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## STEPPE VEGETATION ON SOUTH-FACING SLOPES OF PINGOS, CENTRAL ARCTIC COASTAL PLAIN, ALASKA, U.S.A.

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### ABSTRACT

The hypothesized presence of large regions of grass and forb-dominated "steppe tundra" across Alaska and Siberia during the Pleistocene glacial epochs has led to a search for modern analogs. Evidence is presented for the presence of steppe vegetation on south-facing slopes and summits of pingos within the central Arctic Coastal Plain of Alaska. Vegetation, floristics, soils, and climatic factors are each considered, and together support the idea of an ecologically-physiognomically defined steppe on these sites. Grasses and forbs dominate this vegetation, and *Dryas integrifolia*, which is dominant in most dry sites regionally, is absent or has only minimal cover. Although the floristic evidence indicates that the pingo vegetation is most strongly related to the circumpolar arctic vegetation, the steppe-like vegetation has more North American-Asian and low arctic taxa than do other sites. Soils are Pergelic Cryoborolls, and the microclimates on south slopes have greater daily and annual fluctuations than do other microsites. Other pingo vegetation is related to fellfield and snowbeds. These communities represent the northernmost known examples of steppe in North America, and help explain the complex relationships that can exist within the vegetation of well-drained arctic sites.

### INTRODUCTION

The region known as Beringia remained ice-free during the Pleistocene glaciations (Hopkins, 1967) and was likely a major northern refugium for plants (Hultén, 1937, 1968, 1973). The proposed abundance of grass- and forb-dominated vegetation throughout much of full-glacial late-Pleistocene Beringia (Duvanny Yar interval of Hopkins [1982], approximately 12 to 30 ka) has led to the search for modern vegetation stands that could represent remnants of this previously extensive vegetation (Young, 1982; Yurtsev, 1982). This proposed late-Pleistocene vegetation mosaic has been collectively referred to as steppe tundra, although it is generally recognized that it was an

ecosystem complex with a mosaic of landscapes and associated vegetation rather than a few simple community types. In Alaska, proposed steppe-tundra relicts and steppe-like vegetation have been described from steep, south-facing river bluffs in the interior region (Murray et al., 1983; Armbruster and McGuire, 1985; Howenstein et al., 1985; Juday et al., 1985; Kassler, 1985; Edwards and Armbruster, 1989) and from the Arrigetch Peaks region in the southern Brooks Range (Cooper, 1986). In this paper, we describe steppe vegetation from the Alaskan Arctic Coastal Plain.

We have two primary objectives. The first is to present floristic descriptions of the vegetation of south-facing slopes and summits of pingos on the modern coastal plain. The second is to present evidence that some of the vegetation types found on these sites are physiognomically, floristically, and ecologically related to modern steppe vegetation described from Siberia and interior Alaska. We also discuss the potential and the limitations of the pingos as analogs for Pleistocene conditions.

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## THE STEPPE TUNDRA CONCEPT

Two problems are central to discussions of steppe vegetation in the Arctic. The first involves the classification of modern vegetation dominated by grasses and forbs. The second and more controversial problem is the hypothesized link between these modern types and the Pleistocene Beringian vegetation. At the root of this problem are the connotations of the terms *steppe* and *steppe tundra* originating in the different historical uses of the terms by vegetation scientists and palynologists. *Steppe* is a Russian term traditionally used to describe the vast grasslands of temperate continental Asia, and it gradually became incorporated into the worldwide ecological literature as a physiognomic descriptor of dry, continental grasslands. Modifications such as forest steppe, meadow steppe, shrub steppe, and tundra steppe have been used to describe areas with characteristics primarily of steppe but transitional to other physiognomic types. As a purely physiognomic term, *steppe* is not so dependent on species composition as on vegetation structure (Walter, 1973).

Hibbert (1982) reviewed the history of the steppe tundra concept as it has been applied to the Duvanny Yar Beringian vegetation. European paleontologists recognized as early as the late 19th century that the late-Pleistocene climate and vegetation were different from the present, and the concept of a steppe was invoked to describe a landscape that supported a diverse grazing fauna. Many of the mammals present in the fossil megafaunas found throughout Beringia, such as horse (*Equus caballus*), saiga antelope (*Saiga tatarica*), bison (*Bison priscus*), and woolly mammoth (*Mammuthus primigenius*), required a grassland diet or environment (Guthrie, 1968, 1982; Guthrie and Matthews, 1971; Martin, 1982; Vereshchagin and Baryshnikov, 1982). This abundance of oversized mammals led Guthrie (1982) to suggest the term *mammoth steppe* to describe the biome. Thus, the concept of steppe tundra has gradually developed over the last century to describe a biome that essentially disappeared at the end of the Pleistocene.

Evidence for the vegetation composition of Duvanny Yar Beringia comes from pollen spectra at sites scattered throughout Alaska and northwestern Canada (Livingstone, 1955; Colinvaux, 1964; Rampton, 1971; Matthews, 1974; Ager, 1975, 1982; Giterman et al., 1982; Schweger, 1982; Ritchie, 1984; Ager and Brubaker, 1985; Anderson, 1985). The available evidence consistently indicates that Livingstone's (1955) late Pleistocene Herb Zone pollen assemblage dominated by Gramineae, Cyperaceae, and *Artemisia* is a widespread phenomenon. The character of the landscape associated with this pollen assemblage, however, is a controversial debate. Ritchie (1984; Ritchie and Cwynar, 1982) wrote that the Beringian Duvanny Yar vegetation, at least in northwestern Canada, likely resembled a type of fellfield. Both steppe and fellfield are herbaceous, and Ritchie (1984) has argued that either of these physiognomic types could be interpreted from the same pollen analyses, but that low pollen influx rates and relatively small amounts of organic material in the sediments indicated an open, sparsely vegetated landscape similar to an alpine fellfield. Guthrie (1982) argued that

low pollen influx rates are not necessarily correlated with low biomass in grazing ecosystems, however, because grazing pressure may alter plant allocation patterns toward low reproduction, thereby reducing pollen production.

The complex nature of Beringian vegetation during Duvanny Yar times has been recognized by many authors; as Schweger (1982: 109) described it, "Environmental gradients and vegetation continua were just as much a part of the Wisconsin-age landscape as they are at present." Young (1982), who described the Duvanny Yar vegetation as most likely a mosaic, stated that fellfield types were probably more common in the northern areas of Beringia, grading into steppes in the interior. Edwards and Armbruster (1989) demonstrated the importance of topography to maintenance of extant steppe in interior Alaska. Although herbaceous tundra was overwhelmingly dominant throughout most of Beringia during the Duvanny Yar, the exact nature of the tundra types represented is difficult to reconstruct because of the limitations of routine palynological methods. Because of the controversy surrounding the term *steppe tundra*, in this paper we use *steppe* and *tundra steppe* to describe modern vegetation, and reserve *steppe tundra* specifically for the Pleistocene biome.

## PINGOS OF THE CENTRAL ARCTIC COASTAL PLAIN

Pingos are ice-cored, dome-shaped mounds found in permafrost regions (Mackay, 1979). They are an important component of the Alaskan central Arctic Coastal Plain landscape (D. A. Walker et al., 1985). They may be as high as 50 m, with basal diameters exceeding 1 km, but on the coastal plain most are between 5 and 20 m high, with diameters between 70 and 400 m (Figure 1). They are among the only upland sites on the coastal plain, but have apparently been overlooked as sites of potential steppe vegetation, probably because of their relatively small size. Pingos are not evenly distributed across the coastal plain but are abundant in areas with sand and gravel substrates (D. A. Walker et al., 1985; Ferrians, 1988). The pingos of this study are all within a 70-km radius of Prudhoe Bay, Alaska, to the east, west, and south of the oil field, an area with a relatively dense concentration of pingos (Figure 2).

The Arctic Coastal Plain is a flat region dominated by thaw lakes and ice-wedge polygons. Permafrost is continuous and extends to over 600 m deep in places (Everett, 1980a). Mean annual temperature near the coast at Prudhoe Bay is  $-13^{\circ}\text{C}$ , and there is a steeply warming gradient of temperature inland (Haugen, 1982). Mean annual precipitation is less than 25 cm (D. A. Walker, 1980). Soils are mostly Pergelic Cryaquepts and Pergelic Cryaquolls grading into Histosols (Everett, 1980b). A full description of the regional climate, vegetation, soils, and landforms can be found in Everett and Parkinson (1977), D. A. Walker et al. (1980), D. A. Walker (1985), and D.A. Walker and Everett (1991).

The pingo vegetation is strikingly different from the expanses of wet sedge tundra that dominate the coastal plain. Pingos have a great diversity of habitats, and the complexity of the vegetation pattern is a result of differ-



FIGURE 1. A typical pingo, Prudhoe Bay, Alaska. This feature is 7 m high and has a basal diameter of 110 m.

ences in slope angle, slope aspect, effects of wind, disturbance by animals, site stability, and deposition of snow (Koranda, 1970; D. A. Walker et al., 1985; M. D. Walker, 1990). In addition to these microscale controls, meso- and macroscale patterns related to the coastal climatic gradient and substrate variation are also reflected on pingos.

Vegetation of these pingos is distinct from that on pingos in other parts of the coastal plain (National Petroleum Reserve-Alaska and the Arctic National Wildlife Refuge) and the Noatak River Delta, due to two factors: (1) the exceptional stability of the Prudhoe Bay pingos, and (2) the importance of loess in this ecosystem (D. A. Walker and Everett, 1991). D. A. Walker et al. (1985) described two morphological classes of pingos from the Prudhoe Bay region. One type, which they called "steep-sided pingos," are morphologically similar to pingos described from other arctic regions, particularly the Tuktoyaktuk Peninsula in northwestern Canada (Mackay, 1979). These pingos have relatively steep side slopes, usually between 10 and 30°, and are found exclusively within the boundaries of recognizable drained thaw-lake basins. Thus, their genesis is presumed to be a result of the formation of permafrost in thawed, saturated, coarse sediments following lake drainage, as described by Mackay (1979). The other morphological pingo type was referred to as "broad-based" by D. A. Walker et al. (1985). The broad-based pingos have a greater total volume and gentler side slopes than the steep-sided pingos. Additionally, broad-based pingos are usually found outside the confines of recognizable lake basins. D. A. Walker et al. (1985) speculated, based on a combination of factors including pingo morphology, regional distribution, and soil morphology, that the broad-based pingos are likely an older form that may have dated from

a previous thaw-lake interval, perhaps as early as the Boutellier interval (Hopkins, 1982), approximately 30 to 65 ka. There are no broad-based pingos known from surfaces less than 12,000 years old.

Although the exact age of any given pingo is not known, a unique feature of the Prudhoe Bay pingos is their stability. There are no known collapsed pingos from the Prudhoe Bay region, which is in contrast to the Tuktoyaktuk region, where collapsed and collapsing forms are common (Mackay, 1979). The differences between the regions are likely due to a combination of surface gravels at Prudhoe Bay, giving the pingo surface exceptional stability, and colder mean annual temperatures at Prudhoe Bay. Thus, the potential longevity of these pingos, and the lack of evidence for pingo collapse, indicates that pingos could have remained as stable sites throughout the Holocene, and perhaps even longer.

Loess is still a dominant factor in the Prudhoe Bay region that maintains soil pH at 7.0 to 8.0 throughout most of the region (D. A. Walker and Everett, 1991). Calcareous sediments are carried from limestone deposits at the headwaters of the Sagavanirktok River and redeposited as loess on the coastal plain downwind of the river. This continual input of calcareous material maintains alkaline soil conditions, compared to most of the coastal plain where acidic substrates dominate. Over time, mesic tundra will normally become more acidic due to accumulation of organic acids in peat. Tundra steppe areas in Siberia have been reported primarily from calcareous substrates (Yurtsev, 1982). Loess was much more abundant in northern Alaska during the Duvanny Yar (Hopkins, 1982); therefore, if there are any relicts of the Pleistocene landscape on the coastal plain, the loess-controlled ecosystems are where they are most likely to be found.

