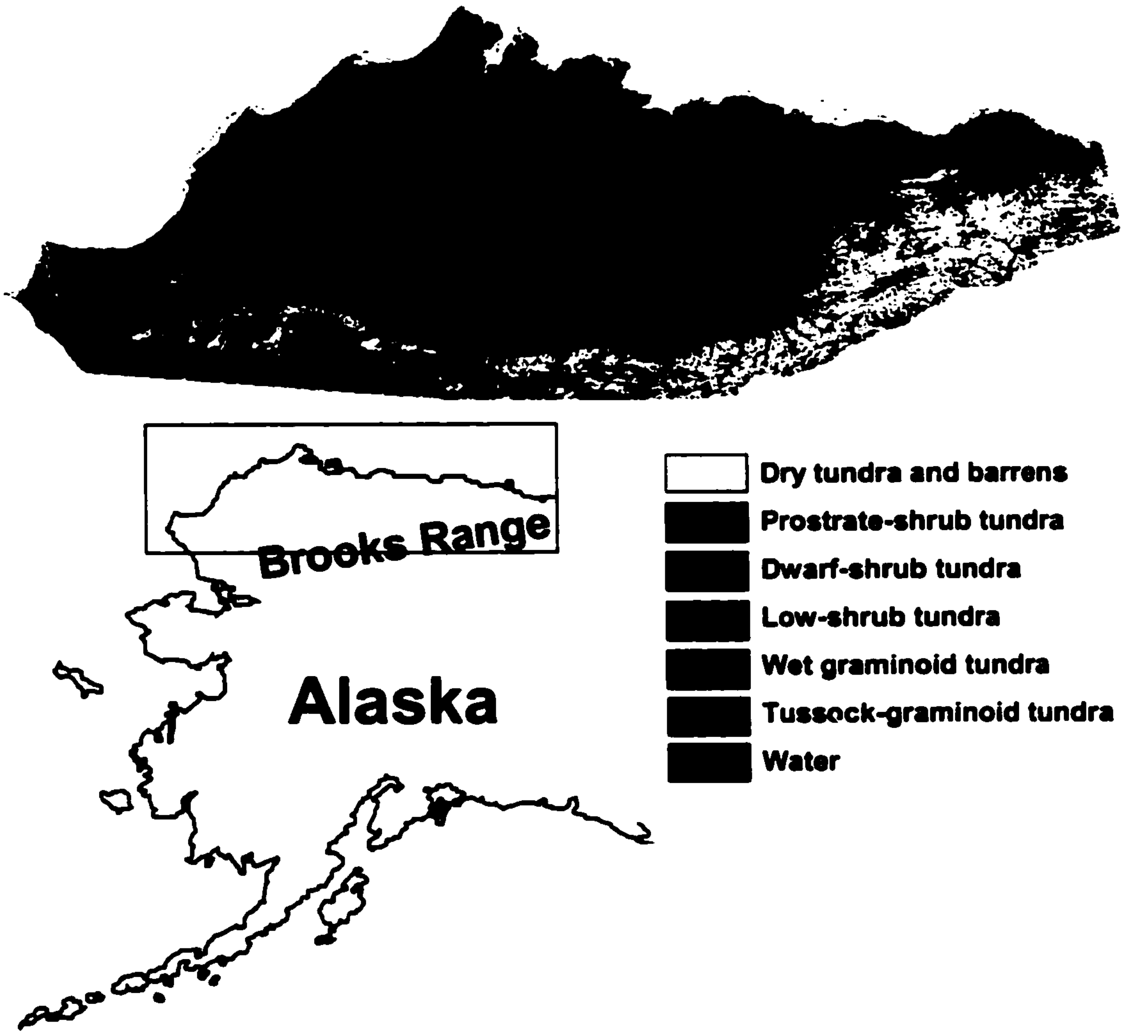

Figure 1.1. Vegetation map of northern Alaska with land-cover categories from Muller et al. (1999).

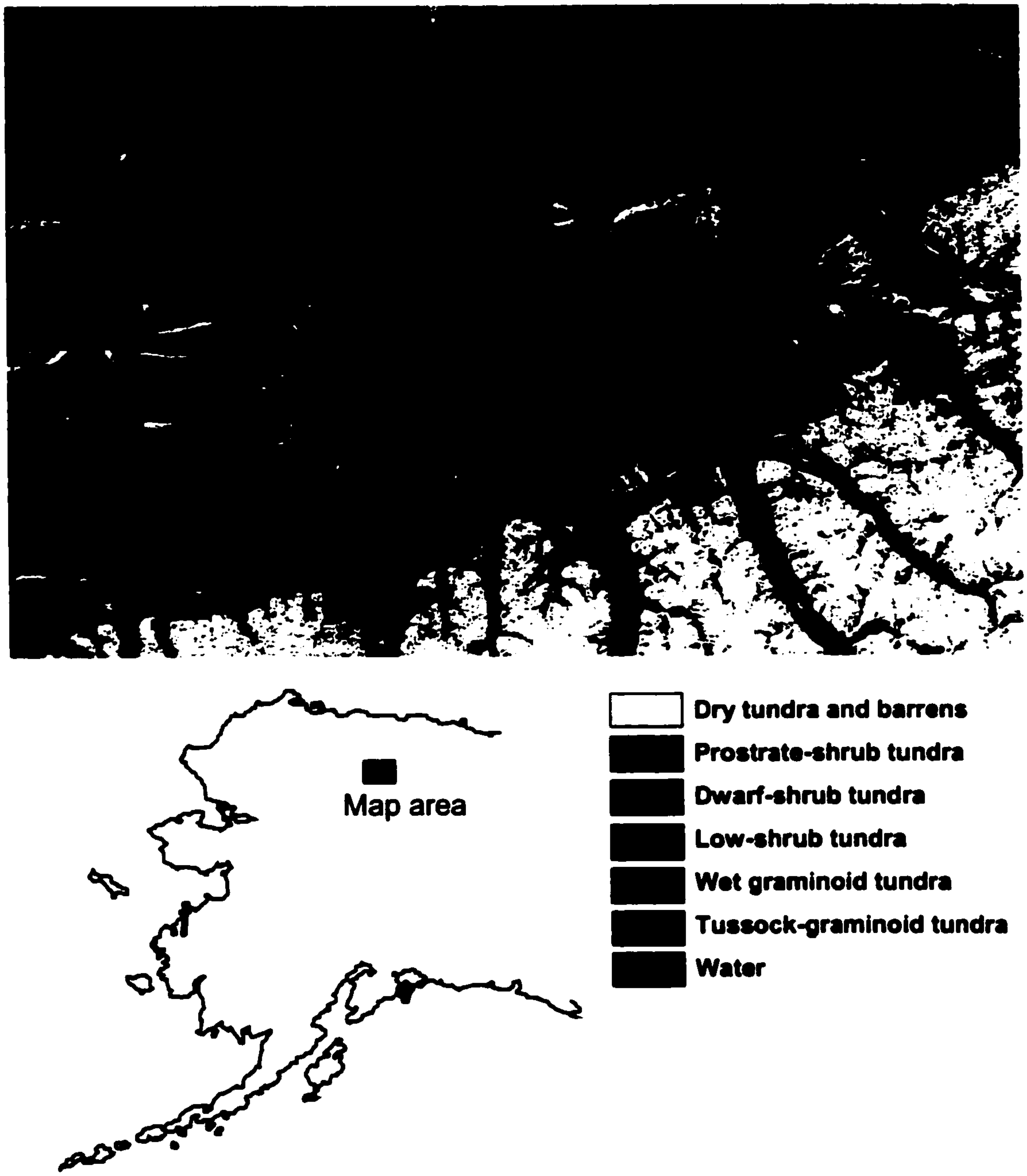

Figure 1.2. Vegetation map of the central Arctic Foothills area of northern Alaska with land-cover categories from Muller et al. (1999).

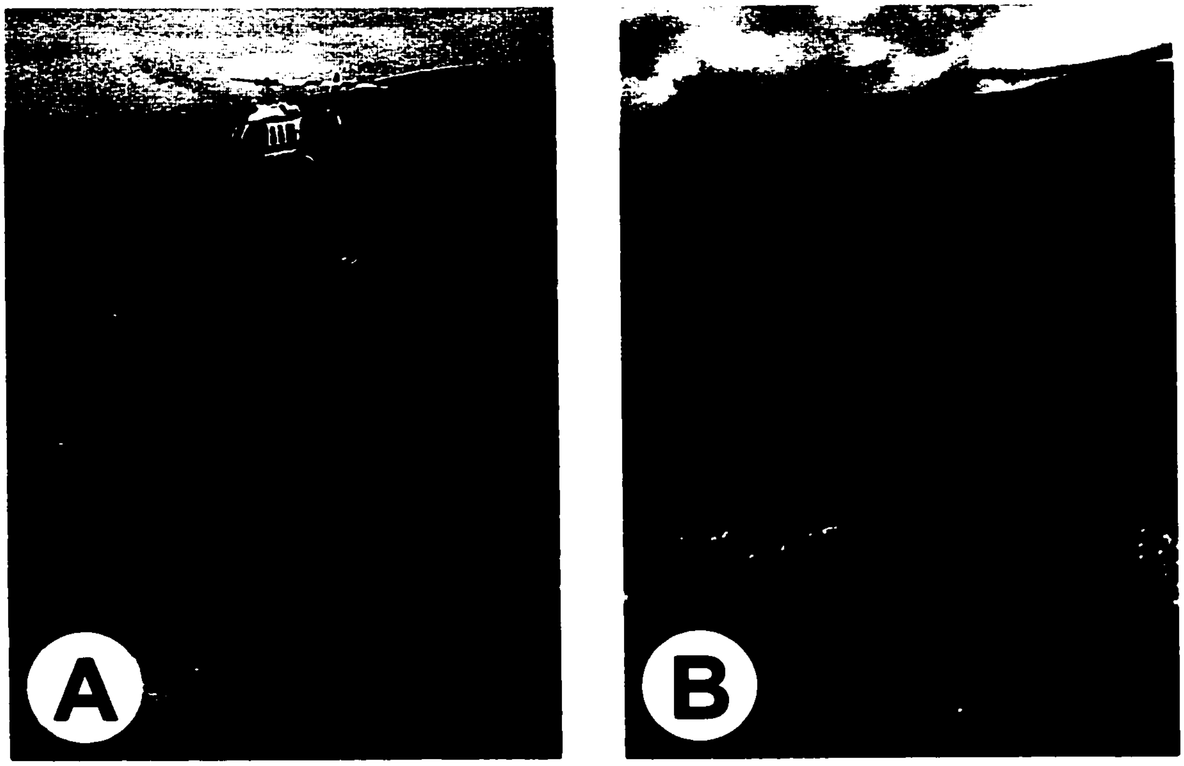

Figure 1.3. Photographs of (A) prostrate-shrub tundra and (B) dwarf-shrub tundra.

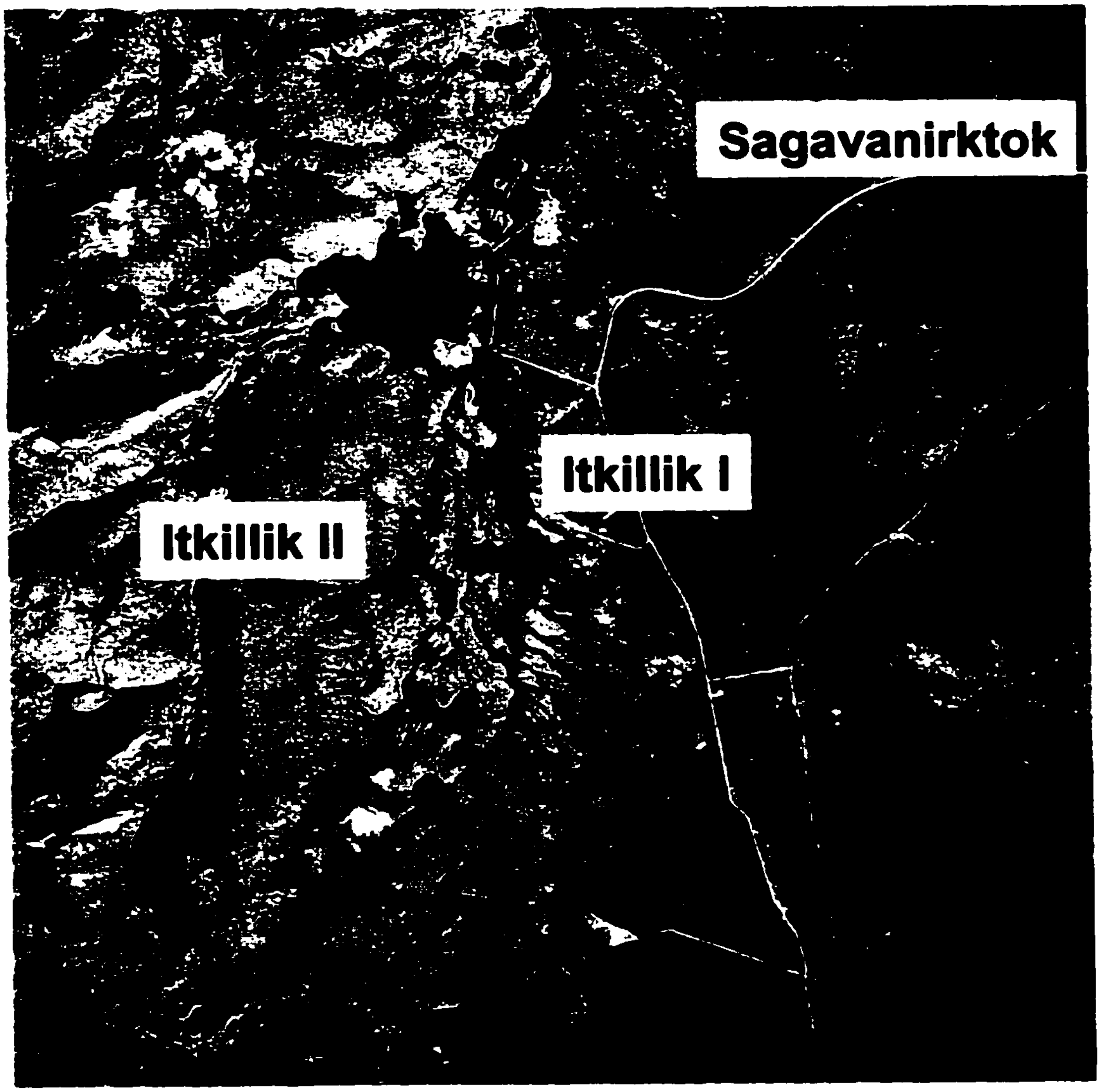

Figure 1.4. False-color aerial photograph of the Toolik Lake area. Dashed line indicates the boundary between the Itkillik II glaciated surface and the older Itkillik I and Sagavanirktok surfaces. Dark red indicates areas of dense vegetation cover; gray indicates sparsely vegetated areas.

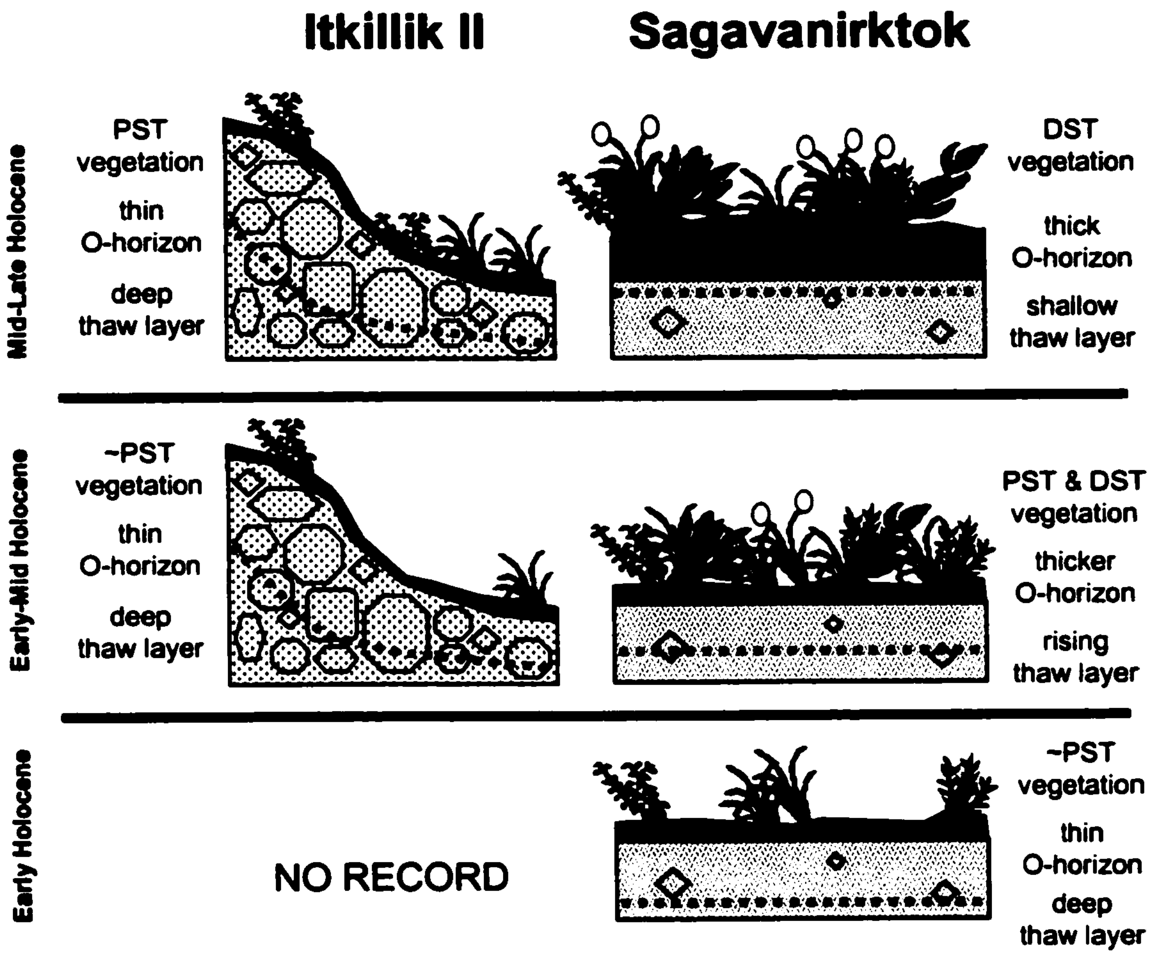

Figure 1.5. Schematic diagram illustrating vegetation and soil characteristics of Itkillik II and Sagavanirktok surface ecosystems before, during, and after the early to middle Holocene increase in effective moisture, as inferred from the Red Green and Upper Capsule pollen records. Dashed lines indicate permafrost thaw depth.

CHAPTER 2: Representation of tundra vegetation by pollen in lake sediments of northern Alaska

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SUMMARY

To better understand the representation of tundra vegetation by pollen data, modern pollen assemblages and pollen accumulation rates (PARs) were analyzed in the surface sediments of lakes of the Arctic Foothills and Arctic Coastal Plain of northern Alaska. Using a detailed land-cover map of the region, we assigned each study site to one of five tundra vegetation 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). 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. Smaller-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. Thus, the pollen data reflect patterns of tundra vegetation related to both regional-scale climatic gradients and landscape-scale edaphic heterogeneity.

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 and 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. 1982; 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 and 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 and Gough 2002), and paleoecological studies may provide insights to this question (Chapter 4).

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 (number of pollen grains cm^{-2} yr^{-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 and 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 2000; Walker et al. 1994, 1995). For example, shrubs occur on the coastal plain in areas where slightly higher topography affords drier soils (Walker and 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 27 lakes in this region, Anderson and 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 43 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, 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 smaller-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. Second, we analyzed pollen in surface cores dated with ^{210}Pb to estimate pollen accumulation rates (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 physiographic 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. 2.1a). 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 and Porter 1975; Hamilton 1994). Landscapes of Anaktuvuk (early Pleistocene), Sagavanirktok (>125,000 years BP), and Itkillik I (>60,000 years 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 years 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^2) 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 and Everett 1991; Walker et al. 1991). Much of the Arctic Coastal Plain is covered with thermokarst lakes (Muller et al. 1999).

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 and 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 pH < 5.5 (Walker et al. 1994; Muller et al. 1999). Dominant taxa include *Betula nana*, *Ledum palustre*, *Vaccinium vitis-idaea*, *V. uliginosum*, *Eriophorum vaginatum*, and *Sphagnum* species (Walker et al. 1994).

In many other settings, including cryoturbated substrates, river terraces, moderately drained terrain where 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* and *Arctostaphylos rubra*); non-tussock-forming Cyperaceae (e.g., *Carex bigelowii*); non-*Sphagnum* mosses (e.g., *Tomentypnum nitens*, *Aulacomnium turgidum*, and *Hypnum bambergeri*); and *Dryas integrifolia* (Walker and 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 *Carex aquatilis*, *Eriophorum angustifolium*, *Dupontia fischeri*, *Alopecurus alpinus*, and *Arctophila fulva* (Walker and 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 *Salix alaxensis*, *S. lanata*, *S. pulchra*, *S. glauca*, and *Alnus crispa* (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 78 lakes across the Arctic Foothills and Arctic Coastal Plain (Fig. 2.1b); 27 of these have been previously described (Anderson and Brubaker 1986). Sites were selected to achieve an even geographic coverage and to represent an array of tundra types. Lake size varied considerably (0.2 to 28.8 km^2), but the majority were between 1 and 4 km^2 in area (Table 2.1). Undisturbed sediment-water interface cores were obtained near the center of each lake using either a 2.5-cm diameter gravity corer or a 5-cm diameter piston corer. Gravity cores were extruded vertically in 2-cm intervals; piston cores were extruded vertically in 0.5-cm intervals between 0-10 cm and in 1-cm intervals between 10-20 cm.

For 70 of the sites, subsamples (1-2 cm^3) 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 100x objectives (12x 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. ^{210}Pb activity was measured 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) modeling. 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 ^{210}Pb flux for the Toolik Lake area (site 276) (Fitzgerald and Engstrom, unpublished data). For each core, a sediment subsample was removed from each level in the interval represented by the sediment accumulation rate (*ca.* 1850 to present). 0.5-cm^3 subsamples were taken from the 0.5-cm-thick levels, and 1-cm^3 subsamples were taken from the 1-cm-thick levels. Those subsamples were combined and homogenized, and a 2-cm^3 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 within a 2-km radius, and assigned the sites to the vegetation type that occupied the largest area (excluding water) within 2 km. Preliminary analyses showed that pollen and vegetation abundances were most strongly related at this distance (Appendix 1). The two lakes classified as moist tussock-graminoid 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 and Everett 1991; Walker et al. 1994) and pollen spectra, sites assigned to the PST vegetation type were split into two categories: Arctic Foothills type (10 sites) and Arctic Coastal Plain type (21 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 and 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 23 taxa that occurred in at least 15 of the 70 samples, as this combination of taxa provided better overall discrimination than other subsets of taxa.

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° x 0.5° global climate data set (New et al. 1999), with locally weighted lapse rates used to adjust for elevation during the interpolation (P. Bartlein, personal communication). DA scores for each site were compared to 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. 2.2 and 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%, *Carex 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 communities by *Carex aquatilis* and *Eriophorum angustifolium* (Walker and 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 and Little 1972; Walker et al. 1994). This distribution generally corresponds to *Betula* pollen percentages >25%, although a few foothills sites had somewhat lower percentages and a few coastal sites have percentages >25%. *Alnus* species (*A. crispa* and *A. tenuifolia*) 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 and Little 1972). The high percentages of *Alnus* pollen at sites in the Arctic Foothills (>20%) reflects the abundance of *Alnus 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 produced by *Picea glauca* and *P. mariana* in the boreal forest region south of the Brooks Range rarely is transported 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 decumbens* and *Salix lanata*) and on the coastal plain (e.g., *Vaccinium vitis-idaea* and *Salix reticulata*) (Hultén 1968; Walker and 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 2.2). 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. 2.4). 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 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 2.3). *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* is common in DST, *Selaginella rupestris* occurs in PST in the Arctic Foothills, and a greater number 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 2 km, this secondary trend presumably represents the smaller-scale heterogeneity within the broader foothills and coastal tundra zones that arises due to 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 Ericaeae 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),* 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* 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* occurs on relatively dry sites within the Arctic Coastal Plain (Walker and 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 2.4). DA axis 1 values were most strongly correlated to July precipitation ($r=0.71$) (Fig. 2.5). 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 not related to any of the climatic variables (Table 2.4). 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 (~4500-8500 grains cm^{-2} yr^{-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 coastal plain PST sites had intermediate values (~1000-3000 grains cm^{-2} yr^{-1}), and the two foothills PST sites had the lower values (~300 grains cm^{-2} yr^{-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 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 and Hussey 1962). Most thermokarst lakes are less than 6 m deep, so bottom sediments may be mixed by windstorms (Black and Barksdale 1949). 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 and Porter 1975). Sediment input to these lakes is likely to be less erratic than in thermokarst lakes, and thus PARs from the Arctic Foothills sites may be more reliable than from coastal plain sites. However, ^{210}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 and Engstrom, unpublished 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 and 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 and 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 since shrub communities have the highest primary production and vegetation cover of the inland tundra types (Shaver et al. 1996; Walker 1999; Williams and 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 *Alnus 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 foothills 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 and 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 and Brubaker 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 smaller-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 *Rubus 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^{-2} yr^{-1}) 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^{-2} yr^{-1}, whereas Holocene PARs range from *ca.* 500 to 25,000 grains cm^{-2} yr^{-1} (Anderson 1985, 1988; Cwynar 1982; 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 and Brubaker 1973; Lehman 1975; Bonny 1978; Davis and 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 geographic pattern of PARs and extra-local pollen percentages, and the similar ranges of modern and fossil PARs. The increase in PARs from 100s to 1000s of grains cm^{-2} yr^{-1} 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 and 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.

Table 2.1. Vegetation type, location, elevation, lake size, and discriminant analysis scores for modern pollen sites. Sites lacking discriminant analysis scores were analyzed only for the pollen accumulation rate study.

Vegetation	Site	Longitude (deg. W)	Latitude (deg. N)	Elev. (meters)	Lake size (km^2)	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

Table 2.1 continued

Vegetation	Site	Longitude (deg. W)	Latitude (deg. N)	Elev. (meters)	Lake size (km^2)	Discriminant Analysis	
						Axis 1	Axis 2
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
Dwarf-shrub	148	144.05	69.41	597	0.5	0.38	1.79
	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
	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	--	--

Table 2.2. Classification results for discriminant analysis of modern pollen samples.

	Predicted group				
Actual 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

Table 2.3. Loadings for each taxon for discriminant analysis axes 1 and 2.

