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Vegetation and Floristics of Pingos, Central Arctic Coastal Plain, Alaska

by

MARILYN DREW WALKER

With many figures, tables and photos in
the text and in the appendices



J. CRAMER

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ABSTRACT

Pingos are dry, ice-cored mounds found in the Arctic. They are relatively common on the Alaskan Arctic Coastal Plain, which is a flat, wet landscape with minimal relief. Pingos are among the few well-drained features in this landscape. This study examined the regional pingo flora and vegetation with regard to environmental gradients, equilibrium biogeography, and successional patterns. The pingo flora is found to be related primarily to northern circumpolar and Asian floras. The vegetation is found to be related to alpine vegetation of Alaska and Canada, to steppe tundras of Siberia, and to northern circumpolar vegetation. Primary controlling environmental gradients are temperature for vascular plants and soil chemistry for cryptogams.

Unique elements occur on dry, south-facing slopes, habitats not found elsewhere in this region. Some of these steppe elements have nonequilibrium species-area relations, suggesting they are remnants of an earlier, more extensive vegetation, and are speculated to be Unique elements occur on dry, south-facing slopes, habitats not found elsewhere in this region. Some of these steppe elements have nonequilibrium species-area relations, suggesting they are remnants of an earlier, more extensive vegetation, and are speculated to be remnants of the 'steppe tundras' thought to have covered much of Alaska during the Pleistocene glaciations.

Vegetation succession was considered in relation to four morphological classes of pingos, proposed as represent-

ing a time sequence. The system is driven by geomorphic processes. The among-pingo floristic variation increases along the sequence through the first three classes and decreases in the fourth class. The decrease in floristic variation in the final class is thought to be controlled by the gentle slopes. Variation is minimal on north slopes and best developed on south slopes in all morphological stages. This pattern may be due to dominance of allogenic over autogenic controls on the cold sites, as well as to a decreased pool of colonizers for these sites. South slopes are the warmest sites regionally, and support many species that are regionally limited to these sites. Thus, contrasting north and south slopes of pingos represent the equivalent of a latitudinal shift.

Pingos are excellent sites on which to study basic ecological questions because of their relatively manageable size, their consistent shapes and substrates, and their great number on the Coastal Plain, which permits repeatable experiments at the landscape level. Conservation of these sites is critical to preserving the total floristic and landscape diversity of the Arctic Coastal Plain. This comprehensive analysis of pingo ecology is a framework for this conservation.

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Dr. Patrick Webber, my dissertation advisor, has encouraged me in all facets of my career since I first came to the study. The Institute of Arctic and Alpine Research (INSTAAR) provided space and facilities in which to complete the work.

Dr. Patrick Webber, my dissertation advisor, has encouraged me in all facets of my career since I first came to the Institute of Arctic and Alpine Research in 1982. He has provided funding, creative ideas, friendship, knowledge, and encouragement throughout the years, and continues to do so, and it has all been deeply appreciated, and perhaps not frequently enough expressed. My husband,

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CHAPTER I

INTRODUCTION

We had paddled and floated most of the day, which at this latitude was 24 hours long, but the wind from the north had made our progress very slow. Our arms and backs ached from paddling and poling the heavily loaded canvas folboats, which frequently had to be pulled off shoals and gravel bars.... During the afternoon as I surveyed the landscape to the north from the river bank, I noticed a dome-like structure on the horizon but couldn't really believe there was anything that high out there.... It was nearly 2 A.M. and the tundra was still brilliantly lit by the arctic sun when we rounded a bank of the meandering Toolik River, and picked out our camp site on the terrace bank six feet above the river. I jumped onto the bank and there not more than 600 yards away was a large conical mound that looked to me like one of the pyramids of Egypt. It rose at least 100 feet above the tundra and had a base of 1000 feet, which made it almost like a mountain on the flat, prairie-like landscape. It was a pingo. [Koranda 1970, pg. 18]

J.J. Koranda's first encounter with a pingo demonstrates the intrigue with which people first view pingos, and illustrates the personal fascination that led to this dissertation. The word 'pingo' was borrowed from the Inuit language by Porsild (1938) to represent a specific type of ice-cored mound found in arctic regions. Early explorers along the Alaskan and Canadian coasts noted and described these features (Richardson 1851; Schrader 1904; Leffingwell 1919).

Pingos are described by Mackay (1979) as "...ice-cored hills which are typically conical in shape and can grow and persist only in permafrost." They may reach as high as 50 m and obtain a diameter over 1 km (Embleton and King 1968; Walker et al. 1985), although in the area studied most are less than 10 m high. Pingos are genetically separated from other types of mounds by the presence of an ice core, which can range from ice-rich sediment to nearly pure ice (Mackay 1979; Pissart 1983).

Objectives

The primary objective of this work is to characterize the vegetation and associated soils of the pingos of a region within the central Arctic Coastal Plain of Alaska (Fig. 1). This is approached with five goals: (1) classifying the vegetation in a form that can be related to other vegetation assemblages, (2) relating environmental gradients to the pingo vegetation, (3) determining the floristic affinities of the pingo flora and comparing this with the regional flora, (4) determining if the number of species on pingos represents an equilibrium constrained by pingo size (area), and (5) characterizing the successional sequences on these pingos.

There are several reasons why the pingos are of ecological interest. Koranda (1970) appears to be the first to mention that pingos would be excellent sites for plant ecological studies. He noted that pingo vegetation is particularly diverse

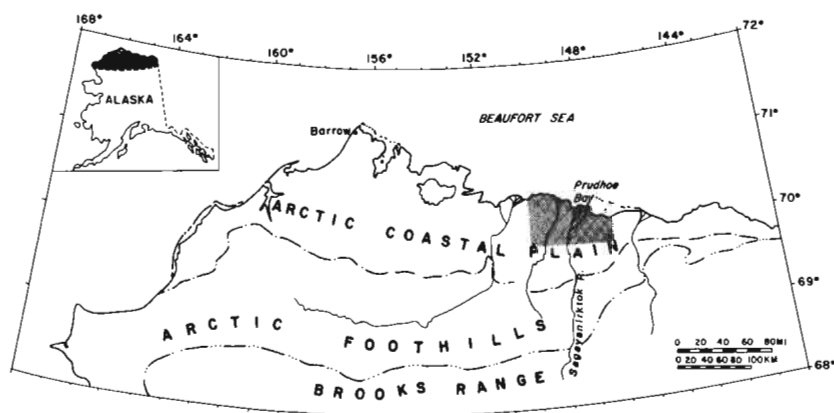


Figure 1. Location of the study on the Alaskan Arctic Coastal Plain. The shaded area represents the approximate boundary of the study region. Physiographic provinces are according to Wahrhaftig (1965).

due to the variety of distinct habitats, which are related to differences in slope, aspect, effects of wind, disturbance by animals, and deposition of snow. Perring (1959, p. 447) envisioned the ideal situation in which to study soils and vegetation of any biome as:

...Two or more isolated hemispherical hills...made of the same parent materials similarly oriented, undisturbed by burning or ploughing and grazed at the same intensity...isolated so that no disturbing local climate would upset the picture, and with strata horizontal so hills...made of the same parent materials similarly oriented, undisturbed by burning or ploughing and grazed at the same intensity...isolated so that no disturbing local climate would upset the picture, and with strata horizontal so that drainage would be similar on all aspects. If soil development had commenced about the same time...the soil and vegetation should be comparable in both areas. In practice hemispherical hills are not very frequent and in the field it is necessary to use samples from scattered sites in an attempt to synthesize the ideal. [emphasis my own]

The northern Alaska pingos represent a condition close to this ideal, with similar parent material, topography, and climate. They are essentially small ecosystems. Few studies have directly examined the ecological effects of slope and aspect in the Arctic (Ritchie 1984), as relatively few situations exist where this can be easily considered, although directional patterns have been reported, for example, by Polunin (1948) and Webber (1971).

A compelling reason to study the ecology of these particular pingos at this time is that most have been impacted to some degree by the oil development in the Prudhoe Bay and Kuparuk regions that is now expanding across much of northeastern Alaska. Because the area is primarily a wetland, the management focus has been primarily on maintaining the wetland integrity and functional values, with essentially no attention to the

dry environments of pingos. At least one pingo has been destroyed completely by construction activities (Walker et al. 1986), and others have had their entire vegetation cover removed. Most within the oil field are littered with surveyors' trash and have obvious vehicle tracks on at least one slope. Several pingos are regularly used as sites for radio towers (Fig. 2).



Figure 2. Pingo no. 5 (Prudhoe Mound) with radio tower on top. This pingo is within the Prudhoe Bay oil field, and most pingos within the oil field have been affected by the development to some degree.

dry environments of pingos. At least one pingo has been destroyed completely by construction activities (Walker et al. 1986), and others have had their entire vegetation cover removed. Most within the oil field are littered with surveyors' trash and have obvious vehicle tracks on at least one slope. Several pingos are regularly used as sites for radio towers (Fig. 2).

Questions and Predictions

At least one slope of several pingos are regularly used as sites for radio towers (Fig. 2).

Questions and Predictions

The central question of this study was, "Are there unique elements of the pingo vegetation, and if so, what are they, and why do they exist?" Pingo vegetation has never been fully described. Koranda (1970), Koranda and Evans (1975), Walker et al. (1985), and Everett (1983a,b) have stated that pingos are unique features in this landscape. The

work of Mackay (1979) in the Tuktoyaktuk Peninsula, N.W.T., Canada, has demonstrated the opportunities for understanding periglacial geomorphic processes through the study of pingos. To date, however, no one has illustrated just what it is about the vegetation and ecology of pingos that makes them so interesting. This general question is too broad to be approached with a single prediction, so a series of three secondary questions have also been asked:

(1) "Are there rare species or communities present on the pingos, and if so, what are their elements?"
 (2) "Do the pingos function as biogeographic islands?" and
 (3) "Is there a successional vegetation sequence on the pingos that is related to their age and geomorphic development?"

(1) "Are there rare species or communities present on the pingos, and if so, what are their elements?"
 (2) "Do the pingos function as biogeographic islands?" and
 (3) "Is there a successional vegetation sequence on the pingos that is related to their age and geomorphic development?"

Question 1: Rare Elements

During the last full glacial¹, the Alaskan vegetation was much different than today, and large expanses of grass-dominated tundra (steppe-tundra) may have been present (Hopkins et al. 1982). Many authors have hypothesized that if there were such environments then they should be present today in areas with appropriate habitat, i.e., in isolated refugia. The Brooks Range, river bluffs in interior Alaska, and scattered sites in Siberia have been demonstrated to have steppe-like plant assemblages that may represent relicts of this type (Yurtsev 1982; Murray et al. 1983; Cooper 1989). Some of the pingos may be very old stable sites that were present during this full glacial period (Rawlinson 1984a; Walker et al. 1985). If so, they may support relicts of this steppe vegetation. The pingos are essentially the only well-drained sites on the coastal plain. It has been presumed that steppe elements are missing from this area due to a lack of habitat, but the dry pingo slopes could potentially support steppe assemblages. Rarity here is defined as not being present regionally, except at these sites, although the species or community may be abundant elsewhere.

Question 2: Pingos as Islands

abundant elsewhere.

Question 2: Pingos as Islands

Both Koranda (1970) and Walker (1985a) stated that the Arctic Coastal Plain pingos are island-like. Walker and Acevedo's (1987) Landsat classification of the Beechey Point quadrangle shows

¹Hopkins' (1982) Duvanny Yar, approximately 12 to 30 ka; there were no glaciers within the region of this study at any time during the Pleistocene.

that 53% of the terrestrial portion of the map is either standing water or wet tundra, while only 39% is moist or dry tundra. They were not able to separate moist and dry tundra, but the dry area is estimated to be a very small percentage of this 39%. At Prudhoe Bay, which includes some of the wetter portions of the Beechey Point Quadrangle, less than 1% is dry tundra (Walker 1985a). The pingos are conspicuous, dry, high points within this landscape, and between the pingos there are only scattered areas that are also dry and could serve as source areas for dispersal of plants to the pingos. Dry sites other than pingos are river bluffs and the tops of high-centered polygons. Thus, the pingos are certainly island-like. They are isolated dry areas surrounded by much wetter habitat, much of it standing or open water, and in this sense they are one of the better terrestrial analogs of oceanic islands. It is hypothesized that because pingos are isolated dry sites they will have species-area relationships similar to islands.

Question 3: Successional Sequence

This question is approached with three specific hypotheses. The first is that because the pingos are in equivalent substrates, the environmental gradients on different pingos will be the same, and there will therefore be a change over time toward a characteristic pingo flora. If this is true, then the floras of oldest pingos will be more similar than floras of younger pingos. This would not mean that a steady state had necessarily been reached, but that within the given time scale there is a point at which the vegetation remains stable for some long period of time.

The second hypothesis is that species composition on the youngest sites is less dependent on site factors than on the oldest sites, because initial community composition is a function of chance events. Margalef (1963, 1968) proposed this idea, and Christensen and Peet (1984) tested and supported the hypothesis in a deciduous forest. It remains to be tested in an arctic environment.