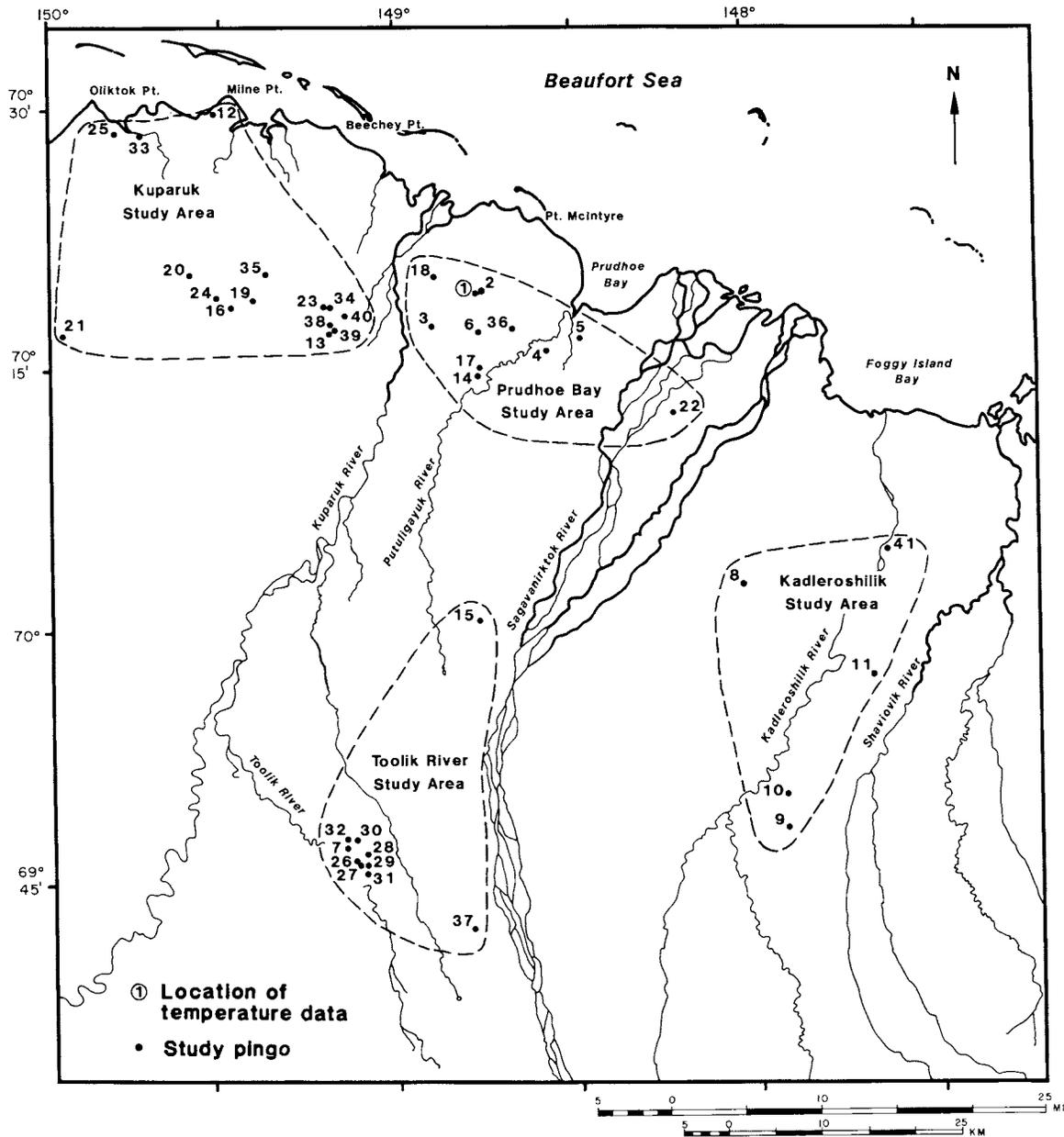
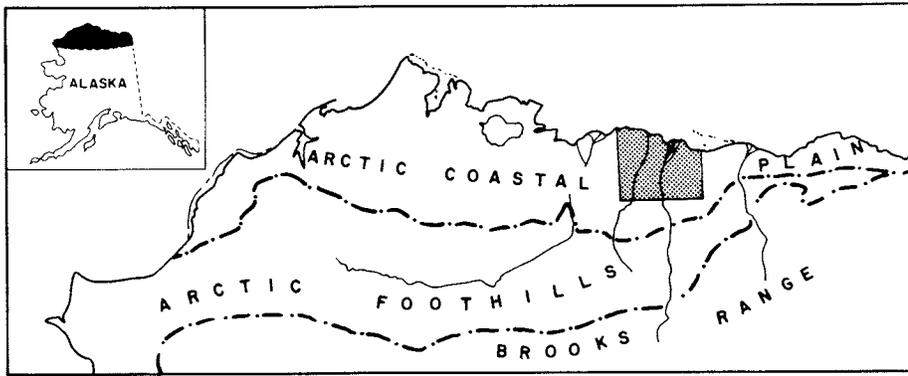


FIGURE 2. Location of sample pingos. The study area was divided into four subareas. Topographic information is from USGS 1:250,000 Beechey Point and Sagavanirktok Quadrangles.

Thus, there are conditions on the pingos possible for the existence of relict Pleistocene vegetation. (1) The pingos are geomorphically stable and long-lived. (2) The pingo slopes have remained dry throughout their existence. (3) The ecosystem is strongly influenced by calcareous loess, which was an important characteristic of the Duvanny Yar ecosystems on the coastal plain. In this paper, we present data from a study that described the soils and vegetation of the central Arctic Coastal Plain pingos (M. D. Walker, 1990). Here we focus on the south-facing slopes, where steppe vegetation occurs.

There is no single, accepted definition for what constitutes steppe vegetation outside the true steppes of central Asia, Europe, and North America. Factors other than vegetation structure (dominated by perennial grasses and forbs, with minimal woody plant cover) that have been stressed in the literature as indicative of steppe include deep, nutrient-rich soils, usually derived from loess, and a continental climate with summer drought

stress (Guthrie, 1982). Yurtsev (1982) stressed floristic gradients, therefore including species composition in the definition. The concept of spatial extensiveness is also frequently invoked. All of these factors taken together, i.e., physiognomy, floristics, soils, and climate, constitute an ecological definition for steppe, as they consider the whole system rather than any one part. Classification is a subjective exercise. There can be no definitive proof that any vegetation entity should be called by one name or another. Using an ecological definition of steppe, we considered the following to be evidence in support of classifying these stands as steppe: (1) domination of the vegetation by grasses and forbs, (2) presence of species described from extant steppes of interior Alaska and Asia, (3) deep, nutrient-rich soils, and (4) warm, dry, microclimates. Finally, we assessed pollen profiles from a small group of sites to determine what similarity, if any, they had to steppe-tundra pollen spectra.

## METHODS

### SAMPLE SITES

Vegetation was sampled from seven specific sites on each of 41 pingos. East-northeast-facing slopes (site 1) are directly exposed to predominant winds and are snow free throughout the year. Summits (site 2) and many south-facing slopes are frequently used by arctic ground squirrels (*Spermophilus parryi*), arctic foxes (*Alopex lagopus*), and perching birds. Leeward (west-southwest-facing) slopes have three distinct snowbed sites associated with depth of snow and drainage (sites 3–5). South-facing upper backslopes (site 6) are usually snow free in winter and are the warmest sites in summer. North-facing upper backslopes (site 7), which are also predominantly snow free in winter, are the coldest sites in summer.

Percentage cover of all vascular and cryptogam species was estimated visually in a 5-m-diameter circular sample plot at each of the seven sites. Soil at each sample site was described and classified using the USDA taxonomy (Soil Survey Staff, 1975).

### MICROCLIMATE

Soil and air temperature data were recorded on a pingo at Prudhoe Bay (Figure 2) in August 1986 in order to characterize the differences in surface temperatures on north- and south-facing slopes compared to the air temperature. Three Belfort continuous strip-chart recording temperature instruments were placed on the north-facing slope, south-facing slope, and summit of the pingo. A 30 × 30 cm, 10-cm deep hole was dug at each surface temperature site and filled with clean gravel. The same gravel source was used for all holes. Temperature probes placed directly below the gravel surface measured ground surface temperature. Slope angles were locally adjusted to 30° on both sides of the pingos to compare north- and south-facing slopes of the same angle.

A standard-height weather shelter was erected approximately 100 m southeast of the pingo, and a single Belfort

instrument measured shelter air temperature and ground temperature at that site simultaneously. The ground temperature probe was in mesic tundra and was buried in clean gravel from the pingo.

### VEGETATION CLASSIFICATION

A three-level, hierarchical, floristically-based vegetation classification was produced using the sorted table analysis method (Mueller-Dombois and Ellenberg, 1974). Differential taxa for each syntaxon were determined according to the rule that the taxa occurred in at least 50% of the samples within a syntaxon, and in less than 33% of the remaining samples. The basic classification unit was the stand type, which corresponds approximately to an association in the sense of Braun-Blanquet (1932), but the informal designations are used until more phytosociological information is available from this region. The three levels of the hierarchy are given the informal designations of "group," "stand type," and "subtype." All plots were classified at least as far as the level of group and stand type. Names of the classification entities include the unit name plus two dominant or characteristic species, for example, Group *Cassiope tetragona*-*Dryas integrifolia*. Vascular plant nomenclature is based on Hultén (1968). Lichen names follow Thomson (1979, 1984), and bryophytes follow Steere (1978) and Steere and Inoue (1978).

### FLORISTIC ANALYSIS

The multiple-character approach of D. A. Walker (1985) was used to examine the floristic affinities of the vegetation (Table 1). Each species was assigned to a class in each of three independent categories which signify different distributional characteristics: (1) broad environmental regions, (2) northernmost limit, and (3) geographic range. Environmental regions were developed from D. A. Walker's (1985) ecological zones and are similar to

biomes. Arctic species are confined wholly to the arctic tundra regions; arctic-alpine species occur also in alpine sites outside the Arctic; arctic-boreal species' ranges extend into the boreal forest region; coastal species are confined to a small strip along the coast, and their ranges may extend outside the Arctic.

The concept of northernmost limit was developed by Young (1971) to elucidate the effects of temperature on arctic species distributions. Many authors have discussed the close relationship between summer temperature and arctic vegetation (Sørensen, 1941; Clebsch, 1957; Böcher, 1959; Cantlon, 1961; Clebsch and Shanks, 1968; Rannie, 1986). Young (1971) noted, in his analysis of the flora of St. Lawrence Island, that the size of arctic floras can be reasonably well predicted on the basis of summer temperature alone. He divided the circumpolar Arctic into four zones on the basis of a summer warmth index, which is the sum of mean monthly temperatures above 0°C. Zone 1 is the coldest and contains only polar deserts; zone 4 is the warmest and corresponds to low arctic regions. Young (1971) classified each vascular species within the flora of St. Lawrence Island into one of these four zones according to their northernmost limit. For taxa not listed in Young (1971), D. A. Walker's (1980) classification of the Prudhoe Bay flora was used, and remaining species were classified using the distribution maps of Hultén (1968). Because of a steep temperature gradient associated with the Beaufort Sea coast, the Prudhoe Bay region encompasses zones 2, 3, and 4 over a relatively small distance (D. A. Walker, 1985). This is a very compressed gradient; only northeastern Siberia has an equivalent situation in the vicinity of the Kolyma River (Young, 1971).