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

Table 2.4. 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

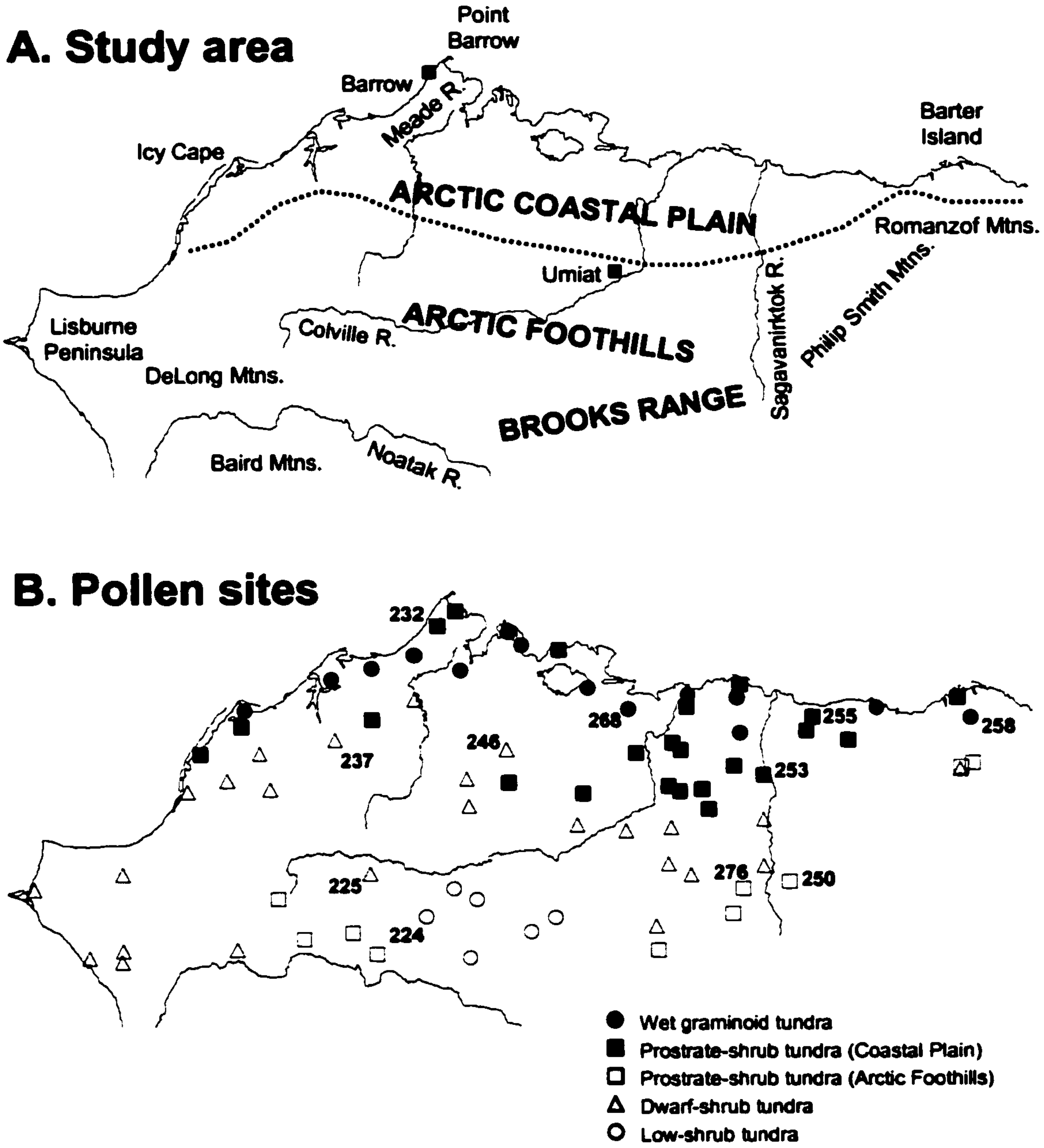

Figure 2.1. (A) Map of northern Alaska showing the major physiographic regions and locations mentioned in the text. Dotted lines indicates the approximate boundary between the Arctic Coastal Plain and Arctic Foothills regions. (B) Locations of study sites. Symbols indicate the dominant vegetation type within a 2-km radius of the lake (Muller et al. 1999). Site numbers are show for sites used in the PAR calibration study.

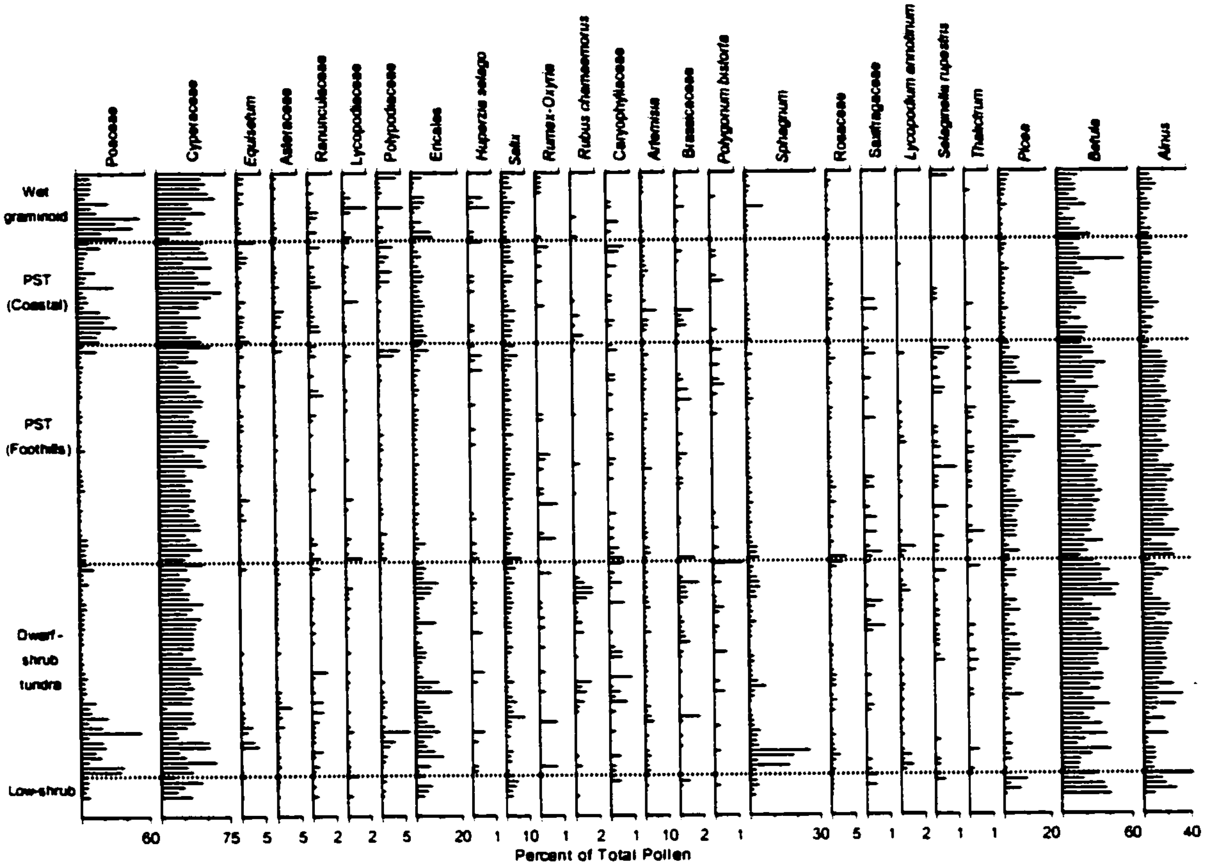

Figure 2.2. Percentage diagram for modern pollen assemblages from northern Alaska. Within each vegetation type, sites are ordered from east to west. Taxa are ordered by their loadings for the first discriminant axis.

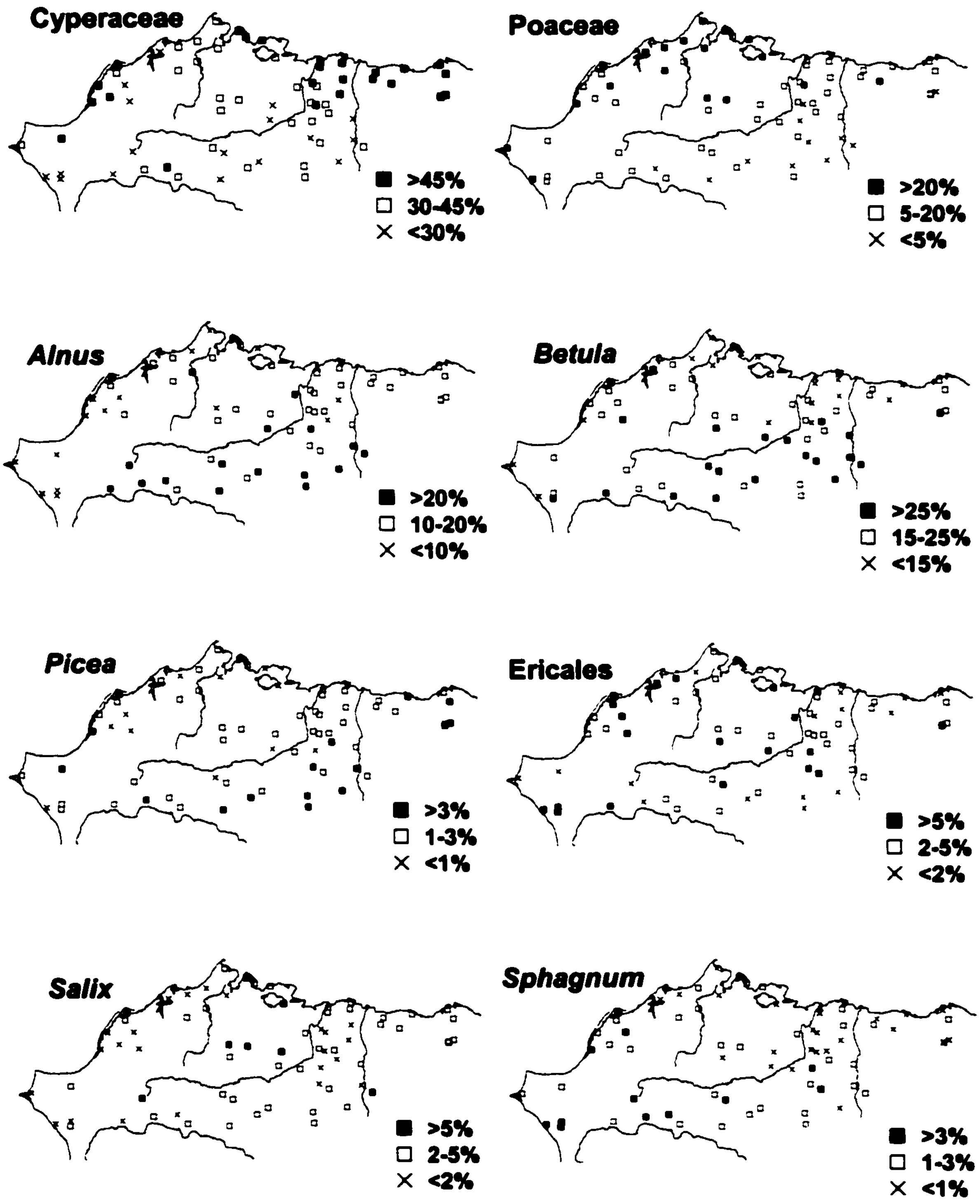

Figure 2.3 Maps of pollen percentage data for the main taxa.

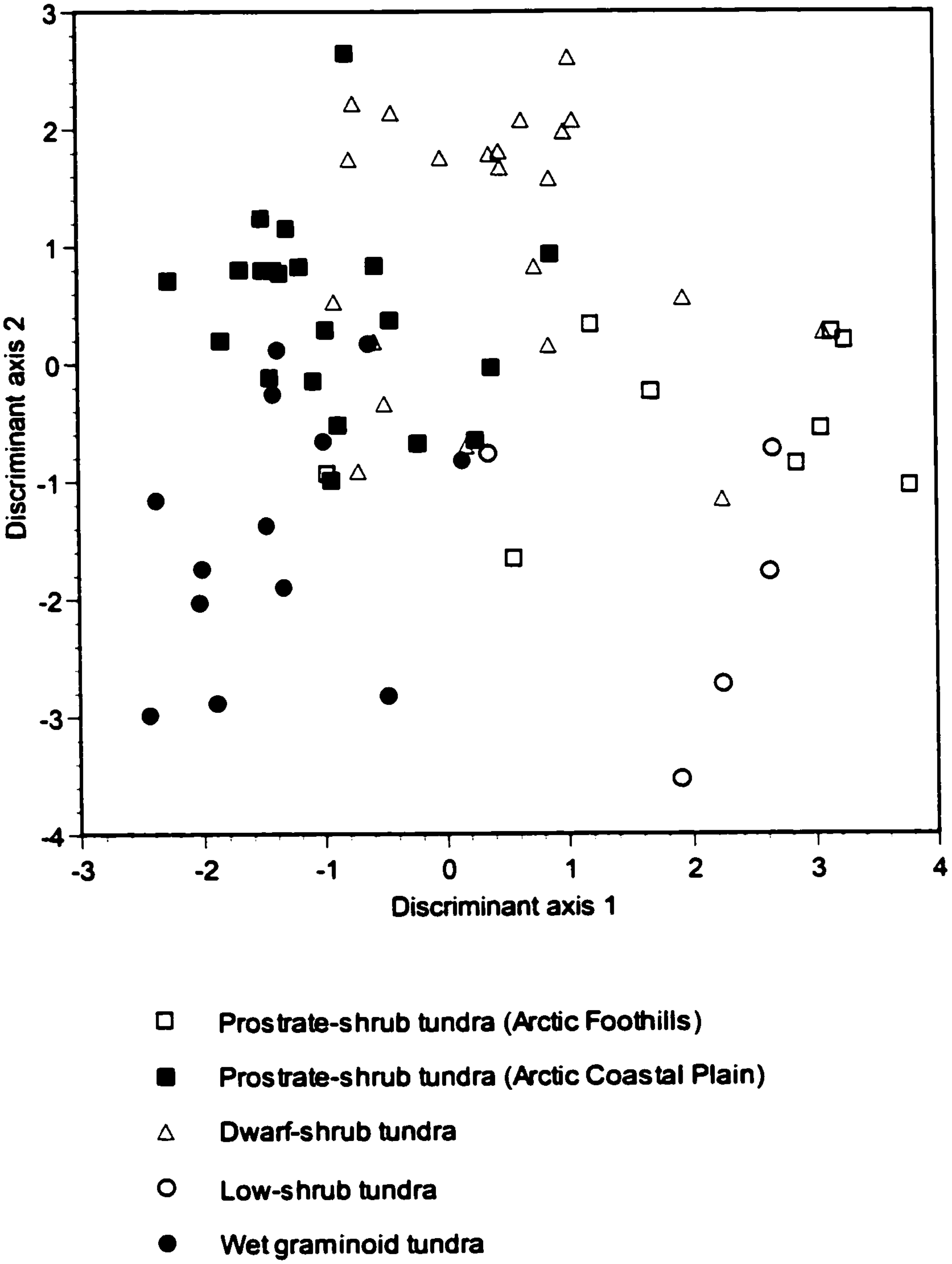

Figure 2.4. Discriminant analysis axis 1 and 2 scores for modern pollen sites from northern Alaska.

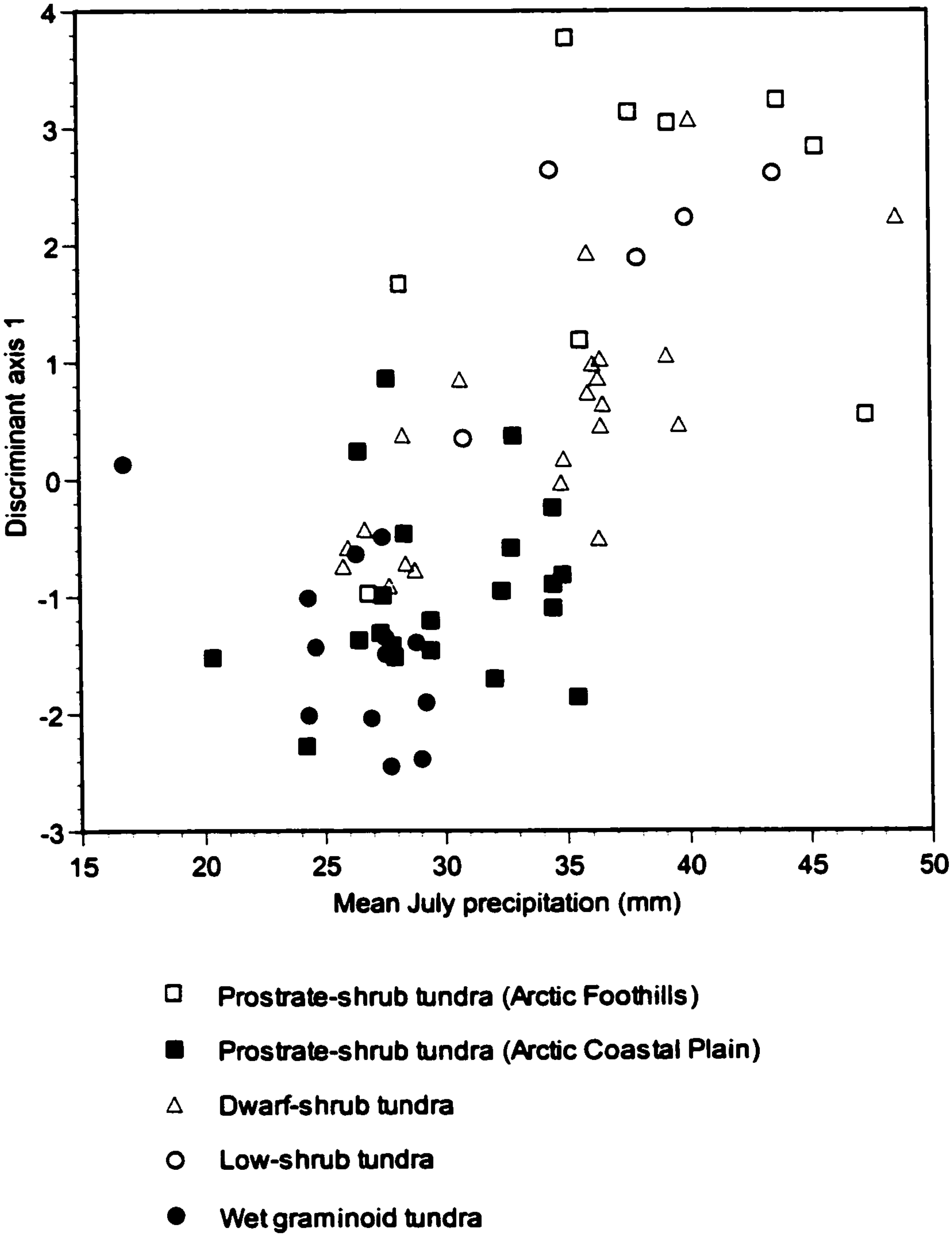

Figure 2.5. Mean July precipitation *versus* discriminant analysis axis 1 values for modern pollen sites from northern Alaska.

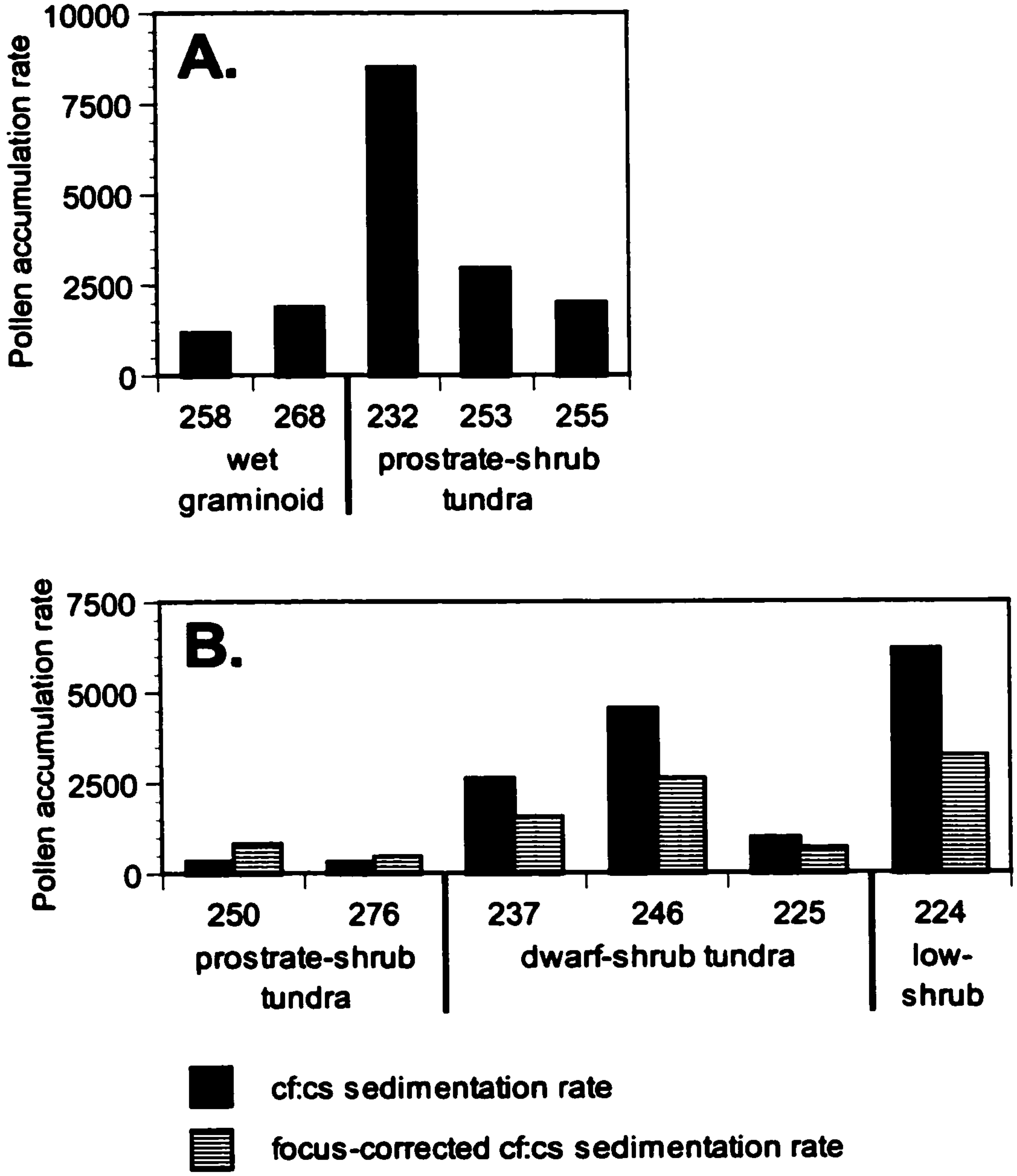

Figure 2.6. Modern pollen accumulation rates (PARs) for lakes on the Arctic Coastal Plain (A) and in the Arctic Foothills (B). Focus-corrected PARs are shown for foothills sites.

CHAPTER 3: Pollen-vegetation calibration for tundra communities in the Arctic Foothills, northern Alaska

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SUMMARY

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 analyzing 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 (*ca.* 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). 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. 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.

INTRODUCTION

Plant community composition and ecosystem properties of arctic tundra are spatially heterogeneous, varying in response to changes in climate and substrate 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 (Nichols 1974; 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; Ritchie et al. 1987). For example, modern pollen 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 and Brubaker 1986; Chapter 2). 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 paleo- and modern ecologists are interested in small-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 and Gough 2002).

To test the correspondence between tundra vegetation and pollen at the landscape scale, we analyzed pollen in the modern sediments of 56 small lakes from the central Arctic Foothills of northern Alaska. The study sites represent two different 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 (DA) 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 DA 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 to the community composition of DST and PST. 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 small-scale patterns of tundra vegetation, and thus helps to define the spatial resolution that is achievable by paleoecological studies in the Arctic.

STUDY AREA

The sites sampled for this study are located in the central Arctic Foothills, an area of rolling uplands north of the Brooks Range (Fig. 3.1). 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 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 (Detterman et al. 1958; Hamilton and Porter 1975; 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 to 11,500 years BP) flowed across the western half of the study area, ending 10 km to the northwest (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 and Bockheim 2001).

Spatial patterns of plant communities in the Arctic Foothills are strongly controlled by topography and substrate characteristics (Walker et al. 1994; Walker and Walker 1996). Sagavanirktok surfaces are dominated by moist dwarf-shrub tussock-graminoid tundra (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 (Hanson 1953; Alexandrova 1980; Bliss and Matveyeva 1992; Muller et al. 1999). We refer to this vegetation as dwarf-shrub tundra (DST). Dominant plants include *Eriophorum vaginatum*, *Sphagnum* species, *Betula nana*, *Ledum palustre*, *Vaccinium vitis-idaea*, and *V. uliginosum* (Walker et al. 1994). Vegetation cover is nearly continuous in DST (<1% bare soil), with a relatively tall plant canopy (~6.5 cm) (Walker et al. 2001). 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 (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). We refer to this vegetation as prostrate-shrub tundra (PST). 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 *Hypnum bambergeri*); and *Dryas integrifolia* (Walker et al. 1994, 1998). PST 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). Vegetation cover is discontinuous in PST (~8% bare soil), with a shorter plant canopy than DST (~3.9 cm). The Itkillik II and Sagavanirktok surfaces have different spectral reflectance (NDVI) values (Walker et al. 1995), related to lower above-ground biomass for PST (~480 g m^{-2}) than for DST (~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 center 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 3.1). The unequal sample size for the two surfaces reflects differences in the density of lakes on Sagavanirktok and Itkillik II landscapes. The intermediate-aged Itkillik I surface was not sampled for this study. Most of the lakes are located within a 200 km^2 area centered on Toolik Lake (Fig. 3.1a), but four additional Sagavanirktok samples were collected from lakes as far as 19 km northeast of Toolik Lake (Fig. 3.1b).

Samples of 2 cm^3 of sediment 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 100x objectives (12x 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 presence of two extra-local pollen types to approximate the absolute amount of local pollen deposited in these sediments (e.g., Maher 1963, 1972). *Alnus* and *Picea* pollen grains were encountered in all of the samples, even though these taxa are not locally present. *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 and Little 1972). By assuming that the pollen rain of *Alnus* and *Picea* is distributed homogeneously throughout the study area, we can express the abundances of the major taxa as a ratio to the sum of *Alnus* and *Picea*, and variations in that ratio should reflect differences in local pollen productivity.

Data analysis

We utilized two multivariate approaches that are commonly used to analyze pollen data: discriminant analysis (DA) and dissimilarity metrics. These techniques were applied to the 56 modern samples to determine whether Sagavanirktok and Itkillik II samples could be differentiated based on their pollen spectra. The analyses were performed using the 28 pollen and spore types that were found in at least eight samples (Table 3.2), as this combination of taxa provided better overall discrimination than other subsets of taxa.

In DA (SPSS 1999), all samples are analyzed 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 pre-determined 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 DA loading for each taxon, as these values show which pollen and spore types were most useful for discriminating between the surfaces (Liu and 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 *versus* between vegetation groups (e.g., Overpeck et al. 1985; Anderson et al. 1989). We used two different dissimilarity metrics (squared chord distance and Canberra metric distance) to make pairwise comparisons of all samples. Squared chord distance (SCD) and Canberra metric distance (CMD) represent two classes of dissimilarity metric that differ in their weighting of rare taxa. 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. 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, 1986; Zweig and Campbell 1993).

Each SCD and CMD measurement between paired pollen samples can be classified as either "within-surface" (Sagavanirktok to Sagavanirktok, or Itkillik II to Itkillik II) or "between-surfaces" (Sagavanirktok to Itkillik II, or *vice versa*). 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. 3.2). However, because 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. 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 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, implicit in the choice of a dissimilarity metric critical value is a trade off between high TPF or TNF. There are a variety of methods used to choose critical values (e.g., Metz 1978; Noe 1983; Schäfer 1989), 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 versus 1-TNF (also known as false positive fraction) can be used to describe the overall performance of the dissimilarity metrics (Fig. 3.2). The area under the ROC curve (AUC) is a measure of how well a given metric differentiates between the within- and between-surface comparisons, with possible values for AUC 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 AUC is judged to be better at discriminating between pollen samples from like and unlike vegetation. There are several methods available to estimate AUC (Bamber 1975; Hanley and McNeil 1982; Centor and Schwartz 1985). We used the sum of rectangles under the ROC curve (Zweig and Campbell 1993).

RESULTS

DA effectively distinguished between lakes from the different glaciated surfaces (eigenvalue = 7.73). All 56 samples were correctly classified (Table 3.3), with the 44 Itkillik II samples occurring below a DA score of 1, and the 12 Sagavanirktok samples with DA scores greater than 3 (Table 3.1, Fig. 3.3). 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 DA results are robust.

Several taxa had higher percentages in samples from one surface or the other (Fig. 3.4). Taxa associated with the Itkillik II surface (DA loading ≤ -0.09) included *Alnus*, *Equisetum*, *Picea*, Polypodiaceae, *Thalictrum*, and Rosaceae. On the other hand, taxa associated with the Sagavanirktok surface (DA loading ≥ 0.09) included *Rubus chamaemorus*, *Sphagnum*, Ericales, Poaceae, Brassicaceae, *Lycopodium annotinum*, Saxifragaceae, Asteraceae, Lycopodiaceae, *Betula*, and *Polygonum bistorta* (Table 3.2). The DA loading for 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. 3.5). Similarly, the ratios of *Betula* pollen to extra-local pollen were substantially higher for the Sagavanirktok surface. *Huperzia selago*, *Artemisia*, *Salix*, *Encalypta*, Caryophyllaceae, *Rumex-Oxyria*, Bryidae, Ranunculaceae, *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. 3.6). However, CMD was more effective than SCD for differentiating between the Sagavanirktok and Itkillik II surfaces. For CMD, within- and below-surface comparisons generally had values <13 and >13, respectively, whereas SCD had more overlap. This observation was confirmed by the ROC analysis (Fig. 3.7), as the AUC was higher for CMD (0.88) than for SCD (0.78).