Finally, it is hypothesized that because at this latitude there are more species at their northernmost limit than at their southernmost limit, diversity will develop more slowly on the cold sites (north slopes and ENE sides) than on the warm sites (south slopes and summits) and will maintain a lower level on the cold sites. Forty-six percent of the Prudhoe Bay flora reaches its northern-

most limit in this region (Walker 1985a). The cold sites, therefore, have a more depauperate flora, and there are fewer species capable of colonizing these sites. Auclair and Goff (1971) found different patterns of diversity in a temperate forest successional sequence on mesic and xeric sites. They stated that in intermediate portions of environmental gradients competition would be most intense, and therefore diversity should be lessened. They also stated that in high-stress environments the dominant climax species may also be the pioneers. This is very similar to Svoboda and Henry's (1987) model for the high arctic. Reinert et al. (1970) found an initial rapid rise in diversity at Glacier Bay, followed by a leveling off, with a maximum stand age of 1500 years.

CHAPTER II

BACKGROUND

Pingos

Mechanism of Formation

Porsild (1938) was the first to propose the theory that the pingos of northern Alaska and northwestern Canada:

...were formed by local upheaval due to expansion following the progressive downward freezing of a body or lens of water of semi-fluid mud or silt enclosed between bedrock and the frozen surface soil, much in the way in which the cork of a bottle is pushed up by the expansion of the water when freezing.

Porsild's theory was essentially correct, although it is now thought that expulsion rather than expansion causes the upheaval (Mackay 1979). Another type of pingo that forms under pressure due to an upslope water source has also been recognized. These two types of pingos have been called closed-system and open-system respectively, but Mackay (1979) suggested that the terms hydrostatic and hydraulic pingos are more appropriate. Certain pingos that would be classified as the closed-system type might not be completely closed, as they could be

hydraulic pingos are more appropriate. Certain pingos that would be classified as the closed-system type might not be completely closed, as they could be connected to an open talik (an unfrozen water-saturated zone in permafrost). The two types are not exclusive, and gradations between them occur when local conditions are such that both types of water sources are available. The pingos in this study are all presumed to be the hydrostatic type, because there is no obvious water source necessary for the formation of hydraulic pingos.

Hydrostatic pingos generally form in drained thaw-lake basins following drainage of lakes greater than 2 m deep (Fig. 3). Lakes of this depth do not freeze to the bottom in winter, which creates a deep talik beneath them. Following drainage, permafrost aggrades into the talik from all sides. As freezing progresses, water is expelled from the pore spaces of sandy or gravelly materials into the remaining unfrozen area, where pressure builds, eventually becoming great enough to push up the overlying sediments and form a pingo (Mackay 1979; Everett 1980a). Any talik that refreezes could potentially form a pingo, for example, under an abandoned stream channel.

This expulsion of water into a mass in the center of the pingo gives rise to injection ice, which results whenever a mass of injected water freezes within sediments (Pissart 1983). Mackay (1979) described three types of ice that are possible in pingos: pore ice, segregated ice, and intrusion ice. The conditions necessary for formation of these various ice types result from the pressure difference between the ice and water phases and also the type of sediments present at the ice-water interface. Some necessary for formation of these various ice types result from the pressure difference between the ice and water phases and also the type of sediments present at the ice-water interface. Some authors have emphasized ice origin as a critical factor in the classification of pingos and in separating pingos from other types of mounds, such as palsas (Pissart 1983), but Mackay (1979) stressed that it is the mound form that identifies a pingo as such and not the origin of ice within. He emphasized that the core may range from icy sediment to

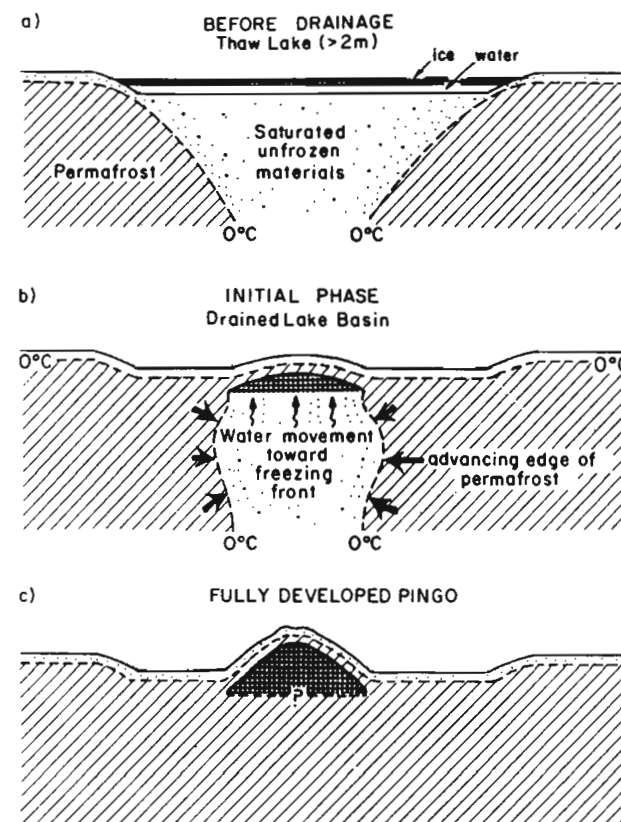


Figure 3. Schematic diagram of pingo formation. In (a), the drained lake phase, a deep thawed area (talik) forms under the lake. Permafrost begins to aggrade following lake drainage (b), and pingo growth is initiated. In (c), a fully developed pingo exists, and in this case is a completely closed system.

Source: Everett, K.R. 1980. Landforms. In: Walker, D.A., K.R. Everett, P.J. Webber and J. Brown. *Geobotanical atlas of the Prudhoe Bay region, Alaska*. Hanover, NH: U.S. Army Cold Regions Research and Engineering Laboratory, CRREL Report 80-19, p. 19.

Source: Everett, K.R. 1980. Landforms. In: Walker, D.A., K.R. Everett, P.J. Webber and J. Brown. *Geobotanical atlas of the Prudhoe Bay region, Alaska*. Hanover, NH: U.S. Army Cold Regions Research and Engineering Laboratory, CRREL Report 80-41, p. 19.

pure ice, and that a continuum exists from flat ground with massive sill ice, to pingos with intrusion ice, to pingos with segregated ice, to flat areas with icy sediment. The pingos of northern Alaska and northwestern Canada are limited to

regions of sand or gravel (Shumskii 1959; Mackay 1962, 1966, 1968, 1973, 1978, 1979; Carter and Galloway 1979; Müller 1962; Walker et al. 1985), but in other parts of the world pingos have grown in bedrock (e.g. Balkwill et al. 1974).

Distribution

Pingos have been described from areas of continuous or discontinuous permafrost in Canada and Greenland (Fraser 1956; Pihlainen et al. 1956; Stager 1956; Craig 1959; Müller 1959; Robitaille 1961; Mackay 1962, 1963a,b, 1966, 1972, 1977a,b, 1979, 1981, 1983; Cruickshank and Colhoun 1965; Pissart and French 1976, 1977; Tarnocai and Netterville 1976; Vernon and Hughes 1976; Hughes 1969; Hughes et al. 1972; Brown and Péwé 1973; Balkwill et al. 1974; French 1975, 1976; Péwé 1975; French and Dutkiewicz 1976; Bennike 1983). They are also known from Siberia (Bobov 1960; Evseev 1976; Yurtsev 1982), Spitsbergen (Åhman 1973; Svensson 1976), Mongolia (Rotnicki and Babinski 1977; Kowalkowski 1978), and the Tibetan Plateau (K.T. Cheng, cited in Mackay 1979, pg. 6). Most recently, pingos have been described from Antarctica (Pickard 1983).

Pingos occur in most areas of the Arctic Coastal Plain where thaw lakes and sandy or gravelly sediments are present (Porsild 1938; Burns 1964; Koranda 1970; Carter and Galloway 1979; Ferrians 1983; Rawlinson 1984a; Walker et al. 1985). Carter and Galloway (1979) mapped the pingos of the National Petroleum Reserve - Alaska (NPR-A). Hydraulic pingos are found throughout central Alaska in the zone of Walker et al. 1985). Carter and Galloway (1979) mapped the pingos of the National Petroleum Reserve - Alaska (NPR-A). Hydraulic pingos are found throughout central Alaska in the zone of discontinuous permafrost, and in valleys of the northern Brooks Range (Holmes et al. 1966, 1968; Hamilton and Obi 1982).

The distribution of pingos in the Prudhoe Bay and Kuparuk oil fields was described and mapped by Walker et al. (1985; Fig. 4) at a scale of 1:63,360, and they described two distinct geomorphic

types of pingos in this area. One is a steep-sided type with small basal diameter and steep slopes, found in drained lake basins (Fig. 5). The other type has gentle slopes and broad base (Fig. 6). The terms steep-sided and broad-based refer to these types as defined by Walker et al. (1985).

Regional Setting

The region of Alaska north of the Brooks Range crest and extending from the Chukchi Sea on the west to the Canadian border has been called the Arctic Slope or North Slope by various authors. The area of this study lies entirely within the Arctic Coastal Plain physiographic province of Wahrhaftig (1965). The nearest alpine areas are in the Brooks Range, which is the northwestern extension of the Rocky Mountain Cordillera, and the geologically distinct Richardson Mountains in northwestern Canada.

Prudhoe Bay is located on the northern coast of Alaska, at latitude 70°N, longitude 148°W. This study covers the area within a 70 km radius of Prudhoe Bay, to the east, west, and south of the region defined by Walker (1985a) (Fig. 1). It includes major portions of the United States Geological Survey 1:250,000-scale Beechey Point and Sagavanirktok quadrangles.

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Regional Landscape Units

Walker and Acevedo (1987) divided the region within the Beechey Point and Sagavanirktok quadrangles into four landscape units: (1) flat thaw-lake plains, (2) gently rolling thaw-lake plains, (3) hills, and (4) river floodplains. All areas include some floodplain units (Fig. 7).

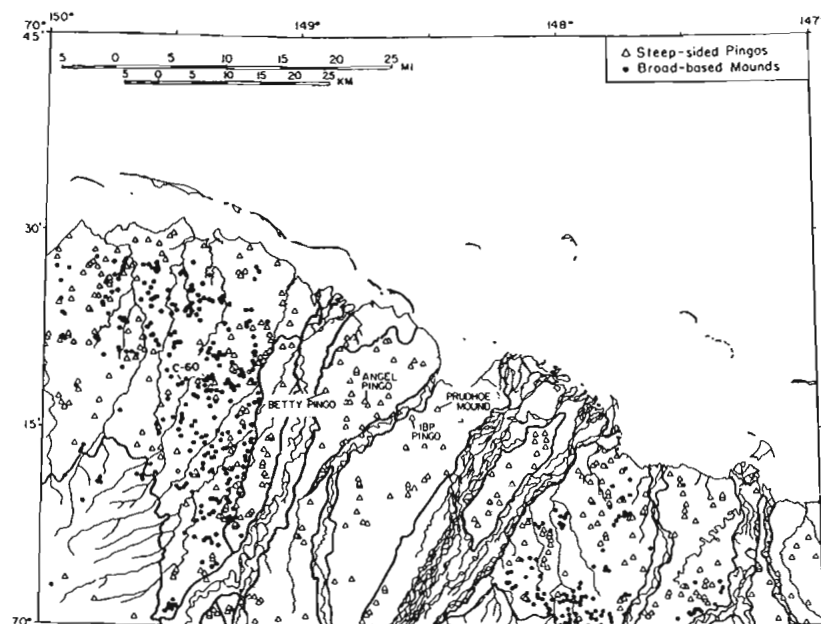


Figure 4. Distribution of pingos on the USGS 1:250,000-scale Beechey Point Quadrangle.

Source: D.A. Walker, M.D. Walker, K.R. Everett and P.J. Webber. 1985. Pingos of the Prudhoe Bay region, Alaska. *Arctic and Alpine Research*, 17:333.

The landscape units of Walker and Acevedo (1987) differ from the definition of landscape proposed by Forman and Godron (1986). In order to keep this distinction clear, the term landscape units is used when referring specifically to the regional units defined by Walker and Acevedo, and the term study areas is used when referring to the landscapes as divided for this study. The term landscape units is used when referring specifically to the regional units defined by Walker and Acevedo, and the term study areas is used when referring to the landscapes as divided for this study.