Geographic range is the continental distribution of a species, which is largely controlled by historic factors. D. A. Walker's (1985) geographic range categories were modified slightly because of our specific interest in Beringia. Five categories were defined. Circumpolar taxa occur on all continents; North American-Asian-European taxa occur on all continents except eastern North America and Greenland; North American-Asian taxa are limited to those two continents; North American taxa are limited to North America; Alaskan-Yukon endemics are limited to Alaska and northwestern Canada.

#### POLLEN ANALYSIS

Pollen was analyzed from soil samples taken from the top 10 cm of vegetation relevés (M. D. Walker [1990] sample nos. 5-6, 33-6, 41-5, 41-15). These are all south-facing slopes. The first number corresponds to the pingo number in Figure 2. The samples were originally collected for soil analysis and were not specifically meant for pollen analysis. Samples were selected to have sufficient organic material present (5-10%), to have had some pollen preservation, and also to be no more than 10 cm deep. The samples likely represent a combination of modern pollen input and reworked material.

Pollen sample preparation followed standard Institute of Arctic and Alpine Research (INSTAAR) procedures

TABLE 1  
*Classes used for the floristic analysis*

Environmental Regions <sup>a</sup>	
Arctic	Restricted to arctic, including alpine regions within arctic
Arctic-alpine	Ranging into nonarctic-alpine regions
Arctic-boreal	Ranging into the boreal zone
Coastal	Restricted to a small strip of land near the coast
Geographic Range	
Circumpolar	On all circumpolar continents
North American-Asian-European	On all circumpolar continents except Greenland
North American-Asian (including Beringian endemics)	On North America and Asia, but absent from Europe
North American	Restricted to North America
Alaskan-Yukon endemic	Restricted to Alaska and the Yukon Territories
Northernmost Limit <sup>b</sup>	
Zone 1	Summer warmth index 0- < 6
Zone 2	Summer warmth index ≤ 6- < 12
Zone 3	Summer warmth index ≤ 12- < 20
Zone 4	Summer warmth index ≤ 20- < 35

<sup>a</sup>Modified from D. A. Walker (1985).

<sup>b</sup>From Young (1971). See text for explanation of summer warmth index.

(Nichols, 1975), modified from Faegri and Iversen (1975). A known weight of sample was prepared, and a tablet containing a known number of exotic marker grains (*Eucalyptus*) was added prior to chemical pollen concentration (Stockmarr, 1971). Pollen was concentrated with a sequence of sodium hydroxide, hydrofluoric acid, and acetolysis treatments. The pollen was stained with fuchsin and mounted in glycerine jelly.

Pollen sums varied from 116 to 202 grains/sample. In sample numbers 41-6 and 5-6, two slides were counted to achieve sums greater than 100 grains. Pollen densities were much higher for the other two samples, and 200 counts were achieved in less than one slide. Pre-Quaternary pollen types were excluded from the pollen count. Pollen identifications were made using the INSTAAR palynology laboratory reference pollen collection and with pollen keys (Kapp, 1969; McAndrews et al., 1973; Moriya, 1976). Percentages were averaged to produce a composite south-facing pingo slope pollen spectrum.

Fifteen modern pollen samples (12 moss polsters and 3 lake sediment samples) collected and counted by Nelson (1979) were averaged in order to represent regional pollen. These are all from the central coastal plain area. Nelson did not describe the vegetation at his sample sites.

TABLE 2  
Differentiating taxa for the three pingo vegetation groups<sup>a</sup>

	<i>P. glauca</i> - <i>P. alpigena</i>	<i>C. rupestris</i> - <i>S. oppositifolia</i>	<i>C. tetragona</i> - <i>D. integrifolia</i>
Number of samples:	56	105	127
<b>Regional Pingo and Dry Site Taxa</b>			
<i>Dryas integrifolia</i>	V 2	V 3	V 3
<i>Lecanora epibryon</i>	V 1	V 2	IV 1
<i>Cetraria cucullata</i>	IV r	V 1	IV 1
<i>Cetraria nivalis</i>	IV r	V 1	IV 1
<i>Thamnolia subuliformis</i>	IV r	V 1	IV 1
<i>Cetraria islandica</i> ssp. <i>islandica</i>	IV r	V +	IV 1
<i>Tortula ruralis</i>	V 1	III r	III +
<i>Rhytidium rugosum</i>	III +	IV 1	IV 1
<i>Distichium capillaceum</i>	III r	IV r	IV +
<i>Thuidium abietinum</i>	IV 1	III r	III +
<i>Physconia muscigena</i>	V +	III r	II r
<i>Cladonia pocillum</i>	III r	III r	III r
<i>Polygonum viviparum</i>	II r	III r	IV r
<i>Dactylina arctica</i>	II r	IV r	III r
<i>Encalypta rhamnoides</i>	III +	III r	II r
<i>Cornicularia divergens</i>	II r	III +	II r
<i>Minuartia arctica</i>	II r	III r	II r
<i>Drepanocladus uncinatus</i>	II r	II r	III 1
<i>Eurynchium pulchellum</i>	II r	II r	III r
<b>Group <i>Poa glauca</i> - <i>Poa alpigena</i> (steppe communities occurring primarily on summits and south-facing slopes)</b>			
<i>Poa glauca</i>	IV 2	I r	I r
<i>Minuartia rubella</i>	IV r	II r	I r
<i>Stellaria longipes</i>	IV r	I r	II r
<i>Poa alpigena</i>	III 2	I r	I r
<b>Taxa common to Groups <i>Poa glauca</i> - <i>Poa alpigena</i> and <i>Carex rupestris</i> - <i>Saxifraga oppositifolia</i></b>			
<i>Oxytropis nigrescens</i> s.l.	III +	III 1	I r
<b>Group <i>Carex rupestris</i> - <i>Saxifraga oppositifolia</i> (communities occurring primarily on east- and north-facing slopes and some steppe communities)</b>			
<i>Carex rupestris</i>	II 1	V 2	II 1
<i>Hypogymnia subobscura</i>	III r	V +	II r
<i>Ochrolechia frigida</i>	II r	IV 1	II 1
<i>Fistulariella almqvistii</i>	II r	IV r	I r
<i>Alectoria nigricans</i>	I r	IV r	II r
<i>Lecanora luteovernalis</i>	I r	III +	I r
<b>Taxa common to Groups <i>Carex rupestris</i> - <i>Saxifraga oppositifolia</i> and <i>Cassiope tetragona</i> - <i>Dryas integrifolia</i></b>			
<i>Ditrichum flexicaule</i>	II r	IV r	IV r
<i>Salix reticulata</i>	II r	III +	V 1
<i>Saxifraga oppositifolia</i>	I r	V 1	III r
<i>Astragalus umbellatus</i>	II r	III +	IV 1
<i>Silene acaulis</i>	I r	III r	III r
<i>Parrya nudicaulis</i> s.l.	I r	III r	III r
<i>Pedicularis lanata</i>	I r	II r	III r
<b>Group <i>Cassiope tetragona</i> - <i>Dryas integrifolia</i> (communities occurring primarily in snowbeds)</b>			
<i>Tomenthypnum nitens</i>	I r	II r	V 2
<i>Cassiope tetragona</i>	.	I r	IV 2
<i>Carex scirpoidea</i>	I r	II 1	IV 1
<i>Pedicularis capitata</i>	II r	II r	IV +
<i>Masonhalea richardsonii</i>	II r	II r	IV +
<i>Papaver macounii</i>	II r	II r	IV r
<i>Salix rotundifolia</i>	II r	I r	III 2
<i>Arctagrostis latifolia</i>	II 1	I r	III +

<sup>a</sup> Complete differentiated relevé tables for each group are in M.D. Walker (1990). Table values are Braun-Blanquet constancy classes (I - >0-20%; II - >20-40%; III - >40-60%; IV - >60-80%; V - >80%), followed by average cover for the group expressed as a cover class (r - ≤0.3%; + - >0.3- <1%; 1 - 1-5%; 2 - >5-25%; 3 - >25-50%; 4 - >50-75%; 5 - >75-100%).

TABLE 3  
Differentiating taxa for the steppe vegetation types<sup>a</sup>

	<i>P. glauca</i> - <i>P. alpigena</i>									
	<i>C. beeringianum</i> - <i>R. pedatifidus</i>			<i>P. glauca</i> - <i>B. pumpellianus</i>						
	FB-LC <sup>b</sup>	TS-PU	Frag.	PH-PA	KM-SG	CO-ST	AG	CP-CN	CF-SN	Typ.
Number of samples:	15	16	4	4	8	8	1	6	2	21
<b>Stand Type <i>Cerastium beeringianum</i>-<i>Ranunculus pedatifidus</i></b>										
<i>Cerastium beeringianum</i>	V 1	V 1	V 1	III +	II r	II r	..	..	..	..
<i>Ranunculus pedatifidus</i>	V 1	V 1	III r	II r	..	II r	..	..	..	..
<i>Papaver lapponicum</i>	V 1	V +	III r	..	..	II r	..	..	..	I r
<i>Draba cinerea</i>	IV r	V r	IV r	III r	II r	II r	V r	I r	..	I r
<b>Subtype <i>Festuca baffinensis</i>-<i>Luzula confusa</i></b>										
<i>Poa arctica</i>	IV 2	II 2	II r	III 1	II +	II 2	..	..	..	I r
<i>Festuca baffinensis</i>	IV 1	II +	..	II 1	I r	III r	..	..	..	I r
<i>Luzula confusa</i>	IV 1	..	..	..	..	I r	..	..	..	..
<i>Rinodina turfacea</i>	IV r	I r	..	II r	I r	II r	..	..	..	I r
<i>Melandrium affine</i>	III r	II r	..	III r	II r	I r	V r	..	..	I r
<i>Saxifraga caespitosa</i>	III r	I r	II r	..	..	..	..	..	..	..
<i>Timmia austriaca</i>	III r	II r	IV r	III 1	III +	II r	..	..	..	I r
<i>Politrichastrum alpinum</i>	III 1	I r	..	..	..	III r	..	..	..	I r
<b>Subtype <i>Trisetum spicatum</i>-<i>Potentilla uniflora</i></b>										
<i>Trisetum spicatum</i>	II 1	V 2	III r	II r	I r	..	..	..	..	..
<i>Potentilla uniflora</i>	I r	V 2	..	..	I r	II +	V 1	..	..	I r
<i>Lloydia serotina</i>	II +	IV 1	..	..	..	II r	..	I r	..	II r
<i>Androsace septentrionalis</i>	I r	III r	II r	III r	I r	II r	V +	..	..	..
<i>Campanula uniflora</i>	..	III +	..	..	..	III r	..	I +	..	I r
<i>Taraxacum phymatocarpum</i>	..	III +	III r	..	..	III r	..	..	..	I r
<b>Stand Type <i>Poa glauca</i>-<i>Bromus pumpellianus</i></b>										
<i>Bromus pumpellianus</i> s.l.	I r	I 1	..	V 3	IV 2	III 2	V r	..	..	..
<i>Bupleurum triradiatum</i>	..	..	..	III +	I r	IV 1	V +	..	..	..
<b>Subtype <i>Potentilla hookeriana</i>-<i>Polemonium acutiflorum</i></b>										
<i>Potentilla hookeriana</i> ssp. <i>hookeriana</i>	I 1	III 1	..	V 2	III +	II r	..	..	..	..
<i>Polemonium acutiflorum</i>	I r	I +	..	IV 2	I r	..	..	..	..	..
<i>Agropyron boreale</i> ssp. <i>hyperarcticum</i>	I 1	II 1	..	III 2	II r	..	..	..	..	..
<i>Draba glabella</i>	I r	I r	..	III r	III r	I r	..	..	..	..
<i>Oxytropis maydelliana</i>	II r	I r	II 1	III r	II r	II r	..	..	..	II +
<b>Subtype <i>Kobresia myosuroides</i>-<i>Salix glauca</i></b>										
<i>Kobresia myosuroides</i>	I +	..	II +	II 1	V 2	III 2	..	V 1	V r	II 1
<i>Salix glauca</i>	I r	I r	..	II 1	V 2	..	..	II r	V +	I r
<i>Arctous rubra</i>	I r	..	..	II r	IV 1	..	..	..	..	I r
<i>Pyrola grandiflora</i>	..	..	..	II r	III +	..	..	..	..	..
<i>Astragalus alpinus</i>	I r	I r	..	II r	III +	..	..	..	..	..
<b>Subtype <i>Carex obtusata</i>-<i>Saxifraga tricuspidata</i></b>										
<i>Carex obtusata</i>	I 1	I r	..	..	I r	V 2	..	..	..	..
<i>Saxifraga tricuspidata</i>	..	I r	..	..	..	V 1	..	..	..	..
<i>Polemonium boreale</i>	II 1	III 1	..	II +	..	IV +	..	..	..	..
<i>Anemone drummondii</i>	..	..	..	..	..	IV r	..	..	..	..
<i>Phlox sibirica</i>	..	..	..	..	..	IV r	..	..	..	..
<i>Cladonia gracilis</i>	..	..	..	..	I r	IV r	..	..	..	I r
<i>Cornicularia aculeata</i>	..	I r	..	..	..	IV r	..	I r	..	..
<i>Parmelia omphalodes</i>	II r	I r	..	..	..	IV r	..	..	..	II r
<i>Minuartia arctica</i>	I r	I r	II r	III 1	II r	IV r	..	I r	III r	II r
<i>Astragalus aboriginum</i>	..	..	..	II r	..	III +	V 1	..	..	..
<i>Saxifraga reflexa</i>	..	..	..	..	..	II +	..	..	..	..
<b>Subtype <i>Artemisia glomerata</i></b>										
<i>Artemisia glomerata</i>	..	I r	..	II r	..	..	V 2	..	..	..
<b>Stand Type <i>Carex rupestris</i>-<i>Oxytropis jordallii</i></b>										
<i>Oxytropis jordallii</i>	I +	I r	..	..	II r	..	..	V 1	V 1	III 1
<b>Subtype <i>Carex petricosa</i>-<i>Carex nardina</i></b>										
<i>Carex petricosa</i>	..	..	..	..	..	..	..	V 2	..	..
<i>Hedysarum alpinum</i> ssp. <i>americanum</i>	..	..	..	II r	I r	..	..	IV +	III 1	..
<i>Carex nardina</i>	..	I r	..	..	..	I r	..	III r	..	..
<i>Braya humilis</i>	..	..	..	..	..	II r	..	III r	..	..
<b>Subtype <i>Carex franklinii</i>-<i>Salix brachycarpa</i> ssp. <i>niphoclada</i></b>										
<i>Carex franklinii</i>	..	..	..	..	..	..	..	V 2	..	..
<i>Salix brachycarpa</i> ssp. <i>niphoclada</i>	I 1	..	..	..	II 1	..	..	V 1	..	..