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 a number of taxa that either dominate or are generally restricted to DST communities. For example, high *Betula* percentages in Sagavanirktok samples reflect the dominance of *Betula nana* in DST (Walker et al. 1994). The pollen and spore patterns for *Rubus chamaemorus*, *Lycopodium annotinum*, and *Polygonum bistorta* were consistent with the common occurrence of the taxa on acidic, organic soils on the Sagavanirktok surface, and their rarity on Itkillik II landscapes (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 Sagvanirktok 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 Ericaceae species in DST, including *Cassiope tetragona*, *Ledum palustre*, *Vaccinium uliginosum*, and *V. vitis-idaea*. Ericales percentages are lower in Itkillik II samples, appropriately reflecting the less frequent occurrence of Ericaceae (e.g., *Arctostaphylos rubra* and *Rhododendron lapponicum*) in PST (Walker et al. 1994). Spores assigned to the Lycopodiaceae category 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). 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. However, the overall cover of Cyperaceae species is higher in DST, mainly due to the abundance of *Eriophorum vaginatum*, the tussock-forming sedge that dominates

Sagavanirktok surface plant communities (Walker et al. 1994). Thus, the ratios of Cyperaceae pollen to extra-local pollen are noteworthy, as the higher ratios for Sagavanirktok than Itkillik II samples indicate that the absolute deposition of Cyperaceae pollen was higher for the Sagavanirktok surface.

The associations of other pollen types with the Sagavanirktok surface are less intuitive because they represent a diverse array of species. However, in each case some of the species can be linked to Sagavanirktok landscapes. For example, Saxifragaceae pollen in these samples was likely derived from *Saxifraga punctuata* and *S. nelsoniana*, both of which are characteristic of DST. Many Poaceae species favor the boggy, acidic conditions of DST, including *Phippsia algida*, *Arctagrostis latifolia*, *Calamagrostis canadensis*, *Arctophila fulva*, and *Dupontia fisheri* (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 *Petasides 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* and *E. arvense* in PST communities (Walker et al. 1994). Although Polypodiaceae species are rare in the central Arctic Foothills, when present they occur in dry, rocky, or calcareous soils (e.g., *Cystopteris fragilis*, *Woodsia alpina*, *W. glabella*, and *Dryopteris fragans*; 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 typically found on rocky slopes (Hultén 1968). Rosaceae pollen in Itkillik II samples is likely from the various species within this family 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 DA 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 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 prefer the boggy conditions that typify Sagavanirktok-aged landscapes (e.g., *Anemone richardsonii*). However, some Ranunculaceae species are found in xeric sites and PST communities, such as *Anemone parviflora* and *Ranunculus pedatifidus* (Hultén 1968; Walker et al. 1994). We anticipated that Bryidae spores would have a strong association with the Itkillik II surface, as many Bryidae species occur in PST communities, including *Aulacomnium acuminatum*, *A. turgidum*, *Meesia uliginosa*, *Tomentypnum nitens*, *Dicranum angustum*, and *Hypnum banbergeri* (Walker et al. 1994). However, Bryidae percentages were noticeably higher only in Itkillik II lakes from the northwestern portion of the study area. This pattern may reflect more abundant moss cover near those lakes, but we are unable to adequately address smaller-scale variability within the Itkillik II landscape in this study. We also expected *Selaginella rupestris* to be classified as an indicator of the Itkillik II landscape, 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

In addition to representing some important differences in tundra community composition between DST and PST, the pollen data also reflect variations in local 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 how pollen productivity varies between the Sagavanirktok and Itkillik II surfaces. 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. Sagavanirktok samples had both lower *Alnus* and *Picea* percentages and higher ratios than Itkillik II samples (Figs. 3.4 and 3.5), indicating that DST has higher pollen productivity than PST, with much of the difference due to higher amounts of *Betula* pollen. The inferred higher pollen productivity presumably results 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; Bonny 1978; Cwynar 1982; Davis and Ford 1982; Guthrie 1985; Magri 1994), 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), paleoenvironmental 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, 1988; Anderson et al. 1988, 1994; Lozhkin et al. 1993; Oswald et al. 1999), and the pollen of these species occurs 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, 1988; Anderson et al. 1988, 1994; Lozhkin et al. 1993; Oswald et al. 1999), and in this study were associated with the drier Itkillik II surface.

On the other hand, with only two exceptions (*Equisetum* and *Selaginella selaginoides*), the pollen and spore types were not restricted to one surface or the other. Thus, because the presence or absence of individual taxa was not entirely faithful for these tundra types, this data set suggests that paleoecological 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 analyzing 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. 3.7). 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. 3.6) 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 modeling 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 than it was possible to perceive differences in the pollen assemblages of sites that are separated by only a few kilometers 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 to the spatial relationship between modern pollen and tundra vegetation, and because the results indicate that pollen data reflect small-scale vegetational patterns, they suggest 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 northwestern Canada were interpreted as indicative of xeric, discontinuous tundra (Cwynar and Ritchie 1980; Cwynar 1982; Ritchie 1982; Ritchie and Cwynar 1982). However, this interpretation was criticized by paleontologists (e.g., Guthrie 1982, 1990), who asserted 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 and Colinvaux 1992), suggesting that a small-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 and 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 small-scale variability of full-glacial vegetation and other past arctic plant communities.

Table 3.1. Locations, number of pollen grains counted, and discriminant analysis scores for the 56 modern pollen sites. Lakes 1-44 are on the Itkillik II glacial surface and 45-56 are on the Sagavanirktok surface.

Lake number	Latitude	Longitude	Pollen grains counted	Discriminant Analysis 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

Table 3.1 continued

Lake number	Latitude	Longitude	Pollen grains counted	Discriminant Analysis score
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

Table 3.2. Discriminant analysis loadings for each taxon.

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

Table 3.3. Classification and cross-validation results for the discriminant analysis of the modern pollen samples.

Classification	Predicted surface	
Actual surface	Itkillik II	Sagavanirktok
Itkillik II	44	0
Sagavanirktok	0	12
Cross-validation	**Predicted surface**	
Actual surface	Itkillik II	Sagavanirktok
Itkillik II	41	3
Sagavanirktok	0	12

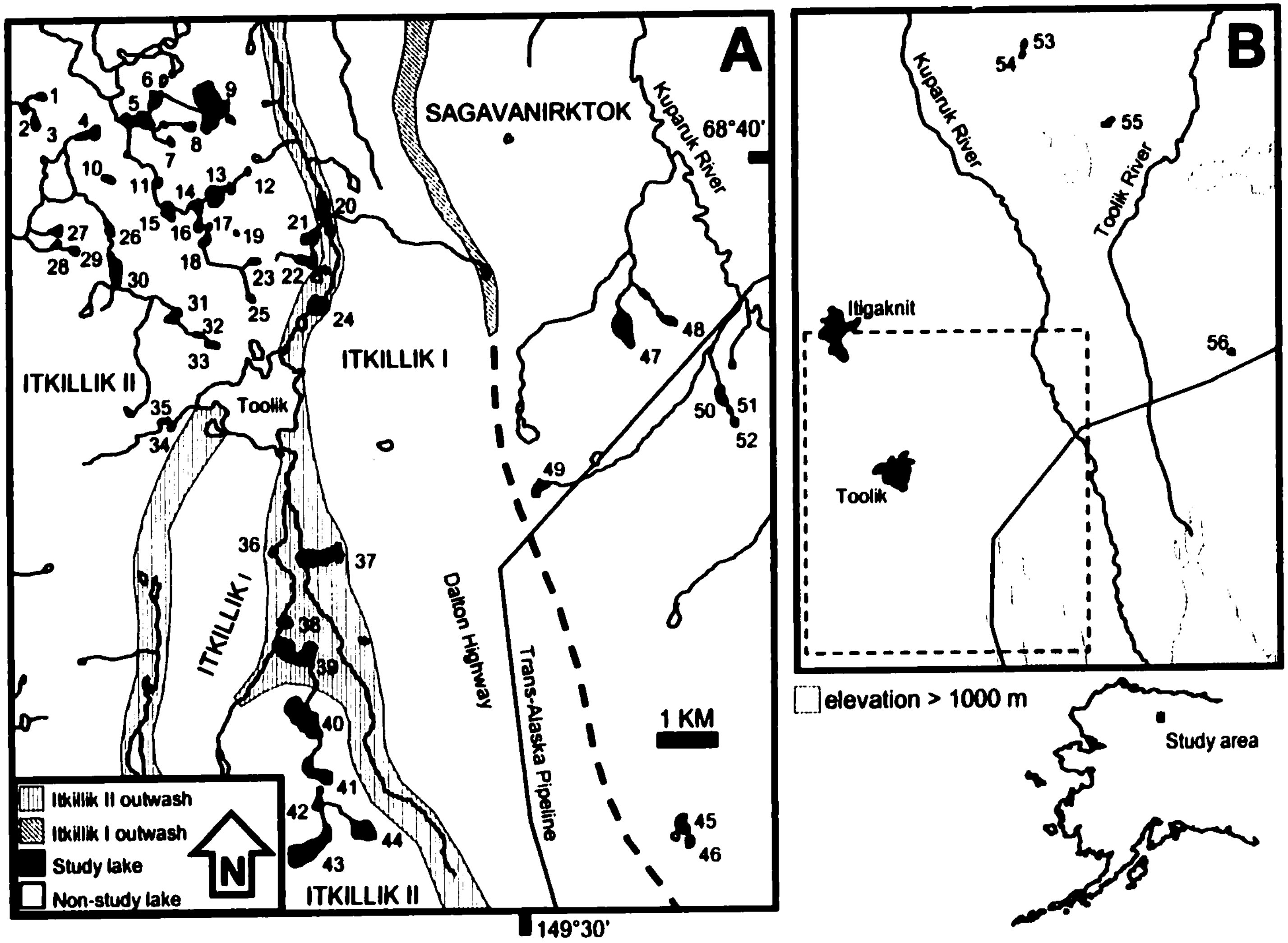

Figure 3.1. Map of the study area indicating study sites for pollen-vegetation calibration research. Glacial geology redrawn from Hamilton (1978) and Walker et al. (1995). Lakes 53-56 are located on Sagavanirktok deposits.

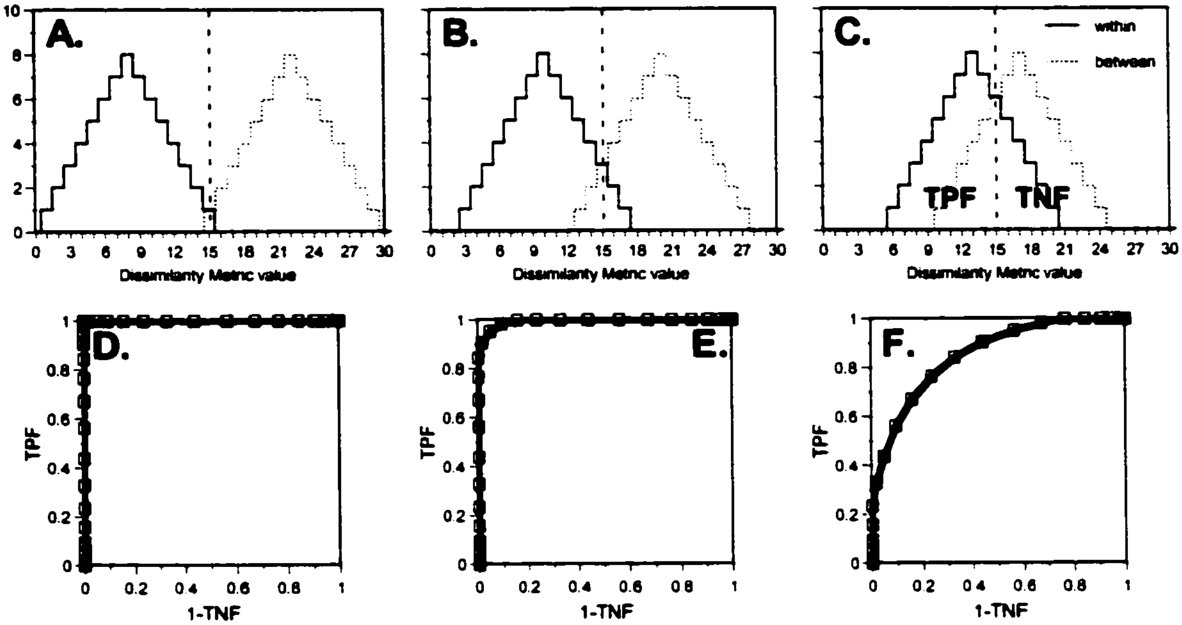

Figure 3.2. Idealized histograms of within- and between-surface dissimilarity metric comparisons (A, B, C) and corresponding receiver operating characteristic (ROC) plots (D, E, F). The first scenario (A, D) has perfect discrimination between like and unlike vegetation types, the second scenario (B, E) is intermediate, and the third scenario (C, F) has considerable overlap between the within- and between-surface histograms. Vertical lines indicate the critical value (15 in each case). An example of the true positive fraction (TPF) and true negative fraction (TNF) is illustrated in Figure 3.2c. TPF is the portion of the within-surface histogram that occurs below a given dissimilarity metric value (in this case 15), and TNF is the portion of the between-surface histogram that occurs above that value.

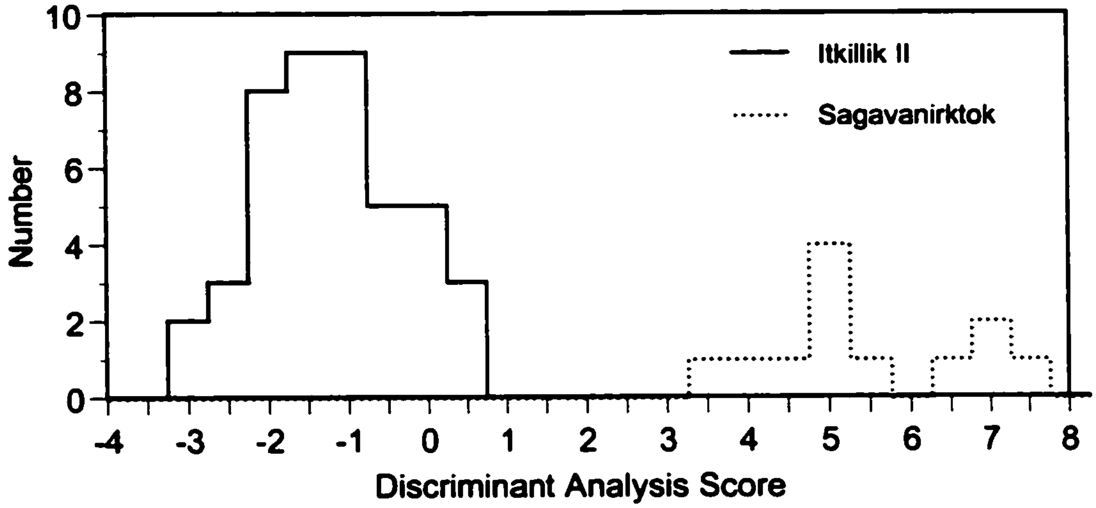

Figure 3.3. Histogram of discriminant scores for 56 modern pollen samples from the Itkillik II and Sagavanirktok glaciated surfaces.

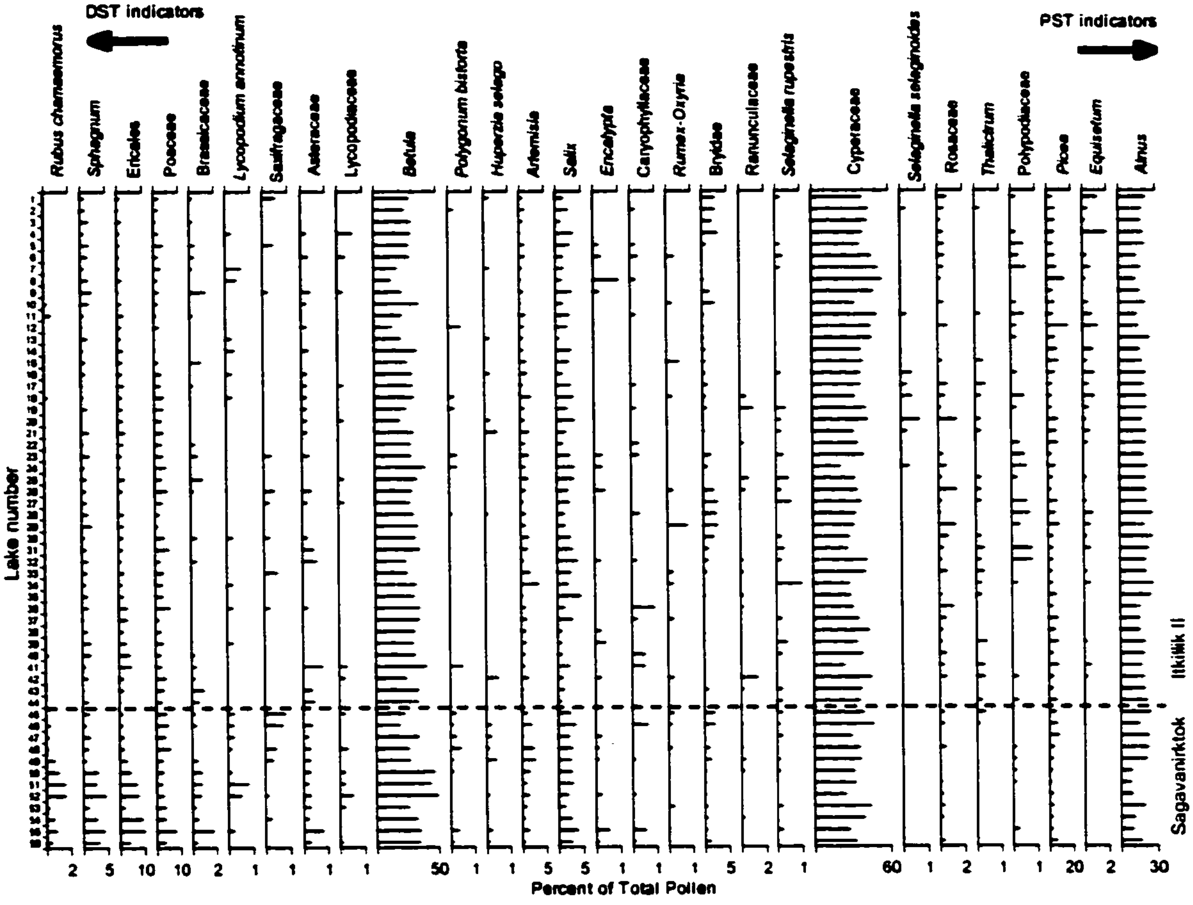

Figure 3.4. Pollen and spore percentage diagram for modern lake-sediment samples from the central Arctic Foothills, northern Alaska (analysis by W.W. Oswald). The pollen and spore taxa are ordered according to their discriminant analysis loadings (Table 3.2). Scales of x axes vary.

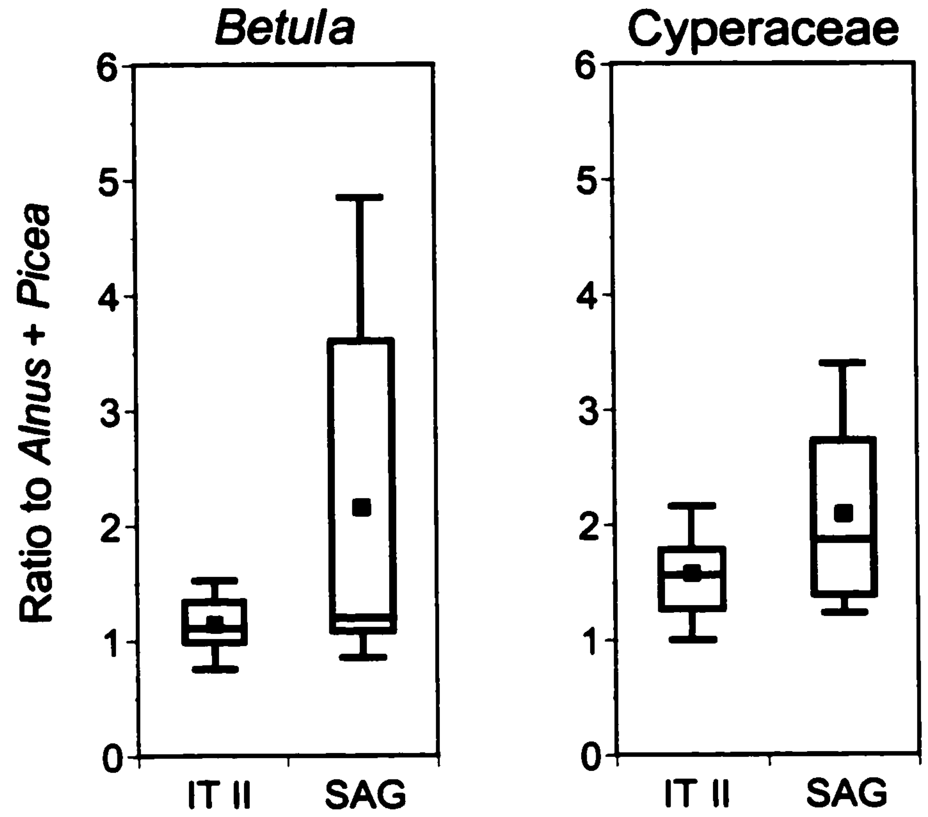

Figure 3.5. Ratios of the major taxa (*Betula* and Cyperaceae) to the sum of *Alnus* and *Picea* pollen. White and gray boxes are Itkillik II and Sagavanirktok samples, respectively. The box represents the 25th and 50th percentiles, the whiskers indicate the 10th and 90th percentiles, the horizontal line shows the median, and the mean is represented by the square.

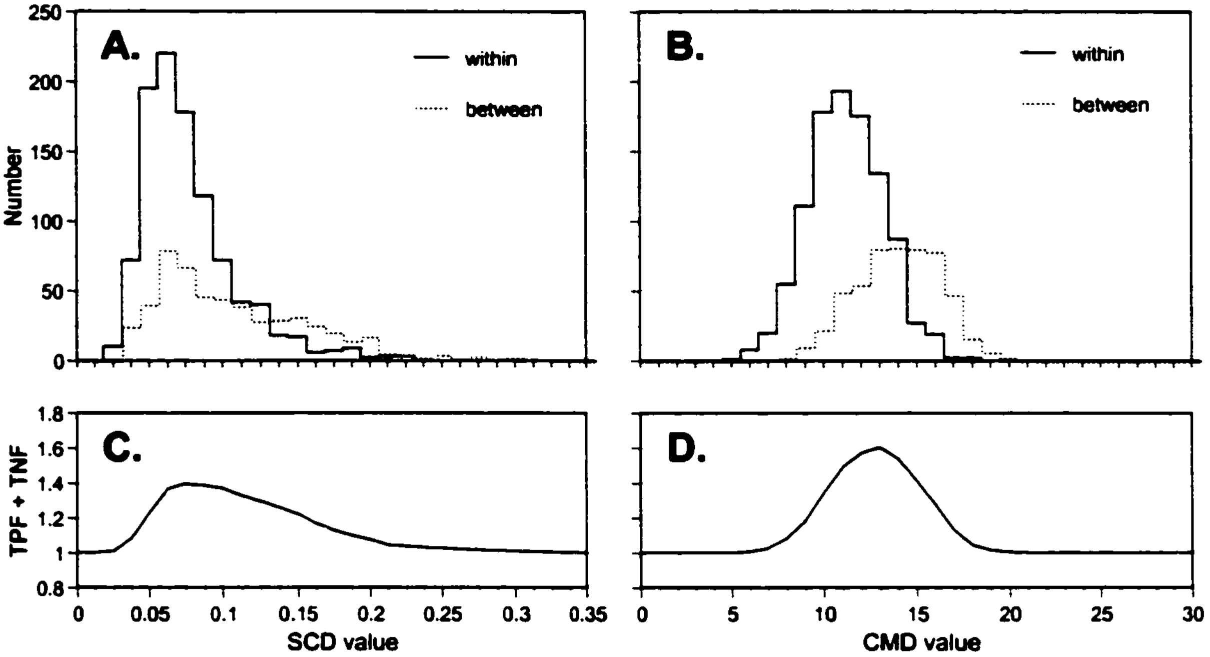

Figure 3.6. Histogram of squared chord distance (A) and Canberra metric distance (B) values for all within- and between-surface comparisons of Sagavanirktok and Itkillik II samples. The maximum TPF + TNF value indicates the critical value for square chord distance (C) and the Canberra metric distance (D).

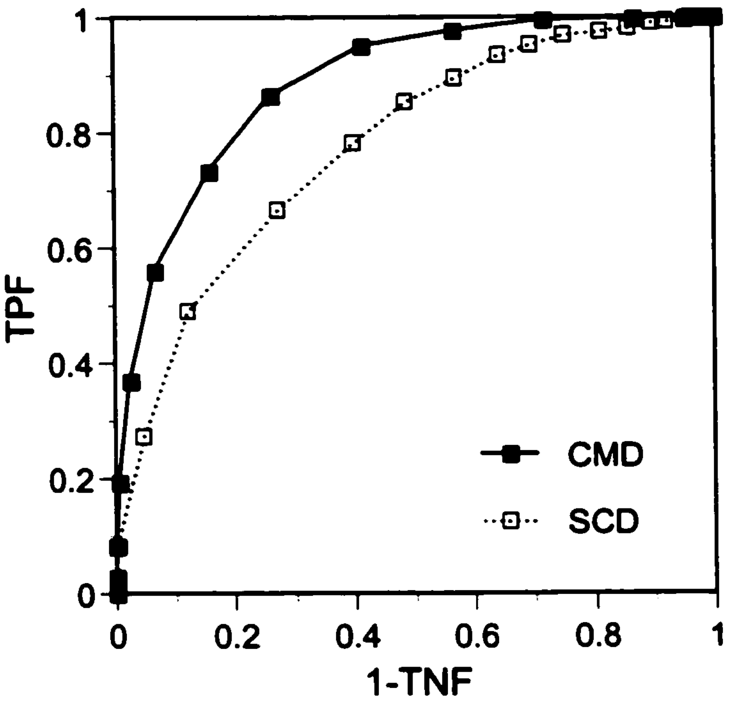

Figure 3.7. Receiver operating characteristic (ROC) plots for squared chord distance (SCD) and Canberra metric distance (CMD) dissimilarity metrics.

CHAPTER 4: Holocene pollen records from the central Arctic Foothills, northern Alaska: testing the role of substrate in the response of tundra to climate change

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SUMMARY

To explore the role of edaphic controls in the response of arctic tundra to climate change, we analyzed Holocene pollen records from lakes in northern Alaska located on glaciated surfaces (Sagavanirktok and Itkillik II) with contrasting soil texture (fine versus coarse), topography (smooth versus irregular), and tundra (dwarf-shrub versus prostrate-shrub). Using indicator taxa, pollen accumulation rates (PARs), and multivariate (Canberra metric distance) comparison of fossil and modern pollen assemblages, we reconstructed the vegetational changes at Upper Capsule Lake (Sagavanirktok surface) and Red Green Lake (Itkillik II surface) in response to increased effective moisture between the early and middle Holocene. In the Red Green record, low PARs and the continuous presence of taxa indicative of prostrate-shrub tundra (PST; *Equisetum*, Polypodiaceae, *Thalictrum*, and Rosaceae) indicate that the vegetation of the Itkillik II surface resembled PST throughout the Holocene. During the warm, dry early Holocene (11,300 to 10,000 cal years BP), PST also occurred on Sagavanirktok surfaces, as evidenced by PST indicators (Bryidae, Polypodiaceae, *Equisetum*, and Rosaceae) in this interval of the Upper Capsule record. However, PST taxa declined, PARs increased, and taxa indicative of dwarf-shrub tundra (DST; *Rubus chamaemorus* and *Lycopodium annotinum*) increased between 10,000 and 7000 cal years BP, suggesting increased vegetation cover and a transition from PST to DST. As climate changed during this interval, we hypothesize that the Sagavanirktok surface experienced increased soil moisture because of its fine-textured soils and smooth topography. This would have led to a series of positive feedbacks involving greater vegetation cover, permafrost aggradation, anoxic and acidic soil

conditions, slower decomposition, and the development of a thick organic layer. In contrast, soil moisture remained low on the better-drained Itkillik II surface, and as a result only minor vegetational changes occurred between the early and middle Holocene. These findings indicate that landscape-scale substrate variations have an important effect on how tundra responds to climate change, which suggests that the response of arctic ecosystems to future climatic variability may be spatially heterogeneous.