The flat thaw-lake plains represent an ancient floodplain surface between the Kuparuk and Sagavanirktok Rivers. This was a glaciofluvial outwash plain during the melting of the Brooks Range glaciers 8,000 to 10,000 BP (Rawlinson 1984b; Walker and Acevedo 1987). The exact age of the surface is not known, but the oldest available radiocarbon date on

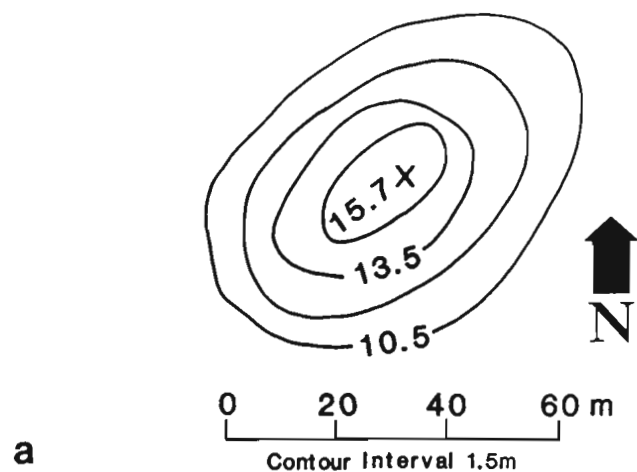
basal peat of $9,330 \pm 150$ BP represents a minimum for initiation of peat formation in the region (Everett 1980b; Walker and Acevedo 1987). The gently rolling thaw-lake plains are an older surface of unknown age.

Landscape Elements

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Landscape Elements

Most of the region's terrain is flat, and the predominant landscape elements are related to the presence of continuous permafrost up to 600 m deep (Everett 1980b). Walker et al. (1986) subdivided landscape elements into two types: (1) landforms, which are large landscape units that may contain within them one or more surface forms, and (2) surface forms, which are smaller-scale units. The



a



b



b

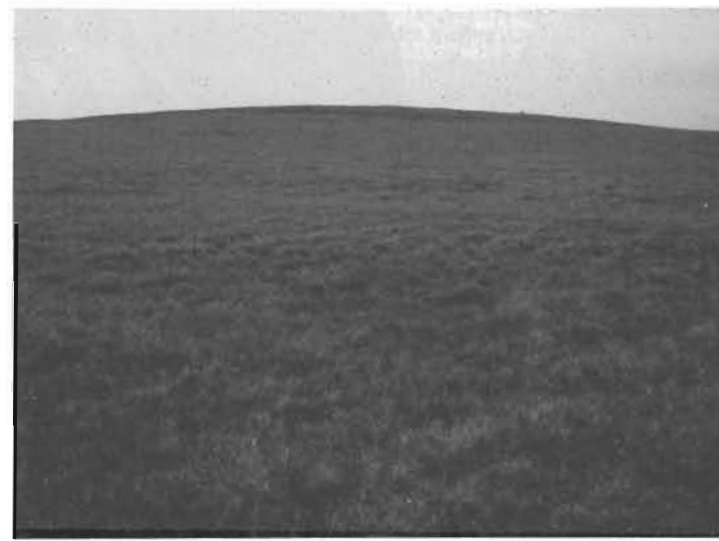
Figure 5. A typical steep-sided pingo (Pingo 1, Flower) at Prudhoe Bay, in plan view (a) and facing north looking at the south slope of the pingo (b). This pingo is 7 m high and 85 m in diameter. Slopes are as steep as 30° . Topographic data adapted from Air Photo Tech (1979).

landscape is dominated by lakes, which occupy 25-30% of the surface, and most lakes have a long axis orientation of

N15°W (perpendicular to the primary wind vector) (Black and Barksdale 1949; Everett 1980a). Most regional landscape



a



b



b

Figure 6. A typical broad-based pingo (Pingo 35, Pingok) in the Kuparuk area, in plan view (a) and facing north looking at the south slope of the pingo from its base (b). This pingo is 13 m high and 350 m in diameter. Slopes range from 5° to 15° . Topographic data adapted from Air Photo Tech (1979).

elements are a result of two related processes, ice-wedge formation and the thaw lake cycle.

A theory of ice-wedge formation based on thermal contraction cracking is generally accepted as the best explanation

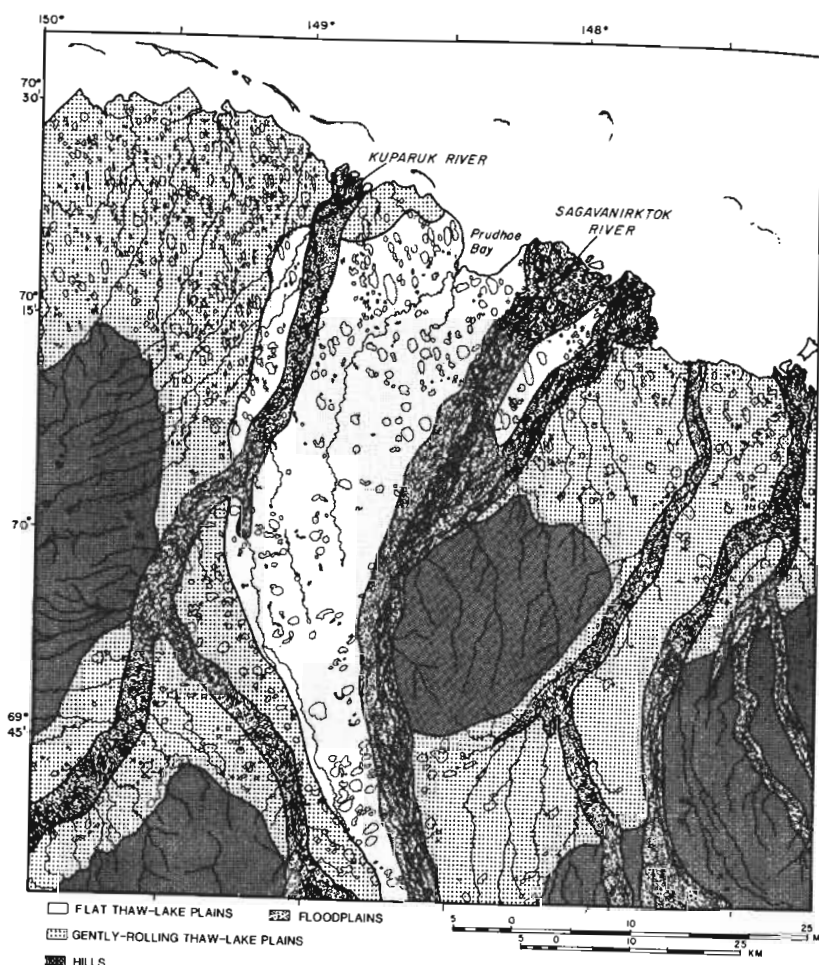


Figure 7. Landscape units of the study region. Units are from Walker and Acevedo (1987).

Figure 7. Landscape units of the study region. Units are from Walker and Acevedo (1987).

for this phenomenon (Leffingwell 1915, 1919; Lachenbruch 1959, 1966). Cracks form in the ground during the winter due to low temperatures, either at the surface or within the permafrost (Mackay 1984). Water flows into these cracks in the springtime and freezes; this process is repeated over the years, and an ice wedge develops. The intersection of the cracks results in a polygonal ground pattern

expressed on the surface. The ice wedge displaces soil around the edge of the polygon, resulting in a raised rim.

A cyclical process of pond and lake formation, followed by subsequent lake drainage and reestablishment of ice wedges, has been called the thaw-lake cycle; this process shapes most of the region's landscape (Hopkins 1949; Britton 1957; Everett 1980a; and others).

The cycle is a result of natural thermo-karst processes, going from ice-wedge polygons to growing lakes to drained lake basins. Pingos may form during the drained lake stage, and are therefore considered part of the thaw-lake cycle. Landforms other than pingos that are associated directly with the thaw-lake cycle include low-centered polygons, high-centered polygons, and strangmoor/disjunct polygon rims. Important elements of the landscape that are not a result of ice wedges or thaw lakes are the large, braided rivers that cross through the region. These have their headwaters in the foothills and mountain valleys of the Brooks Range, and as landscape corridors they have a major influence on the regional vegetation and wildlife.

Climate

Regional climate is characterized by long, cold winters and short, cool summers (Walker 1980). Mean annual temperature at the Prudhoe Bay (Deadhorse) airport is -13°C . Mean annual precipitation is quite low, around 25 cm. There is a maritime influence along the coast that leads to different summer climates between the coastal and inland areas of this study (Haugen and Brown 1980). The southern extent of the maritime influence is unknown, but is best expressed as a north to south gradient. Summer conditions at the coast are predominantly cloudy, moist, cool, and windy with temperatures within a few degrees of freezing, while clear skies and more variable wind speed and direction are prevalent inland.

Winter climate is probably more uniform across the area, although most available data are from Prudhoe Bay.

Monthly means for January through March are around -30°C , and the sun is down for 49 days (Gavin 1973; Walker 1985a).

Precipitation near the coast is frequent in the summer, but total amounts are small. Away from the coast precipitation events become less frequent but produce more moisture, so that the net result is approximately equal amounts across the region (Kane and Carlson 1973; Dingman et al. 1980; Haugen and Brown 1980).

Geology

The area lies within the broad geographical area called Beringia that includes the portions of northeastern Asia and northwestern North America that lay outside the Plio-Pleistocene continental ice sheets (Fig. 8) (Hopkins 1967, 1982). Five glacial sequences are recognized in the Brooks Range; none of these reached as far north as the study region. From oldest to youngest they are: (1) Gunsight Mountain (Tertiary), (2) Anaktuvuk River (early Pleistocene), (3) Sagavanirktok River (middle Pleistocene), (4) Itkillik Phase I (early Wisconsin), and Phase II (late Wisconsin), and (5) Fan Mountain neoglacial (Hamilton 1982, 1983, 1986; Hamilton and Hopkins 1982). The Gunsight Mountain drift is the furthest north, and reaches its northern extent approximately 35 km south of the southernmost pingo sampled.

Surficial geology is dominated by unconsolidated late Cenozoic fluvial, glaciofluvial, eolian, and lacustrine sediments collectively called the Gubik formation, but contained within this unit are a number of distinct and different aged units (Smith and Mertie 1930; O'Sullivan

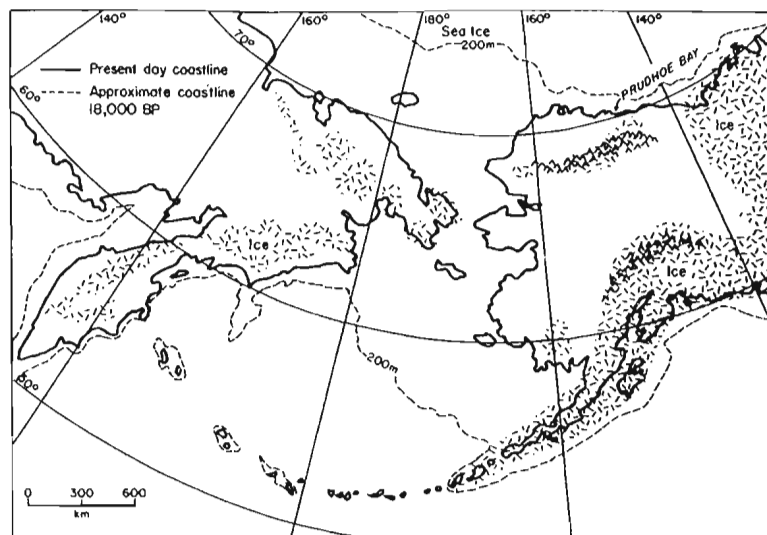


Figure 8. Hypothetical reconstruction of Beringia 18,000 BP. Continental ice sheets and mountain glaciers are shown with the stippled pattern (adapted from Barry 1982).

1961; Black 1964; Rawlinson 1984b; Brigham 1985). There are also a few scattered areas of marine sediments.

The flat thaw-lake plains are a combination of alluvium and glaciofluvial outwash, with a few isolated coastal occurrences of Flaxman marine deposits and Sangamon-age sand and gravel deposits (Rawlinson 1984b, 1986a,b,c,d,e; Hickmott 1986a,b). A surface layer of loess and peat 0.5 to 1 m deep overlies most of this surface (Everett 1980b; Rawlinson 1984b). The area's drainage history is complex, but it is evident that the Putuligayuk River was once the primary channel for the Sagavanirktok River and perhaps also the Kugaruk River (Rawlinson 1984b). A sandy gravel outwash 3 to 5 m deep is of Birch and Duvanny Yar age (see Chapter III for dates) and has been termed the Putuligayuk outwash by Rawlinson (1984b).

A layer of sandy gravel alluvium approximately 7 m thick (the Putuligayuk alluvium) underlies the Putuligayuk outwash (Rawlinson 1984b).

The gently rolling thaw-lake plains are covered by a layer of peat and are similar to the flat thaw-lake plains, but have more relief and represent older surfaces. Rawlinson (1984b) described a sequence of three terraces from the Colville River eastward toward the Kugaruk River. These same terraces are repeated on the gently rolling thaw-lake plains east of the Sagavanirktok River. The region of this study that is within the gently rolling thaw-lake plains is to the east of the oldest of these terraces, Colville terrace I. This surface is a combination of Ugnuravik sand and gravel, which are speculated to be Sangamon age (Rawlinson 1984b).

The major areas of hills, Franklin Bluffs and the White Hills, represent isolated Tertiary surfaces of the Sagavanirktok formation (Payne et al. 1951). Floodplains throughout the region consist of Holocene gravelly sand and silt; peat has formed in less active areas.