<sup>a</sup> Complete differentiated relevé tables are in M.D. Walker (1990). Table values are Braun-Blanquet constancy classes (I - >0-20%; II - >20-40%; III - >40-60%; IV - >60-80%; V - >80%), followed by average cover expressed as a cover class (r - ≤0.3%; + - >0.3-1%; 1 - 1-5%; 2 - >5-25%; 3 - >25-50%; 4 - >50-75%; >75-100%).

<sup>b</sup> FB-LC - *Festuca baffinensis* - *Luzula confusa*; TS-PU - *Trisetum spicatum* - *Potentilla uniflora*; Frag. - fragment; PH-PA - *Potentilla hookeriana* - *Polemonium acutiflorum*; CO-ST - *Carex obtusata* - *Saxifraga tricuspidata*; AG - *Artemisia glomerata*; CP-CN - *Carex petricosa* - *Carex nardina*; CF-SN - *Carex franklinii* - *Salix brachycarpa* ssp. *niphoclada*; Typ. - typicum.

## RESULTS

### VEGETATION ANALYSIS

The three classification groups defined on the pingos correspond to the physiognomic-ecological categories of steppe, fellfield, and snowbed, but their formal classification was based on differentiating taxa (Westhoff and

van der Maarel, 1978), not on physiognomy (Table 2). Of the 26 taxa in Table 2 that differentiate the three groups, only one, *Cassiope tetragona*, is completely absent from any given group. Twenty taxa are common to all pingo vegetation. It is notable that 17 of these are

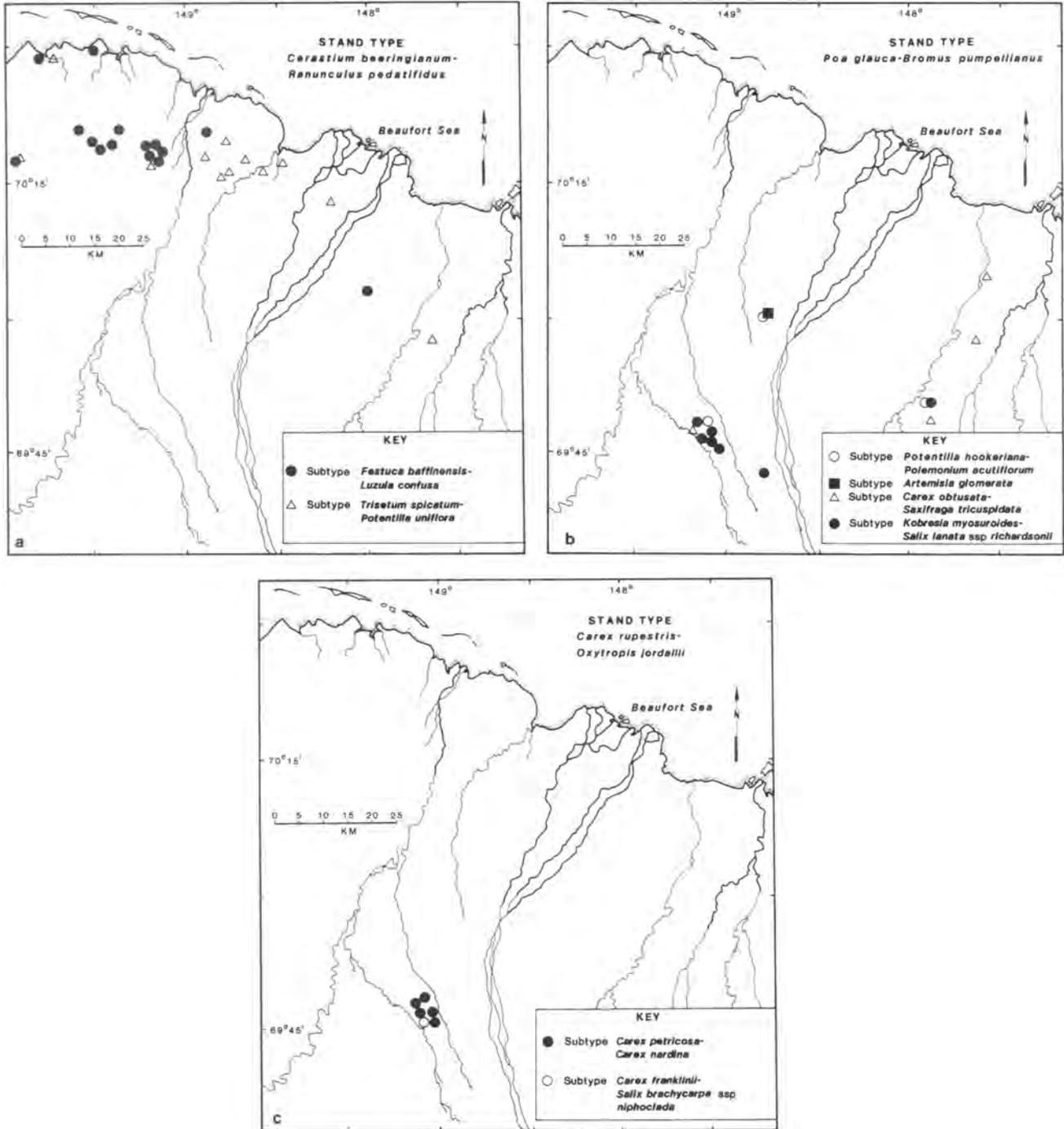


FIGURE 3. Distribution of (a) Stand Type *Cerastium beeringianum*-*Ranunculus pedatifidus* and its subtypes, (b) Stand Type *Poa glauca*-*Bromus pumpellianus* and its subtypes, and (c) steppe subtypes within Stand Type *Carex rupestris*-*Oxytropis jordalii*.

cryptogams (nine lichens and eight mosses). The three widespread vascular taxa include a dwarf shrub, *Dryas integrifolia*, and two forbs, *Minuartia arctica* and *Polygonum viviparum*. There are no widespread grasses.

Steppe-like vegetation occurs on well-drained sites, primarily south-facing slopes and summits that are dominated by graminoids and erect forbs and with minimal cover of *Dryas integrifolia* and cushion plants. These stands are placed into Group *Poa glauca*-*Poa alpigena*. This group has two steppe stand types, *Cerastium beerianum*-*Ranunculus pedatifidus* and *Poa glauca*-*Bromus pumpellianus*, with six subtypes (Table 3). Although *Dryas integrifolia* occurs in many of these sites, it has low relative cover and abundance here, and the dominant species in most of these areas are a combination of forbs and grasses. Many stand types within this group have not been described previously.

Fellfield-like vegetation is placed into Group *Carex rupestris*-*Saxifraga oppositifolia*, which is found on exposed, north-, and northeast-facing slopes. These sites have low vascular species diversity and cover, with an abundance of cushion and mat-forming plants and crustose lichens, and are ecologically similar to high alpine and high arctic sites. Five of six differential taxa are lichens, and seven taxa are in common with Group *Cassiope tetragona*-*Dryas integrifolia*. Most of the stand types in this group are not steppe types, but one, *Carex rupestris*-*Oxytropis jordalii*, has two steppe subtypes.

Snowbeds are placed into Group *Cassiope tetragona*-*Dryas integrifolia*. These sites are usually dominated by dwarf ericaceous shrubs, and are similar to snowbed types described elsewhere in the Arctic (Aleksandrova, 1980; Nams and Freedman, 1987a, b).

#### STEPPE STAND TYPE DESCRIPTIONS

All stand types and subtypes within Group *Poa glauca*-*Poa alpigena* are described here, as well as the steppe subtypes within Stand Type *Carex rupestris*-*Oxytropis jordalii* (in Group *Carex rupestris*-*Saxifraga oppositifolia*). Distributions of the steppe stand types and subtypes indicate a strong locational component (Figure 3). The best examples of steppe are found within Subtype *Carex obtusata*-*Saxifraga oppositifolia*, which is limited to sites greater than 15 km inland.

#### Stand Type *Cerastium beerianum*-*Ranunculus pedatifidus*

This type is most common on animal-disturbed summits, but is also found on south-facing slopes near the coast. It is equivalent to the moist *Festuca baffinensis*, *Papaver macounii*, *Ranunculus pedatifidus* forb, grass tundra described at Prudhoe Bay by D. A. Walker (1985), which he associated with areas of high animal use. Coverage of *Dryas integrifolia* is variable in this type, and ranges from absent to 50%, but with a low mean value of 11%. Other important species include *Papaver lapponicum* and *Draba cinerea*. Forbs and grasses are dominant overall, and this is considered a steppe type. Soils are sandy, and species associated with the coast and rivers

are common and include *Potentilla pulchella*, *Antennaria friesiana*, and *Alopecurus alpinus*. Two subtypes are recognized with differentiating taxa, and a group of four floristically depauperate stands were not further characterized.