INTRODUCTION

Arctic tundra is spatially heterogeneous, with variations in ecosystem processes and plant community composition occurring at a variety of spatial scales (e.g., Walker 2000). At the scale of the entire circumarctic region, the primary variations in vegetation result from the latitudinal climatic gradient. Growing seasons are shorter and colder at higher latitudes, and as a result there is a northward decrease in primary productivity, diversity, biomass, plant stature, and carbon storage (e.g., Young 1971; Alexandrova 1980; Yurtsev 1994; Walker 2000). Tundra ecosystems also vary at smaller spatial scales (1-100 km), typically in response to edaphic heterogeneity caused by variations in parent material, eolian deposition, or glacial history (e.g., Elvebakk 1994; Walker 2000). The resulting variations in geomorphology, soil pH, or soil texture within a latitudinal climatic zone can strongly influence ecosystem processes and plant community membership, especially via effects on soil moisture (Walker et al. 1994; Muller et al. 1999).

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

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

In this paper, we use a paleoecological approach to examine substrate controls on tundra ecosystem response to climate change. By reconstructing the vegetation history of sites that differ in landform and soil characteristics, we examined how substrate influenced ecological changes induced by past climate change. The study was conducted in the central Arctic Foothills of northern Alaska, an ideal setting for this research due to its Pleistocene glacial history and resultant edaphic variability. We analyzed pollen records from lakes on contrasting glaciated surfaces, one with flat topography and fine-textured soils, the other with greater relief and coarse-textured soils. The sites are only 11 km apart, ensuring that they experienced the same climatic changes during the Holocene (i.e., the past 10,000 ^{14}C years or 11,500 calibrated ^{14}C years). Specifically, we examine the response of these sites to the onset of cool, moist climatic conditions between the early and middle Holocene, using knowledge of the modern pollen-vegetation relationships for this area to achieve a detailed interpretation of the vegetational history.

STUDY AREA

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

The Arctic Foothills have been glaciated repeatedly, and geomorphic evidence of three major Pleistocene glacial advances exists in the study area (Fig. 4.1). The Sagavanirktok glaciation (>125,000 years BP) covered the entire study area, and surfaces of this age remain exposed in the eastern portion of the area (Hamilton 1978). Late Pleistocene glacial advances were largely restricted to the Brooks Range, but glaciers reached the western portion of the study area via the Atigun and Itkillik valleys during two intervals: the Itkillik I (>60,000 years BP) and Itkillik II (24,000 to 11,500 years BP) glaciations (Hamilton and Porter 1975). Landscapes of Sagavanirktok and Itkillik I age have been subjected to long periods of mass wasting, weathering, and loess deposition. As a result, these areas have gently rolling topography and fine-textured soils. In contrast, areas glaciated by the Itkillik II ice advance have more irregular topography and coarser, better-drained soils (Hamilton 1978, 1994; Bockheim et al. 1998; Munroe and Bockheim 2001).

Sagavanirktok surfaces are dominated by moist dwarf-shrub tussock-graminoid tundra (also called moist acidic tundra; Walker et al. 1995). We refer to this vegetation as dwarf-shrub tundra (DST). Dominant plants in DST communities include dwarf shrubs (e.g., *Betula nana*, *Ledum palustre*, *Vaccinium vitis-idaea*, *V. uliginosum*); the tussock-forming sedge *Eriophorum vaginatum*; and a thick layer of *Sphagnum* mosses (Walker et al. 1994). Vegetation cover is nearly continuous in DST (<1% bare soil), and the plant canopy is relatively tall (~6.5 cm) (Walker et al. 2001). Shrub communities dominated by *Salix* species are also common on the Sagavanirktok landscape, particularly in water tracks and other riparian settings (Walker et al. 1994; Muller et al. 1999). Itkillik II surfaces are dominated by 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). Because the coarse-textured moraines and gravelly slopes that typify the Itkillik II landscape hold less moisture than Sagavanirktok soils, the substrate is relatively dry and overall vegetation cover is lower in PST (~8% bare soil) than DST (Walker et al. 2001). PST has a shorter canopy (~3.9 cm) than DST, and the dominant taxa include non-tussock Cyperaceae (e.g., *Carex bigelowii*); prostrate shrubs (e.g., *Salix arctica* and *Arctostaphylos rubra*); non-*Sphagnum* mosses (e.g., *Tomentypnum nitens*, *Aulacomnium turgidum*, and *Hypnum bambergeri*); and *Dryas integrifolia* (Walker et al. 1994, 1998).

In a related study, Oswald et al. (Chapter 3) found that lakes on Itkillik II and Sagavanirktok surfaces could be differentiated based on their modern pollen assemblages, and also that the modern pollen spectra of Itkillik II and Sagavanirktok samples realistically reflected the community composition of PST and DST, respectively. For example, Sagavanirktok surface samples have relatively high pollen or spore percentages of many taxa that are either prevalent in or restricted to DST, including *Rubus chamaemorus*, *Sphagnum*, Ericales, *Lycopodium annotinum*, *Betula*, and *Polygonum bistorta*. In contrast, Itkillik II samples have lower percentages of the DST indicator taxa, and relatively higher percentages of taxa associated with PST, including *Equisetum*, *Thalictrum*, Rosaceae, and Polypodiaceae.

We selected two study sites in watersheds with plant communities representing the main vegetation types of the Sagavanirktok and Itkillik II surfaces. Red Green Lake (informal name, 68° 39.2' N, 149° 40.9' W) is located on the Itkillik II surface about 3 km northwest of Toolik Lake, the location of the Arctic Long Term Ecological Research site (Fig. 4.1). The 2 ha lake (3.2 m maximum depth) is located in a *ca.* 50 ha watershed dominated by PST. It has a single outlet stream that flows west into the Itkillik River. Upper Capsule Lake (informal name; 68° 37.8' N, 149° 24.6' N) sits on the Sagavanirktok surface about 7 km east of Toolik Lake. It is 1 ha in area (5.7 m maximum depth), and is located in a *ca.* 350 ha watershed dominated by DST and shrub communities. A single outlet stream flows northward through two other small lakes before reaching the Kuparuk River.

HOLOCENE CLIMATE HISTORY

Knowledge of the Holocene climate history of northern Alaska is based on various types of paleoclimatic evidence, including fossil pollen data, plant and insect macrofossils, lake-sediment geochemistry from sites in northern and interior Alaska, lake-level reconstructions from interior Alaska, and General Circulation Model (GCM) predictions. Our understanding of the mechanisms and patterns of past climate change remains uncertain, but there are some general aspects of Holocene climate history that are agreed upon. For example, climate became warmer and wetter during the late glacial period (14,000 to 11,500 cal years BP) as summer insolation increased, the Bering land bridge began to flood, and the influence of the Laurentide ice sheet on large-scale circulation patterns began to diminish (COHMAP 1988; Bartlein et al. 1992). Lake levels in interior Alaska rose rapidly during this interval (Abbott et al. 2000; Edwards et al. 2001) and shrub *Betula* expanded throughout northern Alaska (e.g., Anderson and Brubaker 1994).

By the early Holocene (11,500 to 8500 cal years BP), the Laurentide ice sheet exerted little influence on circulation patterns in Alaska and summer insolation reached a relative maximum (COHMAP 1988; Bartlein et al. 1992). Lake-level data indicate that precipitation was probably still lower than present (Abbott et al. 2000; Edwards et al. 2001), whereas temperatures were relatively warm. In northern Alaska, several types of paleoclimatic evidence suggest that summer temperatures may have even been warmer than present. For example, *Populus* wood dated to this interval occurs at sites beyond its modern range (Detterman 1970; Hopkins et al. 1981; Betancourt et al. 1984; Nelson and Carter 1987), and *Populus* pollen occurs in lake sediments at a site north of the modern limit of *Populus* (Oswald et al. 1999). There are several explanations for the early Holocene expansion of *Populus* (e.g., Bartlein et al. 1995; Hu et al. 1998), but the positive correlation between *Populus balsamifera* radial growth and summer temperature (Edwards and Dunwiddie 1985; Lev 1987) indicates that it may have been a response to warm conditions. In addition, few glaciers in the central Brooks Range persisted during this interval (Ellis and Calkin 1979), and early Holocene fluvial deposits from the northern Arctic Foothills contain insects indicative of well-drained substrates and summer temperatures 2°C warmer than present (Nelson and Carter 1987).

Summer insolation decreased after 8500 cal years BP (Bartlein et al. 1992), and effective moisture increased in response to either cooler temperatures, increased precipitation, or both (Hu et al. 1998; Anderson et al. 2001; Edwards et al. 2001). Between 8500 and 6500 cal years BP, the increase in effective moisture crossed a threshold that permitted the expansion of *Alnus* throughout Alaska (e.g., Anderson and Brubaker 1994; Brubaker et al. 2001), including the region north of the Brooks Range (e.g., Eisner 1991; Oswald et al. 1999). The boundary conditions that control large-scale climatic variability reach their modern levels after 6500 cal years BP (Bartlein et al. 1992), and pollen and lake-level records from interior and northern Alaska give no indication of major climatic variations during this interval (e.g., Anderson and Brubaker 1994; Abbott et al. 2000). However, century-scale climatic variations are indicated by other evidence, including Brooks Range glacial advances, beach ridge dynamics along the northwest coast, dune activity in the Kobuk Valley, and lake-sediment geochemistry (e.g., Ellis and Calkin 1984; Calkin 1988; Mason and Jordan 1993; Anderson et al. 2001; Mann et al. 2002). There is particularly strong evidence for warm, dry conditions during the Medieval Warm Period, *ca.* 1100-600 cal years BP, and cool, wet conditions during the Little Ice Age, *ca.* 600-200 cal years BP (Hu et al. 2001; Mann et al. 2002).

METHODS

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

Sediment subsamples (1 cm^3) were dried at 90°C and ashed at 550°C to calculate loss-on-ignition (LOI). Subsamples of 2 or 3 cm^3 were prepared for pollen analysis following standard procedures for organic-poor sediments (Cwynar et al. 1979; PALE 1994). Tablets containing *Lycopodium clavatum* spores were added to the subsamples to allow estimation of pollen concentrations and pollen accumulation rates (Stockmarr 1971). Pollen residues were stained with safranin, mounted in silicone oil, and microscopically examined using 40 and 100x objectives (12x eyepieces). Non-*Sphagnum* moss (Bryidae) spores were classified according to Brubaker et al. (1998) and ascomycete spores were identified following van Geel (1972, 1978; van Geel et al. 1982). At least 300 pollen grains of terrestrial plant taxa were counted for each sample, and all pollen and spore abundances are expressed as a percentage of the sum of identified and unidentified pollen grains.

To interpret the fossil pollen assemblages, we relied upon previous studies of the modern relationships between pollen data and patterns of different tundra communities in northern Alaska (Chapter 2), in particular the landscape-scale patterns of PST and DST on the Itkillik II and Sagavanirktok surfaces (Chapter 3). Our interpretation involved several approaches, including analysis of indicator taxa, multivariate comparison of pollen assemblages, and calculation of pollen accumulation rates (PARs). First, we examined patterns of individual pollen and spore types that are known to be indicative of modern plant communities or specific environmental conditions (indicator taxa; e.g., Cwynar 1982). Taxa were classified as indicators (Table 4.1) based on their association with DST or PST in a modern pollen-calibration study for this area (Chapter 3), as well as other calibration studies for northern Alaska (Brubaker et al. 1998; Chapter 2). Second, we compared entire pollen assemblages between fossil and modern samples using a multivariate dissimilarity metric (modern analog method; e.g., Overpeck et al. 1985). For each record, we calculated the Canberra metric distance (CMD) between each fossil pollen assemblage and each of the modern pollen assemblages from the Itkillik II and Sagavanirktok surfaces. CMD is a dissimilarity metric in which the distance between multivariate samples is strongly influenced by minor taxa, and it was shown to be more effective than the widely applied squared chord distance for distinguishing between the Itkillik II and Sagavanirktok modern pollen assemblages (Chapter 3). As an index of the similarity of each fossil sample to modern PST and DST plant communities, we calculated its average CMD to the Itkillik II ($n = 44$) and Sagavanirktok ($n = 12$) modern samples. Analyses of the modern pollen data set identified a CMD of 13 as the "critical value" for distinguishing between like and unlike plant communities. Lastly, to approximate the overall vegetation cover of past plant communities, fossil PARs (number of grains cm^{-2} $year^{-1}$) were compared to modern PARs from northern Alaska. The link between PARs and tundra vegetation cover has been disputed (e.g., Guthrie 1985, 1990), but Oswald et al. (Chapter 2) found that patterns of vegetation cover were broadly reflected by modern PARs in the Arctic Foothills.

CORE STRATIGRAPHY AND CHRONOLOGY

The Red Green Lake sediment core (Fig. 4.2) consists of coarse sand (285-239 cm) overlain by inorganic, irregularly banded, gray-brown silt (239-109 cm) and dark organic silt (109-0 cm). Mollusk shells are abundant between 200 and 160 cm. LOI is low (<10%) below 200 cm, and higher (30-50%) above 200 cm. Pollen was not analyzed below 240 cm due to very low pollen concentrations. The base of the Upper Capsule Lake core is inorganic silt (328-327 cm) overlain by peaty organic sediment (327-310 cm) with high LOI (50-60%). Between 310-273 cm, the sediment is gray-brown silt with diffuse bands, and the upper 273 cm of the core is dark organic silt. LOI values decrease above 310 cm (12-32%).

For both records, dating control is provided by accelerator mass spectrometry (AMS) ^{14}C analyses of plant fragments sieved (>500 μm) from the sediment (Fig. 4.2, Table 4.2). Seven ages were obtained for the Red Green core, one of which (202-203 cm) is the average of three ^{14}C dates for different plant materials from the same depth (Appendix 1). The dates were converted to calibrated ages with the CALIB 4.1 program (Stuiver and Reimer 1993). The age of the 16-21 cm sample was rejected because it was anomalously old relative to the age-depth relationship for the other dates from the core (Fig. 4.2). The age-depth model used to calculate PARs and to assign sample ages is based on linear interpolation between the six remaining calibrated ^{14}C ages.

We obtained nine ages for the Upper Capsule record, two of which (155-157 and 310-311 cm) are the average age of multiple ^{14}C dates for different plant materials from the same depth (Appendix 1). These dates were also converted to calibrated ages using CALIB. We reject the dates for 100-101 and 207-208 cm, which are younger than would be expected based on the age-depth relationship for the other dates (Fig. 4.2). The ages of the lowest samples (310-311 and 325-326 cm) are statistically the same, indicating that the organic peat at the base of the core was deposited rapidly, and thus the age from 325-326 cm is not included in the age-depth model. PAR calculations and age assignments are based on linear interpolation between the six remaining calibrated ^{14}C ages.

VEGETATION HISTORY

Early Holocene (Zone 1: 11,300-10,000 cal years BP)

The records from the two lakes begin at different times, and only the Upper Capsule record covers the early Holocene interval (Fig. 4.3). The Sagavanirktok surface was not glaciated during the late Pleistocene (Hamilton 1978), but the Upper Capsule basin appears to have been dry during the Itkillik II glaciation, perhaps due to low precipitation. The peaty basal sediments of the Upper Capsule core suggest that the basin first contained a bog or wetland, but the statistically identical ^{14}C dates at the bottom and top of the peat indicate that the conditions favoring the accumulation of organic sediments were short-lived. The change from peat to silty sediment indicates that the lake began to fill around 11,300 cal years BP. In contrast, the lack of record from Red Green Lake (Fig. 4.4) during this part of the Holocene may indicate that Itkillik II landscapes were unstable due to recent glacial retreat, the continued presence of stagnant ice, and low vegetation cover.

UC-1 pollen assemblages (Fig. 4.3) are dominated by Cyperaceae (~50%), *Betula* (~35%), Ericales (5-20%), *Salix* (~5%), and *Sphagnum* (~5%), with minor taxa indicative of the modern vegetation of the Itkillik II surface, including *Thalictrum*, Polypodiaceae, *Equisetum*, *Encalypta*, Bryidae, and *Selaginella rupestris* (Chapter 2). These assemblages reflect tundra dominated by Cyperaceae species and prostrate shrubs (*Salix* and Ericaceae), probably not unlike modern PST. Indeed, the comparison of UC-1 assemblages with modern pollen spectra (Fig. 4.5) suggests that the early Holocene vegetation near Upper Capsule was analogous to the current tundra of the Itkillik II surface (CMD <13). Taxa indicative of mesic tundra (*Betula* and *Sphagnum*) are present in UC-1, but the similarity of their percentages with modern pollen spectra of the Itkillik II surface suggests that they were uncommon. For example, *Betula* and *Sphagnum* percentages in UC-1 are comparable to those in modern lake sediments from the Itkillik II surface (~35% and ~2%, respectively), where *Betula nana* and *Sphagnum* species are rare at present (Walker et al. 1994). The presence of *Populus* pollen in UC-1 corroborates other evidence that *Populus balsamifera* occurred north of the Brooks Range during the early Holocene (Detterman et al. 1970; Hopkins et al. 1981; Betancourt et al. 1984; Oswald et al. 1999).

The source of the ascomycete spores in UC-1 assemblages is uncertain, but they may have been produced by either ascomycetes living in the soil or by the fungal component of fruticose lichens. If the spores were derived from soil ascomycetes, their abundance may reflect moderate soil moisture conditions, as most tundra fungi are negatively affected by excessively wet or dry soils (Dowding and Widden 1974; Flanagan and Scarborough 1974; Miller and Laursen 1974). Alternatively, the spores may reflect past lichen cover, as ascomycetes are the fungal partner for the overwhelming majority of lichens (Hale 1953), and fruticose lichens are presently widespread in northern Alaska (Thomson 1979), particularly in relatively xeric tundra like PST (Evans et al. 1989; Walker et al. 1994). However, the production of spores by lichenized ascomycetes is relatively low compared to other ascomycetes (J. Ammirati, personal communication), so this explanation is less likely. In either case the presence of ascomycete spores in UC-1 is consistent with our characterization of the early Holocene vegetation of the Sagavanirktok surface as similar to modern PST, as this type of tundra has both moderately drained soils and high lichen cover.

Early-Middle Holocene transition (Zone 2: 10,000 to 7000 cal years BP)

In UC-2, Cyperaceae percentages decrease to 25-40%, *Betula* percentages increase to 40-50%, and minor taxa are indicative of both PST and DST. Taxa associated with modern PST are still present (*Selaginella rupestris*, *Encalypta*, Polypodiaceae, and *Equisetum*), and percentages of Rosaceae, another PST indicator, are even higher than in UC-1. However, Bryidae percentages are lower than in UC-1 and taxa indicative of modern DST (*Rubus chamaemorus*, *Polygonum bistorta*, *Lycopodium annotinum*, and Lycopodiaceae) are regularly encountered. The presence of both PST and DST indicators in UC-2 spectra is manifest in the multivariate analyses (Fig. 4.5), which indicate that the fossil assemblages are not analogous to modern vegetation of either the Itkillik II or the Sagavanirktok surface (CMD >13). Overall, these palynological changes suggest that both PST and DST species occurred on the Sagavanirktok surface during this transitional period. PST species were probably still present in the steeper, better-drained portions of the landscape, but *Betula nana* and other DST species were able to establish in mesic sites.

The Red Green Lake record (Fig. 4.4) begins at 8400 cal years BP, in the middle of zone 2. The lake probably started to fill at this time as a result of the regional increase in effective moisture (Edwards et al. 2001). Total PARs are low (<700 grains cm^{-2} yr^{-1}) throughout RG-2, suggesting sparse overall vegetation cover (Fig. 4.6). *Betula* pollen increases from 30 to 60% and Cyperaceae percentages decrease from 60 to 25%. However, the low PARs for these taxa indicate that *Betula nana* and Cyperaceae species were not abundant. The minor taxa (Rosaceae, *Selaginella rupestris*, Bryidae, Polypodiaceae, and *Equisetum*) are indicative of PST, and ascospores are also present. Comparison with the modern spectra suggests that the vegetation of RG-2 was similar to the current tundra of the Itkillik II surface (CMV <13), especially during the upper portion of this zone. The relatively high percentages of *Encalypta*, Bryidae, and Polypodiaceae spores in the lower portion of RG-2 indicate that the vegetation near Red Green was actually drier and more open than modern PST tundra prior to around 8000 cal years BP.

Middle Holocene (Zone 3: 7000-3000 cal years BP)

At both sites, increased percentages of *Picea* and *Alnus ca.* 7000 cal years BP reflect the expansion of these taxa in the regional vegetation. Records from northern Alaska show that *Picea glauca* and *P. mariana* reach their modern range limits in the southern foothills of the central Brooks Range between 8000 and 7000 cal years BP (e.g., Brubaker et al. 1983; Anderson and Brubaker 1994). However, it is unlikely that either *Picea* species occurred in the Arctic Foothills during this interval, as *Picea* percentages in UC-3 and RG-3 do not exceed modern values. *Alnus crispa* occurs north of the Brooks Range (Viereck and Little 1972), but is not currently found in the study area. Percentages of *Alnus* are slightly higher than modern between 7000-5000 cal years BP, similar to other sites in the central and western Brooks Range (e.g., Anderson and Brubaker 1994), suggesting that *Alnus* species were more abundant in the regional vegetation than they are at present.

In UC-3, PST taxa decrease in abundance, DST taxa increase in abundance, and pollen assemblages become analogous to the modern spectra of the Sagavanirktok surface (CMD <13). Specifically, *Salix* percentages decline slightly between UC-2 and UC-3, and most PST indicators (Rosaceae, Bryidae, Polypodiaceae, and *Equisetum*) are either absent or very rare in UC-3. On the other hand, percentages of DST indicators, including

Ericales, *Rubus chamaemorus*, *Lycopodium annotinum*, Lycopodiaceae, and *Sphagnum*, either increase or remain relatively high. These changes mark the end of the transition from PST dominance to the DST ecosystem that exists today in the Upper Capsule watershed. By 7000 cal years BP, Upper Capsule pollen assemblages indicate that DST had come to dominate those portions of the landscape that were occupied by PST in the preceding zone, and the increase in PARs, particularly for *Betula*, suggests that vegetation cover was higher overall. A coincident decrease in ascomycete spore abundance may reflect in increase in soil moisture that was unfavorable to soil ascomycetes, or perhaps reduced lichen cover on the Sagavanirktok surface. The latter interpretation is consistent with the recent finding that the abundance of lichens decreases in response to increased vascular plant biomass (Cornelissen et al. 2001).

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

Late Holocene (Zone 4: 3000 cal years BP to present)

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

In addition, changes in pollen and *Pediastrum* percentages within zone 4 indicate further variations in climate and vegetation during the past two millennia. In the Red Green record, *Pediastrum* percentages decline between 1500 and 500 cal years BP, and pollen assemblages from this interval exhibit increased similarity to the modern assemblages of the Sagavanirktok surface (CMD <13), although the palynological changes are minor. There is a more obvious change in the Upper Capsule record, as the similarity to Itkillik II modern pollen assemblages increases abruptly at 1500 cal years BP (CMD <13). The changes in pollen percentages are subtle, but it appears that the increased similarity to Itkillik II modern vegetation results from slight decreases in the percentages of Lycopodiaceae, *Sphagnum*, Asteraceae, and *Betula*. However, the Red Green and Upper Capsule fossil assemblages remain more similar to the modern assemblages of their corresponding surface during this interval, and after 500 cal years BP they become less similar to the modern assemblages of the contrasting surface. Taken together, these changes may reflect the response of both terrestrial and aquatic ecosystems to the century-scale climatic variations that occurred during the late Holocene, including the Medieval Warm Period and the Little Ice Age (e.g., Calkin 1988; Hu et al. 2001; Mann et al. 2002). However, the chronology and sampling frequency of these records are not adequate for a more detailed examination of the environmental and ecological changes of the late Holocene.

DISCUSSION

Edaphic controls on ecosystem response to climate change

The differences in geomorphology and soil texture between the Itkillik II and Sagavanirktok glaciated surfaces were likely responsible for the disparate vegetational responses at Red Green and Upper Capsule to the climatic changes of the early to middle Holocene. As effective moisture increased between 10,000 and 7000 cal years BP, we hypothesize that a more pronounced increase in soil moisture occurred on the Sagavanirktok surface because its fine-textured soils and flat landforms retained more water than the better-drained substrates of the Itkillik II surface (Fig. 4.7). Higher soil moisture fostered an increase in plant cover on Sagavanirktok landscapes, which initiated a series of ecological and hydrological changes leading ultimately to the transition from PST to DST. Most important were the effects of the vegetation on the depth of the summer permafrost thaw layer. First, the increase in plant cover, in particular the upright, woody species, such as *Betula nana* and *Vaccinium uliginosum*, would have shaded the ground and thus reduced the amount of energy reaching the soil. Second, these woody, dwarf-shrub species, as well as mosses, contributed slowly decomposing litter to the soil (Hobbie 1996), thus helping to create a thicker organic layer. Third, the deep layer of organic litter, mosses, and sedge tussocks would have further reduced thermal conductance to the soil, and together these changes would have caused a major reduction in soil temperature and reduced soil thawing (Benninghoff 1952; Klinger 1996; Young et al. 1997). Shallower permafrost thawing impeded soil drainage, leading to anoxic and acidic soil conditions. The combination of cold soil temperatures, increased abundance of recalcitrant litter, and especially soil anoxia and acidity, would have greatly reduced decomposition rates (Hobbie 1996; Johnson et al. 1996). In turn, even thicker organic layers contributed further to permafrost aggradation (Van Cleve et al. 1991). The outcome of this transition can be seen today, as soils of DST have thicker organic horizons (~20 cm *versus* ~10 cm) and shallower active layers (~40 cm *versus* ~55 cm) than soils of PST (Bockheim et al. 1998; Walker et al. 2001).

The pollen records from Upper Capsule and Red Green Lakes shed new light on the origin of the differences between DST and PST. The importance of the ecological and hydrological feedbacks in DST has been noted previously (e.g., Walker et al. 1989, 1994), but the manner in which these differences arose is not clearly understood. Jorgenson (1984) made the insightful observation that different tundra ecosystems occupied the Sagavanirktok and Itkillik II glaciated surfaces, leading to the hypothesis that plant community succession occurred in response to long-term landscape evolution. This hypothesis suggested that as glacial deposits in the Arctic Foothills aged over millennia, they experienced mass wasting, slope reduction, eolian deposition, the development of a thick layer of organic matter and vegetation (especially *Sphagnum*), and ice aggradation (Jorgenson 1984; Walker et al. 1989, 1994). As these changes proceeded, there was a gradual succession from PST to DST. Because the changes in landform and soil characteristics were viewed as the primary drivers of ecosystem change, this hypothesis emphasized the importance of landscape evolution over climate change in the development of DST ecosystems. More recently, pollen records from northern Alaska have helped to clarify our understanding of the role of climate in ecosystem change (e.g., Walker et al. 1995), and the records from Red Green and Upper Capsule illustrate even more clearly that DST does not result solely from landscape evolution. The topography and soil texture of glaciated landscapes most likely were transformed over many thousands of years, but the ecological changes associated with the switch from PST to DST occurred more rapidly. At Upper Capsule, DST developed over a relatively short interval (*ca.* 3000 years) when cool, moist climatic conditions acted upon the smooth topography and fine-textured soils of the Sagavanirktok surface.

Comparison with other pollen records

The changes in the Red Green and Upper Capsule records are consistent with other pollen records from the Arctic Foothills and elsewhere in northern Alaska, suggesting that edaphic controls on the vegetational response to Holocene climate change were important throughout the region. Nearby sites on the Sagavanirktok surface show a gradual change from PST to DST during the middle Holocene, similar to the transition at Upper Capsule.

For example, at Oil Lake (2 km northwest of Upper Capsule), PST indicators (*Equisetum* and Polypodiaceae) have highest percentages *ca.* 12,500-10,000 cal years BP, slightly lower percentages during the transition from 10,000-7000 cal years BP, and are nearly absent after 7000 cal years BP. On the other hand, DST indicators (*Lycopodium annotinum* and Ericales) are present in low percentages during the transitional period, but become more abundant (including *Rubus chamaemorus* and *Polygonum bistorta*) after 7000 cal years BP (Eisner and Colinvaux 1992; Oswald and Brubaker, unpublished data). Pollen records from a peat deposit at Imnavait Creek (10 km east of Upper Capsule) and Ahaliorak Lake (60 km northwest of the study area, Anaktuvuk surface) lack the temporal resolution to perceive the details of this transition, but in general their stratigraphy is consistent with the Upper Capsule record. The Imnavait Creek record has relatively high percentages of PST indicators (*Equisetum* and Rosaceae) during the early Holocene (Eisner 1991), whereas the Ahaliorak record has higher percentages of Ericales pollen in the late Holocene than in the early Holocene (Eisner and Colinvaux 1990; Anderson and Brubaker, unpublished data).