Soils

Four United States Department of Agriculture soil orders are represented regionally: Histosols, Entisols, Inceptisols, and Mollisols (Everett 1975, 1980c; Everett and Parkinson 1977; Parkinson 1978; Walker 1985a). U.S. Soil Conservation Service maps are not available for this region, and soil mapping has been done as part of geobotanical mapping within the oil field (Everett 1980c; Walker et al. 1986; and others). The primary environmental gradients controlling regional soils are drainage, disturbance, age, and deposition of calcareous loess.

Soils of wet tundra are either Pergelic Cryofibrists or Pergelic Cryohemists, or in regions where calcareous eolian loess is important Histic Pergelic Cryaquepts are found (Everett and Parkinson 1977). In this case, environmental conditions at the site would normally lead to a Histosol, but the input of eolian mineral material dilutes the surface horizon such that it is classified as mineral rather than organic.

Soils of moist sites are Pergelic Cryaquolls, Pergelic Ruptic Aqueptic Cryaquolls, or Pergelic Cryosaprists. The primary difference between the first two types is related to frost disturbance, with Pergelic Ruptic Aqueptic Cryaquolls found primarily in frost scar terrain, often in close association with Pergelic Cryaquolls. Pergelic Cryaquolls may be

found on any relatively undisturbed upland surface with moderate drainage. Pergelic Cryosaprists are distinguished from Pergelic Cryaquolls by the presence of an organic surface horizon (Everett and Parkinson 1977; Everett 1980c).

Pergelic Cryorthents and Pergelic Cryosaprists are soils of active alluvium and sand dunes, respectively. These Entisols have little or no differentiation of horizons; they represent either young surfaces or chronic disturbances (Everett 1980c; Walker 1985a). In the absence of disturbance, soils of well-drained sites, including most pingos, are either Pergelic Cryoborolls or Calcic Pergelic Cryoborolls. Dry soils throughout the region have abundant free carbonates present due to carbonate-rich parent materials, but the concentration of this carbonate within the soil subhorizons is a function of time, leading to a Calcic Pergelic Cryoboroll (Parkinson 1978).

Arctic Vegetation

The literature of the vegetation of the circumpolar Arctic is vast; much of this literature is in Russian and German and has not been translated into English. The synthesis work of Aleksandrova (1980) provided a much needed overview. Studies of large regions include the work of Böcher (1938) in Greenland, Bliss (1977) on Devon Island, and Spetzman provided a much needed overview. Studies of large regions include the work of Böcher (1938) in Greenland, Bliss (1977) on Devon Island, and Spetzman (1959) in Alaska.

Studies of Arctic Coastal Plain vegetation have been concentrated mainly around Barrow and the area within the National Petroleum Reserve - Alaska (NPR-A) (Cantlon 1961; Britton 1967; Komárková and Webber 1976, 1978, 1980a; Brown et al. 1980; Ebersole 1985). Other North Slope vegetation studies, outside of the immediate Prudhoe Bay

region, include Hanson (1951, 1953), Johnson et al. (1966), Anderson (1974), Dean and Chesemore (1974), Young (1974), Racine (1976), Racine and Anderson (1979), and Walker (1985b; Walker and Acevedo 1987). These cover the Beechey Point and Sagavanirktok Quadrangles, the Noatak and Kobuk river valleys, the Seward Peninsula, the Cape Thompson area, Kuskokwim Flats, and Eagle Summit. Studies of alpine areas include Jordal (1951), Lambert (1968), Batten (1977), and Cooper (1983, 1986). Gill's (1971) Mackenzie River Delta study is also pertinent.

Little work had been done in the Prudhoe Bay region prior to its selection as a secondary study site for the U.S. Tundra Biome program under the auspices of the International Biological Program (IBP) in the early 1970's (Brown 1975). Much of what has been done is directly related to impacts from the oil development and was funded by oil companies as required to meet permitting and environmental impact assessment needs. The vegetation within the Prudhoe Bay region was described by Brown (1975) and Walker (1985a; Walker et al. 1980). Detailed geobotanical maps of much of the Prudhoe Bay oil field have been made at a scale of 1:6,000 (Walker and Webber 1980a, Walker et al. 1986). Koranda's (1960) work on Franklin Bluffs, a relict Tertiary surface southeast of Prudhoe Bay, was one of the first detailed studies in this area, but it concentrated on the bluffs, which are atypical. The work of Komárková and Webber (1980b), Murray et al. (1980), and Walker and Webber (1980b) along the Dalton Highway, described the vegetation and flora along a north to south transect from Prudhoe Bay to the Yukon River. Viereck and Dyrness (1980;

Viereck et al. 1986) have synthesized the classification systems in use in Alaska.

Pingo vegetation has been briefly covered in a number of studies. Walker (1985a) described the major communities on the pingos within the Prudhoe Bay region, and Ito (1978) described the vegetation of several pingos in the vicinity of Tuktoyaktuk, N.W.T., Canada. Burns (1964) described several small pingos in the Yukon-Kuskokwim river delta region, but it is unclear whether or not these were truly pingos or some other type of ice-cored mound such as a palsa. There are also references to pingo vegetation in Mackay (1973, 1976) and Andreev and Perfilov (1975).

Vegetation of the Study Region

Aleksandrova (1980) divided the Arctic into two regions, the tundra region and the polar deserts. Using her classification, the region of this study is within the Alaska subprovince of the Chukotka-Alaska province of the subarctic tundra subregion of the tundra region, but is rather near the northern border between the arctic and subarctic tundras, and contains elements of both. Thus, she relates the vegetation of this region more closely to Siberia than to most of the North American Arctic, but she separates it at the subprovince level due to a number of differences, including the species that form the northern tree limit. All of Alaska, except the southeastern panhandle, the extreme northwest of Canada west of the Mackenzie River, and the Chukotka region of Siberia are collectively known as Beringia (Yurtsev 1974a; Hopkins et al. 1982). The non-mountainous portions of Beringia were not glaciated during the Pleistocene, and the continents were connected via a land

bridge because of lowered sea levels (Hopkins 1967; Fig. 8). The mesic tundra throughout this area is similar, dominated by *Eriophorum vaginatum* and *Carex lugens* tussock tundra, which are less abundant east of the Mackenzie River (Aleksandrova 1980).

The Prudhoe Bay vegetation differs from most of the coastal plain by the rarity of *Eriophorum vaginatum*. Walker (1985a) described the stand types at Prudhoe Bay. Dry areas are dominated by *Dryas integrifolia*; *Carex rupestris*, *Oxytropis nigrescens*, *Saxifraga oppositifolia*, and *Lecanora epibryon* are also common. Plant cover in dry sites is often incomplete, and crustose lichens may be abundant. Moist tundra in mesic uplands is dominated by *Eriophorum angustifolium*, *Dryas integrifolia*, *Tomenthypnum nitens*, and *Carex aquatilis*. Fruticose lichens are abundant in all but the wettest sites. Wet tundra is dominated by *Carex aquatilis*, and these sites have few dicots present. *Carex aquatilis* and *Arctophila fulva* are the predominant emergent species.

The study region extends beyond the oil field and includes large expanses of tussock sedge, dwarf shrub tundra dominated by *Eriophorum vaginatum*, *Carex lugens*, and species of *Salix* and other dwarf shrubs.

Environmental Gradients

lugens, and species of *Salix* and other dwarf shrubs.

Environmental Gradients

The relationship of vegetation to the landscape and its environment has been an important part of modern vegetation science from its beginnings in Europe in the latter part of the last century. It was Ramensky (1924, 1930), Gleason (1926), and Lenoble (1927), however, who first argued that classification into discrete units was not a natural model, but that

vegetation varies continuously across a landscape. This idea of gradients was developed in North America by Whittaker (1948, 1951, 1967, 1973), Curtis and others (Curtis and McIntosh 1951; Brown and Curtis 1952), Ellenberg (1950, 1952), and Perring (1958). It was considered a radical departure from the strict European school of classification and was not readily accepted by most phytosociologists (Shimwell 1971). In the past several decades, however, classification and gradient analysis have come to be recognized as complementary techniques that when used together can give the best understanding of vegetation patterns and their causes (Waring and Major 1964).

It has been fairly recently that gradient analyses have been regularly done in conjunction with descriptive studies, as there were few reliable and consistent methods available. For this reason there are few such studies in the arctic. Webber (1971) was the first study that concentrated on techniques of gradient analysis in arctic regions. He cites as earlier studies Summerhayes and Elton (1928), Hansen (1930), Seidenfaden and Sørensen (1937), Böcher (1954), Aleksandrova (1960), Beschel (1963), Raup (1965), and Johnson et al. (1966), but none of these were really gradient analyses as the term is applied today. Cantlon (1961) first pointed out the need for such studies in Alaska, and Walker (1985a) followed and Johnson et al. (1966), but none of these were really gradient analyses as the term is applied today. Cantlon (1961) first pointed out the need for such studies in Alaska, and Walker (1985a) followed his model of considering the vegetation of Prudhoe Bay in terms of three scales of environmental gradients (micro-, meso-, and macroscale). Other studies that have directly considered gradients include Bliss (1956), Gill (1971), Webber (1978; Webber et al. 1980), Cooper (1983), Odasz (1983), and Ebersole (1985).

The field of landscape ecology, which is still emerging in North America (Naveh and Lieberman 1984; Forman and Godron 1986), takes gradient analysis another step, from community-level gradients to landscape-level gradients. This field has been active in Europe for some time (Troll 1950, 1968; Neef 1963, 1967; Haase 1964; Schmithusen 1964, 1967; Bobek and Schmithusen 1967). It has come into popular usage in North America relatively recently (e.g. Komárková 1976). This type of approach is useful in northern Alaska, where there are large, unbroken expanses of tundra. The present study views vegetation at the level of the landscape, as well as on the smaller scale of the community.

Floristics

Floristics and vegetation are closely related topics, but whereas vegetation studies concentrate on regional patterns and communities, floristics is the study of the flora and its history. The regional flora contains the building blocks for communities. The work of Hultén (1937, 1958, 1962, 1963a,b, 1968), Löve and Löve (1963), Johnson and Packer (1967), Young (1971, 1976, 1982), Murray (1978, 1979, 1980; Murray et al. 1983), Yurtsev (1962, 1963, 1972a,b, 1974a,b, 1978, 1982), Walker (1985a), and Cooper (1989) have all dealt with floristics directly.

The arctic contains only about 600 indigenous species, and about 200 of Young (1971, 1976, 1982), Murray (1978, 1979, 1980; Murray et al. 1983), Yurtsev (1962, 1963, 1972a,b, 1974a,b, 1978, 1982), Walker (1985a), and Cooper (1989) have all dealt with floristics directly.

The arctic contains only about 600 indigenous species, and about 200 of these are circumpolar (Löve 1959). The Bering land bridge served as a migration route between Asia and North America for many species during the Pleistocene. Because of this connection, and also because Alaska was isolated to the east

flora is a combination of circumpolar and Beringian species, including Alaskan endemics (Hultén 1968). The floristic link between Alaska and Asia was first described by Hultén (1937), and the more recent work by Yurtsev (1982) and Murray (1980; Murray et al. 1983) has continued to elucidate this connection and its role in the formation of the modern vegetation.

Because of its importance to these trans-continental migrants, the Pleistocene environment of the land bridge and Beringia in general has generated considerable interest (Hopkins 1967; Hopkins et al. 1982). Many workers have envisioned that much of this area was a steppe-tundra (Hibbert 1982). The first use of this term and concept was from German and Russian paleontologists, who were trying to imagine an environment that could have supported a large ungulate fauna. Nehring (1890) discovered these Pleistocene vertebrate faunas in central Europe, and he wrote of a "steppe climate with an arctic tinge to it" (Nehring 1895). Tugarinov (1929), a Russian paleontologist, further developed the concept, and made the suggestion that the mammalian fossil associations found in northern Asia, Europe, and Alaska represented actual faunal assemblages, and were not just together due to some type of depositional coincidence. This is a matter of considerable debate today, as there has been little stratigraphic control in the major paleontological finds (Matthews 1982).

The history of the steppe-tundra concept was based on the existence of large, grazing animals now associated with grassland and shrub steppes, rather than on direct evidence from the pollen or plant microfossil records. Following

independent evidence from European, Russian, and North American palynologists developed that supported the idea. When the Soviet picture of a cold, dry, environment was first presented in the U.S. in 1965 (Giterman and Golubeva 1967), it was very similar to the independent conclusions drawn by Colinvaux (1964) from Imuruk Lake cores. Earlier, Livingstone (1955, 1957) recognized three pollen zones from two lakes in northern Alaska, an herb zone, dominated by grasses, sedges, and species of *Artemisia*, a birch zone, and an alder zone, the most recent. These three zones have held up remarkably well in other studies (Anderson 1982; Nelson 1982a; Brubaker et al. 1983; Baker 1984; Wilson 1984), and the herb zone has been postulated to represent this steppe-tundra type. Yurtsev (1982) described the modern pollen rain from Wrangel Island, which he considers a good modern example of a northern steppe-tundra type, and it is quite similar to many of the herb-zone pollen spectra, with high amounts of grasses, *Artemisia* spp., and *Selaginella sibirica*. Ritchie (1984; Cwynar and Ritchie 1980) has argued that there is no concrete evidence for these steppe-tundra assemblages, and that the herb zone probably represents a fellfield type of vegetation.