Subtype *Festuca baffinensis*-*Luzula confusa* is found only on summits, and the flora of this subtype has a distinctly alpine character. Three of the more common species, *Saxifraga caespitosa*, *Festuca brachyphylla*, and *Papaver lapponicum*, are listed by Cooper (1986) as present on the most exposed, high alpine sites in the Arrigetch Peaks region of the Brooks Range. Seven of the ten differentiating and associated vascular species are listed by Cooper as present in the Arrigetch flora.

Subtype *Trisetum spicatum*-*Potentilla uniflora* occurs primarily on summits, but it was also found on five south slopes. These sites are highly disturbed by animals such as arctic fox, arctic ground squirrel, and birds (M. D. Walker, 1990). Like the previous subtype, these sites have a distinctly alpine character, and are dominated by grasses and forbs. This subtype grades into Stand Type *Poa glauca*-*Bromus pumpellianus*.

#### Stand Type *Poa glauca*-*Bromus pumpellianus*

This stand type contains good examples of steppe. *Bupleurum triradiatum*, an arctic-alpine species common in this type, is also an important component of south-facing steppes in interior Alaska (Edwards and Armbruster, 1989). Although this stand type is found on some of the steepest slopes, they are also exceptionally stable, with no evidence of frost action or other geomorphic disturbance. They are, however, heavily used by arctic ground squirrels. The type is equally divided between summits and south slopes, and is fairly varied, with four subtypes. *Dryas integrifolia* is of minimal importance.

Subtype *Potentilla hookeriana*-*Polemonium acutiflorum* was described from the summits and a south slope of three pingos. These sites often have a high cover of grasses and a meadow-like appearance (Figure 4). Other important species are *Agropyron boreale* ssp. *hyperarcticum*, *Draba glabella*, and *Oxytropis maydelliana*. This subtype had considerable evidence of use by arctic fox.

Subtype *Kobresia myosuroides*-*Salix glauca* was found mainly on summits of a group of pingos near the Toolik River. It is characterized by the presence of erect willows (*Salix* spp.). *Salix lanata* may be present, as well as the dwarf shrub *Arctous rubra*; *Calamagrostis purpurascens* is an associated species. The importance of dwarf shrubs precludes this as a steppe type, but both *K. myosuroides* and *C. purpurascens* indicate a relationship to the steppes. *Calamagrostis purpurascens* is a dominant species on the Greenland steppes (Böcher, 1954, 1963), interior Alaska (Murray et al., 1983; Edwards and Armbruster, 1989), and Wrangel Island (Yurtsev, 1982). These sites are more heavily disturbed by arctic ground squirrels than any other type, and the ground surface is often complex, with multiple burrow openings.

Subtype *Carex obtusata*-*Saxifraga tricuspidata* was found in eight sites, all to the east and south of the main

Prudhoe Bay area. These are the best examples of steppe vegetation on the pingos (Figure 5). *Dryas integrifolia* has less than 1% cover or is absent. Important species include *Anemone drummondii*, *Phlox sibirica*, *Polemonium boreale*, *Minuartia arctica*, *Astragalus aboriginum*, and *Saxifraga reflexa*. Several range disjunctions are found here, including *Saxifraga reflexa*, *Pulsatilla patens*, and *Eritrichium aretioides*. *Erigeron muirii*, which is endemic to the North Slope of the Brooks Range and occurs primarily in the foothills, is present in several of these stands. *Carex obtusata* and *Pulsatilla patens* are important in many modern steppe types of Siberia, particularly the meadow steppes (Aleksandrova, 1980; Yurtsev, 1982), and in the steppes on interior Alaska (Murray et al., 1983; Edwards and Armbruster, 1989). Similar vegetation is also found on south-facing sandstone outcrops in the northern foothills of the Brooks Range (D. A. Walker

et al., 1989; M. D. Walker et al., 1989).

Subtype *Artemisia glomerata* was represented by only a single stand. This same vegetation is found on extremely exposed south-facing sandstone outcrops in the foothills. It has few species and is dominated by *Artemisia glomerata*, with *Poa glauca*, *Bromus pumpellianus*, and *Bupleurum triradiatum* also conspicuous. It shares few species with other subtypes.

#### Stand Type *Carex rupestris*-*Oxytropis jordalii*

This stand type is found on south-facing slopes on the more northern pingos sampled, primarily to the north of the 70° latitude line. The steppe subtypes, however, are restricted to a group of pingos near the Toolik River, in the southern end of the study area. Subtype *Carex petricosa*-*Carex nardina* is related to the herbaceous-cryophyte vegetation that Yurtsev (1982) stated has the general



FIGURE 4. Subtype *Potentilla hookeriana*-*Polemonium acutiflorum* on the south slope of pingo 15.



FIGURE 5. Subtype *Carex obtusata*-*Saxifraga tricuspidata* on pingo 41.

aspect of a steppe but is characterized by arctic-alpine species. Other differentiating vascular species are *Hedysarum alpinum* ssp. *americanum* and *Braya glabella*. *Kobresia myosuroides* was present in all but one of the stands.

Subtype *Carex franklinii*-*Salix brachycarpa* ssp. *niphoclada* is represented by a single stand on the summit and south slope of one pingo. It is very similar to subtype *Carex petricosa*-*Carex nardina*, but neither of these species are present in this type.

#### FLORISTIC ANALYSIS

M. D. Walker (1990) recorded 232 vascular taxa, 218 species, 113 genera, and 32 families on these 41 pingos. Within the area of study, 19 of these are restricted taxa known only from the pingos (Table 4). This regional restriction does not imply that these taxa are rare throughout their range, only that they are restricted to specific habitats within the area considered here. These restricted taxa are consistently most common on south-facing slopes, although they represent only a small proportion of the given taxa in any sample (Figure 6). The lowest occurrences of restricted taxa are in snowbeds. This is because snowbeds are not limited to pingos but are fairly common regionally, whereas stable, windblown south- and north-facing slopes are rare on the coastal plain, occurring primarily on pingos.

The floristic affinities of the restricted taxa are distinct from those of the other members of the pingo flora ("widespread species" in Figure 7). Restricted taxa are mostly Zone 4, whereas the widespread taxa are primarily Zone 2 and Zone 3 ( $\chi^2 = 208.29$ ,  $p < 0.001$ ). Over half the restricted taxa are North American-Asian, whereas nearly half the widespread taxa are circumpolar ( $\chi^2 = 57.73$ ,  $p < 0.001$ ). There is also a slightly higher proportion of North American species and Alaskan-Yukon endemics in the restricted group. The restricted taxa do not differ from the remaining pingo flora with regard to environmental regions ( $\chi^2 = 4.04$ , ns).

#### POLLEN

Pollen from the pingo soils differs from the modern samples analyzed by Nelson (1979) from moist and wet tundra in the Prudhoe Bay area (Figure 8;  $\chi^2 = 208.29$ ,  $p < 0.001$ ). *Alnus*, *Betula*, *Picea*, and *Pinus* have been combined into one category as long-distance taxa. The pingo pollen spectrum has lesser percentages of long-distance taxa, *Salix*, and *Ericales*, approximately the same percentages of Gramineae and *Artemisia*, and greater amounts of Cyperaceae, Caryophyllaceae, other forbs, and spores. Influx rates cannot be calculated because of the way in which the data were collected, and comparison of percentages is difficult. The extent to which the differences are due to differential preservation of certain pollen types in soils as compared to moss polsters and lake sediments is also difficult to assess.

The degree to which the pollen is characteristic of the modern vegetation differs considerably among the four samples, indicated by Pearson correlation coefficients

between relative vegetation cover and relative pollen percent, with long-distance taxa and spores removed from the pollen sum ( $r^2 = 0.01, 0.12, 0.50, 0.83$ ). The two low correlations were both samples in which pre-Quaternary pollen types were found, indicating the samples were not purely recent pollen. Although *Artemisia* was present in the vegetation at only two sites, it was represented in the pollen spectrum at three sites (Figure 9). Of the two samples which had *Artemisia* present in the vegetation, it was over-represented in the pollen spectrum in one case and greatly under-represented in another. The relative abundance of *Artemisia* pollen in these samples appears

TABLE 4  
Taxa that are primarily restricted to pingos within the study region

<i>Anemone drummondii</i>	<i>Erigeron muirii</i>
<i>Braya humilis</i> ssp. <i>richardsonii</i>	<i>Erysimum pallasii</i>
<i>Carex franklinii</i>	<i>Eritrichium aretioides</i>
<i>Carex glacialis</i>	<i>Luzula arcuata</i>
<i>Carex nardina</i>	<i>Pulsatilla patens</i>
<i>Carex obtusata</i>	<i>Saxifraga davurica</i>
<i>Carex petricosa</i>	<i>Saxifraga reflexa</i>
<i>Carex supina</i> ssp. <i>spaniocarpa</i>	<i>Selaginella sibirica</i>
<i>Draba fladnizensis</i>	<i>Stellaria umbellata</i>
<i>Draba subcapitata</i>	

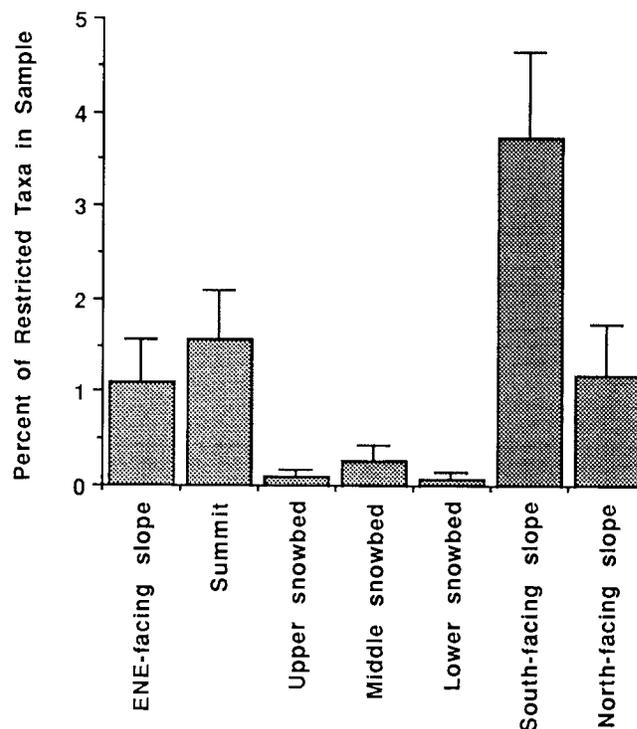


FIGURE 6. Distribution of restricted species (Table 5) among the seven sampling sites. Data are shown as percentage of species in a sample rather than absolute frequency, because there are significant differences in species richness among microsites (M. D. Walker and D. A. Walker, 1988). Error bars represent the standard error.