Similar changes are evident at several sites in the western Brooks Range that, like Upper Capsule, were not glaciated during the late Pleistocene. In pollen records from the Kobuk and Noatak drainages, percentages of Polypodiaceae and *Equisetum* are generally high during the early Holocene, and a transition occurs between the early and middle Holocene to assemblages featuring higher percentages of Ericales, *Sphagnum*, and *Lycopodium* (Anderson 1985, 1988; Anderson et al. 1994). These sites differ from Red Green and Upper Capsule in that they have higher percentages of *Betula*, *Alnus*, and *Sphagnum* and lower percentages of Cyperaceae during the Holocene. The pollen record from Tukuto Lake in the western Arctic Foothills shares many of the same stratigraphic patterns as the Upper Capsule record, including an interval when both PST and DST indicator taxa are present. During the beginning of the Holocene, Tukuto assemblages have relatively high percentages of Polypodiaceae and *Equisetum* spores. That zone is followed by the transitional period in which the PST indicators are present at low percentages and DST indicators (Ericales and *Rubus chamaemorus*) also occur. Lastly, there is a switch to DST *ca.* 7000 cal years BP indicated by the near absence of PST taxa and increased percentages of Ericales (Oswald et al. 1999). A notable difference between this record and that of Upper Capsule is that *Lycopodium annotinum* percentages decrease after 7000 cal years BP at Tukuto but not at Upper Capsule. In addition, the record from Red Green Lake is similar to two pollen records from recently glaciated sites in the western Brooks Range. Etivlik Lake (Itkillik II surface) and Feniak Lake (Itkillik I surface) have relatively high percentages of *Equisetum* and Polypodiaceae spores in the early Holocene, but do not exhibit the change to DST in the middle Holocene that characterizes records from older glaciated surfaces (Eisner and Colinvaux 1992; Oswald et al. 1999).

The consistent patterns of indicator taxa in these records suggests that the early to middle Holocene changes in vegetation observed in the central Arctic Foothills occurred regionally, but with some variability related to geographic and edaphic factors. In both the central Arctic Foothills and the western Brooks Range, tundra apparently similar to modern PST was present at the beginning of the Holocene. However, between *ca.* 10,000 and 7000 cal years BP there was a transition from PST to DST on Sagavanirktok and other old surfaces, after which PST taxa were no longer abundant in the vegetation. In contrast, the pollen records from Red Green Lake and other sites on recently glaciated surfaces show that areas with coarse-textured substrates did not undergo this vegetational change. Instead, these surfaces have been occupied by tundra not unlike modern PST since at least 8500 cal years BP.

Implications

The finding that Sagavanirktok and other old surface ecosystem experienced a stronger vegetational response to Holocene climatic change than their recently glaciated counterparts suggests that old, weathered landscapes may be more susceptible to major environmental changes in the future. If, as in the early Holocene, future warming results in lower effective moisture in northern Alaska, we might expect the complex feedbacks of the DST ecosystems to be disrupted. For example, warmer conditions might reduce soil moisture and accelerate soil decomposition rates (e.g., Hobbie 1996), reducing vegetation cover and the depth of the organic layer, and thus leading to deeper permafrost thawing and even drier soils. In contrast, the vegetation of Itkillik II surface was relatively insensitive to past climate change, and therefore may not be as strongly affected by future warming as the Sagavanirktok surface. Because their coarse-texture results in inherently low water-holding capacity, Itkillik II soils will likely support relatively xeric, sparse tundra vegetation regardless of climate. The effect of substrate on ecosystem sensitivity to climate change may also be important at the circumarctic scale. Substrate varies greatly across the Arctic, with heterogeneity occurring at variety of spatial scales, and resulting from many different factors (e.g., glacial history, parent material, or eolian deposition; Walker et al. 1998; Walker 2000). The critical role of substrate in the Holocene ecosystem history of the central Arctic Foothills suggests that this edaphic variability may impart strong spatial heterogeneity on how arctic tundra ecosystems respond to future climate change.

Table 4.1. Taxa indicative of the vegetation of the Itkillik II surface (PST) and the Sagavanirktok surface (DST) according to modern pollen-vegetation calibration study (Chapter 3). *Encalypta* is also considered a PST indicator following Brubaker et al. (1998).

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

Table 4.2. Radiocarbon dates from Red Green and Upper Capsule lake-sediment records. Calibrated ages in bold were used in age-depth model. See Appendix 1 for discussion of average ages from multiple dates.

Depth (cm)	^{14}C years BP	CAMS number	Material	Mass (mg C)	+1 SD [Calibrated ^{14}C age(s) BP] –1 SD
Red Green					
16-21	2910 ± 100	69507	Unidentified plant & insect fragments	0.06	3236 [3061, 3046, 3037, 3007, 3003] 2886
69-70	1790 ± 50	54625	Terrestrial moss fragments	0.16	1816 [**1710**] 1627
123-124	3110 ± 60	54626	Moss fragments & stems	0.47	3382 [**3350**] 3265
202-203	7116 ± 73	---	Average age for 3 dates[a]	---	8001 [7940, **7885**, 7882] 7859
214-216	7490 ± 100	64011	Moss & semi-woody pieces	0.09	8389 [**8335**] 8180
229-230	7500 ± 70	54627	Wood & moss fragments	0.17	8385 [**8341**] 8195
275-276	7800 ± 140	64012	Semi-woody fragment	0.06	8928 [**8590**] 8413

Table 4.2 continued

Depth (cm)	^{14}C years BP	CAMS number	Material	Mass (mg C)	+1 SD [Calibrated ^{14}C age(s) BP] −1 SD
Upper Capsule					
75-76	1670 ± 50	66740	Moss fragments	1.37	1687 [**1553**] 1524
100-101	650 ± 80	54634	*Betula* & other leaf fragments	0.08	668 [649, 578, 572] 549
155-157	3705 ± 67	—	Average age for 2 of 3 dates[b]	—	4148 [4081, **4030**, 3993] 3929
207-208	1070 ± 50	64013	Terrestrial moss fragments	0.51	1051 [966] 932
230-231	6610 ± 60	54635	Woody & semi-woody pieces	0.41	7569 [7551, 7542, **7505**, 7499, 7484] 7431
250-251	8200 ± 50	66744	Terrestrial moss fragments[c]	1.08	9268 [9238, 9220, 9187, **9178**, 9130, 9095, 9093] 9030
260-261	8220 ± 50	54636	Leaf, terrestrial moss, & graminoid pieces	0.47	9395 [9248, 9216, 9208, **9198**, 9192, 9172, 9133] 9033
310-311	9957 ± 32	—	Average age for 6 of 7 dates[d]	—	11545 [11333, 11321, **11298**, 11270, 11262] 11257
325-326	9790 ± 50	54637	Unidentified plant & woody fragments	0.71	11226 [**11196**] 11172

[a] Average of CAMS 66737, 66738, and 66739

[b] Average of CAMS 66741 and 66743; 66742 not used

[c] Second sample from this level (CAMS 66745) not used

[d] Average of CAMS 66734, 66735, 66736, 66746, 66748, and 66749; 66747 not used

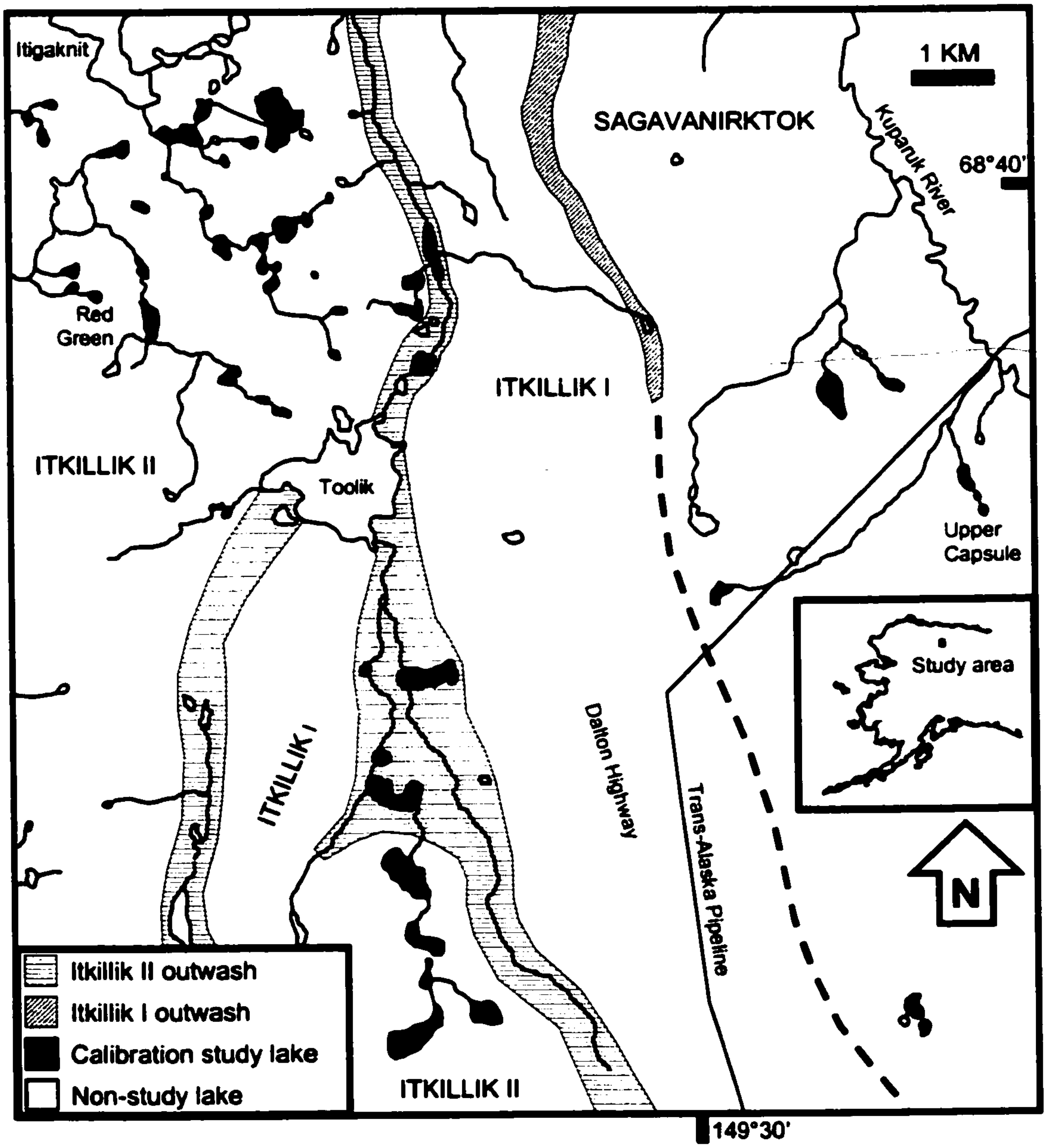

Figure 4.1. Map of the study area with locations of Red Green Lake (RG) and Upper Capsule Lake (UC). Glacial geology is redrawn from Hamilton (1978) and Walker et al. (1995). The dashed line indicates the boundary between the Itkillik I and Sagavanirktok surfaces. Lakes drawn in black were sampled for the pollen-vegetation calibration study (Chapter 3). Four additional pollen-vegetation calibration study lakes are located as far as 19 km northeast of this study area (beyond map boundary).

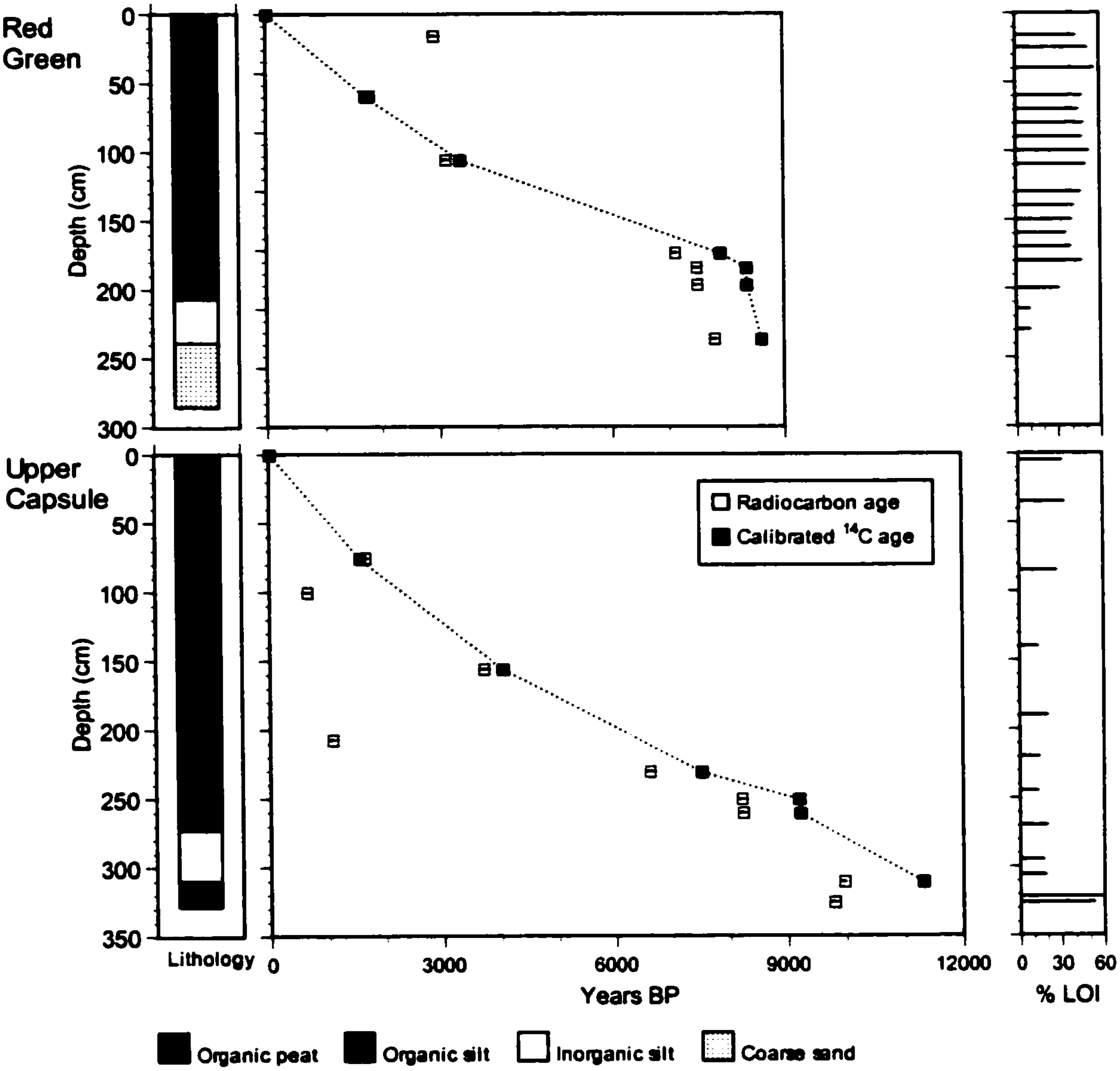

Figure 4.2. Lithology, chronology, and percent weight loss-on-ignition (% LOI) for sediment cores from Red Green Lake and Upper Capsule Lake. The age-depth plots show radiocarbon ages (with ± 1 S.D. indicated by horizontal line within each symbol) and calibrated ^{14}C ages for those dates included in the age-depth model.

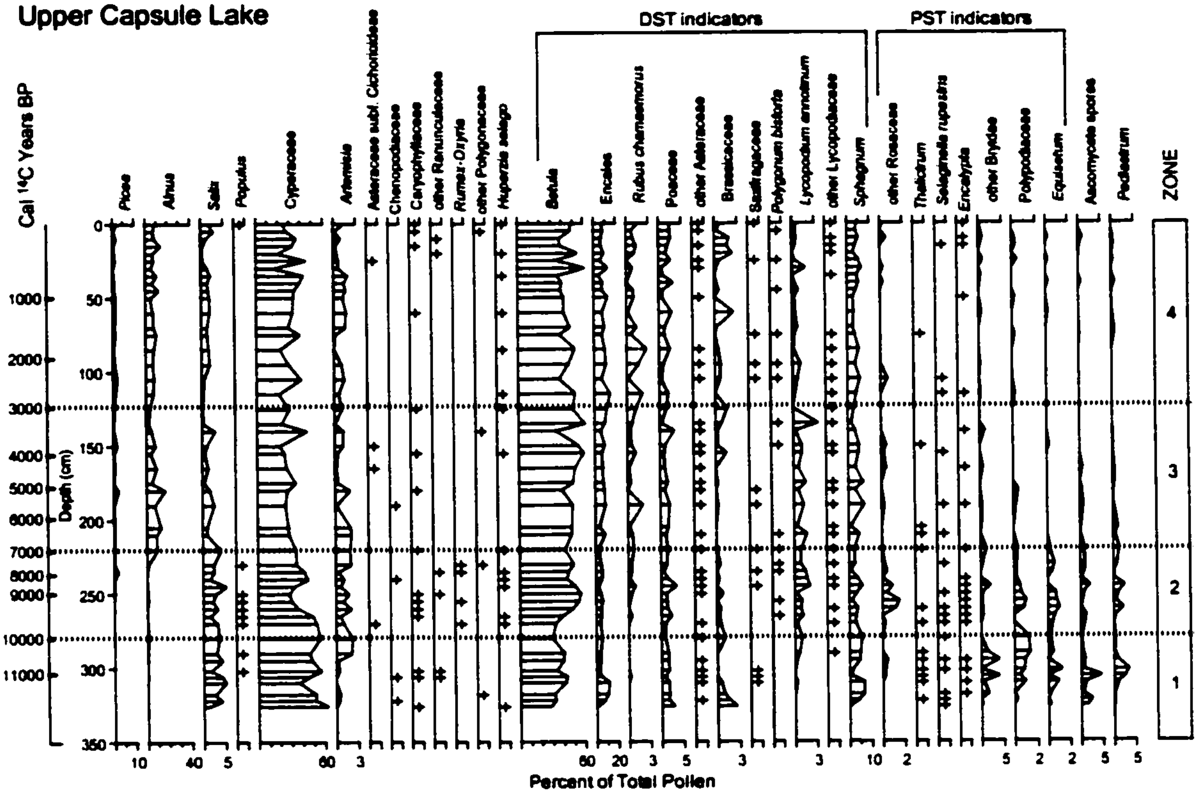

Figure 4.3. Pollen and spore percentage diagram for Upper Capsule Lake (analysis by W. Oswald). Pollen, spores, and *Pediastrum* are expressed as a percentage of the total pollen sum. Scales of the x axes vary. Taxa are classified as indicators of DST or PST vegetation based on their patterns in modern pollen assemblages (Table 4.1). Symbols (+) indicate <2%.

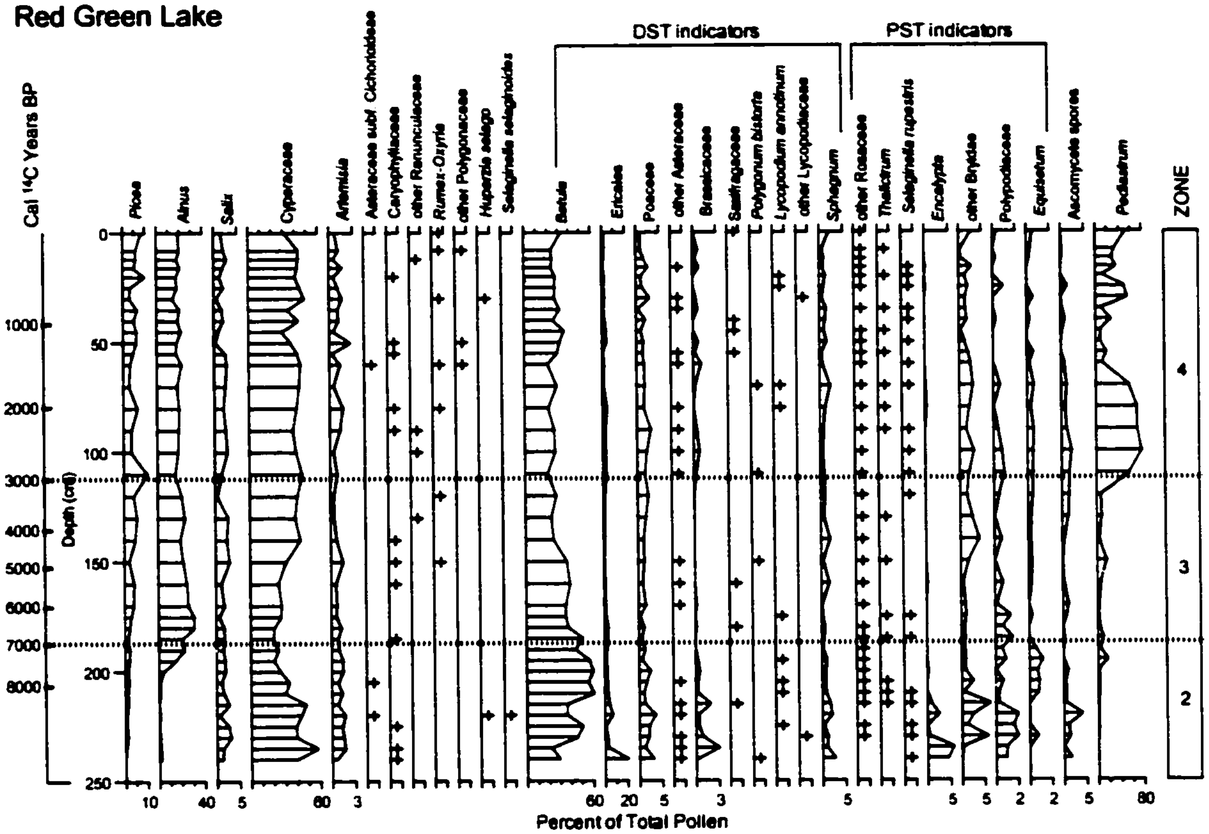

Figure 4.4. Pollen and spore percentage diagram for Red Green Lake (analysis by W. Oswald). Pollen, spores, and *Pediastrum* are expressed as a percentage of the total pollen sum. Scales of the x axes vary. Taxa are classified as indicators of DST or PST vegetation based on their patterns in modern pollen assemblages (Table 4.1). Symbols (+) indicate <2%.

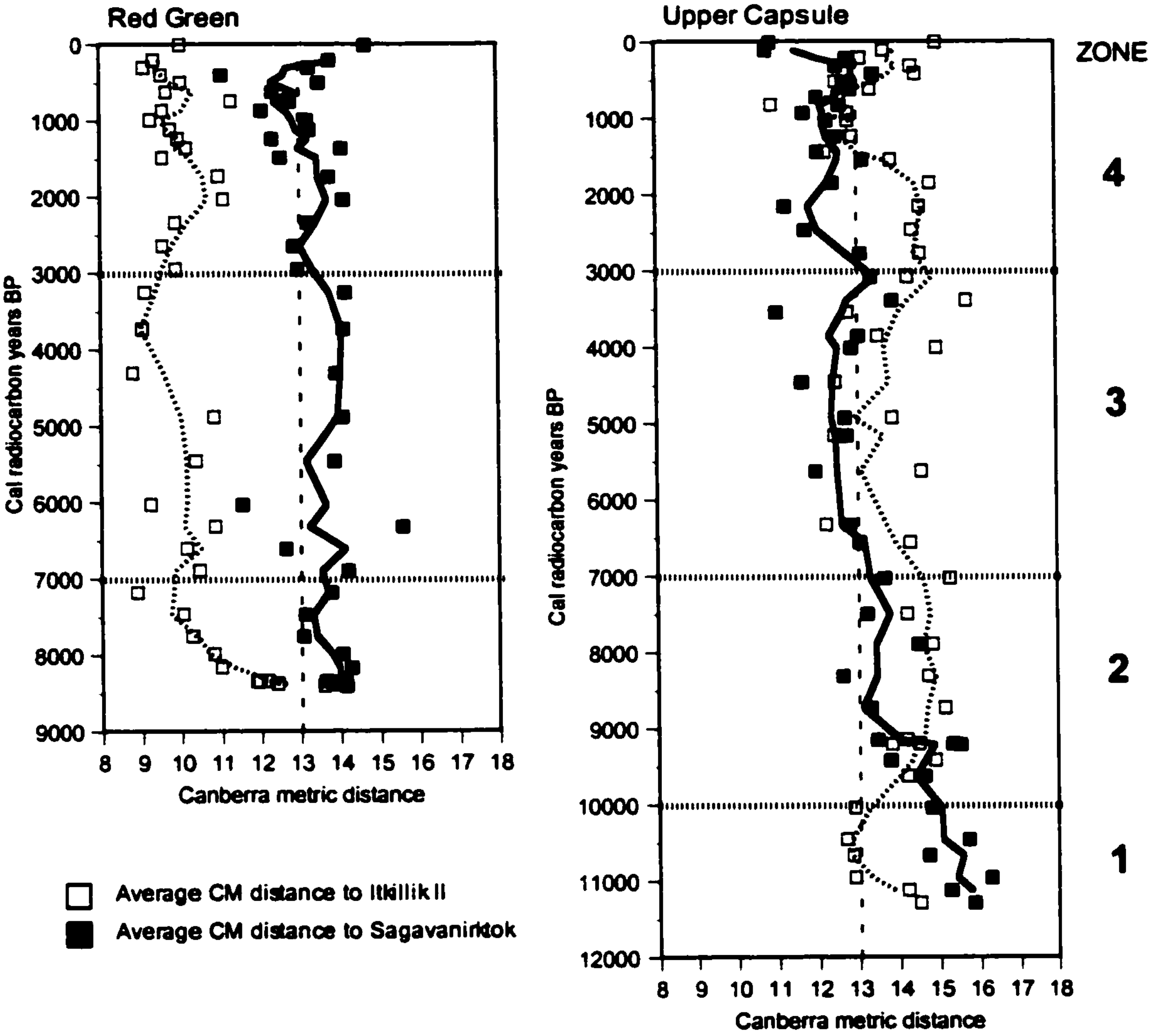

Figure 4.5. Canberra metric distance (CMD) comparison of Red Green and Upper Capsule fossil pollen assemblages with modern pollen assemblages from the Itkillik II and Sagavanirtok surfaces. Each point is the average value of a fossil assemblage to the modern samples of either the Itkillik II or Sagavanirktok surface. Summary lines are 3-point moving averages. The vertical lines show the CMD critical value separating samples from like (CMD <13) and unlike (CMD >13) vegetation types (Chapter 3).