Island Biogeography

Since the publication of MacArthur and Wilson's theory of island biogeography in 1967, there have been a multitude of studies attempting to verify or refute the theory or fit specific data to it. This theory states that the number of species on an island represents an equilibrium between extinction rates and

Island Biogeography

depend on distance from source areas; extinction rates depend on island size. The theory predicts that the number of species on an island, S , is exponentially related to the area of the island:

$$S = cA^z \quad (1)$$

Data have been published for plants and animals, on oceanic islands and archipelagoes (Terborgh 1973; Diamond et al. 1976; Linhart 1980; Nilsson and Nilsson 1978, 1982, 1983) as well as terrestrial habitat patches (Culver 1970; Vuilleumier 1970; Brown 1971; Cook 1974; Johnson 1975; Behle 1978; Crowe 1979; Riebesell 1982; Murray et al. 1983). No arctic data have ever been applied to the theory, although Young (1982) recognized its significance in relationship to the steppe-tundra question, because if modern steppe-tundras are relict, they should have non-equilibrium biogeography.

The theory leads to three specific predictions: 1) that turnover of species occurs, 2) that the species-area curve will be steepest for the most isolated islands and steeper on islands than on equivalent mainland areas, and 3) that a dynamic equilibrium is in fact operating (Williamson 1981). The value of z in equation (1) represents the slope of the line defined by the species-area equation, and most attention has centered on this aspect. Gould (1979), however, pointed out that when the slopes of two equations are equal, the ratio of their dynamic equilibrium is in fact operating (Williamson 1981). The value of z in equation (1) represents the slope of the line defined by the species-area equation, and most attention has centered on this aspect. Gould (1979), however, pointed out that when the slopes of two equations are equal, the ratio of their intercepts, c , represents the relative species richness of different regions of similar size. Some data suggest that isolation lowers the value of c , rather than having a direct effect on z (Slud 1976).

MacArthur and Wilson did not make specific predictions about the value of z , but they did present empirical data suggesting that for equilibrium island populations it should fall between .24 and .35, and for mainland sites, or subsamples within an island, it should be between .12 and .17. Slopes outside these ranges have been interpreted as representing nonequilibrium conditions. Nonequilibrium would be expected in areas where islands have formed from isolation of a previously extensive habitat, such as mountaintops that were isolated by climatic change during the Holocene, or oceanic islands in the Bering Strait that were continuous with the exposed continental shelf during the Pleistocene (Brown 1971; Riebesell 1982; Young 1982). In these situations, extinction rates are expected to exceed colonization rates, as these areas have gone from part of the mainland to islands, and it takes longer to reach an equilibrium from too many species than from too few species for a given area (MacArthur and Wilson 1967). Once a viable population is established, it will tend to persist. MacArthur and Wilson (1967) hypothesized that on mainlands the lower z values are a result of the presence of small populations of many species in an area that belong to a larger, viable population. On an island these small populations could not persist. High colonization rates, as compared to extinction rates, should lead to decreased values of z , as colonization rate is more dependent on area than it is on isolation.

Predictions concerning turnover and equilibrium have been difficult to treat. The prediction of species turnover does not address the time scales involved.

small systems, while others (e.g. Gilbert 1980) have claimed that because turnover has not been shown in most cases, the theory is nullified. It has also been shown that observed turnover often represents sampling error (Lynch and Johnson 1974; Simberloff 1976; Nilsson and Nilsson 1982). It is true that this prediction cannot be invalidated, but this does not make the theory intractable. Colonization and subsequent extinction of some species have been well documented in successional studies (e.g. Crocker and Major 1955, and many others). Arctic plants are relatively long-lived (Billings 1973), so it would be difficult to definitively demonstrate turnover for a given area in the Arctic. For the present study it is assumed that turnover has occurred at some point in time.

Succession

Because the pingos may well be some of the oldest stable sites on the coastal plain, they are logical sites on which to study succession. Within the last decade studies of plant succession have concentrated on mechanisms driving succession and the evolutionary consequences of succession (e.g. Pickett 1976; Peet and Christensen 1980; Christensen and Peet 1984; Tilman 1986). In tandem with these experimental studies have come a series of models of succession that attempt to define the process as a generalized one driven by similar forces in all environments (e.g. Connell and Slatyer 1977; Tilman 1985). Clements' (1916) original concept was that all recently exposed surfaces will eventually become inhabited by plants, and that this process of going from barren ground to

existing environmental factors at the site. This concept of the climatic climax contains within it the concept of convergence, that is, change within a community to a particular stand type, the climax type. This concept was inherent in the earliest successional descriptions (Cowles 1899; Cooper 1916; Clements 1916, 1928).

Since these earliest works, two critical questions have emerged from successional studies in many different environments: (1) whether or not there is convergence toward a characteristic climatic climax type, and (2) the importance of site factors or characteristics as opposed to chance immigration in determining both the initial and final species composition (Margalef 1963, 1968; Connell and Slatyer 1977; Matthews 1979a,b; Christensen and Peet 1984; Matthews and Whittaker 1987). Margalef (1963, 1968) and Egler (1954, 1975) both recognized that initial species composition is likely to be controlled by the chance arrival of species at the sites, although they predicted entirely different outcomes from this initially apparently random assemblage. Matthews and Whittaker (1987) concluded that species composition differences along environmental gradients increase rather than decrease over time, and Pineda et al. (1981) and Christensen and Peet (1984) came to a similar conclusion.

Arctic Studies

There have been rather numerous descriptive studies of succession in northern Alaska and other regions of the Arctic, many associated with river alluvium (Polunin 1936; Spetzman 1951; Bliss

Arctic Studies

and Peterson 1980; L.R. Walker and Chapin 1986; Walker et al. 1986; Cargill and Chapin 1987; Svoboda and Henry 1987). Churchill and Hanson (1958) reviewed concepts of arctic succession. Peterson and Billings' work related coastal plain succession to natural geomorphic cycles (the thaw-lake cycle in particular), and the pingos are part of the same cycle.

Svoboda and Henry (1987) have presented a model for succession in high arctic environments. It addresses the problem that in the most extreme environments, where plants are at the very limits of their tolerance range, succession as it is generally understood does not seem to occur. This model predicts that in marginal environments, competition is of little importance, as few species are able to exist at all, and these may not persist over any period of time. Savile (1960) also wrote of decreased competition in the High Arctic, and Griggs (1934) wrote that arctic environments are ruderal or weedy. Vascular plant communities in such settings will not develop high enough cover to build up a substantial amount of soil organics. Thus, the site remains in an early sere for a long period of time, perhaps indefinitely.

Taking Svoboda and Henry's work one step further, one can envision a gradient from these most extreme environments, at the very limit of plant growth, to some point farther south where successional processes, as they have generally been described, are acting. At this point, perhaps indeterminately,

Taking Svoboda and Henry's work one step further, one can envision a gradient from these most extreme environments, at the very limit of plant growth, to some point farther south where successional processes, as they have generally been described, are acting. At this more southerly point, competition is controlling most species' distributions, not environmental stresses. The study region probably falls somewhere in the middle of this gradient, and so is an

METHODS

Study Areas

The region was divided into four broad study areas (Fig. 9): (1) the Prudhoe Bay area, including all of the Prudhoe Bay oil field between the Kuparuk River and the Sagavanirktok River main (east) channel, extending approximately 40 km to the south from the coast, (2) the Kuparuk oil field, including all of the area west of the Kuparuk River that was accessible by road in 1984, extending from the coast approximately 30 km south, (3) the Toolik River area, including all of the coastal plain west of the Sagavanirktok River beginning at the southern edge of the Prudhoe Bay area and extending south to the northern tip of the White Hills, and (4) the Kadleroshilik area, including all of the coastal plain east of the Sagavanirktok River and west of the Shaviovik River, extending approximately 56 km south from the coast. Each study area has a unique combination of geologic and climatic factors, making them separate landscape types. The Prudhoe Bay and Toolik River study areas are within the flat thaw-lake plains, and the Kuparuk and Kadleroshilik areas are in the gently rolling thaw-lake plains.

Field Study

rate landscape types. The Prudhoe Bay and Toolik River study areas are within the flat thaw-lake plains, and the Kuparuk and Kadleroshilik areas are in the gently rolling thaw-lake plains.

Field Study

Forty-one pingos were sampled from the four study areas (Fig. 9, Table 1). The original study plan was to sample equally from the four study areas, but the relative inaccessibility of the Toolik and

samples from these regions. A few sites within the Toolik River area could be sampled from the Dalton Highway; otherwise transportation in these two areas was by air, limiting the amount of time spent in these regions.

Each pingo listed in Table 1 was assigned a name and number. If a pingo was assigned a name on U.S. Geological Survey (USGS) maps then that name was used. This was the case for Prudhoe Mound (no. 5), Jones Mound (no. 12), and Thetis Mound (no. 33). These sites are all near the coast and were described and named by early explorers. Many pingos had benchmarks on top, and in this case the benchmark name was used. This was the case for Betty (no. 3), Angel (no. 6), Beny (no. 7), Hale (no. 14), Percy (no. 15), and Michelle (no. 18). The remaining names are unofficial.

Sampling was opportunistic, and in the Prudhoe Bay and Kuparuk areas the existing road network was used to reach the sampling sites (Fig. 10). Within Prudhoe Bay, all pingos at least 5 m high were sampled. In the Kuparuk area, pingos closest to the road were sampled. All pingos in the Kadleroshilik area had to be accessed by air, and since this was done in conjunction with other unrelated studies these samples are essentially random. Kadleroshilik Pingo (no. 41) is Prudhoe Bay, all pingos at least 5 m high were sampled. In the Kuparuk area, pingos closest to the road were sampled. All pingos in the Kadleroshilik area had to be accessed by air, and since this was done in conjunction with other unrelated studies these samples are essentially random. Kadleroshilik Pingo (no. 41) is perhaps the largest pingo in the world, and it was chosen for this reason. In the Toolik River area, pingos 15 and 37 were reached by road, and the remainder were sampled in a single extended camping

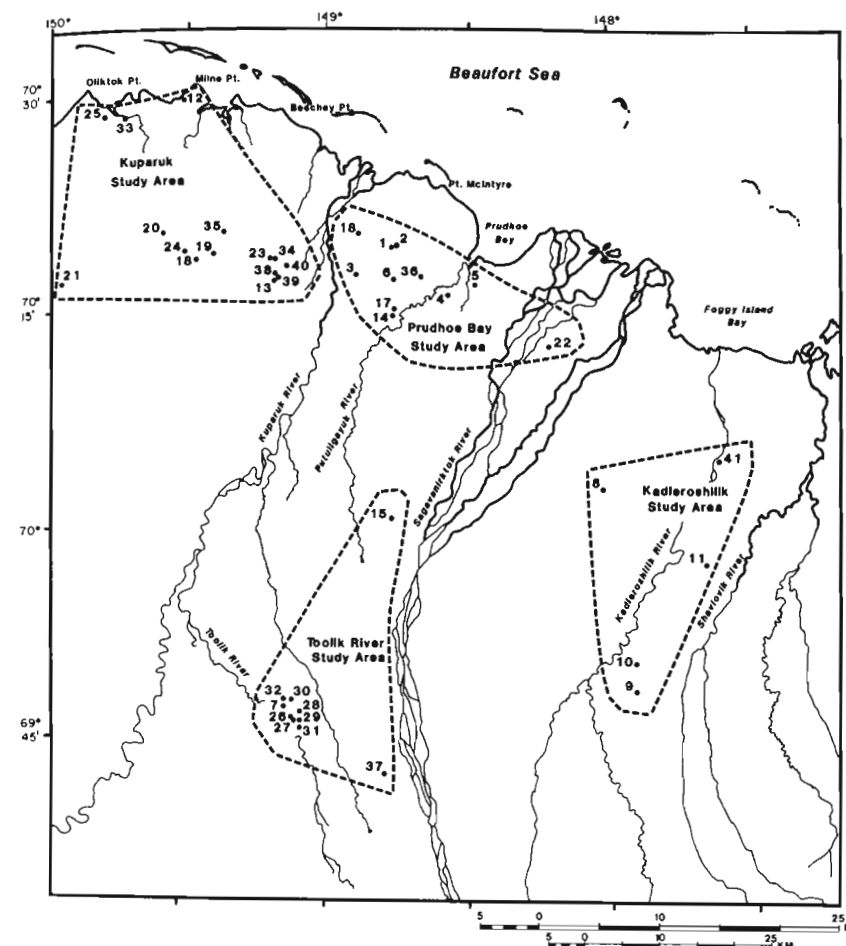


Figure 9. Location of sample pingos and study areas. Topographic information from USGS 1:250,000-scale Beechey Point and Sagavanirktok quadrangles.