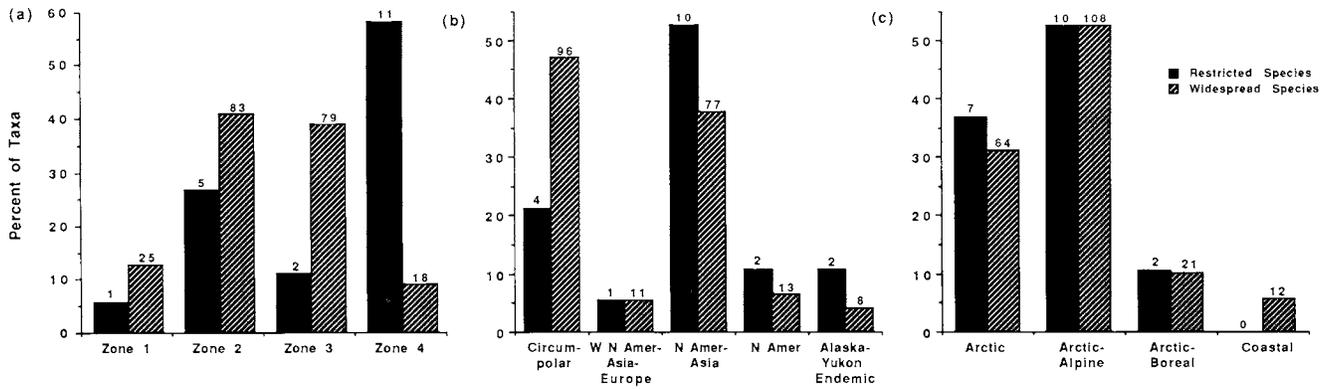


FIGURE 7. Distribution of species among the (a) northern limit types, (b) geographic range categories, and (c) environmental regions. Number of species is on top of each bar.

to be related more to the distance of the sites from the coast, where *Artemisia* is most abundant regionally, than to its relative abundance in the plant community at the pollen sampling site. Other forb taxa, such as the Caryophyllaceae, appear to be better indicators of site vegetation.

While it would be premature to draw broad conclusions from only four samples, these data establish two important things. First, the pingo pollen spectra, at least for the south-facing slopes that we examined, are distinct from the regional spectra. Thus, modern pollen rain studies of these sites could be useful for determining pollen spectra for these community types. Second, *Artemisia* is probably not a good pollen indicator of the presence of *Artemisia* reasonably close to the sampling site. *Artemisia* pollen is most abundant in coastal sites, where it is locally common on unstable dunes and river bars.

#### SOILS

Pingos form following drainage of deep thaw lakes, and much of the organic material in pingo soils probably originated in the lake phase. The combined processes of colluviation, soil creep, and digging by squirrels and foxes incorporate this organic material into the subsurface layers. The result is a deep, well-drained, mineral soil that is rich in organics. The soil is colonized and stabilized by grasses, which further enhances the formation of a deep, dark-colored surface horizon. Soils associated with the steppe types are primarily Pergelic Cryoborolls (41 of 59 profiles). Pergelic Cryoborolls are differentiated from other Mollisols solely on the basis of temperature, but pedological processes in well-drained arctic soils are, in most cases, the same or analogous to processes that occur in temperate regions, although rates may be slowed (Ugolini, 1986). Mollisols are characterized by the U.S. Soil Taxonomy (Soil Survey Staff, 1975) as “. . . the very dark colored, base-rich soils of the steppes,” although they are also found in the boreal regions on well-drained calcareous sites (Everett and Parkinson, 1977). Pergelic Cryoborolls are essentially limited to pingos on the coastal

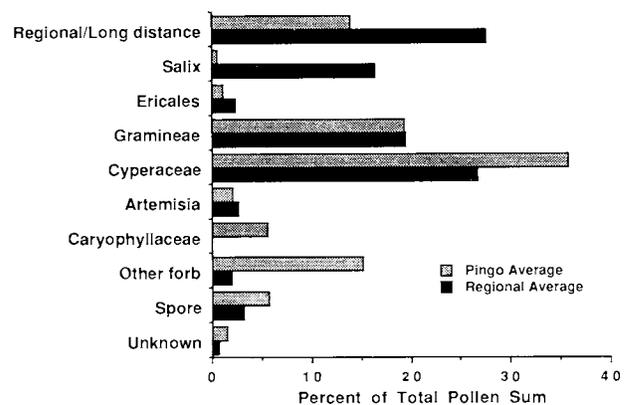


FIGURE 8. Comparison of mean pollen percentages for four south-facing pingo slopes (pingo average) with the average of 15 modern pollen samples (regional average) from Nelson (1979).

plain. Their genesis is a result of a combination of factors which include the mechanism of pingo genesis and the pingo flora and fauna.

Three Pergelic Cryoboroll soils were recognized. Typical Pergelic Cryoborolls have no additional characteristics. Calcic Pergelic Cryoborolls have secondary accumulations of carbonate (Bk horizons) (Everett and Parkinson, 1977) which are a result of calcareous loess becoming incorporated into the soil. Pacific Pergelic Cryoborolls have overthickened mollic epipedons (>40 cm thick) (M. D. Walker, 1990). The latter often occur on pingo summits, where animals mix organic-rich materials into the soil. Summit areas are typically grassy, which stabilizes the soil and further enhances Mollisol development.

Other soil types less frequently found on south-facing slopes and summits of pingos in this study include Pergelic Cryumbrepts (six profiles) and Pergelic Cryochrepts (six profiles). The former occur where either pH or base saturation is too low to meet the requirements for a Mollisol as defined by the USDA criteria (Soil Survey Staff, 1975). The latter occur when the surface horizon is too thin to qualify as a Mollisol.

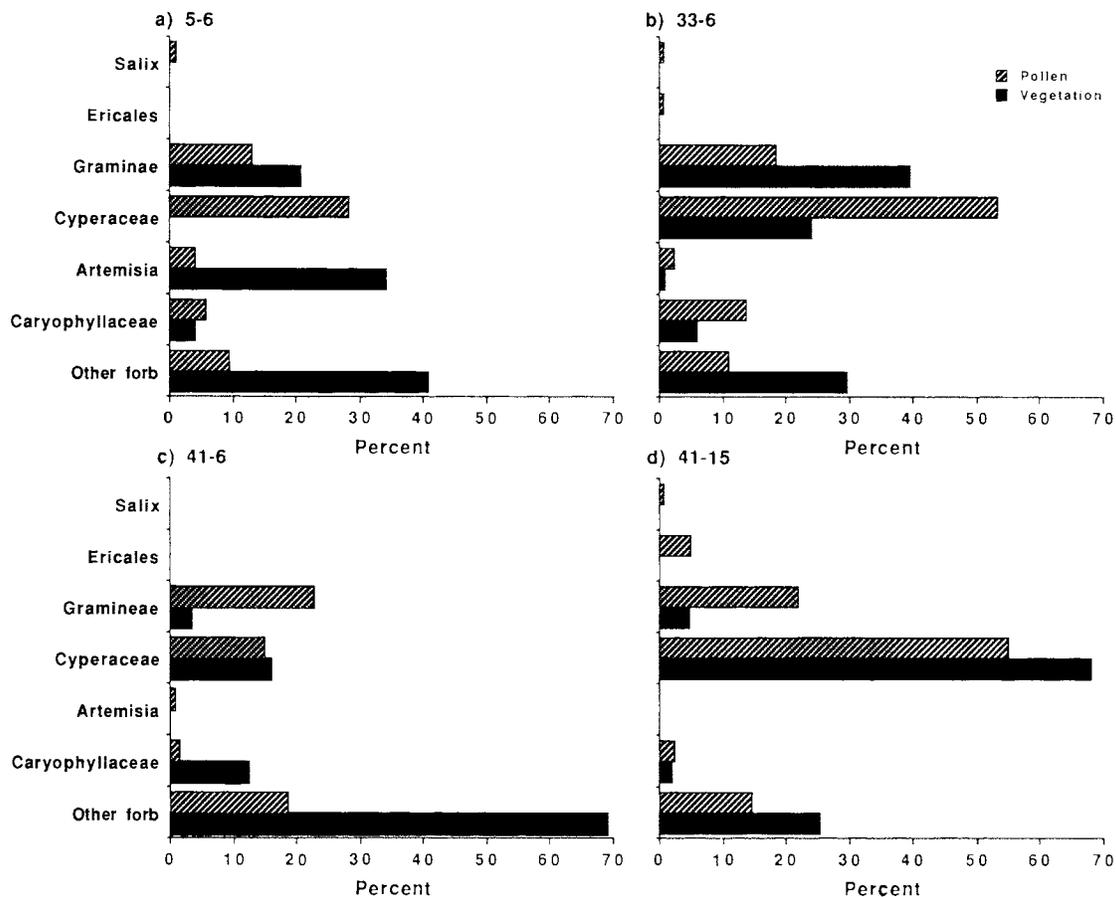


FIGURE 9. Pollen percentages adjusted to exclude long-distance taxa (*Alnus*, *Betula*, *Picea*, *Pinus*) compared to relative percentages of the same groups in the vegetation samples. Samples 5-6 (a) and 33-6 (b) are coastal sites classified as Subtype *Trisetum spicatum*-*Potentilla hookeriana*, and samples 41-6 (c) and 41-15 (d) are inland sites classified as Subtype *Carex obtusata*-*Saxifraga tricuspidata* (Figures 2 and 3).

#### MICROCLIMATES

The south slope of the instrumented pingo had the highest maximum daily temperature of the five sites measured, and it also had the lowest minimum (Table 5). South slope temperature fluctuated as much as 27°C in a single day. This effect is due to the low sun angle at this latitude (70°N), so that steep, south-facing slopes receive more radiation at midday than level slopes. At midnight, however, when both sun angle and ambient air temperatures are lowest, south slopes are in shadow, whereas north-facing and flat sites receive some incoming radiation from the midnight sun. Although there are no winter climate data available for pingos or equivalent sites, it is likely that annual (winter vs. summer) soil tem-

perature fluctuations are also greatest on south-facing pingo slopes. We expect mid-winter temperatures to differ little between north- and south-facing slopes because the sun is continually below the horizon. Both north- and south-facing slopes are snow free in winter, and therefore lack the climatic buffering of snow cover. South-facing slopes of pingos, therefore, have both more extreme diurnal and annual fluctuations in surface temperature than do flat, mesic surfaces or north-facing slopes. Although these could not be considered continental microclimates in the classic sense, they do represent the continental extreme of the gradient of microclimates present in northern Alaska today.

#### DISCUSSION

##### APPROPRIATENESS OF THE STEPPE CLASSIFICATION

Pingos are distinct from the majority of the Alaskan Arctic Coastal Plain landscape because of their great habitat diversity. In particular, the steep, stable, south-

facing slopes are essentially limited to pingos on the coastal plain, and are much warmer in summer than any other coastal plain sites. The pingo plant communities consist of some types that are very much like alpine fell-

TABLE 5  
*Mean temperature (°C), August 1986, for standard-height shelter, mesic tundra next to shelter, and pingo summit, south-facing slope, and north-facing slope*

	Minimum	Maximum	Daily fluctuation	Mean
Standard-height shelter	2.1 ± .42 <sup>a</sup>	7.1 ± .94	5.0 ± .72	4.6 ± .63
Range	-2.0 - 6.6	-0.7 - 17.1	0.3 - 14.1	-0.9 - 11.8
Number of days	30	30	30	30
Mesic tundra	2.2 ± .27	9.0 ± .82	6.1 ± .80	5.1 ± .49
Range	0.9 - 4.4	2.4 - 16.0	1.5 - 14.0	1.6 - 9.0
Number of days	20	22	18	18
Pingo summit	2.4 ± .27	11.2 ± .94	8.8 ± .83	6.8 ± .56
Range	0 - 5.2	2.5 - 21.3	1.4 - 18.3	1.6 - 12.2
Number of days	30	30	30	30
Pingo south slope	1.4 ± .46	14.0 ± 1.5	12.7 ± 1.2	7.7 ± .90
Range	-2.5 - 5.5	1.8 - 31.5	2.7 - 26.8	-0.1 - 18.1
Number of days	30	30	30	30
Pingo north slope	1.6 ± .34	8.2 ± .75	6.8 ± .57	4.8 ± .50
Range	-1.3 - 4.7	1.5 - 14.8	1.6 - 12.1	0.1 - 9.4
Number of days	30	29	29	29

<sup>a</sup>Second figure is standard error of the mean.

fields, with widely-spaced cushion and mat plants, and skeletal soils (M. D. Walker, 1990). Many of the dominant species in these fellfield-like areas, such as *Oxytropis nigrescens*, are endemic to arctic-alpine Beringia. There are also the steppe communities, however, with much higher coverage of erect forbs and grasses and greater total plant cover. The vegetation structure, including both physiognomy and composition, the floristics, and the soils of these sites all support their classification as steppe. They have abundant graminoids, and their species composition reflects ties to other tundra steppe communities.