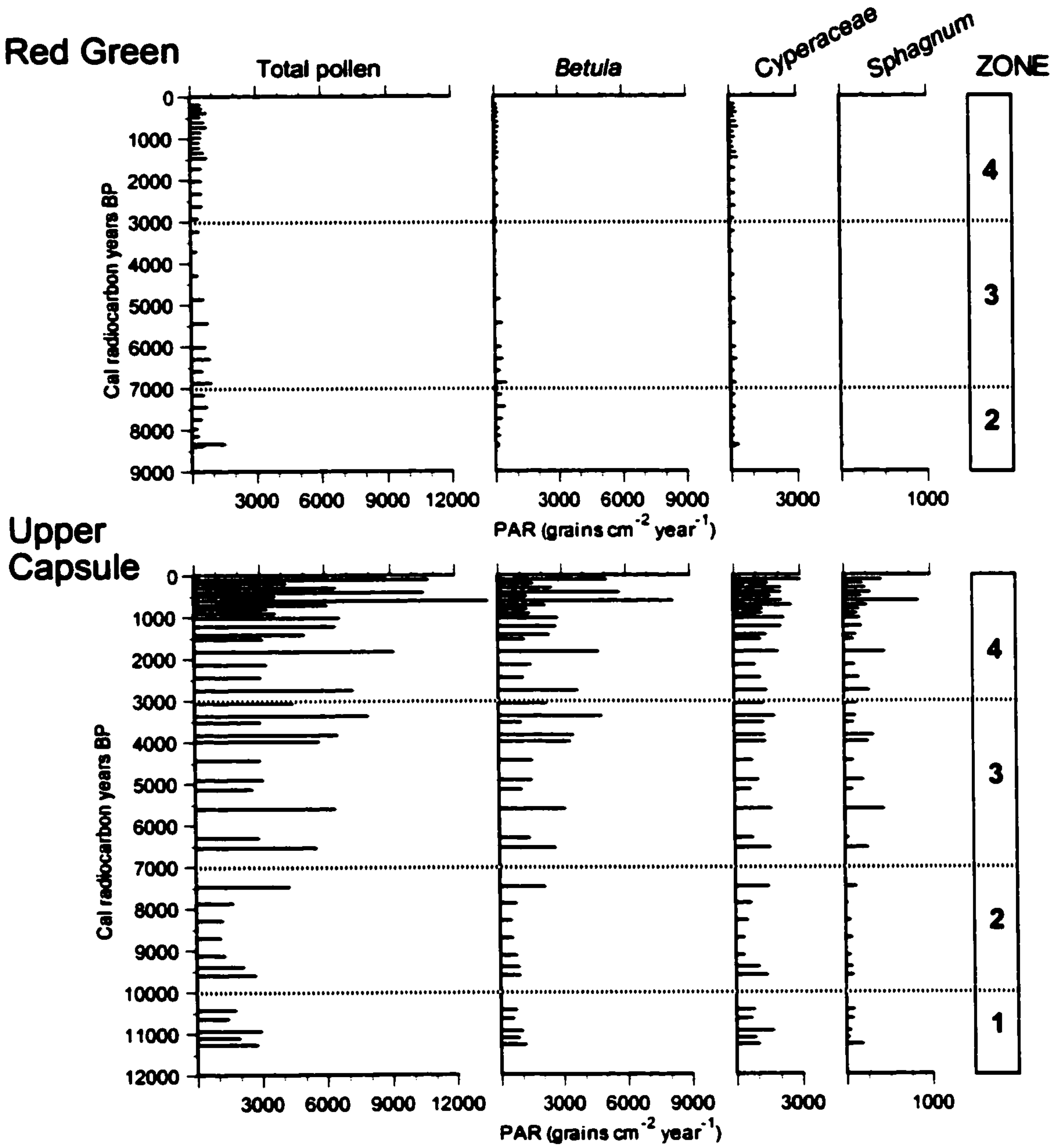

Figure 4.6. Total pollen accumulation rates (PARs) and PARs for selected taxa in the records from Red Green Lake (RG) and Upper Capsule Lake (UC). Five levels with artificially inflated PARs are not shown. Those levels include RG 220 cm = 4319 grains cm^{-2} year^{-1}, RG 225 cm = 21,128 grains cm^{-2} year^{-1}, RG 230 cm = 1511 grains cm^{-2} year^{-1}, UC 255 cm = 54,571 grains cm^{-2} year^{-1}, and UC 260 cm = 40,669 grains cm^{-2} year^{-1}. Scale of x axis for *Sphagnum* differs from other taxa.

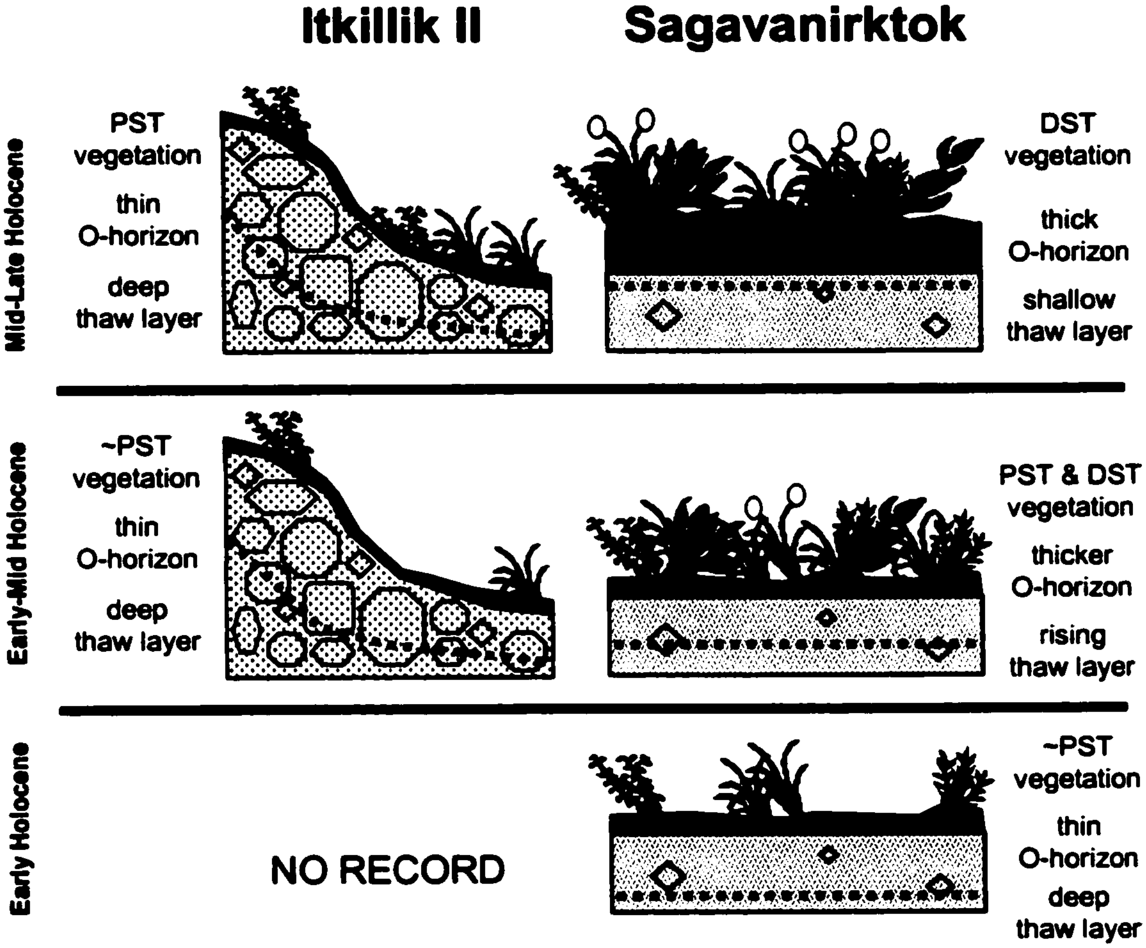

Figure 4.7. Schematic diagram illustrating vegetation and soil characteristics of Itkillik II and Sagavanirktok surface ecosystems before, during, and after the early to middle Holocene increase in effective moisture, as inferred from the Red Green and Upper Capsule pollen records. Dashed lines indicate permafrost thaw depth.

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APPENDIX 1: Pollen representation of tundra in the Arctic Foothills, northern Alaska: relationships between pollen and vegetation abundance

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SUMMARY

To determine the spatial scale of tundra vegetation represented by lake-sediment pollen data, pollen and plant community abundance were compared for 56 lakes in the central Arctic Foothills of northern Alaska. Using vegetation data from a land-cover map of northern Alaska, we determined the percent cover of several tundra types within concentric circular plots extending to 5000 m from the center of each lake. Dwarf-shrub tundra (DST) and low-shrub tundra (LST) were common on Sagavanirktok and Itkillik I glaciated surfaces, whereas prostrate-shrub tundra (PST) and wet graminoid tundra (WGT) were common on the younger Itkillik II glaciated surface. To approximate the relevant pollen source area for this data set, we examined the relationship between pollen and spore percentages and percent cover of the four main tundra types, and determined the plot radii at which these variables were best correlated. *Betula* and *Rubus chamaemorus* pollen percentages were best correlated to LST between 1750 and 2500 m. *Equisetum*, Polypodiaceae, and Bryidae spore percentages had highest correlations with WGT cover at 3000, 2000, and 4000 m, respectively, and their correlations with PST cover reached an asymptote between 500 and 3000 m. Percentages of several taxa were best correlated with DST at distances between 500 and 1500 m, including *Rubus chamaemorus*, *Sphagnum*, Ericales, Poaceae, Brassicaceae, and Asteraceae. These patterns suggest that pollen data reflect relatively small-scale (<2 km) patterns of tundra vegetation in the central Arctic Foothills.

INTRODUCTION

Lake-sediment pollen records are widely used to reconstruct past vegetation (e.g., Wright et al. 1993), although the spatial scale represented by pollen data is often not well understood (e.g., Jackson 1994). This is particularly true in the Arctic, where palynology has been considered a "blunt instrument" for paleoecological research (Colinvaux 1967), in part because of the unclear spatial resolution of pollen records (e.g., Colinvaux 1964, Anderson et al. 1994, Gajewski et al. 1995). Consequently, the interpretation of past spatial patterns of arctic vegetation is often vague or speculative (e.g., Oswald et al. 1999).

Empirical and modeling studies show that pollen source area, the area that produces that component of the pollen rain that varies in response to differences in vegetation from location to location, is related to the size of the sedimentary basin (e.g., Bradshaw and Webb 1985; Prentice 1985; Sugita 1994). Large sedimentary basis, such as large lakes (>150 ha), collect pollen from a large geographic area and thus are thought to reflect regional patterns of vegetation (e.g., Jacobson and Bradshaw 1981). Small sedimentary basins, such as small lakes and forest hollows (<1 ha), apparently provide records of smaller-scale patterns of vegetation (e.g., Jacobson and Bradshaw 1981; Calcote 1995). However, the theoretical understanding of the spatial scale represented by pollen records is based primarily on what has been learned in temperate, forested areas, and thus may not be applicable to arctic tundra. In tundra ecosystems, many of the pollen types are insect-dispersed rather than wind-dispersed, and the smaller stature of the vegetation may result in different patterns of pollen dispersal than in forests.

We conducted a study in the Arctic Foothills of northern Alaska to explore the relationship between geographic patterns of tundra plant communities and lake-sediment pollen signatures. By comparing modern pollen data with vegetation cover at a variety of distances from study lakes, we attempted to determine the spatial scale at which the pollen best reflects the surrounding vegetation.

STUDY AREA

This research was conducted in the Toolik Lake area of the central Arctic Foothills. The study area (Fig. 5.1) can be divided into two major landscape units with different topography, soils, and tundra plant communities; these differences are attributable to their different glacial histories (Detterman et al. 1958; Hamilton and Porter 1975; Hamilton 1994). Most surfaces in the study area are glacial drift and outwash dating to the Sagavanirktok River (>125,000 years BP) or Itkillik I (>60,000 years BP) glacial advances from the Brooks Range (Hamilton 1978). These landscapes have been modified by long periods of weathering, mass wastage, and eolian deposition, and thus are characterized by rolling topography and clayey-to-silty soil textures (Hamilton 1994). Active layers are shallow on old landscapes, resulting in poor drainage and acidic, waterlogged soils (Walker et al. 1989, 1994). The more recent Itkillik II glacial advance (24,000 to 11,500 years BP) covered the southwestern portion of the study area. This landscape has steeper, better drained, and more irregular terrain (Hamilton 1994), and its soils have higher pH, thinner organic horizons, and deeper thaw layers (Bockheim et al. 1998; Munroe and Bockheim 2001).

The distribution of tundra communities in this area (Fig. 5.2) is strongly controlled by the variations in topography and soils (Walker et al. 1994; Walker and Walker 1996). The Sagavanirktok and Itkillik I surfaces are occupied primarily by moist dwarf-shrub tussock-graminoid tundra (dwarf-shrub tundra; DST) the typical tussock tundra found in many parts of the Arctic (Hanson 1953; Alexandrova 1980; Bliss and Matveyeva 1992; Muller et al. 1999). Dominant plants include *Eriophorum vaginatum*, *Sphagnum* species, *Betula nana*, *Ledum palustre*, *Vaccinium vitis-idaea*, and *V. uliginosum* (Walker et al. 1994). Moist low-shrub tundra and other shrublands (low-shrub tundra; LST) are also common on the older glacial surfaces, particularly in riparian areas (Walker et al. 1994; Muller et al. 1999). *Eriophorum angustifolium* and *Salix* species dominate LST (Walker et al. 1994). Moist graminoid prostrate-shrub tundra (prostrate-shrub tundra; PST) dominates the Itkillik II landscape. PST features non-tussock Cyperaceae (e.g. *Carex bigelowii*); prostrate shrubs (e.g., *Salix arctica* and *S. reticulata*); non-*Sphagnum* mosses (e.g., *Tomentypnum nitens*, *Aulacomnium turgidum*, and *Hypnum bambergeri*); and *Dryas integrifolia* (Walker et al. 1994, 1998). Wet graminoid tundra (WGT) is also common on Itkillik II landscapes in this area, especially in fens. *Carex aquatilis* and

Eriophorum angustifolium are the dominant species (Walker et al. 1994; Muller et al. 1999). Dry tundra and barrens communities (Muller et al. 1999) are rare near Toolik Lake, but do occur on Imnavait Mountain and other highlands in the northern portion of the study area.

METHODS

We collected sediment-water interface samples from 56 small-to-medium-sized (<25 ha) lakes on the Sagavanirktok and Itkillik II glaciated surfaces in the central Arctic Foothills (Fig. 5.1). Samples were taken near the center of each basin using either a gravity corer or a piston surface-sediment sampler. The uppermost 1-2 cm of the sediment core was used for pollen analysis, and 2 cm^3 samples were prepared according to 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 100x objectives (12x eyepieces). Non-*Sphagnum* moss (Bryidae) spores were classified following Brubaker et al. (1998). At least 350 pollen grains of terrestrial plant taxa were counted for each sample. Pollen and spore abundance was expressed as a percentage of the sum of all identified and unidentified pollen grains.

The plant community data were derived from a land-cover map of northern Alaska created by Muller et al. (1999). The map has eight broad land-cover categories, six of which occur in this study area: DST, LST, PST, WGT, dry tundra and barrens, and water. We used ArcView 3.2 software (ESRI 1996) to measure the coverage of these land-cover categories in a series of concentric circles centered on the 56 study lakes. Measurements were taken for circular plots with radii of 250, 500, 750, 1000, 1250, 1500, 1750, 2000, 2500, 3000, 3500, 4000, 4500, and 5000 m. Vegetation cover was expressed as a percentage of the non-water land cover in each circular plot.

To determine the geographic area that is reflected by the lake-sediment pollen data, we calculated the correlation between the percentage value for each pollen and spore type and the percentage cover of each vegetation type for all 56 lakes at each of the 14 plot-radius distances. We then plotted these correlation values against plot radius to determine the distance at which the pollen and vegetation percentages are best correlated. In this type of analysis we assume that pollen inputs are equal from all directions (Sugita 1993); this pattern is more likely true for insect-dispersed than wind-dispersed pollen types.

RESULTS

Several of the taxa were more abundant in samples from one glaciated surface or the other (Fig. 5.3). Sagavanirktok surface lakes had relatively high percentages of *Rubus chamaemorus*, *Sphagnum*, Ericales, Poaceae, Brassicaceae, *Lycopodium annotinum*, Saxifragaceae, Asteraceae, Lycopodiaceae (excluding *L. annotinum* and *Huperzia selago*), *Betula*, and *Polygonum bistorta*. Itkillik II surface lakes had relatively higher percentages of *Alnus*, *Equisetum*, *Picea*, Polypodiaceae, *Thalictrum*, and Rosaceae. The correspondence between pollen assemblages and the vegetation of the Sagavanirktok and Itkillik II surfaces is discussed in detail elsewhere (Chapter 3).

In general, DST and LST surround Sagavanirktok lakes, whereas PST and WGT surround Itkillik II lakes (Figs. 5.2 and 5.4). However, several of the lakes south of Toolik Lake are located in DST vegetation, even though they sit on Itkillik II outwash. In some cases, vegetation changes dramatically with increasing distance from the lake. For example, lake 38 has high percent cover of PST within 750 m, but DST and LST dominate beyond that distance. On the other hand, a number of other lakes have proportionally the same vegetation cover in all of the different-size circular plots up to 5000 m. Maximum percentage values for DST, LST, PST, and WGT in any plot are 80, 70, 85, and 35%, respectively. As the dry tundra and barrens category never occurred at greater than 8%, it was excluded from the subsequent analyses.

We examined how the relationship between pollen and plant community abundance changed with increasing plot size (Fig. 5.5), and plotted combinations of pollen or spore types and vegetation types that were significantly correlated ($p<0.01$) at any distance

(Fig. 5.6). *Betula* and *Rubus chamaemorus* pollen percentages were correlated with the abundance of LST, and both taxa had a peak in correlation coefficients between 1750 and 2500 m (r=0.48 and 0.41, respectively). Six different taxa were correlated with DST percent cover. Poaceae reached an asymptote at 750 m with a correlation of 0.37. Asteraceae and Brassicaceae had correlation peaks of 0.47 and 0.43, respectively, at a distance of 750, after which their correlation values decreased quickly to around 0.3 at 1750 m. Ericales, *Rubus chamaemorus*, and *Sphagnum* also had their highest r values at 750 m (0.54, 0.53, and 0.45, respectively). Their correlations decreased sharply between 1000 and 1750, then increased gradually.

Equisetum, Polypodiaceae, and Bryidae percentages were correlated with the abundance of PST. Their correlations increased dramatically from 250 to 500, at which point Bryidae appears to reach an asymptote at an r of around 0.4. *Equisetum* r values gradually increased to 0.52 at 3000 m, whereas Polypodiaceae was best correlated to PST at 2500 m (r=0.44). These three taxa were also correlated with the abundance of WGT. Polypodiaceae correlations increased to 0.46 over the first 2000 m, then decreased after 2500 m. For *Equisetum*, correlation values rose quickly between 250 and 1000 m, then increased at a slower rate until they reach a maximum value of 0.55 at 3000 m. There was not a clear peak in the correlations between Bryidae percentages and WGT abundance, but they may have reached an asymptote at 4500 m where r=0.57. *Alnus* pollen percentages were also correlated with the abundance of both PST and WGT, but these data are not shown. We do not consider this relationship to be informative in this case because *Alnus* does not occur in the study area. Oswald et al. (Chapter 3) provide a more detailed discussion of the pattern of *Alnus* percentages in these samples.

DISCUSSION

Sugita (1993) introduced the concept of "relevant source area" for pollen, defined as the area beyond which the correlation with plant abundance does not improve. As the vegetation data in our study was at the level of the plant community rather that individual species, we did not estimate relevant pollen source area exactly as Sugita (1993) envisioned, or as others have attempted to do with empirical studies (e.g., Calcote 1995). However, as the plant communities examined in this study are defined in part by the presence or abundance of key plants (Walker et al. 1994), we can assume that each geographic area classified as a given vegetation type has roughly the same percent cover of the component species. Thus, if the abundance of a certain vegetation type (e.g. DST tundra) increased with plot radius, we can probably assume that the abundance of taxa associated with that vegetation type (e.g., *Sphagnum*) also increased in abundance. Therefore, if we found that the correlation between a vegetation type and a pollen type does not improve beyond some distance, then we have indirectly estimated the relevant source area for that taxon.

In the Toolik Lake area, the correlations between pollen and vegetation types did reach asymptotes or peaks as study plot radius increases from 250 to 5000 m. However, the distance at which modern lake-sediment pollen percentages were best correlated with the surrounding tundra vegetation varied somewhat between pollen taxa and vegetation types. For DST, the significantly correlated taxa reached peaks or asymptotes between 500 and 1000 m, whereas the best correlations for LST were between 1750 and 2500 m. For WGT, Polypodiaceae, *Equisetum*, and Bryidae each had its highest correlation at a different plot radius (2000, 3000, and 4500 m, respectively). It was somewhat more difficult to define the distance at which the pollen data reflects the abundance of PST, as the correlated taxa reached an asymptote at 500 m, but achieved their highest r values with larger vegetation plots (radii between 2000 and 3000 m). Despite this variability, it appears that the pollen data generally reflect landscape-scale vegetation patterns. For the most part, the sample sites fall within a few 100 m of the boundary between the Itkillik I and Itkillik II glacial surfaces, which marks the major change in plant community abundance. As the size of our vegetation study plots increased to 1000-2000 m radii, they crossed that vegetational boundary and in many cases the correlation between vegetation and pollen abundance decreased sharply.

These findings confirm the results of a related study (Chapter 3) which defined indicator pollen and spore taxa for the vegetation of the Sagavanirktok and Itkillik II landscapes. Similar to Oswald et al. (Chapter 3), we found that Sagavanirktok surface plant communities (DST and LST) are characterized by *Rubus chamaemorus*, *Betula*, *Sphagnum*, Ericales, Poaceae, Brassicaceae, and Asteraceae, whereas Itkillik II plant communities (PST and WGT) are characterized by *Equisetum* and Polypodiaceae. Moreover, the approach used in this study illustrates that the pollen data reflect even smaller-scale patterns of plant community variability. For example, lakes on the western edge of the study area (samples 1-4 and 26-30) had higher percent cover values of PST tundra than Itkillik II surface lakes closer to the boundary with the Itkillik I landscape (e.g., samples 20 and 24, Fig. 5.4). These lakes also had the highest Bryidae spore percentages in our data set, which is consistent with the fact that PST plant communities have high abundance of mosses, such as *Tomentypnum nitens* (Walker et al. 1994). Thus, the fact that the correlation between PST and Bryidae spore abundance reached an asymptote at only 500 m suggests that the pollen data reflect the variability of plant community patterns within the Itkillik II landscape. At the coarser scale examined by Oswald et al. (Chapter 3), these details of the pollen-vegetation relationship are less easily recognized.

Interestingly, the relevant source area for these pollen and spore taxa appears to be related to plant community rather than dispersal vector. We expected that those types that are dispersed primarily by wind (e.g., *Betula* and Poaceae) would have larger source areas than insect-dispersed types (e.g., *Rubus chamaemorus*, Brassicaceae, and Asteraceae). However, no such pattern was apparent, and instead the distance at which the best pollen-vegetation correlation occurs seems to depend upon the vegetation type. For example, for LST *Rubus chamaemorus* and *Betula* both reach their highest correlation at 1750 m, whereas for DST tundra all six of the taxa have relevant source areas between 500 and 1000 m. This suggests that vegetation patch size and distribution may influence the assessment of pollen source area, as those plant communities with relatively small patch size (WGT and LST) were characterized by larger source areas than those with larger patch size (PST and DST). However, regardless of the effect of patch size, the relevant source areas for all taxa were quite small, suggesting that even wind-dispersed pollen grains like those of *Betula* and Poaceae tend to not travel great distances.

In fact, we can use these data to roughly estimate the percentage of the observed *Betula* pollen that is of extra-local origin. Since *Betula nana* is virtually absent from the PST and WGT plant communities (Walker et al. 1994), we can assume that the percentage of *Betula* pollen in lakes without DST and LST represents its background abundance. Thus, the y-intercept in graphs of *Betula* pollen percentage versus the summed percent cover of DST and LST provides an estimation of how much *Betula* pollen travels into lakes where *Betula nana* is not present in the surrounding vegetation (Fig. 5.7). Depending on the size of the plot where these variables are compared, the y-intercept varied between 20 and 27%, which suggests that the *Betula* percentage must reach at least 20% to indicate the local presence of *Betula nana*. Interestingly, Anderson and Brubaker (1986) defined 20% as the *Betula* pollen percentage corresponding to the northern range limit of *Betula nana* in Alaska.

Most of the research on relevant pollen source area has focused on very small sedimentary basins, such as forest hollows and moss polsters (e.g., Jackson and Wong 1994; Sugita 1994; Calcote 1995; Gavin and Brubaker 1999), whereas only a few studies have addressed this topic using lake-sediment pollen data. Bradshaw and Webb (1985) compared tree-inventory data collected on a 1-km^2 grid with modern pollen data from lakes in the mixed hardwood-conifer region of Wisconsin. For small lakes (<9 ha), there was good correspondence between pollen and plant abundance within 2.3 km and 4.5 km radii, but the plant-vegetation correlations were not assessed for plots with smaller radii. Jackson (1990) examined this relationship at a smaller scale using pollen assemblages from small ponds (0.1 to 0.5 ha) in northern New York and southern New England. Comparison of those pollen data with basal area data from surrounding deciduous and mixed conifer-hardwood forests indicated that poorly-dispersed pollen types (*Picea* and

Tsuga) represented nearby vegetation (<500 m) and well-dispersed types (*Quercus*, *Pinus*, and *Betula*) came from sources >1000 m from the ponds. Using a simulation approach, Sugita (1994) examined relevant pollen source area for small (0.8 ha) and medium-sized (19.6 ha) lakes in closed hemlock-hardwood forests of northern Michigan. In that study, small and medium lakes had relevant pollen source areas of 300-400 m and 600-800 m, respectively. Similarly, simulations by Sugita et al. (1999) suggest that small lakes (3.14 ha) in open agricultural and semi-open forested landscapes in southern Sweden have relevant pollen sources areas of 800-1000 m. Our results from the Toolik Lake area are generally consistent with these studies, as the pollen-vegetation correlation peaks and asymptotes indicating the relevant pollen source area usually occurred between 500 and 2000 m. Thus, despite differences in vegetation structure and vectors of pollen dispersal, it does not appear that arctic tundra ecosystems have substantially larger relevant pollen source areas than do forests.

For the assessment of relevant pollen source area to be possible, the pollen data must be compared to an appropriate vegetation data set. We can determine the distance at which the correlation no longer improves only if there is some variability in the abundance of the different vegetation types as sampling plot radius increases. For example, nearly all of the pollen-vegetation correlation curves for the DST, LST, and WGT vegetation types decreased after reaching a peak value. This decline occurred because vegetation beyond the optimal sampling distance contributes less pollen to the lakes, and therefore its inclusion results in weaker correlations. However, the PST vegetation type had a different pattern, with no obvious peak in correlation values. This results from the lack of variability in the relative abundance of PST beyond 750-1000 m (Fig. 5.4). As plot radius increased, PST accounted for approximately the same percent cover for a given lake. Itkillik II surface lakes almost always had percent cover values of either 50-60 or 60-85%, whereas Sagavanirktok lakes had either 0-25 or 25-50% PST cover. The arrangement of lakes and vegetation patches on this landscape simply does not allow us to define the decline in pollen-vegetation correlation that we see in the other vegetation types. However, the sharp increase in correlations at small distances and marginal improvement thereafter suggests that the relevant pollen source area is approximately 500 m for Polypodiaceae and Bryidae, although it may be somewhat larger for *Equisetum*.

The relatively small pollen source areas (500-2000 m) in the Toolik area provide further evidence that palynology in the Arctic as not necessarily as "blunt" as previously assumed (e.g., Colinvaux 1967). The patterns of several pollen and spore taxa accurately reflect the spatial occurrence of plant communities related to topographic and substrate differences between the Itkillik II and Sagavanirktok glacial surfaces. Comparison of the pollen data with species-level vegetation data would likely enhance our understanding of pollen-vegetation relationships for tundra, especially for key taxa such as *Betula* and *Sphagnum*. However, the relevant pollen source distances documented in this study clearly permit the detection of landscape-scale patterns of tundra vegetation, which suggests that fossil pollen records can be used to reconstruct the small-scale spatial variability of past arctic vegetation.