Field Sampling Procedures

Field sampling consisted of: 1) data for the entire pingo, and 2) data from seven sample plots on each pingo. Table 1 lists the data and information that were taken for the entire pingo. Diameter was measured on the north and west sides of the pingo by two people using a 100 m fiberglass fabric tape. If the pingo was

measured, the opposite side was used. The bottom margin of the pingo was defined as the point at which there was a noticeable break in slope or change in vegetation. In a few cases there was no abrupt change, and in this instance it was estimated as a point on the landscape where the slope was zero. A common problem was the presence of a colluvial

Field Sampling Procedures

Field sampling consisted of: 1) data for the entire pingo, and 2) data from seven sample plots on each pingo. Table 2 lists the data and information that were taken for the entire pingo. Diameter was measured on the north and west sides of the pingo by two people using a 100 m fiberglass fabric tape. If the pingo was

measured, the opposite side was used. The bottom margin of the pingo was defined as the point at which there was a noticeable break in slope or change in vegetation. In a few cases there was no abrupt change, and in this instance it was estimated as a point on the landscape where the slope was zero. A common problem was the presence of a colluvial

Table 1. Locations of the forty-one pingos and the microsites sampled on each pingo. Microsite numbers refer to locations shown in Fig. 12.

Number	Name	Latitude/Longitude	Study Area	Microsites Sampled
1	Flower	70°20'N, 148°47'W	Prudhoe Bay	1 through 7
2	Flower 2	70°17'N, 148°47'W	Prudhoe Bay	1 through 7
3	Betty	70°17'N, 148°54'W	Prudhoe Bay	1 through 7
4	IBP ¹	70°16'N, 148°34'W	Prudhoe Bay	1 through 7
5	Prudhoe Mound	70°17'N, 148°29'W	Prudhoe Bay	1 through 7
6	Angel	70°17'N, 148°46'W	Prudhoe Bay	1 through 7
7	Beny ²	69°47'N, 149°08'W	Toolik River	1 through 7
8	Mandy	70°02'N, 148°01'W	Kadleroshilik	1 through 7
9	Grizzly	69°48'N, 147°54'W	Kadleroshilik	1 through 7, plus additional erect low shrub community on south slope
10	DAW	69°50'N, 147°55'W	Kadleroshilik	1 through 5 plus additional snowbank community, erect low shrub community on south slope
11	NLP	69°56'N, 147°41'W	Kadleroshilik	1 through 7
12	Jones Mound	70°30'N, 149°31'W	Kuparuk	1, 2, 4 through 7
13	Everett	70°17'N, 148°11'W	Kuparuk	1 through 7, plus additional late-lying snowbank at base of leeward side
14	Hale	70°15'N, 148°46'W	Prudhoe Bay	1 through 7
15	Percy	70°00'N, 148°46'W	Toolik River	1 through 7, plus additional steppe community on south slope
16	C60 ³	70°18'N, 149°27'W	Kuparuk	1 through 7
17	Gull	70°20'N, 148°47'W	Prudhoe Bay	1 through 7
18	Michelle	70°20'N, 148°54'W	Prudhoe Bay	1 through 7
19	Kit	70°19'N, 149°24'W	Kuparuk	1 through 7
20	Lupine	70°20'N, 149°34'W	Kuparuk	1 through 7
21	Bone	70°17'N, 149°57'W	Kuparuk	1 through 7
22	Sagavanirktok	70°12'N, 149°12'W	Prudhoe Bay	1 through 7
23	Loon	70°18'N, 149°12'W	Kuparuk	1 through 7
24	Webber	70°18'N, 149°31'W	Kuparuk	1 through 7
25	Oliktok	70°28'N, 149°48'W	Kuparuk	1 through 7
26	Moose	69°46'N, 149°07'W	Toolik River	1 through 7
27	Caribou	69°46'N, 149°07'W	Toolik River	2, 4 through 7
28	Bone	70°17'N, 149°57'W	Kuparuk	1 through 7
29	Sagavanirktok	70°12'N, 149°12'W	Prudhoe Bay	1 through 7
30	Loon	70°18'N, 149°12'W	Kuparuk	1 through 7
31	Webber	70°18'N, 149°31'W	Kuparuk	1 through 7
32	Oliktok	70°28'N, 149°48'W	Kuparuk	1 through 7
33	Moose	69°46'N, 149°07'W	Toolik River	1 through 7
34	Caribou	69°46'N, 149°07'W	Toolik River	2, 4 through 7
35	Parmigan	69°47'N, 149°04'W	Toolik River	1 through 7
36	Dowitcher	69°46'N, 149°05'W	Toolik River	2 through 7
37	Jaeger	69°47'N, 149°07'W	Toolik River	1 through 7
38	Eagle	69°48'N, 149°07'W	Toolik River	1 through 7
39	Longspur	69°48'N, 149°09'W	Toolik River	2 through 7, plus frost boil in moist tundra in polygon trough on SW

Table 1 (continued).

34	Euphrates	70°18'N, 149°11'W	Kuparuk	1 through 7
35	Pingok	70°27'N, 149°22'W	Kuparuk	1 through 7
36	Nancy	70°17'N, 148°40'W	Prudhoe Bay	1 through 7
37	Pintail	69°43'N, 148°48'W	Toolik River	2 through 7, plus additional snowbed community
38	Porsild	70°17'N, 149°11'W	Kuparuk	1 through 7
39	Koranda	70°17'N, 149°10'W	Kuparuk	1 through 3, 5 through 7
40	Muffin	70°17'N, 149°10'W	Kuparuk	1 through 7
41	Kadleroshilik Mound	70°03'N, 147°35'W	Kadleroshilik	1 through 7, plus five additional snowbank communities, fellfield in valley on top, tussock tundra area, and two additional south slope communities

¹ Called "Weather Pingo" by Brockett (1982) and Rawlinson (1984); lies within the IBP study area.

² Called "Toolik Pingo" by Koranda (1970).

³ Name used by Brockett (1982).

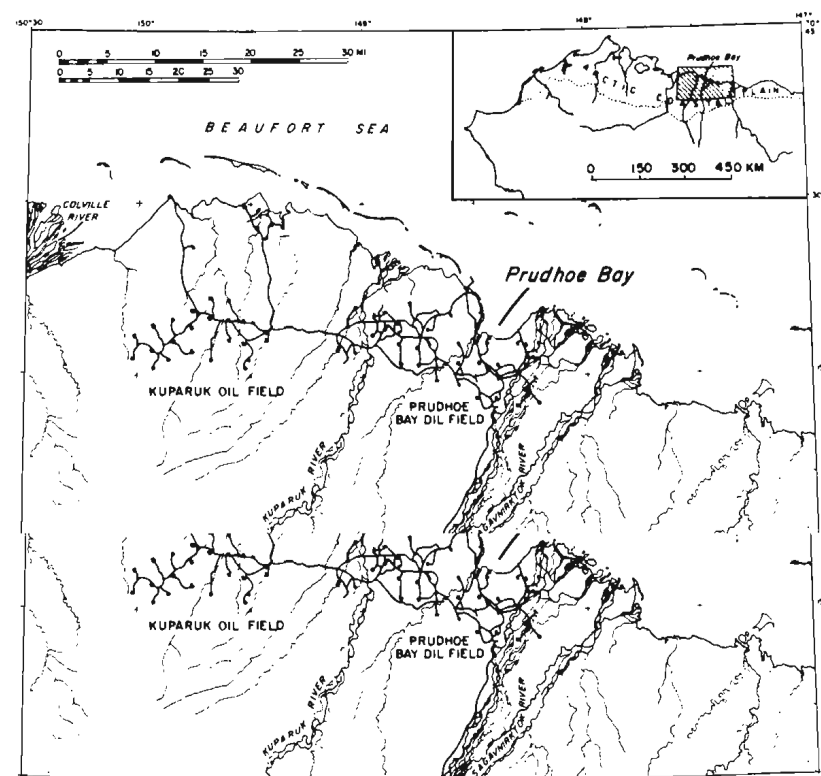


Figure 10. Map of the road network in the Prudhoe Bay and Kuparuk oil fields. Sampling within these regions was constrained to sites that could be easily reached from a road.

Source: D.A. Walker, M.D. Walker, K.R. Everett and P.J. Webber. 1985. Pingos of the Prudhoe Bay and Kuparuk oil fields. *Journal of Geology* 93: 17-33.

Table 2. List of data recorded for each pingo.

Information	Measurement Type
Height	meters
North-south diameter	meters
East-west diameter	meters
Shape	Describe, note deviations from expected hemispherical shape, characterize slope angle on all sides
Type	Steep-sided or broad-based
Disturbance	Description, intensity (scalar)
Landscape unit and regional terrain type	Units of Walker and Acevedo (1987)
Geomorphic features	Describe, indicate size and extent on pingo (includes ice wedges, polygons, contraction cracks, unstable slopes, colluvial apron, etc.)
Surrounding vegetation	Walker (1983) level B units
Distance to coast	kilometers
Distance to nearest pingo	kilometers
Distance to major rivers	kilometers to Sagavanirktok, Kuparuk, Toolik, Putuligayuk, and Kadleroshilik rivers

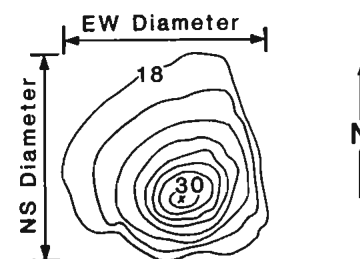
changes, one each at the top and bottom of the colluvial apron. This feature was well developed on some pingos and missing on others. When there was a clear colluvial apron present, two separate diameter measurements were made, one of the entire pingo, and one of the area above the colluvial apron.

Height was estimated by standing at the base of the pingo and locating with a leveling device the point on the slope one of the entire pingo, and one of the area above the colluvial apron.

Height was estimated by standing at the base of the pingo and locating with a leveling device the point on the slope that was level with the eye. The investigator then walked to this spot and repeated the procedure. Height was determined by multiplying the height of the observer's eye by the number of increments necessary to reach the top. Elevation is accurate to within one-half meter. Height was estimated on at least two sides of the pingo. A third estimate was

made if these differed by more than 0.5 m. Estimates were averaged to obtain the final value. Surface area was estimated by presuming the pingo was a perfect spherical sector (Fig. 11).

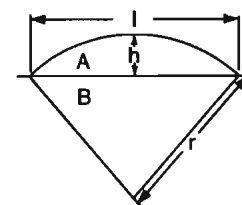
Scalar measurements were taken on type and extent of the disturbances present on the pingo (Tables 3 to 5). The primary purpose of the scalars was to aid in note-taking and to give a degree of constancy to the descriptions. The re-type and extent of the disturbances present on the pingo (Tables 3 to 5). The primary purpose of the scalars was to aid in note-taking and to give a degree of constancy to the descriptions. The remainder of the information was primarily descriptive. Information on landscape units and regional terrain type was according to Walker and Acevedo (1987) (Table 6). Distances to the coast and to rivers were obtained from USGS 1:250,000 Beechey Point and Sagavanirktok quadrangles. Distance to the nearest pingo was measured on 1:60,000



Topographic map of pingo no. 24
(Contour interval = 1.5m)

$$\text{Estimated diameter} = \frac{\text{NS} + \text{EW}}{2}$$

Area of a spherical sector:



$$\text{Pingo area } (A_A) = A_T - A_B$$

$$A_A = \frac{\pi r^2 h}{2}$$

Figure 11. Diagram illustrating the method used to estimate diameter and total surface area. A and B are three dimensional shapes shown in side view. A_A is the estimated surface area.

CIR photographs. Photographs of the entire pingo were taken from four compass directions on the ground, and vertical or slightly oblique aerial photographs were taken when a plane or helicopter was available (pingo nos. 1 through 11 entire pingo were taken from four compass directions on the ground, and vertical or slightly oblique aerial photographs were taken when a plane or helicopter was available (pingo nos. 1 through 11 and 41).

A complete vascular plant species list was made prior to sampling any vegetation. This survey took 20 to 60 minutes depending on the size of the area. At the end of sampling the pingo was checked again for any species that might have been missed.

Detailed vegetation and soil descriptions were made at the same seven microsites on each pingo (Fig. 12). These seven microsites consistently show the major community types on a given pingo, although there are often minor types not included within these microsites. The samples were located by first locating the microsite on the pingo, and then visually determining the predominant vegetation at that microsite. A stake was placed in the center of the dominant vegetation type, so that the entire sample would be within a region of homogeneous

Table 3. Scalar values to measure amount of debris and structures on entire pingo.

Scalar	Meaning
0	no debris or structures
1	small bits of trash present, easily removed
2	small permanent structure (<i>e.g.</i> benchmark) present or somewhat larger debris
3	considerable debris present that is not easily removed
4	large permanent structure present or large abandoned machinery
5	entire surface disturbed, covered by debris or structures

Table 4. Scalar values used to measure excavation disturbance on the entire pingo.

Scalar	Meaning
0	no excavation
1	minor excavation; 1 to 5 small pits < 0.5 m diameter
2	moderate excavation; many small pits or 1 pit 0.5 to 1.5 m diameter
3	major excavation; more than 1 pit > 0.5 m diameter
4	small open pit mine
5	extensively mined

Table 5. Scalar values used to measure degree of vehicle disturbance on entire pingo.