Yurtsev (1982) has demonstrated from his extensive work in Siberia that a complete transition exists from the true steppes in interior Asia to the tundra steppes of the northern coast. He described this transition in terms of floristics, climate, and associated soils, with the most extreme tundra steppes found on Wrangel Island. The Wrangel Island landscape has no known equivalent on the Chukotka mainland, and the steppe associations there are best developed on south-facing slopes with gravelly soils. The island is floristically very rich, and because of its location on the polar shelf and its isolation from the mainland, it is particularly important for identification of potential relict vegetation. Ericaceous heath species that dominate most modern dry arctic sites are missing entirely from the Wrangel Island flora. The pingo steppes, particularly Subtype *Carex obtusata-Saxifraga tricuspidata*, are most similar to the cryoxerophyte vegetation described on relatively warm, south-facing slopes on Wrangel Island.

Another significant use of the term steppe to describe modern arctic vegetation is the work of Böcher in Greenland (1954, 1963). He described associations dominated by *Calamagrostis purpurascens* and *Carex supina* ssp. *spaniocarpa* as steppes, calling the *Calamagrostis pur-*

*purascens* associations the "tall grass prairie" of Greenland (Böcher, 1963: 219). Related vegetation dominated by *Festuca brachyphylla* and *Kobresia myosuroides* was described by Böcher as transitional to the steppe types. Vegetation of steep, south-facing bluffs in interior Alaska is related to the Greenland vegetation, with *Calamagrostis purpurascens* and *Carex supina* both important (Murray et al., 1983; Howenstein, et al., 1985; Juday et al., 1985). Steppe vegetation on some south-facing river bluffs in the Alaskan interior shows continual gradation with alpine tundra vegetation (Edwards and Armbruster, 1989).

Taxa restricted to pingos are primarily arctic-alpine, North American-Asian, low arctic. The increased importance of North American-Asian taxa indicates a floristic tie to Asia, and therefore to Beringia, because the Bering Land Bridge is the only dispersal route that has existed between the continents. The great importance of Zone 4 taxa (the warmest arctic zone) indicates ties to the Brooks Range and interior Alaska. Finally, the Pergelic Cryoboroll soils, found regionally only on pingos (Everett and Parkinson, 1977), are in many ways more similar to soils of the Great Plains than they are to the predominantly organic and wetland soils that cover most of the coastal plain. The major factor in common between the pingo soils and other coastal plain soils is that they are all underlain by permafrost, but the pingo soils are much more deeply thawed, usually to greater than 1 m, so that permafrost is not the major factor affecting their genesis. The presence of well-defined secondary carbonate horizons indicates soil processes similar to those in temperate grasslands. Yurtsev (1982) described the presence of secondary carbonates in soils at many of the Siberian steppe sites, and the soils found on south-facing bluffs in interior Alaska have well-defined secondary carbonate horizons (D. A. Walker, personal observation).

A potential criticism of classification of the pingo communities as steppe is their lack of *Artemisia*. While *Artemisia* is an important indicator species of the Herb Zone pollen assemblage, this indicates its increased regional abundance during the Duvanny Yar, but not necessarily its occurrence in every community. *Artemisia* is not considered a critical steppe indicator in modern vegetation. Several species of *Artemisia* occur abundantly on the coastal plain today, usually associated with unstable, sandy soils. The pingo pollen spectra indicate that *Artemisia* is likely to be present in pollen spectra when it is locally abundant, although it may not necessarily be present at the sampling site.

#### POTENTIAL AND LIMITATIONS OF THE PINGOS AS STEPPE TUNDRA ANALOGS

Does this pingo vegetation, which is quite different from the mesic sedge tundra that covers most of the modern Coastal Plain, represent a relict of the proposed Pleistocene steppe tundra, or is it merely a reflection of modern flora and climate? There are several problems with trying to answer this question conclusively. The first is simply that we can never determine the precise floristic composition of past communities. Instead, we can develop only a broad regional picture and an idea of broad topographic vegetation gradients with carefully selected fossil sites (e.g., Schweger, 1982). Another problem is the dynamic nature of vegetation. True relicts will be found where environmental conditions have remained such that species can persist, and where there is a barrier to immigration such that the community is not changed by new colonizers. Wrangel Island is an example of such a situation, and the absence of ericaceous shrubs there probably reflects its relict status.

Pingos, however, are relatively small sites that are not isolated from the surrounding tundra by an impassable or even restrictive barrier, as an island would be. Pingo vegetation represents an integration of past events with present climate, environment, and flora (D. A. Walker et al., 1985; M. D. Walker, 1990). Species able to colonize pingos can readily do so from surrounding sites. It is likely that at least some of the species present in the pingo steppes are remnants that have been able to maintain their existence because of the environmental conditions present on pingos today. Subtype *Carex obtusata-Saxifraga tricuspidata*, in particular, is characterized by a substantial number of range disjunctions and rare species, and it is difficult to explain their existence as a unit based on long-distance dispersal. It is more likely that these small, disjunct stands represent, in part, contraction of a unit that was once more continuous and abundant regionally. In contrast, Stand Type *Cerastium beeringianum-Ranunculus pedatifidus* is made up almost entirely of species that are now common on most dry sites across the coastal plain, and thus probably represents a relatively recent aggregation of species.

Given these inherent limitations, what is the value of discussing potential links between the modern pingo vegetation and Pleistocene Beringian landscapes? The exact

nature of the landscape and climate changes that occurred in northern Alaska during the Pleistocene-Holocene boundary are unknown, and eastern and western regions may have had different full glacial conditions, with mesic tundra and snowbed communities in the west changing to a more sparse, xeric landscape in the east (Cwynar and Ritchie, 1980; Cwynar, 1982; Ritchie and Cwynar, 1982; Wilson, 1984; Anderson, 1988). Since the present environment of the central coastal plain is primarily wet tundra (D. A. Walker, 1985), the overall direction of the landscape change with time has been toward wetter conditions. This change would have been accompanied by a change in the abundance and distribution of species. The Duvanny Yar landscape would have had a very different mix of communities, with types considered distinct today juxtaposed and intergrading. Murray et al. (1983) made the important point that during glacial conditions the mountain and steppe flora and vegetation would have mingled, and therefore ". . . the abundance of arctic-alpine cryophytes in . . . pollen spectra is not fatal to the idea of a steppe-like vegetation."

The value of the pingos lies not so much in their exact duplication of the Pleistocene landscape, which would be impossible to prove in any case, but in the information they can give us about species-community-environment relationships in dry tundra, which was so abundant during the Duvanny Yar (Hopkins, 1982). What separates pingos from other dry sites is their size and their stability. Dry tundra on the coastal plain is generally limited, with the exception of pingos, to very small patches that range in size from as little as a few square meters to areas perhaps as large as 1000 m<sup>2</sup>, for example on the tops of high-centered polygons and along river terraces. Even these largest areas, however, are unstable and transient over fairly short time scales because of the dynamics of the coastal plain landscape (Black and Barksdale, 1949; Everett, 1980a). Pingos are large enough and long-lived enough to develop distinct well-defined communities. Some of the pingos within the Prudhoe Bay region of northern Alaska may be very old sites that were present during the Duvanny Yar or earlier (Rawlinson, 1983; D. A. Walker et al., 1985).

These steppe communities are the first that have been described from arctic Alaska, and represent a northern extreme for steppe in North America. They also represent the only extensive, well-developed dry tundra communities on the Alaskan Coastal Plain. As such, they have value as analogs for past landscapes and for understanding environmental controls on modern arctic vegetation.

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#### REFERENCES CITED

- Ager, T. A., 1975: Late Quaternary environmental history of the Tanana Valley, Alaska. *Ohio State University, Institute of Polar Studies Report*, 54. 117 pp.
- , 1982: Vegetation history of western Alaska during the Wisconsin glacial interval and the Holocene. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*. New York: Academic Press, 75-94.
- Ager, T. A. and Brubaker, L. B., 1985: Quaternary palynology and vegetational history of Alaska. In Bryant, V. M. and Holloway, R. G. (eds.), *Pollen Records of Late-Quaternary North American Sediments*. Dallas: American Association of Stratigraphic Palynologists, 353-385.
- Aleksandrova, V. D., 1980: *The Arctic and Antarctic: Their Division into Geobotanical Areas*. (Translated from the Russian by Doris Löve.) Cambridge: Cambridge University Press. 247 pp.
- Anderson, P. M., 1985: Late Quaternary vegetational change in the Kotzebue Sound area, northern Alaska. *Quaternary Research*, 24: 307-321.
- , 1988: Late Quaternary pollen records from the Kobuk and Noatak River drainages, northwestern Alaska. *Quaternary Research*, 29: 263-276.
- Armbruster, W. S. and McGuire, A. D., 1985: Environmental controls over the development of steppe vegetation on south-facing bluffs in interior Alaska. In: *Proceedings, 36th Arctic Science Conference*, Fairbanks, Alaska, 169.
- Black, R. F. and Barksdale, W. L., 1949: Oriented lakes of northern Alaska. *Journal of Geology*, 57: 105-118.
- Böcher, T. W., 1954: Oceanic and continental vegetational complexes in southwest Greenland. *Meddelelser om Grønland*, 148(1). 336 pp.
- , 1959: Floristic and ecological studies in middle west Greenland. *Meddelelser om Grønland*, 156(5). 68 pp.
- , 1963: Phytogeography of middle west Greenland. *Meddelelser om Grønland*, 148(3). 289 pp.
- Braun-Blanquet, J., 1932: *Plant Sociology: The Study of Plant Communities*. (Translated by G. D. Fuller and H. S. Conard.) New York: McGraw-Hill. 439 pp.
- Cantlon, J. E., 1961: Plant cover in relation to macro-, meso- and micro-relief. Final Report, Office of Naval Research, Grants No. ONR-208 and 216. 128 pp.
- Clebsch, E. E. C., 1957: The summer season climatic and vegetational gradient between Point Barrow and Meade River, Alaska. M.S. thesis, University of Tennessee. 60 pp.
- Clebsch, E. E. C. and Shanks, R. E., 1968: Summer climatic gradients and vegetation near Barrow, Alaska. *Arctic*, 21: 161-171.
- Colinvaux, P. A., 1964: The environment of the Bering Land Bridge. *Ecological Monographs*, 34: 297-329.
- Cooper, D. J., 1986: Arctic-alpine tundra vegetation of the Arrigetch Creek Valley, Brooks Range, Alaska. *Phytocoenologia*, 14: 467-555.
- Cwynar, L. C., 1982: A late-Quaternary vegetation history from Hanging Lake, northern Yukon. *Ecological Monographs*, 52: 1-24.
- Cwynar, L. C. and Ritchie, J. C., 1980: Arctic steppe-tundra: A Yukon perspective. *Science*, 208: 1375-1377.
- Edwards, M. E. and Armbruster, W. S., 1989: A tundra-steppe transition on Kathul Mountain, Alaska, U.S.A. *Arctic and Alpine Research*, 21: 296-304.
- Everett, K. R., 1980a: Geology and permafrost. In Walker, D. A., Everett, K. R., Brown, J., and Webber, P. J. (eds.), *Geobotanical Atlas of the Prudhoe Bay Region, Alaska*. U.S. Army Cold Regions Research and Engineering Laboratory, CRREL Report, 80-14: 8-9.
- , 1980b: Soils. In Walker, D. A., Everett, K. R., Brown, J., and Webber, P. J. (eds.), *Geobotanical Atlas of the Prudhoe Bay Region, Alaska*. U.S. Army Cold Regions Research and Engineering Laboratory, CRREL Report, 80-14: 20-23.
- Everett, K. R. and Parkinson, R. J., 1977: Soil and landform associations, Prudhoe Bay, Alaska, U.S.A. *Arctic and Alpine Research*, 9: 1-19.
- Fægri, K. and Iversen, J., 1975: *Textbook of Pollen Analysis*. 3rd ed. New York: Hafner. 295 pp.
- Ferrians, O., 1988: Pingos in Alaska: A review. In: *Proceedings, Permafrost: Fifth International Conference*. Washington, D.C.: National Academy Press, 734-739.
- Giterman, R. E., Sher, A. V., and Matthews, J. V., Jr., 1982: Comparison of the development of steppe-tundra environments in west and east Beringia: Pollen and macrofossil evidence from key sections. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*. New York: Academic Press, 43-74.
- Guthrie, R. D., 1968: Paleoecology of the large mammal community in interior Alaska during the late Pleistocene. *American Midland Naturalist*, 79: 346-363.
- , 1982: Mammals of the mammoth steppe as paleoenvironmental indicators. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*. New York: Academic Press, 307-328.
- Guthrie, R. D. and Matthews, J. V., Jr., 1971: The Cape Deceit fauna—early Pleistocene mammalian assemblage from the Alaskan Arctic. *Quaternary Research*, 1: 474-510.
- Haugen, R. K., 1982: Climate of remote areas in north-central Alaska, 1957-1979 summary. U.S. Army Cold Regions Research and Engineering Laboratory, CRREL Report, 80-14. 110 pp.
- Hibbert, D., 1982: History of the steppe-tundra concept. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*. New York: Academic Press, 153-156.
- Hopkins, D. M. (ed.), 1967: *The Bering Land Bridge*. Stanford: Stanford University Press. 495 pp.
- , 1982: Aspects of the paleogeography of Beringia during