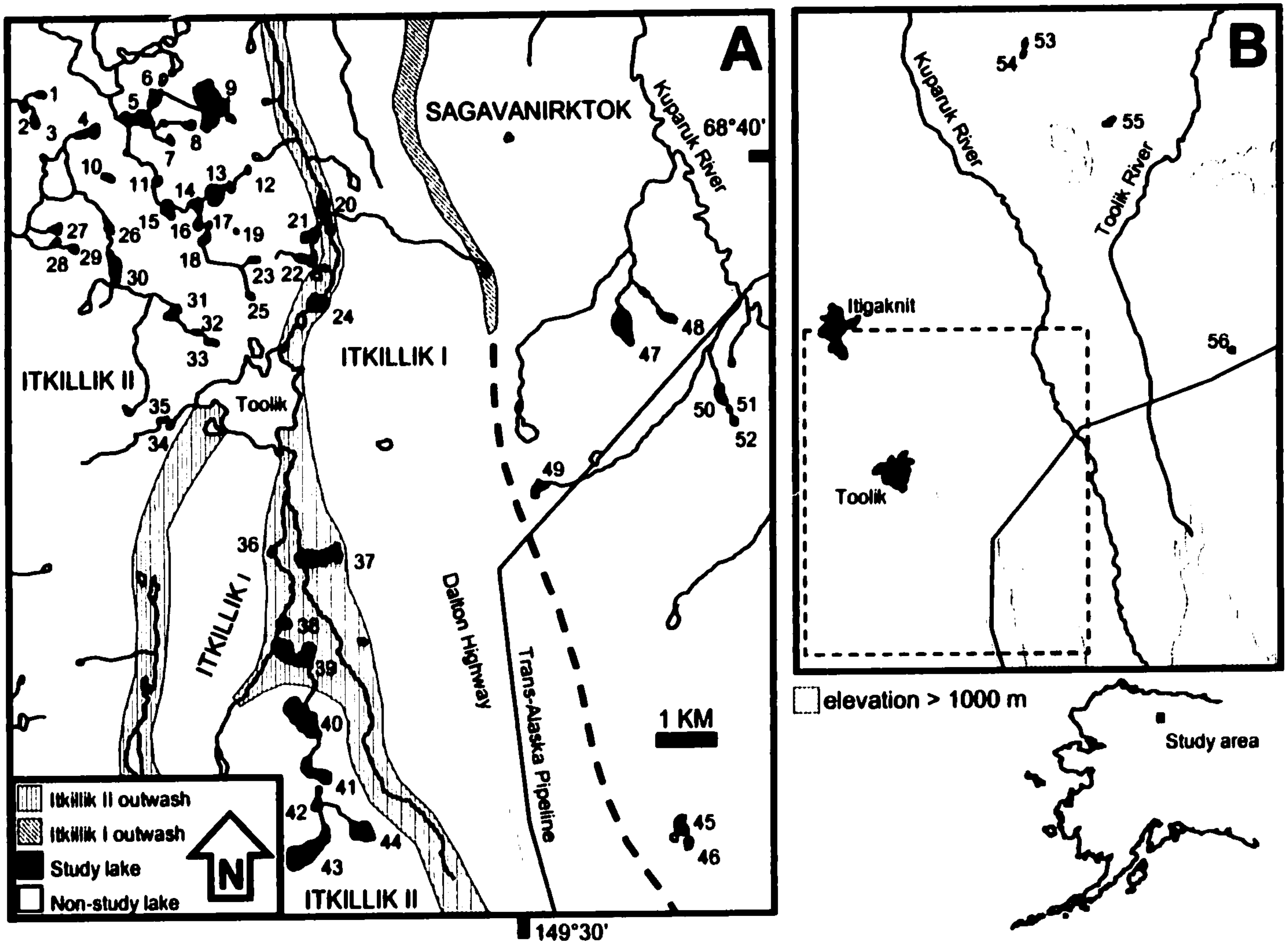

Figure 5.1. Map of the study area indicating study sites for pollen-vegetation calibration research. Glacial geology redrawn from Hamilton (1978) and Walker et al. (1995). Lakes 53-56 are located on Sagavanirktok deposits.

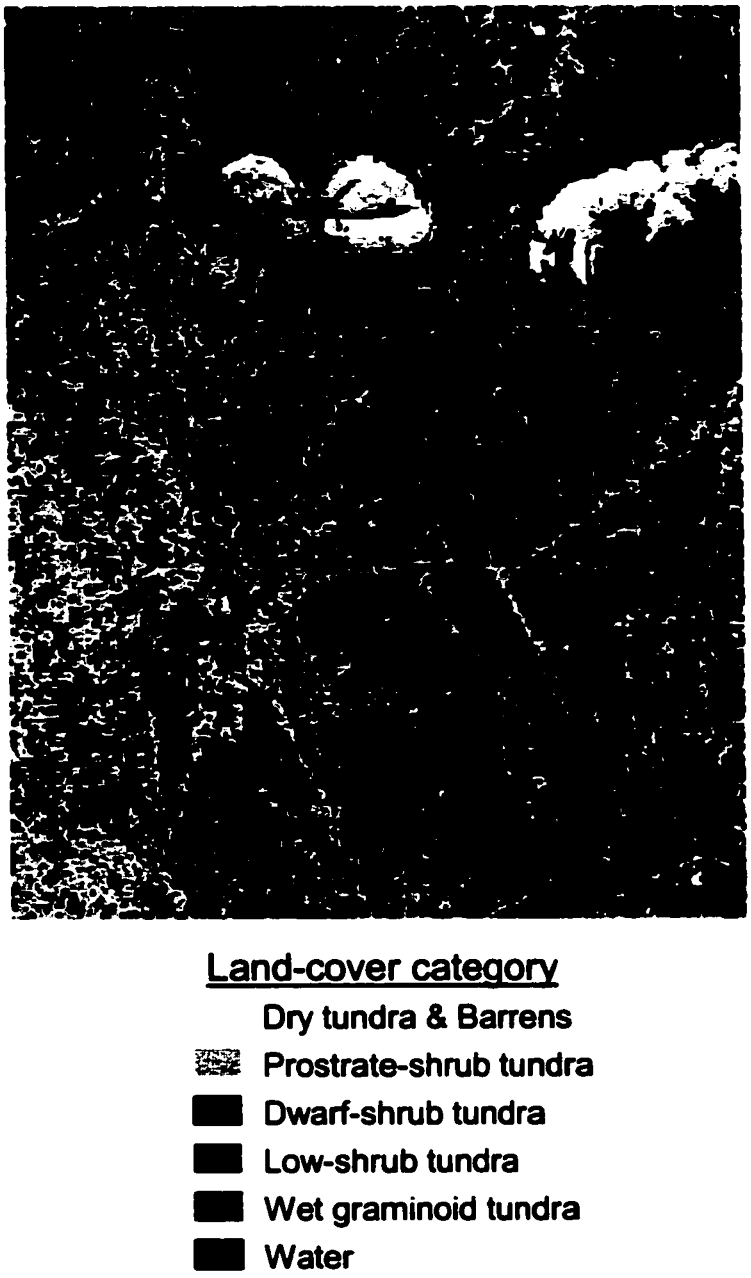

Figure 5.2. Vegetation map for the Toolik Lake area of the central Arctic Foothills using land-cover data from Muller et al. (1999). Map covers the same area as Figure 5.1b.

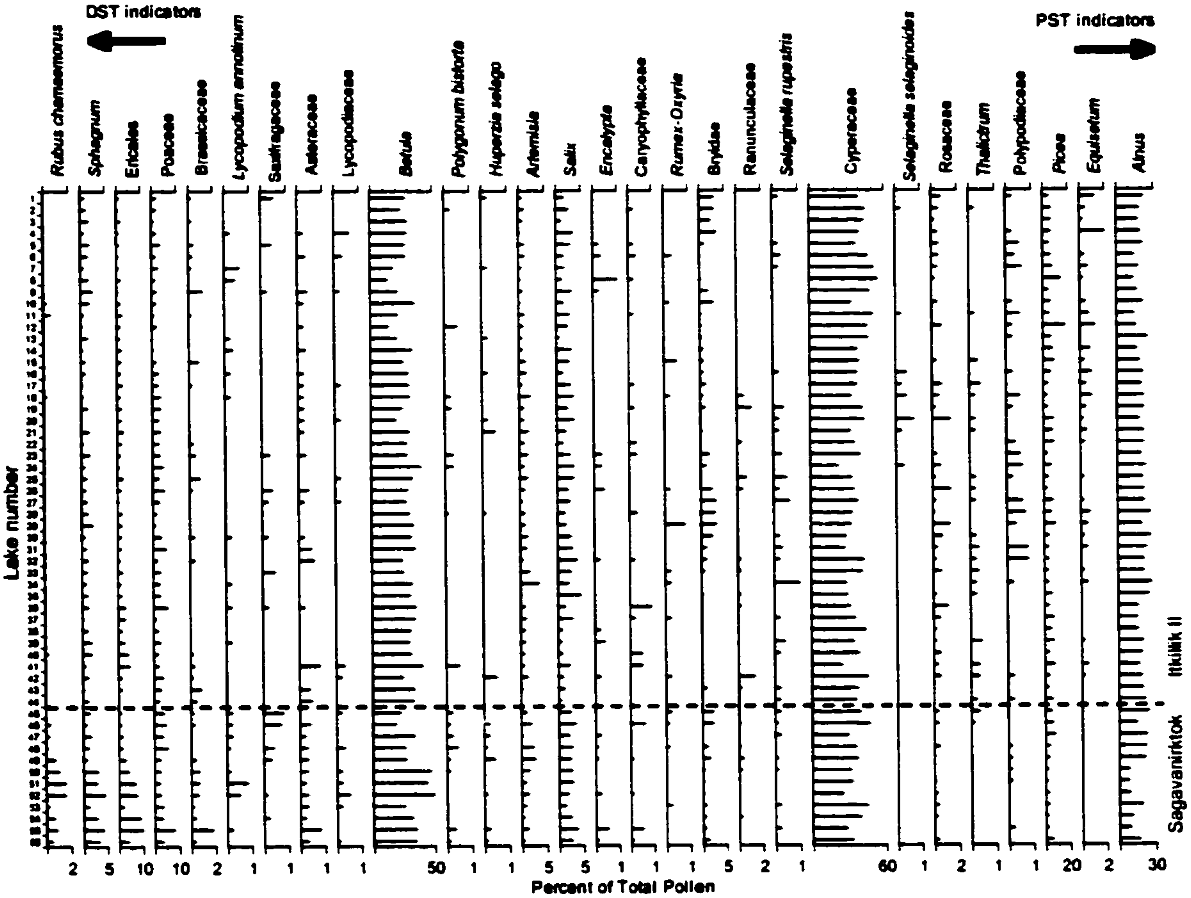

Figure 5.3. Pollen and spore percentage diagram for modern lake-sediment samples from the central Arctic Foothills, northern Alaska (see Chapter 3 for a detailed discussion of these data). Scales of x axes vary.

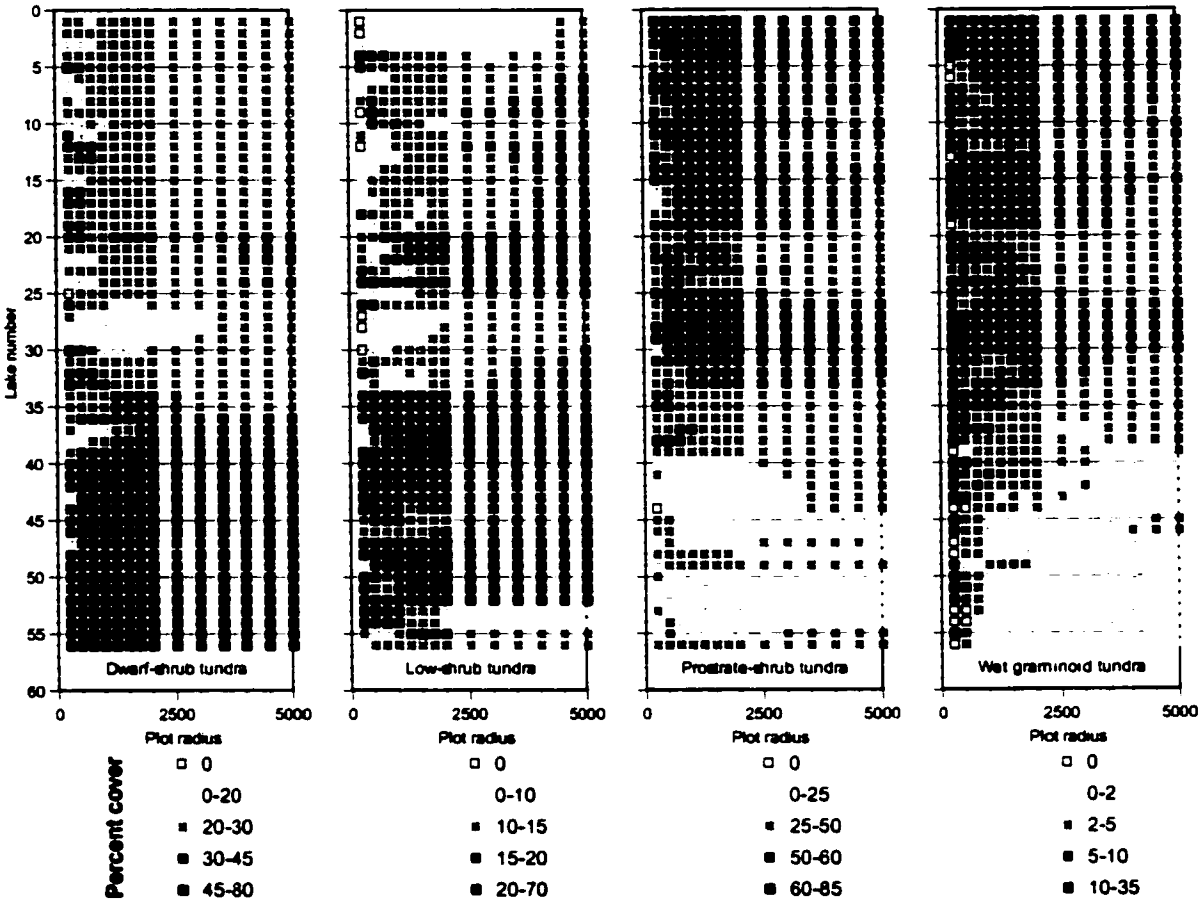

Figure 5.4. Changes in vegetation cover with distance from the study lakes. Boxes show the percent cover of each tundra type for each vegetation plot radius for each of the 56 lakes. Lakes 1-44 are located on the Itkillik II surface, and lakes 45-56 are located on the Sagavanirktok surface. Vegetation data is from the land-cover map by Muller et al. (1999).

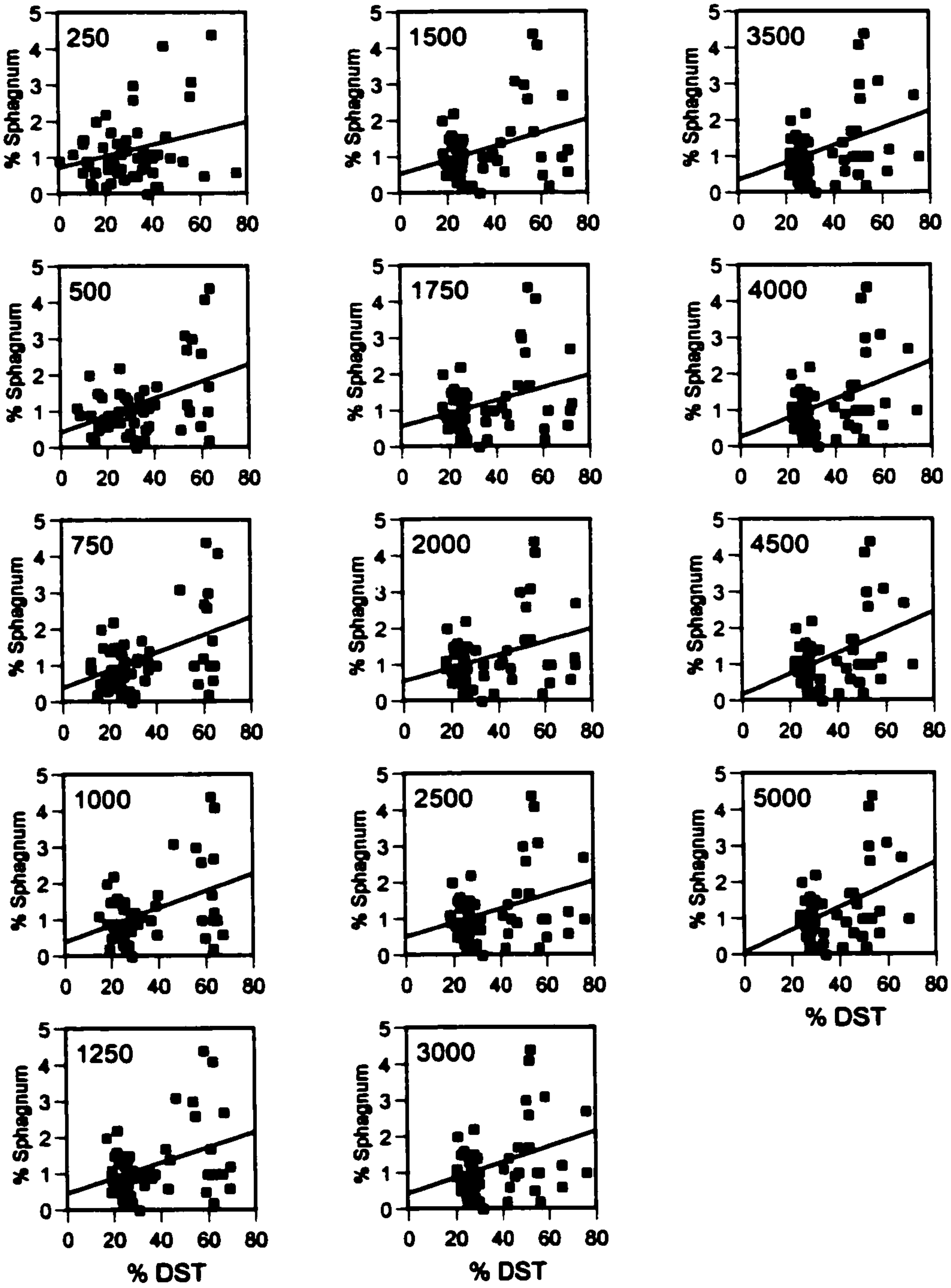

Figure 5.5. Relationship between *Sphagnum* spore percentages and percent cover of dwarf-shrub tundra (DST) for the 56 study lakes at each of the vegetation plot radii distances. All other combinations of vegetation and pollen or spore types were also examined (not shown).

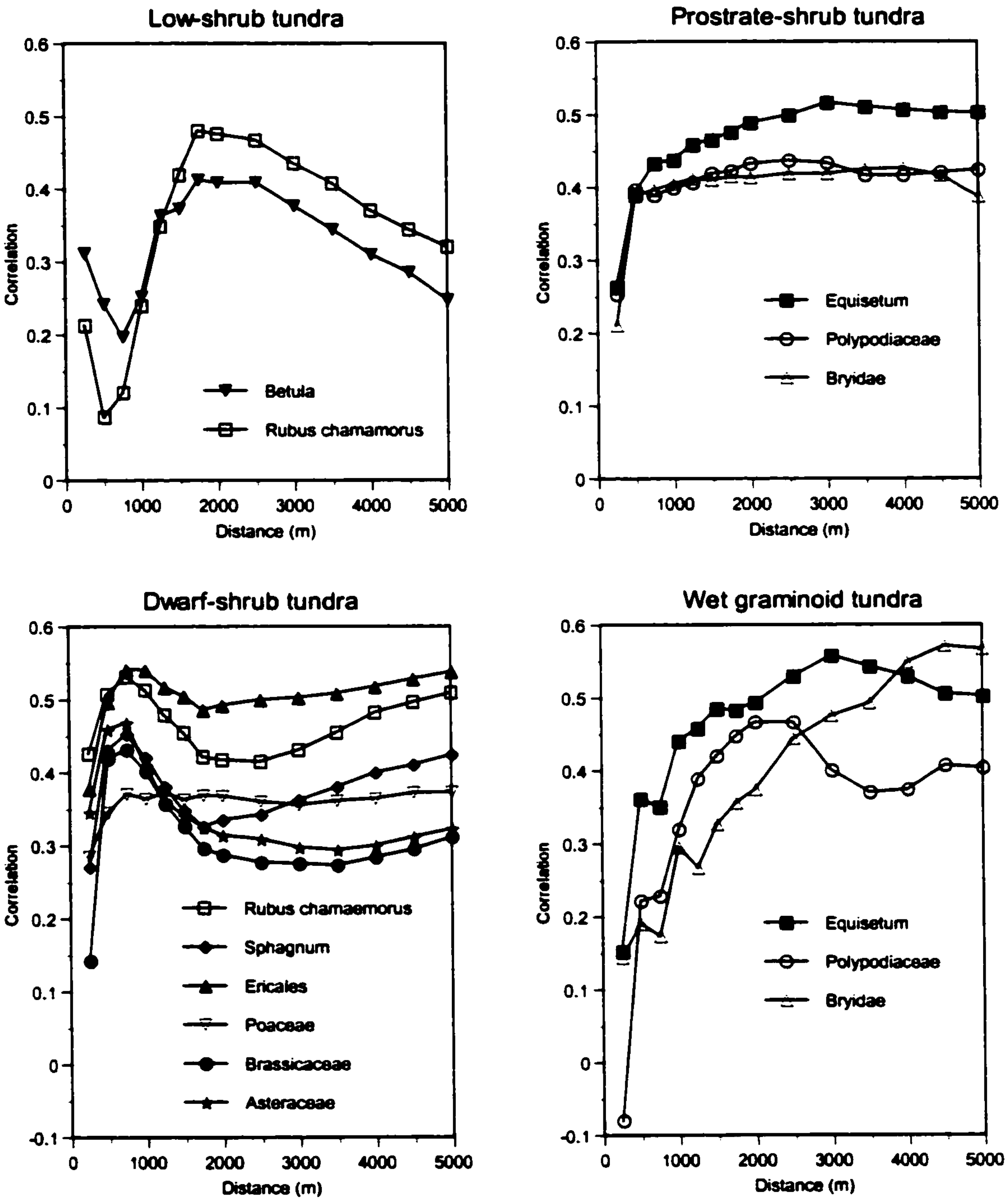

Figure 5.6. Changes in pollen-vegetation correlation with distance from the study lakes. Pollen and spore types were graphed if this correlation was significant ($p<0.01$) for at least one of the 14 plot radii distances.

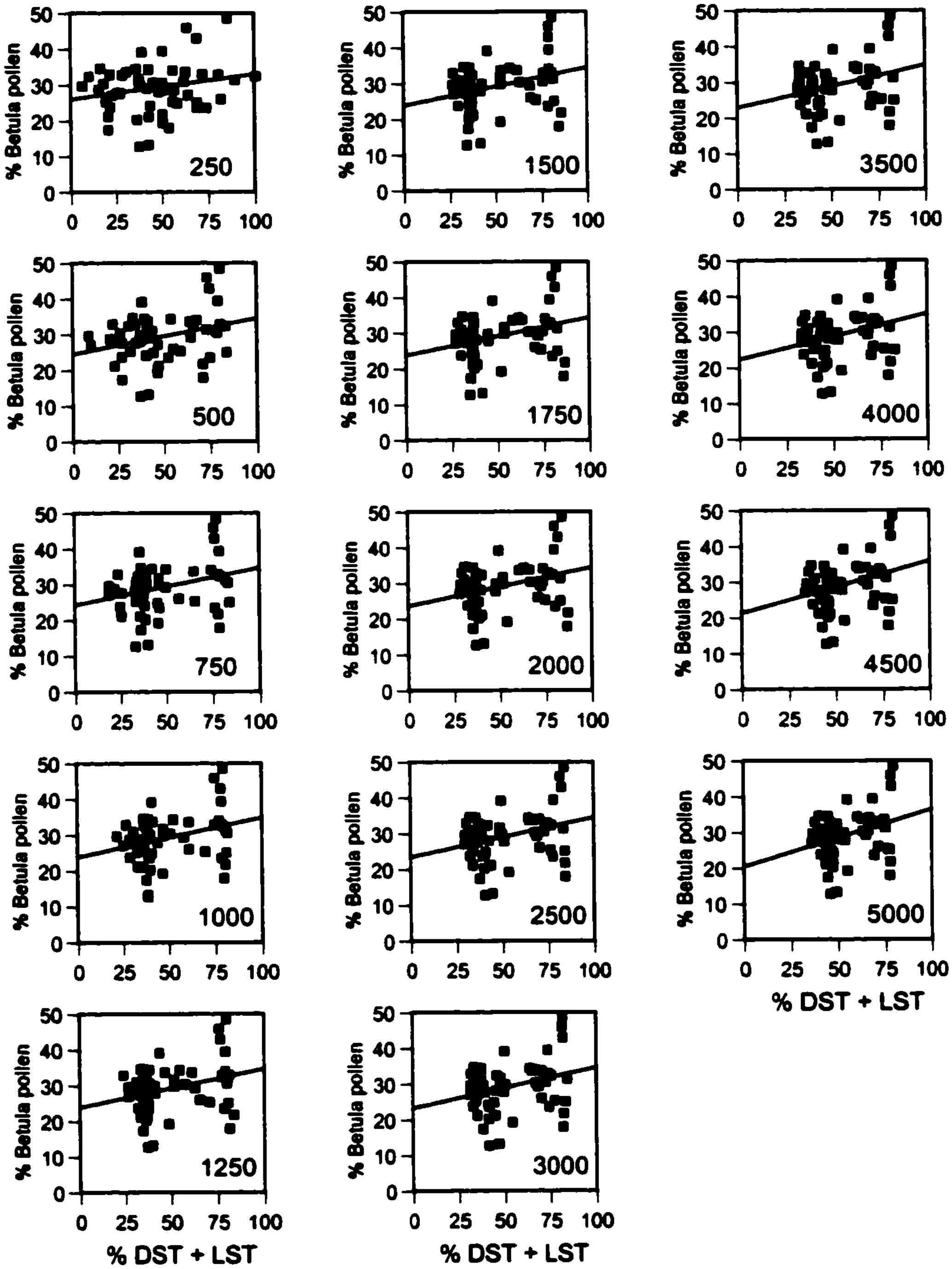

Figure 5.7. Relationship between *Betula* pollen percentages and the combined percent cover of dwarf-shrub tundra (DST) and low-shrub tundra (LST) for the 56 study lakes at each of the vegetation plot radii distances.

APPENDIX 2: Effects of sample size and type on radiocarbon dating of arctic and subarctic lake sediments

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SUMMARY

Dating lake sediments with accelerator mass spectrometry (AMS) ^{14}C analysis of plant macrofossils overcomes the main problem associated with dating bulk sediment samples, namely contamination by old organic matter, but a substantial number of AMS dates from arctic and subarctic sites appear to be erroneous. We conducted a series of ^{14}C dating experiments to test the effects of sample size and type. In the sample-size experiments, ^{14}C dates were obtained for different sized pieces of single woody macrofossils, and statistically equivalent ages were found for subsamples as small as 0.05 mg C. In the sample-type experiments, ^{14}C dates were obtained for different plant macrofossils sieved from the same depth in the sediment, and in several cases there were significant discrepancies between dates for different plant tissues. In general, wood and charcoal were older than other materials, often by more than 500 years. This pattern suggests that ^{14}C dates for woody macrofossils may misrepresent the age of the sediment, probably due to their longer terrestrial residence time and the potential inbuilt age of long-lived plants. This study helps us understand why some ^{14}C samples have anomalous

dates, and may also guide the selection of ^{14}C samples in future studies of lake-sediment records.

INTRODUCTION

High quality chronology is vital in paleoecology, particularly in efforts to understand rates of ecosystem reponses to environmental change and feedbacks between the geosphere and biosphere (e.g., Sarnthein et al. 2000). Lake-sediment records are examined widely for the variety of information they contain about the past, including rapid environmental and ecosystem variability (e.g., Allen et al. 1999; Newnham and Lowe 2000; Clark et al. 2002), and in general the chronology of these records is based on ^{14}C dating. Prior to the development of accelerator mass spectrometry (AMS), lake records were usually dated via ^{14}C analysis of bulk sediments, which in some circumstances is complicated by the contamination of the sediments by old organic matter (e.g., Olsson 1974). This problem is thought to be acute in the northern high latitudes, where organic matter decomposes slowly and may reside in permafrost for long periods of time before being eroded into lake basins (e.g., Nelson et al. 1988; Abbott and Stafford 1996). The development of AMS ^{14}C dating makes it possible to obtain ages for individual plant macrofossils, potentially avoiding problems associated with dating mixtures of contemporaneous and older organic matter in bulk sediment samples. When both techniques are applied to the same record, ages for AMS-dated plant macrofossils are often hundreds of years younger than ages for bulk sediment from the same core depth (e.g., Cwynar and Watts 1989; Törnqvist et al. 1992). However, AMS dating is not free of problems, especially in arctic and boreal regions. Many AMS-dated sediment cores from Alaska and northeastern Siberia suffer from age reversals: dates that are anomalously old or young compared with the age-depth relationship for the majority of dates from a core (e.g., Oswald et al. 1999; Brubaker et al. 2001; Lozhkin et al. 2001; Mann et al. 2001). We hypothesize that these unreliable dates likely result from two main factors: the size and type of the material dated.

AMS analyses of standardized laboratory samples have demonstrated that reasonable analytical precision can be obtained for organic carbon samples <2 mg (e.g., Kirner et al. 1996; Von Reden et al. 1998; Hua et al. 2001). The possibility of obtaining dates from very small macrofossils is a major advantage of AMS when dating records from northern lakes, where in many cases only very small plant fragments are preserved in the sediment. However, age reversals observed at such sites often involve relatively small samples, and in most cases the problematic ages are younger than would be expected based on the age-depth trend for the other samples in the record (e.g., Oswald et al. 1999; Andreev et al. 2001). Given these observations it is important to assess the lower size threshold with empirical results from "real-life" samples.