Scalar	Meaning
0	no disturbance
1	very minor disturbance; well-recovered vegetation in 1 track
2	minor disturbance; well-recovered vegetation in more than 1 track
3	moderate disturbance; 2 to 5 tracks with poorly recovered vegetation
4	major disturbance; large areas disturbed by multiple tracks, poorly recovered vegetation
5	severe disturbance; <60% of original vegetation remains
6	very severe disturbance; <30% of original vegetation remains

Table 6. Codes used for general landscape and regional terrain type descriptions.

<u>Code</u>	<u>General Landscape Unit</u>
1	drained thaw-lake basin
2	inter-thaw-lake area
3	lake
4	fluvial area
5	other (specify)
<u>Code</u>	<u>Regional Terrain Type</u>
4	fluvial area
5	other (specify)
<u>Code</u>	<u>Regional Terrain Type</u>
1	flat thaw-lake plain
2	gently rolling thaw-lake plain
3	floodplain
4	hills

ANGEL PINGO, PRUDHOE BAY REGION, ALASKA

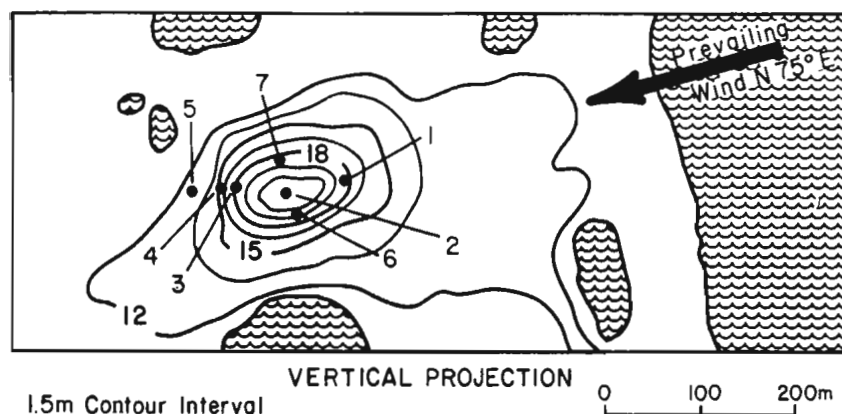


Figure 12. Topographic map of Pingo 6 (Angel) with a 1.5 m contour interval. The seven microsites sampling locations are labeled as (1) ENE wind-exposed, (2) summit, (3) dry leeward side above snowbank, (4) middle of snowbank on leeward side (well-drained), (5) bottom of snowbank at leeward base of pingo (poorly-drained), (6) south slope, (7) north slope. (Topographic information from Air Photo Tech 1979.)

vegetation. Sample centers were all located at the same time, and a sketch of their locations was made.

In a few cases one or more of the microsites were apparently not present. The most common example was the wind-exposed side, which was often missing on pingos located more than 40 km from the coast. A microsite was considered missing if the vegetation at that location was contiguous and homogeneous with another sampled site. A less common problem was the presence of more than one vegetation type at a given location. This was most common on the south slopes, where there was often one type associated with animal dens and another relatively undisturbed type. If the additional vegetation type covered more than 30 percent of the surface area it was sampled as a separate

relevé. Table 1 lists the microsites sampled for each pingo.

Vegetation was described in 12.5 m² relevés. Relevés were established by measuring out a circle 2 m from the stake, to form a 12.5 m² area. This size relevé is within the range recommended by Westhoff and Maarel (1978) for these vegetation types, and it is small enough to remain within homogeneous stands if the center point is carefully chosen. Low erect shrub (0.5 m height) communities were present at some of the more southern sites, and in these areas the relevé size was doubled to 25 m² by measuring a circle of radius 2.8 m. This is the minimal area recommended for sampling shrub communities (Westhoff and Maarel 1978), where larger relevés are necessary in order to adequately characterize the vegetation.

Table 7. List of growth forms used for cover estimates in relevés.

Erect low shrub (15 to 50 cm)
Dwarf shrub (5 to 15 cm)
Prostrate shrub (<5cm)
Graminoid
Forb (includes pteridophytes)
Moss
Crustose lichen
Foliose lichen
Fruticose lichen
Bare ground
Rock

Visual estimates of percentage cover were made first for growth form (Table 7), and this total value was then distributed between the individual species within the growth form. Values between one half and one percent were recorded as a '++', values less than one half percent as '+'. Small lichens and hepatics (for example *Anastrophyllum minutum*) were often missed in the field, but were included in the data later when observed in the laboratory and recorded simply as present (cover value of '+').

Visual estimates of cover allow for extremely efficient data collection, and they were quite suitable for the purposes of this study. The primary purpose was to document the presence of all species within a microsite, and cover was used as a quick estimate of relative dominance. The presence of species directly outside the relevé but not included within was noted. Gauch (1982) warns that attempts at exact quantification of plant cover yield little or no extra information for the amount of effort involved, and Poore (1962) states that it is not often possible to collect enough exact quantitative data to determine community patterns, and

that attempts to do so may hinder progress. Community data are inherently noisy, and this noise is often greater than the errors from visual estimation (Orlócí 1978). The use of visual estimates of cover rather than a more time consuming method greatly increased the total number of pingos sampled, which increases the amount of confidence in the descriptions of the vegetation types. Enough different pingos were sampled that the relative regional rarity, or commonness, of a given vegetation type can be stated with a fairly high degree of confidence. The placing of relevés in this manner represents regular sampling, which is recommended for determining responses to environmental gradients (Gauch 1982). A number of physical factors were also measured at each plot. Soil moisture, disturbance by ground squirrels, fox, lemmings, bear, caribou, birds, and humans, exposure to wind, snow cover, site moisture, and stability were estimated using scalar values (Tables 8 to 13). More quantitative physical measurements were impractical or impossible for these variables.

Table 8. Scalar values used to measure exposure to winds at individual plots.

Scalar	Meaning
1	protected from winds
2	moderate exposure to winds
3	exposed to winds
4	very exposed to winds

Table 9. Scalar values used to measure soil moisture at each plot (modified from Komárková and Scott 1983).

Scalar	Meaning
1	very dry; very small amount of moisture, soil does not stick together
2	dry; small amount of moisture, soil somewhat sticks together
3	damp; noticeable amount of moisture, soil sticks together but crumbles
4	damp to moist; very noticeable amount of moisture, soil clumps
5	moist; moderate amount of moisture, soil binds but can be broken apart
6	moist to wet; considerable amount of moisture, soil binds and sticks to fingers
7	wet; very considerable amount of moisture, drops of water can be squeezed from soil
6	moist to wet; considerable amount of moisture, soil binds and sticks to fingers
7	wet; very considerable amount of moisture, drops of water can be squeezed from soil
8	very wet; large amount of moisture can be squeezed from soil
9	saturated; very large amount of moisture, water drips from soil
10	very saturated; extremely large amount of moisture, soil is more liquid than solid

Table 10. Scalar values used to measure human and animal disturbance at each plot.

Scalar	Meaning
0	no sign present
1	some sign present, no visible disturbance
2	minor disturbance or extensive sign
3	moderate disturbance; small dens or light grazing
4	major disturbance; multiple dens or noticeable trampling
5	very major disturbance; very extensive tunneling or large pit

Table 11. Scalar values used to measure stability at individual plots.

Scalar	Meaning
1	stable
2	subject to occasional disturbance
3	subject to prolonged but slow disturbance such as solifluction
2	subject to occasional disturbance
3	subject to prolonged but slow disturbance such as solifluction
4	annually disturbed
5	disturbed more than once annually

Table 12. Scalar values used to measure duration of snowbank following melt out at each plot.

Scalar	Meaning
1	snow-free all year
2	snow-free most of winter, some snow cover persists after storms but is blown free soon afterward
3	snow-free prior to regional melt out but with snow most of winter
4	snow-free immediately after melt out
5	snowbank persists 1 to 2 weeks after melt out
6	snowbank persists 3 to 4 weeks after melt out
7	snowbank persists 4 to 8 weeks after melt out
8	snowbank persists 8 to 12 weeks after melt out
9	very short snow-free period
10	snow covered all year

Table 13. Scalar values used to measure site moisture at each plot (modified from Komárková and Scott 1983).

Scalar	Meaning
1	extremely xeric, almost no moisture; no plant growth
2	very xeric, very small amount of moisture; dry sand dunes
3	xeric, small amount of moisture; stabilized sand dunes
4	subxeric, noticeable amount of moisture; well-drained slopes, ridges
5	subxeric to mesic, very noticeable amount of moisture; flat, gently sloping surfaces
6	mesic sites, moderate amount of moisture; flat shallow depressions
7	mesic to subhygric, considerable amount of moisture; depressions
8	subhygric, very considerable amount of moisture; saturated but with < 5% standing water < 10 cm deep
9	hygric, large amount of moisture; 100% of surface under water 10 to 50 cm deep; lake margins, shallow ponds and streams
10	hydric, very large amount of moisture; 100% of surface under water 50 to 150 cm deep; lakes, streams

Species Identification

Specimens of all vascular plants and cryptogams were collected from each plot, pressed, and returned to the laboratory for identification. Additionally, voucher specimens of all species recorded in the study were collected. Vascular specimens were deposited in the University of Colorado and University of Alaska herbaria. Hultén (1968) was the primary reference for the majority of the vascular plants, and Polunin (1959), Wiggins and Thomas (1962), and Welsh (1974) were also occasionally used. Argus (1973) was used for *Salix*, and Mulligan (1970, 1971a,b, 1972, 1974a,b, 1975, 1976) was used for *Draba*. Dr. David Murray, curator of the University of Alaska Herbarium, verified most of the vascular specimens, and Dr. William Weber of the University of Colorado Herbarium also verified a large group. Nomenclature is according to Hultén (1968), with the exception of a few species not included there.

Bryophytes and lichens were collected from each plot as a group, dried, returned to the laboratory, sorted, and placed into packets prior to identification. Sources used for identification of bryophytes were Nyholm (1954-1969), Arnell (1956), Lawton (1971), and Crum and Anderson (1981), and for lichens Hale (1979), Karnefelt (1979), and Thomson (1979, 1984). A small subset of lichens was sent to Dr. John Thomson. Bryophytes were Nyholm (1954-1969), Arnell (1956), Lawton (1971), and Crum and Anderson (1981), and for lichens Hale (1979), Karnefelt (1979), and Thomson (1979, 1984). A small subset of lichens was sent to Dr. John Thomson of the University of Wisconsin for verification. Because of inexperience with these groups, particularly the bryophytes, and also because of time constraints and inherent difficulties with these groups, many specimens were identified only to genus or family level. Specific problems

are discussed in Appendix A, annotated species list.

Climate and Snow

Climate data. Limited climatic data were recorded on Pingo 1 in August 1986. Three Belfort continuous strip-chart recording temperature instruments were placed on the north slope (N0°E), south slope (N180°E), and summit of the pingo. A 30 x 30 x 60 cm hole was dug next to each instrument and filled with clean gravel. The same gravel source was used for all holes. Temperature probes were placed directly below the surface in this gravel in order to measure ground surface temperature. Slope angle on both sides was 30°. The instruments were calibrated indoors before setting them in the field, and again after set up.

A weather shelter was erected approximately 100 m southeast of the pingo. A single Belfort instrument inside measured shelter air temperature and ground temperature simultaneously. The ground temperature probe was treated in the same manner as it was on the pingo. Solar radiation was measured by a pyrhemeter placed on top of the shelter.

Snow transects. Transects of snow depth were made in May 1986 on pingos 1, 3, 4, and 24, when the snow pack was at or near maximum depth (Benson et al. 1975). A point on the summit was selected as the starting point for the

Snow transects. Transects of snow depth were made in May 1986 on pingos 1, 3, 4, and 24, when the snow pack was at or near maximum depth (Benson et al. 1975). A point on the summit was selected as the starting point for the transects. A 100 m tape was laid out from this point along the direction of the transect, and measurements of snow depth were taken every one to three meters using an avalanche probe ski pole. The intent was to characterize the shape and extent of the snow cover, so that in

many areas measurements every meter were not necessary. Transects were taken due north and south, and also along the primary wind vector (N75°E and N255°E). The broad-based pingo, no. 24, was measured along an east-west transect instead of along the primary wind vector. Length of the transects varied; transects were at least 100 m long, and ended when the snow depth leveled off and was therefore presumed to be away from any snow accumulation caused by the pingo. Transects were marked every 100 m and at the end with a brightly colored stake, so they could be easily relocated the following summer.

The snow transects were surveyed in August 1986 using a Wild Heerbrugg tripod-mounted level and a stadia rod. The level was set up on the transect starting point, and the elevation difference between that point and selected points every one to three meters along the transect was measured. Care was taken to get sufficient data to characterize breaks in slope. Snow and elevation data were combined to produce illustrations of snowbank shape. Vegetation along the transect was recorded by naming the plant communities according to visual dominants (Walker 1983), and then noting the extent of each community along the transect meter marks.

Climate indices. Because it was impossible to collect temperature data from and then noting the extent of each community along the transect meter marks.