- the late Pleistocene. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*. New York: Academic Press, 3–28.
- Howenstein, R. E., Murray, D. F., and Armbruster, W. S., 1985: Vegetation ecology of south-facing bluffs in subarctic interior Alaska. In: *Proceedings, 36th Arctic Science Conference*, Fairbanks, Alaska, 167.
- Hultén, E., 1937: *Outline of the History of Arctic and Boreal Biota during the Quaternary Period: Their evolution during and after the glacial period as indicated by the equiformal progressive areas of plant species*. (1972 reprint.) Germany: Strauss and Cramer. 168 pp.
- , 1968: *Flora of Alaska and Neighboring Territories: A Manual of the Vascular Plants*. Stanford: Stanford University Press. 1008 pp.
- , 1973: Supplement to the *Flora of Alaska and Neighboring Territories*. A study in the flora of Alaska and the transberingian connection. *Botaniska Notiser*, 126: 459–512.
- Juday, G. P., Batten, A. R., and McGuire, A. D., 1985: The south-facing Volkmar Bluff meadows: Composition and setting. In *Proceedings, 36th Arctic Science Conference*, Fairbanks, Alaska, 170.
- Kapp, R. O., 1969: *How to Know Pollen and Spores*. Dubuque: Brown. 249 pp.
- Kassler, K. C., 1985: Floristic analysis of certain south-facing bluffs along the Yukon River and Tanana River in interior Alaska. In: *Proceedings, 36th Arctic Science Conference*, Fairbanks, Alaska, 166.
- Koranda, J. J., 1970: Pingos. *Pacific Discovery*, 23: 18–24.
- Livingstone, D. A., 1955: Some pollen profiles from arctic Alaska. *Ecology*, 36: 587–600.
- Mackay, J. R., 1979: Pingos of the Tuktoyaktuk Peninsula area, Northwest Territories. *Géographie Physique et Quaternaire*, 33: 3–61.
- Martin, P. S., 1982: The pattern and meaning of holarctic mammoth extinction. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*. New York: Academic Press, 399–408.
- Matthews, J. V., Jr., 1974: Quaternary environments at Cape Deceit (Seward Peninsula, Alaska): Evolution of a tundra ecosystem. *Geological Society of America Bulletin*, 85: 1353–1385.
- McAndrews, J. H., Berti, A. A., and Norris, G., 1973: *Key to the Quaternary Pollen and Spores of the Great Lakes Region*. Toronto: Life Science Miscellaneous Publication, Royal Ontario Museum. 61 pp.
- Moriya, K., 1976: *Flora and Palynomorphs of Alaska*. Tokyo: Kodansha Ltd. 366 pp.
- Mueller-Dombois, D. and Ellenberg, H., 1974: *Aims and Methods of Vegetation Ecology*. New York: Wiley. 547 pp.
- Murray, D. F., Murray, B. M., Yurtsev, B. A., and Howenstein, R. H., 1983: Biogeographic significance of the steppe vegetation in subarctic Alaska. In: *Proceedings, Permafrost: Fourth International Conference*. Washington, D.C.: National Academy Press, 883–888.
- Nams, M. L. N. and Freedman, B., 1987a: Ecology of heath communities dominated by *Cassiope tetragona* at Alexandra fiord, Ellesmere Island, Canada. *Holarctic Ecology*, 10: 22–31.
- , 1987b: Phenology and resource allocation in a high arctic evergreen dwarf shrub, *Cassiope tetragona*. *Holarctic Ecology*, 10: 128–136.
- Nelson, R. E., 1979: Quaternary environments of the Arctic Slope of Alaska. M.S. thesis, University of Washington, Seattle. 141 pp.
- Nichols, H., 1975: Palynological and paleoclimatic study of the late Quaternary displacement of the boreal forest-tundra ecotone in Keewatin and Mackenzie, N.W.T., Canada. *University of Colorado, Institute of Arctic and Alpine Research, Occasional Paper*, 15. 87 pp.
- Rampton, V. N., 1971: Late Quaternary vegetational and climatic history of the Snag-Klutlan area, southwestern Yukon Territory, Canada. *Geological Society of America Bulletin*, 82: 959–978.
- Rannie, W. F., 1986: Summer air temperature and number of vascular species in arctic Canada. *Arctic*, 39: 133–137.
- Rawlinson, S. E. (ed.), 1983: *Guidebook to Permafrost and Related Features, Prudhoe Bay, Alaska*. Fourth International Conference on Permafrost, University of Alaska, Guidebook 5. Alaska Department of Natural Resources, Division of Geological and Geophysical Surveys. 177 pp.
- Ritchie, J. C., 1984: *Past and Present Vegetation of the Far Northwest of Canada*. Toronto: University of Toronto Press. 251 pp.
- Ritchie, J. C. and Cwynar, L. C., 1982: The late Quaternary vegetation of the north Yukon. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*. New York: Academic Press, 113–126.
- Schweger, C. E., 1982: Late Pleistocene vegetation of eastern Beringia: Pollen analysis of dated alluvium. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*. New York: Academic Press, 95–112.
- Soil Survey Staff, 1975: *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys*. U.S. Department of Agriculture Handbook No. 436. Washington, D.C.: Soil Conservation Service. 745 pp.
- Sørensen, T., 1941: Temperature relations and phenology of the Northeast Greenland flowering plants. *Meddelelser om Grønland*, 125(9). 305 pp.
- Steere, W. C., 1978: *The Mosses of Alaska*. Vaduz: Strauss and Cramer. 508 pp.
- Steere, W. C. and Inoue, H., 1978: The Hepaticae of arctic Alaska. *Journal of the Hattori Botanical Laboratory*, 44: 251–345.
- Stockmarr, J., 1971: Tablets with spores used in absolute pollen analysis. *Pollen et Spores*, 13: 615–621.
- Thomson, J. W., 1979: *Lichens of the Alaskan Arctic Slope*. Toronto: University of Toronto Press. 314 pp.
- , 1984: *American Arctic Lichens. I. The Macrolichens*. New York: Columbia University Press. 504 pp.
- Ugolini, F. C., 1986: Pedogenic zonation in the well-drained soils of the arctic regions. *Quaternary Research*, 26: 100–120.
- Vereshchagin, N. K. and Baryshnikov, G. F., 1982: Paleoecology of the mammoth fauna in the Eurasian arctic. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*. New York: Academic Press, 267–297.
- Walker, D. A., 1980: Climate. In Walker, D. A., Everett, K. R., Brown, J., and Webber, P. J. (eds.), *Geobotanical Atlas of the Prudhoe Bay Region, Alaska*. U.S. Army Cold Regions Research and Engineering Laboratory, CRREL Report, 80-14: 10–13.
- , 1985: Vegetation and environmental gradients of the Prudhoe Bay region, Alaska. U.S. Army Cold Regions Research and Engineering Laboratory, CRREL Report, 85-14. 239 pp.
- Walker, D. A., Binnian, E., Evans, B. M., Lederer, N. D., Nordstrand, E., and Webber, P. J., 1989: Terrain, vegetation and landscape evolution of the R4D research site, Brooks

- Range Foothills, Alaska. *Holarctic Ecology*, 12: 238–261.
- Walker, D. A. and Everett, K. R., 1991: Loess ecosystems of Northern Alaska: Regional gradient and toposequence at Prudhoe Bay. *Ecological Monographs* (in press).
- Walker, D. A., Everett, K. R., Brown, J., and Webber, P. J., 1980: *Geobotanical Atlas of the Prudhoe Bay Region, Alaska. U.S. Army Cold Regions Research and Engineering Laboratory, CRREL Report*, 80-14. 69 pp.
- Walker, D. A., Walker, M. D., Everett, K. R., and Webber, P. J., 1985: Pingos of the Prudhoe Bay Region, Alaska, U.S.A. *Arctic and Alpine Research*, 17: 321–336.
- Walker, M. D., 1990: *Vegetation and Floristics of Pingos, Central Arctic Coastal Plain, Alaska*. Dissertationes Botanicae, 149. Stuttgart: J. Cramer. 283 pp.
- Walker, M. D. and Walker, D. A., 1988: Vegetation-environment relationships at two scales on pingos. *Bulletin of the Ecological Society of America*, 69 (suppl. 2): 332.
- Walker, M. D., Walker, D. A., and Everett, K. R., 1989: Wetland soils and vegetation, Arctic Foothills, Alaska. *U.S. Fish and Wildlife Service Biological Report* 89(7). 89 pp.
- Walter, H., 1973: *Vegetation of the Earth and Ecological Systems of Geo-Biosphere*. New York: Springer-Verlag. 274 pp.
- Westhoff, V. and Maarel, E. van der, 1978: The Braun-Blanquet approach. In Whittaker, R. H. (ed.), *Classification of Plant Communities*. The Hague: Junk, 287–399.
- Wilson, M. J., 1984: Modern and Holocene environments of the North Slope of Alaska. M.A. thesis, University of Colorado, Boulder. 252 pp.
- Young, S. B., 1971: The vascular flora of St. Lawrence Island with special reference to floristic zonation in the arctic regions. *Contributions of the Gray Herbarium*, 102: 11–115.
- , 1982: The vegetation of land-bridge Beringia. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*. New York: Academic Press, 179–194.
- Yurtsev, B. A., 1982: Relicts of the xerophyte vegetation of Beringia in northeastern Asia. In Hopkins, D. M., Matthews, J. V., Jr., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*. New York: Academic Press, 157–178.

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