Issues related to sample type arise because lake sediments from arctic and subarctic regions often have few macrofossils. In most cases a single type of macrofossil is not present throughout a core, and thus the chronology for the record is based on ages from a variety of different macrofossil types (e.g., seeds, woody, leaves from different taxa). Furthermore, because of the small size of most macrofossils in northern lake sediments, several different macrofossil types may be combined in a single ^{14}C sample (e.g., Oswald et al. 1999). Macrofossils from aquatic plants are usually avoided because of the possibility of old-carbon reservoir effects in arctic and subarctic lakes (e.g., MacDonald et al. 1987; Abbott and Stafford 1996). However, little is known of systematic biases in the ^{14}C ages of terrestrial plant macrofossils arising from differences in taphonomy or susceptibility to contamination by old or young carbon.

To explore the consequences of differing sample size and type, we conducted a series of AMS ^{14}C dating experiments on materials from sediment cores from northeastern Siberia and Alaska. To test the importance of sample size, ^{14}C dates were obtained for different-sized pieces of a single macrofossil. To examine the importance of sample type, dates were obtained for several different types of plant material from the same depth in the sediment. These experiments (1) help us interpret anomalous ^{14}C dates, and (2) guide the choice of ^{14}C samples for future studies of lake-sediment records from the northern high latitudes.

METHODS

Sampling, pre-treatment, and ^{14}C age determination

Sediment cores were collected from the study lakes (Table 6.1) using a modified square-rod piston-sampler 4.5 cm in diameter (Wright et al. 1984). At selected core depths, 1-2 cm sections of the core were washed through a 500 µm mesh screen with distilled water. The >500 µm fraction was examined using a dissecting microscope, and plant macrofossils were removed using clean tweezers. We selected samples with abundant macrofossils to conduct sample-size and sample-type experiments. For the sample-size experiments, woody macrofossils were spit into 2 to 6 different-sized pieces using a sharp, clean blade. For the sample-type experiments, 2 to 7 different plant macrofossils were chosen from a single 1-2 cm thick sample. To remove exterior contaminants, samples were heated at 70°C for 15 minutes in 1 M HCl, followed by 45 minutes in 1 M KOH, and finally 15 minutes in 1 M HCl. Following this pretreatment, samples were stored in 0.1 M HCl in glass vials with teflon-lined screw caps. ^{14}C analyses were conducted at the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory. ^{14}C ages were determined assuming $\delta^{13}C$ values of -25‰ (Stuiver and Polach 1977).

Data analysis

We used a subroutine in CALIB 4.1 (Stuiver and Reimer 1993) to test for statistically significant ($p<0.05$) age differences between subsamples from a given depth. The subroutine determines the pooled average (weighted mean) of the ^{14}C dates, calculates the test statistic T from the weighted sum of the differences between each sample age and the pooled average, and compares T to a X^2 (chi-square) distribution for n-1 samples. If T is less than X^2, the dates do not differ statistically (Ward and Wilson 1978).

One of several possible explanations (see below) for age discrepancies between samples in the sample-type experiments is that the slow sedimentation rate of these lakes results in a relatively long period of macrofossil accumulation being represented by each 1-2 cm thick interval of a core. To assess the importance of this factor, it was necessary to convert the dates to calibrated (cal) ^{14}C ages (using CALIB 4.1) so that age differences between dates could be compared to estimates of the sedimentation rate for that interval. For each sample-type experiment, we calculated a range of sedimentation rates, including (1) the mean sedimentation rate for the core, and (2) one or more estimates based on linear and polynomial age models fit to either all or some portion of the calibrated ^{14}C dates for the core. When referring to the age difference between the calibrated ages of samples with multiple intercepts, we use the age difference between the nearest intercepts.

RESULTS

Sample-size experiments

^{14}C analyses of different-sized pieces of the same woody macrofossil returned statistically equivalent dates for samples from Upper Capsule 310-311 cm, Malyii Kretchet 121-122 cm, Ahaliorak 32-33 cm, and Vadopadnoye 48-50 cm (Fig. 6.1, Table 6.2). In the case of Vadopadnoye 26-28 cm, the dates for the two smallest subsamples (mass < 0.04 mg C) were somewhat younger than those of larger subsamples, but these values were not significantly different due to their large standard deviations (280 and 550 ^{14}C years). Radiocarbon ages were significantly different for dates on the subsamples of two macrofossils from Malyii Kretchet 85-86 cm. For sample 85-86 (b), the two ages differed by 1330 ^{14}C (1673 cal) years. For sample 85-86 (a), the dates for the two larger samples were identical (3320 ^{14}C years BP), but the small (0.02 mg C) and very small (0.01 mg C) samples were 910 ^{14}C (1206 cal) years younger and 1870 ^{14}C (2364 cal) years older than this date, respectively.

Sample-type experiments

^{14}C dates obtained for different plant materials from the same depth in a core were statistically equivalent in only one case (Red Green 202-203 cm), whereas at least one date was significantly different in the other eight cases (Fig. 6.2, Table 6.3). For Upper Capsule 155-157 cm, graminoid fragments dated at least 1530 ^{14}C (1866 cal) years older than the other materials, and for Upper Capsule 250-251 cm, graminoid and moss dates differed by 270 ^{14}C (252 cal) years. For Upper Capsule 310-311 cm, six of the seven dates (including the three dates on different-sized pieces of the same woody macrofossil, see above) did not differ statistically. The date for moss fragments was younger by at least 440 ^{14}C (685 cal) years. For Grizzly 39-40 cm, five macrofossils had statistically equivalent ages, but the date for charcoal was at least 1500 ^{14}C (1289 cal) years older. Similarly, four of the ages from Grizzly 133-135 cm were not statistically different, but wood and charcoal macrofossils were older by at least 575 and 730 ^{14}C (665 and 830 cal) years, respectively. For Grizzly 292-293 cm, the dates from three different pieces of wood differed by as much as 520 ^{14}C (476 cal) years. All three dates for Okpilak 478-479 cm are significantly different from each other. The seed was youngest, but with a large standard deviation due to its small size. The wood and moss fragments differed by 430 ^{14}C (600 cal) years. The chronological order of these three plant tissues was the same for the samples from Ahaliorak 31-32 cm. The seed had the youngest date, the moss fragments were 400 ^{14}C (598 cal) years older than the seed, and the large piece of wood was 310 ^{14}C (358 cal) years older than the moss. The very small (0.01 mg C) woody twig was at least 2000 ^{14}C (2768 cal) years older than the other materials.

DISCUSSION

The finding that pieces of the same macrofossil larger than 0.05 mg C did not have significantly different ^{14}C dates suggests that there is a sample-size threshold for reliable age determinations. Two analytical factors likely contribute to this result. First, the contribution of the background correction to both the precision and accuracy of the ^{14}C measurement probably becomes significant when sample size approaches this threshold (Brown and Southon 1997). Second, the completeness of the graphitization reaction is uncertain when samples are very small. However, even when samples are large enough to avoid these analytical problems, the dates often have such large standard deviations (>100 years) that they may not provide adequate chronological control for high-resolution records. Obviously, the level of uncertainty that is acceptable will vary depending on the objective of the research. In general, the results of the size experiments are consistent with the sample-size guidelines of most AMS laboratories (e.g., Kirner et al. 1996; Von Reden et al. 1998; Hua et al. 2001), and these findings suggest that the size threshold for "real-life" samples is similar to that found for standardized laboratory samples.

The results of the sample-type experiments are of greater concern to current dating practices for northern lake sediments. In many cases, different types of macrofossils from the same core depth differed by more than 500 ^{14}C years (Table 6.4). Although some of these differences are clearly attributable to small sample size (e.g., 0.02 mg C seed in Okpilak 478-479 cm, 0.01 mg C wood in Ahaliorak 31-32 cm), most age discrepancies occurred where the samples were larger than the 0.05 mg C size threshold. Factors that might contribute to age differences include (1) ^{14}C source or fractionation differences between plants, (2) the slow sedimentation rates of these lakes, (3) taphonomic differences among macrofossil types, and (4) differences in susceptibility to contamination.

First, if plants obtain carbon directly from the lake water, macrofossil ^{14}C ages may appear too old as a result of a reservoir effect (e.g., Abbott and Stafford 1996). For example, MacDonald et al. (1987) found that ^{14}C ages of aquatic moss macrofossils from western Canada were more than 1500 years older than their terrestrial counterparts. However, the moss samples analyzed in this study were from terrestrial or perhaps riparian mosses, and thus should not be affected by this problem. Furthermore, moss macrofossils never had the oldest age in the type experiments, suggesting an atmospheric source of carbon, as would be the case for the other plant types. Alternatively, the observed age discrepancies may result from differences in ^{14}C fractionation among plant species (Aitken 1993). Differences in ^{14}C depletion can be accounted for by adjusting ^{14}C values relative to measured ^{13}C values (Craig 1953), but in this study ^{14}C dates were calculated assuming δ^{13}C values of -25‰ (Stuiver and Polach 1977), which is almost certainly within 5‰ of the actual δ^{13}C value. A δ^{13}C departure from -25‰ of 1‰ corresponds to an age difference of roughly 16 years, and hence the fractionation correction for these dates would be at most 80 years. Because this adjustment is much smaller than the age disparities (>250 years), the fractionation effect is not likely the main cause of the ^{14}C differences among macrofossils from the same core depth.

Second, the slow sedimentation rates of the lakes in this study potentially result in the accumulation of macrofossils of widely different ages in a 1-2 cm thick section of the core. To test the importance of this effect, we compared the age discrepancies between different macrofossils with estimated sedimentation rates for each sample (Table 6.4). The sedimentation rates varied from ~10 years/cm (Grizzly 292-293 cm, Okpilak 478-479 cm) to ~150-200 years/cm (Ahaliorak 31-32 cm). However, even for those samples that spanned 2 cm, the amount of time elapsed during sedimentation was small (<100 years) compared to the age differences between macrofossils (>250 years), and thus this factor does not appear to account for the discrepancies.

Third, the age discrepancies may also result from taphonomic differences among macrofossil types. The most striking result of the sample-type experiments was that wood and charcoal were older than other macrofossils (Fig. 6.2). The amount of the offset was inconsistent, with age differences varying from tens to thousands of years, but this trend occurred all but one of the experiments (i.e., Upper Capsule 155-157 cm) in which woody macrofossils were dated. Because woody macrofossils are relatively large and decay-resistant (Hobbie 1996), they are likely to remain on the landscape longer than smaller, more readily decomposed plant tissues. This effect could be quite important in arctic and subarctic regions where cold climates slow decomposition and organic matter may reside in permafrost for long intervals before being incorporated into lake sediments. Alternatively, dates on these wood and charcoal may be older due to an "inbuilt age" effect (e.g., McFadgen 1982; Gavin 2001). Because woody plants maintain old tissues as part of their structure, wood layers located at some depth within a branch or stem may be substantially older than recent growth. Thus, even if the remains of a woody plant were washed into a lake as soon as the plant died, a ^{14}C date on a piece of wood might appear significantly older than the rest of the sediment if the dated tissues formed early in the life of that plant. This type of error may be important in tundra and particularly problematic in boreal forest ecosystems, as woody tundra plants have been observed to reach 30-55 years (Warren Wilson 1964; Shaver 1986), while boreal forest trees in interior Alaska often live beyond 250 years (e.g., Van Cleve et al. 1983).

Lastly, another explanation for the tendency for woody samples to be older than non-woody materials is that some macrofossil types are more susceptible to contamination than others. For example, perhaps the moss and leaf fragments have younger ^{14}C dates than the woody macrofossils not because they have shorter terrestrial residence times, but because they are more easily contaminated by modern carbon. These non-woody macrofossils are generally flat or filamentous, and therefore their surface area to volume ratio is larger than that of wood and charcoal pieces. Thus, these macrofossils might be more susceptible to laboratory contamination. On the other hand, it is possible that woody tissues have some propensity for contamination by old carbon, perhaps because of their rough surface texture. The sample pretreatment routine should remove impurities from the surface of the macrofossils, but it is possible that some contaminating young or old carbon remains on the samples. However, contamination by modern carbon is much more likely to have an important age effect than that by old carbon, as the substantially higher ^{14}C activity of young carbon creates a larger magnitude dating error than old carbon for the same amount of contaminant (Olsson 1974).

CONCLUSIONS

The results of this study provide specific insights for dating lake sediments from high northern latitudes, but they are also relevant to the general use of ^{14}C analysis in Quaternary science. The sample size experiments demonstrate that statistically equivalent ^{14}C dates could be obtained for very small (0.05 mg C) subsamples of "real-life" plant macrofossils. The ability to date such small materials is crucial for understanding the chronology of macrofossil-poor sediments, including those from many northern lakes, as well as for other scenarios where only very small amounts of organic matter are available for dating (e.g., large lakes, full-glacial sediments). However, the experiments involving ^{14}C analysis of different plant tissues from the same depth in the sediment suggest that some macrofossil types may provide erroneous ages. Wood and charcoal were generally older than other types of plant remains, and in several cases the dates for these materials exceeded other dates by more than 500 ^{14}C years. We attribute this pattern to the slower decomposition and longer terrestrial residence time of woody macrofossils in arctic and subarctic environments, and perhaps to the "inbuilt age" effect that may occur in ecosystems with long-lived plants.

Because woody macrofossils are commonly selected for ^{14}C dating (e.g., Oswald et al. 1999; Anderson and Lozhkin 2001; Gavin et al. 2001; Lozhkin et al. 2001), the conclusion that they may not provide accurate dates for paleoenvironmental records from lake sediments is distressing. In some studies an error of the magnitude observed in these experiments would not alter the interpretation, but when the objective is to reconstruct past environmental change at the scale of centuries or decades, as is increasingly the case (Hu et al. 2001), an error of 500 years is unacceptable. This type of age bias is not only a potential problem in the high northern latitudes, but also in mid-latitude regions where intervals of the past were characterized by cold conditions and permafrost. Fortunately, we can use the results of this study and other ^{14}C dating experiments (e.g., Turney et al. 2000; Nilsson et al. 2001) to guide the selection of samples so that the risk of erroneous dates is minimized.

Table 6.1. Study sites

Lake	Location	Region	Vegetation
Grizzly	62°43'N, 144°12'W	Copper River, Alaska	*Picea* boreal forest
Upper Capsule	68°38'N, 149°25'W	North Slope, Alaska	Moist dwarf-shrub tussock graminoid tundra
Red Green	68°39'N, 149°41'W	North Slope, Alaska	Moist graminoid prostrate-shrub tundra
Okpilak	69°50'N, 143°50'W	North Slope, Alaska	Moist graminoid prostrate-shrub tundra
Ahaliorak	68°55'N, 151°20'W	North Slope, Alaska	Moist dwarf-shrub tussock graminoid tundra
Vadopadnoye	59°24'N, 150°39'E	Priokhot'ye, Russia	*Larix dahurica* forest
Malyii Kretchet	64°28'N, 175°19'E	Anadyr Basin, Chukotka, Russia	*Pinus pumila-Alnus* shrub tundra

Table 6.2. ^{14}C size experiments.

Sample	Material	Mass (mg C)	CAMS No.	^{14}C age BP	+1 SD [cal ^{14}C age(s) BP] −1 SD
Ahaliorak 32-33 cm	wood	0.34	66732	9280 ± 50	10556 [10488, 10440, 10429] 10291
	wood	1.11	66733	9320 ± 40	10577 [10548, 10522, 10505] 10428
	wood	0.06	66731	9350 ± 180	11040 [10559] 10244
Malyii Kretchet 85-65 cm	wood (a)	0.02	48503	2410 ± 330	2846 [2358] 2011
	wood (a)	0.07	48501	3320 ± 120	3691 [3564] 3400
	wood (a)	0.04	48502	3320 ± 190	3827 [3564] 3359
	wood (a)	0.01	48504	5190 ± 550	6501 [5928] 5322
	wood (b)	0.03	48500	3170 ± 240	3684 [3381] 3077
	wood (b)	0.11	48499	4500 ± 90	5311 [5277, 5172, 5123, 5108, 5068, 5055, 5054] 4974
Malyii Kretchet 121-122 cm	wood	0.49	66730	8230 ± 40	9395 [9253, 9215, 9212, 9171, 9138] 9091
	wood	1.23	66750	8300 ± 60	9465 [9397, 9385, 9370, 9360, 9346, 9343, 9297] 9146
	wood	0.12	66729	8370 ± 80	9488 [9465, 9453, 9428, 9335, 9332] 9280
Vadopadnoye 26-28 cm	wood	0.01	49702	2330 ± 550	2989 [2346] 1707
	wood	0.03	49701	2830 ± 280	3352 [2946, 2935, 2928] 2736
	wood	0.07	49697	2990 ± 120	3353 [3207, 3184, 3164] 2963
	wood	0.06	49698	2990 ± 130	3357 [3207, 3184, 3164] 2955
	wood	0.1	49700	3000 ± 90	3339 [3208, 3179, 3169] 3003
	wood	0.07	49699	3040 ± 120	3379 [3315, 3312, 3257] 3076
	wood	0.08	49696	3050 ± 100	3376 [3318, 3309, 3296, 3293, 3265] 3080
Vadopadnoye 48-50 cm	wood	0.06	50792	4170 ± 140	4856 [4812, 4757, 4726, 4722, 4708, 4668, 4654] 4449
	wood	0.08	50793	4180 ± 110	4848 [4815, 4754, 4730, 4718, 4711, 4666, 4659] 4530
	wood	0.22	50795	4270 ± 60	4866 [4837] 4827
	wood	0.17	50794	4290 ± 60	4870 [4847] 4830

Table 6.3. ^{14}C type experiments.

Sample	Material	Mass (mg C)	CAMS No.	^{14}C age BP	+1 SD [cal ^{14}C age(s) BP] −1 SD
Ahaliorak 31-32 cm	Seed	0.07	76814	8680 ± 130	9906 [9624, 9623, 9600, 9586, 9581, 9568, 9562] 9533
	mosses (terrestrial)	0.14	76813	9080 ± 80	10357 [10222] 10189
	Wood	1.00	76812	9390 ± 50	10687 [10636, 10613, 10580] 10512
	Wood	0.01	44522	11390 ± 60	13745 [13404] 13171
Grizzly 39-40 cm	conifer periderm	0.17	82318	95 ± 45	265 [235, 235, 62, 40, 0] 0
	Mosses	0.10	82319	100 ± 70	274 [240, 232, 126, 125, 65, 38, 0] 0
	wood	0.32	82314	150 ± 40	280 [268, 216, 144, 19, 3] 1
	deciduous periderm	0.30	82317	175 ± 40	286 [275, 174, 149, 10, 4] 2
	Picea needle	0.37	82313	180 ± 40	288 [277, 173, 150, 8, 4] 2
	Charcoal	0.93	82316	1685 ± 30	1687 [1566] 1538
Grizzly 133-135 cm	*Picea* conescale	0.37	82322	4125 ± 35	4810 [4786, 4767, 4613, 4596, 4587] 4533
	Mosses	0.42	82326	4160 ± 40	4825 [4810, 4759, 4704, 4670, 4650] 4574
	deciduous periderm	1.01	82324	4180 ± 40	4828 [4815, 4754, 4730, 4718, 4711, 4666, 4659] 4627
	conifer periderm	0.89	82325	4190 ± 40	4829 [4822, 4749, 4733] 4647
	Picea needle	0.94	82320	4225 ± 40	4835 [4828] 4662
	wood	0.95	82321	4800 ± 45	5593 [5585, 5497, 5493] 5479
	Charcoal	0.97	82323	4955 ± 40	5726 [5658] 5613
Grizzly 292-293 cm	wood	0.94	59340	6910 ± 40	7786 [7719, 7709, 7698] 7675
	wood	0.95	59339	7100 ± 50	7961 [7937, 7889, 7878] 7864
	Charcoal	0.99	59341	7430 ± 50	8332 [8278, 8269, 8195] 8176
Okpilak 478-479 cm	Seed	0.02	76817	6750 ± 380	7943 [7607, 7600, 7589] 7272
	mosses (terrestrial)	0.26	76816	7660 ± 50	8451 [8412] 8392
	Wood	1.00	76815	8090 ± 40	9028 [9012] 9005
Red Green 202-203 cm	Leaf	0.08	66737	7060 ± 100	7965 [7927, 7897, 7868] 7758
	mosses (terrestrial)	0.04	66738	7140 ± 220	8174 [7956] 7736
	Wood	0.07	66739	7190 ± 120	8155 [7998, 7993, 7975] 7871

Table 6.3 continued

Sample	Material	Mass (mg C)	CAMS No.	^{14}C age BP	+1 SD [cal ^{14}C age(s) BP] −1 SD
Upper Capsule 155-157 cm	leaf fragments	0.05	66741	3670 ± 120	4152 [3982] 3833
	semi-woody fragments	0.08	66743	3720 ± 80	4221 [4086, 4025, 4020] 3930
	graminoid leaf fragments	0.05	66742	5250 ± 130	6196 [5990, 5965, 5952] 5908
Upper Capsule 250-251 cm	mosses (terrestrial)	1.08	66744	8200 ± 50	9268 [9238, 9220, 9187, 9178, 9130, 9095, 9093] 9030
	graminoid leaf fragments	0.11	66745	8470 ± 90	9534 [9490] 9334
Upper Capsule 310-311 cm	mosses (terrestrial)	0.08	66747	9270 ± 120	10666 [10482, 10442, 10428] 10242
	graminoid leaf fragments	0.11	66749	9710 ± 100	11201 [11167] 10872
	Seed	0.07	66748	9920 ± 150	11631 [11257] 11186
	Wood	1.42	66746	10010 ± 50	11626 [11547, 11509, 11405, 11390, 11342] 11261

Table 6.4. Sample age differences for the ^{14}C type experiments

Sample	^{14}C age difference[a]	Calibrated ^{14}C age difference[b]	Sediment accumulation (years/sample)[c]
Upper Capsule 155-157 cm	1530	1866	72.9 - 96.1
Upper Capsule 250-251 cm	270	252	36.5 - 44.7
Upper Capsule 310-311 cm	440	685	28.8 - 36.5
Grizzly 39-40 cm	1500	1289	23.8 - 29.1
Grizzly 133-135 cm	575 - 730	665 - 830	47.6 - 71.2
Grizzly 292-293 cm	520	476	9.7 - 23.8
Okpilak 478-479 cm	430	600	6.1 - 13.31
Ahaliorak 31-32 cm	310 - 400	358 - 598	151.3 - 206.5

[a] For multiple significant age discrepancies between subsamples, we list the range of age differences.

[b] When comparing calibrated ages of samples with multiple intercepts, we refer to the age difference between the nearest intercepts.

[c] Range of sediment accumulation rates including the mean sedimentation rate and estimates based on reasonable linear and polynomial age models fit to either all or some portion of the calibrated ^{14}C dates for that record.

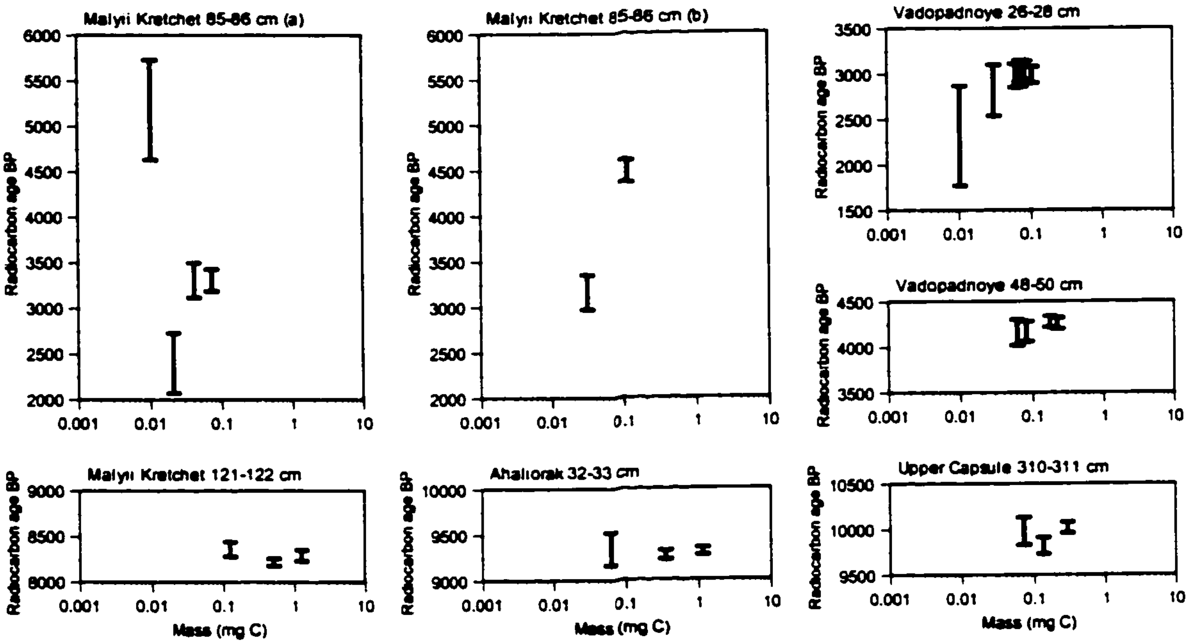

Figure 6.1. Plots of ^{14}C age versus sample mass for different-sized pieces of the same woody macrofossil. Error bars are the ^{14}C age ± 1 S.D.

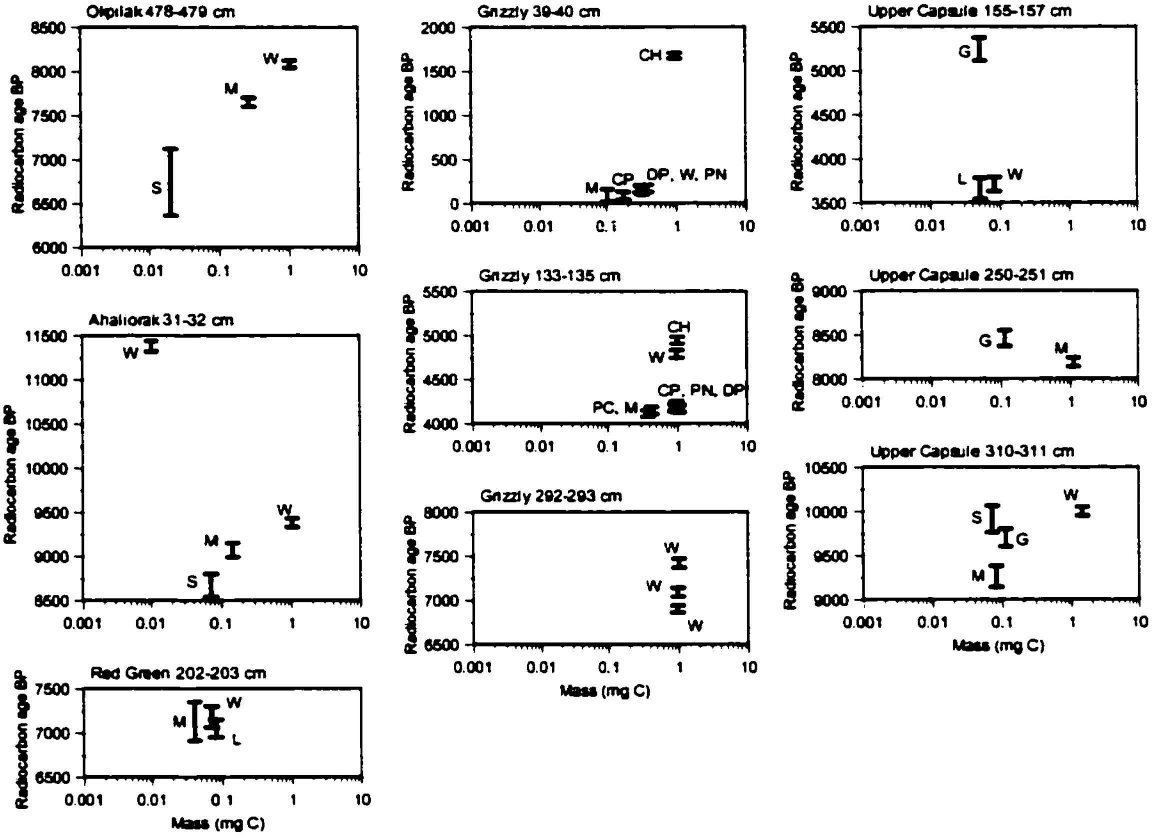

Figure 6.2. Plots of ^{14}C age versus sample mass for different types of macrofossil from the same core depth. Error bars are the ^{14}C age ± 1 S.D. W = woody, M = moss, S = seed, L = leaf, CH = charcoal, CP = conifer periderm, DP = deciduous periderm, PN = *Picea* needle, PC = *Picea* conescale, G = graminoid leaf.

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Publications

Oswald, W.W., L.B. Brubaker, and P.M. Anderson. 1999. Late Quaternary vegetational history of the Howard Pass area, northwestern Alaska. Canadian Journal of Botany 77: 570-581.

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