Climate indices. Because it was impossible to collect temperature data from each plot, two indices of regional temperature and microclimate were used instead. Haugen and Brown's (1980) regressions of temperature and thaw-degree-days indicate that both variables are highly correlated ($r \geq .90$) with distance to the coast. Thus, distance to the coast was used in the analysis as a meas-

ure of temperature. This is more direct than estimating temperature values from the regression and using that as a value; the relationship with other variables would be the same in either case.

Temperature as estimated by the Haugen and Brown equations is useful for looking at regional trends, but cannot be used to compare microclimatic effects. For this, equivalent latitude was calculated for each plot, based on Lee's (1962) equation:

$$\theta' = \arcsin(\sin k \cos h \cos \theta + \cos k \sin \theta) \quad (2)$$

where: θ' - equivalent latitude
 k - degrees of slope from horizontal
 h - azimuthal degrees from north
 θ - actual latitude.

Equivalent latitude is a measure of potential solar radiation and is therefore an indirect measure of temperature. Ideally, a temperature estimate would account for regional variation in conjunction with slope and aspect differences. This is particularly important in arctic regions where the low sun angle amplifies solar radiation differences.

Soils

Field methods. Soils were described by solar radiation differences.

Soils

Field methods. Soils were described immediately next to the vegetation samples. A pit was dug to 60 cm or to permafrost, whichever came first, and soils were described according to Soil Survey Staff (1975). Carbonate and silt morphologies were also described (Gile et al. 1966, Forman and Miller 1984). A small sample (approximately 150 g) was

collected from each horizon. Soils were not described on pingo 41, but the uppermost horizon was collected at each relevé.

Laboratory analyses. Soil pH was determined on the uppermost horizon (A or O horizon) in the laboratory. Approximately 5 g of soil were mixed with distilled water until a saturated paste (Jackson 1959) was formed, which was left covered for one hour; then pH was measured with a Chemtrix Type 400 pH meter.

Analyses of organics and carbonate minerals were done on surface horizons of all samples from pingos 1-6, 13, and 16. Percentage organic carbon and organic matter were determined using the Walkley-Black potassium dichromate method (Walkley and Black 1935). Percentages of calcite (CaCO_3) and dolomite (MgCO_3) were determined using a Chittick gasometric apparatus that measures liberated CO_2 following addition of HCl (Dreimanis 1962; Nelson 1982b). Carbonate equivalent was calculated as the sum of the calcite and dolomite percentages.

Two variables necessary for classification of these soils are percentage organic carbon by weight and base saturation. For those soils on which laboratory analyses were not completed, organic carbon was estimated based on the color, feel, and taste of the soil in the field. Very few of these soils are sufficiently thin. For those soils on which laboratory analyses were not completed, organic carbon was estimated based on the color, feel, and taste of the soil in the field. Very few of these soils are sufficiently organic to be classified as histic, so this was not a major problem. Base saturation does not need to be known exactly, but it is necessary to determine if it is at least 50%, which is the minimum needed to classify a soil as a Mollisol. Base saturation is correlated with pH, and was

presumed to be at least 50% when the pH was greater than 5.5.

Geological Nomenclature

Hopkins (1982) proposed a time-stratigraphic nomenclature corresponding to major phases of the Wisconsin-Weichselian climatic cycles in Beringia, covering the interval between 120,000 and 8,000 BP. This nomenclature will be used whenever possible. The intervals and corresponding Brooks Range glacial sequences are in Fig. 13.

Data Analysis

Data Management

Data were entered onto the CYBER computer at the University of Colorado for analysis. At each stage of data entrance or reduction, a series of checks was used to ensure accuracy. FORTRAN programs designed specifically for reduction and analysis of community data samples were used for the majority of the analyses (Walker 1986). These programs primarily allow for display of the data in a wide variety of formats. This allowed for checking of the data directly against the field notes. The SPSS statistics package (Nie et al. 1975, Hull and Nie 1979) was used to generate all statistics except where otherwise noted. Descriptive statistics are presented directly against the field notes. The SPSS statistics package (Nie et al. 1975, Hull and Nie 1979) was used to generate all statistics except where otherwise noted. Descriptive statistics are presented in the text as mean \pm standard error of the mean.

Classification

The primary goal of the classification was to develop a useful set of entities

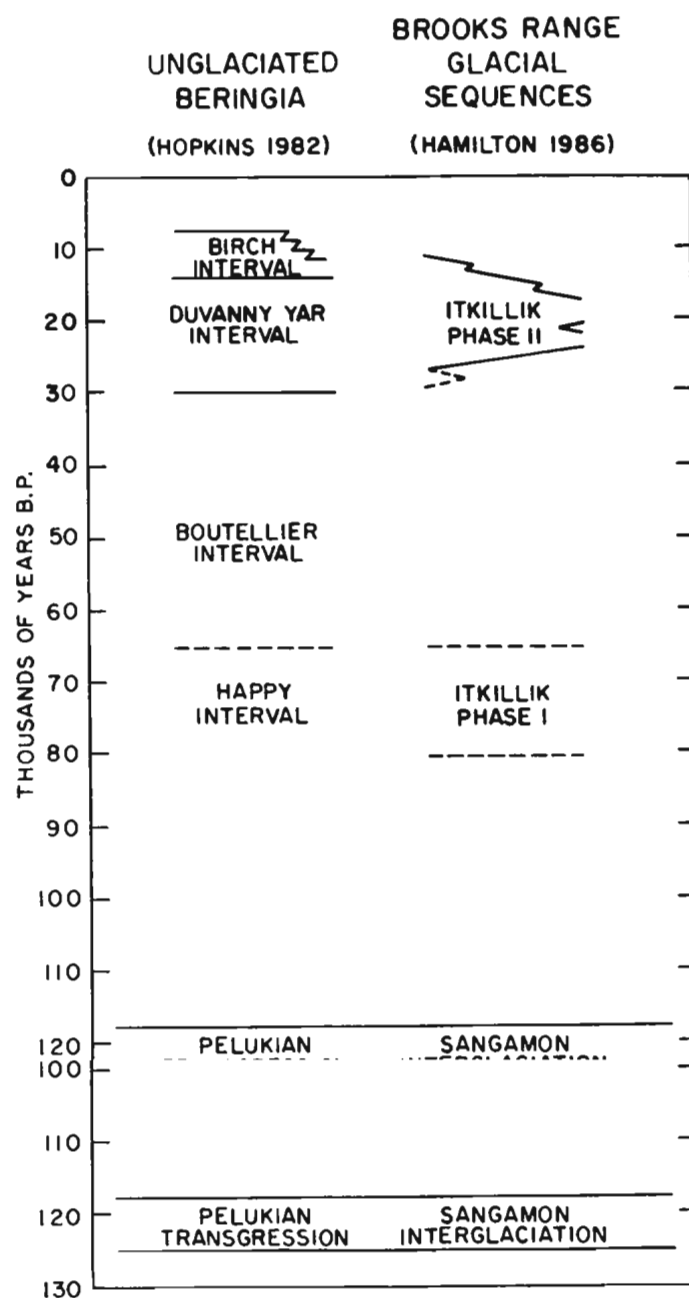


Figure 13. Hopkins' (1982) time-stratigraphic sequence for the non-glaciated portions of Beringia, and the corresponding Brooks Range glacial sequences of Hamilton (1986). (Redrawn from Hopkins [1982] in part.)

(stand types) that could be used to describe the pingo vegetation and on which further analyses could be based. The arranged table technique of Braun-Blanquet (1932) is considered by many to represent the most efficient and meaningful classification tool available (Moore et al. 1970, Westhoff and Maarel 1978). An important difference between a purely mathematical arrangement and a hand arrangement is that a hand-arranged table can be developed reflecting regional patterns and trends that cannot be rigidly defined mathematically.

Classification of species and samples into an arranged table was done using a three-step process. The first step was to split the samples into three subsets, one containing samples from the ENE wind-exposed sides and north slopes (microsites 1 and 7), one containing samples from the summits and south slopes (microsites 2 and 6), and one containing samples from the snowbeds (microsites 3, 4, and 5). Reciprocal averaging (RA) ordination was applied to the data in each subset using FORTRAN program DECORANA (Hill 1979), and a table of species by samples was produced according to the order along the first RA axis. RA results in maximum correlation between species and sample scores, and is therefore useful as a tool for preliminary arrangement. This was followed by hand sorting of the tables to produce the final classes. FORTRAN program LISTEML, written by Margaret Eccles, was used to produce the sorted tables.

A three-level hierarchical classification was used. From highest to lowest, hierarchical levels were: (1) group, (2) stand type, and (3) facies. The standard syntaxa names of association, alliance, and order were not used in order to avoid

producing new units that were inadequately or incompletely described, because the regional vegetation is not well understood nor has it been described in this system. The groups as defined represent the three data subsets, and are most comparable to the alliance concept. The stand type was the basic unit, and all samples were assigned at least this far. Most stand types could be further divided, and this division was called the facies. In one instance, two facies formed a distinct group within a stand type, but were still obviously allied to that stand type. This was defined as a subtype, and was used only in this one case.

The table was arranged by differentiating species, which is how the entities were defined. A species was considered differentiating if it occurred in at least 50% of the samples in a given entity, and in no more than 33% of the remaining samples. A second class of species was defined that were in less than 50% of the samples, but that were highly faithful to the entity. These are termed associated species, and they occur in either at least 40% of the samples in an entity and in no more than 25% of the remaining samples, or at least 50% of their total occurrences are in that entity. Associated species are placed separately underneath differentiating species in the table. Entity names consist of the level followed by two or three species that are most important in defining the entity. An example would be Stand Type *Cerastium beeringianum*-*Ranunculus pedatifidus*.

Ordination

Ordination is a method of arranging non-discrete data in an orderly spatial structure. It reduces complex

multivariate data into low dimensionality. Detrended correspondence analysis (DCA) (Hill 1979, Hill and Gauch 1980) was the method used to produce the ordinations. DCA is an eigenanalysis technique which, although it uses a different computational route, is really a specialized type of principal components analysis that takes into account, and corrects for, the inherent nonlinear structure of community sample data (Pielou 1984). DCA has been widely used and is accepted as a standard technique. Output from the ordination is a series of four scores for each sample and species, which represent coordinates in four-dimensional space. These are usually represented two at a time, so that two-dimensional plots can be drawn. DCA units are consistent and have extrinsic meaning. They are called "SD units" (for average standard deviation of species turnover, Gauch 1982), and one SD represents approximately a 50% change in sample composition. Wartenberg et al. (1987) have cautioned that there may be a problem with the definition of SD units in concrete terms, because the method used to rescale the axes is essentially an arbitrary mathematical model not necessarily related to ecological reality. Nevertheless, SD units are still a useful measure of floristic distance, and DCA axes represent changes in floristic composition of samples. DCA ordinations were done using program DECORANA (Hill 1979). Plots of the ordination were produced with program PICTURE.

Twelve separate ordinations were completed. The first three were based on the flora of each pingo using presence and absence data (i.e. each species present is given an abundance of 1). These

were done for all species, for vascular species only, and for cryptogam species only. The next set was based on the individual sample plot data. This included an overall ordination of all plots, separate ordinations for each of the four morphological classes, and separate ordinations for each of the seven microsites.

Relationship between ordination and classification. Ordination was also used as a tool to relate the classification units to each other and to the environmental variables in the manner of Webber (1971) and Komárková (1979). A composite sample was calculated for each classification unit. This composite contained all species found in all samples within the unit. The calculated abundance value was the mean cover for that species across all the samples. This composite set was then ordinated and plotted in two dimensions. Environmental data were correlated with ordination axes using Spearman rank correlation (Sokal and Rohlf 1969).

Floristics

Floristic analyses were done for vascular species using a slightly modified version of the method of Walker (1985a). Each species is assigned a value in three independent categories: (1) broad environmental region, (2) northernmost limit, and (3) geographic range. Table 14 lists the units in each category. Floristic analyses were done for vascular species using a slightly modified version of the method of Walker (1985a). Each species is assigned a value in three independent categories: (1) broad environmental region, (2) northernmost limit, and (3) geographic range. Table 14 lists the units in each category. The environmental regions were called ecological zones by Walker (1985a), but their definition represents a combination of physiographic and vegetation factors, so environmental regions seems a more appropriate term. Northernmost limit

Table 14. Classes used for the floristic analysis. Environmental regions and geographic ranges are modified from D.A. Walker (1985a); northern limit is from Young (1971).

Environmental Regions:	Arctic Arctic-alpine Arctic-boreal Coastal
Geographic Range:	Circumpolar W N America-Asia-Europe N America-Asia N America Western N America Eastern N America N America-Asia, concentrated in N America N America-Asia, concentrated in Asia Beringian endemic Alaskan-Yukon endemic
Northernmost Limit:	Zone 1 Zone 2 Zone 3 Zone 4

was defined using Young's (1971) zones. I used Walker's (1985a) classifications in most cases, but I checked each one against the maps in Hultén (1968) and made revisions as necessary. The geographic range categories used by Walker (1985a) had a single category for North American-Asian species. This is perhaps the most important category with regard to this study, because Walker demonstrated that these species are primarily found in dry habitats. Thus, I divided it into four categories: (1) North American-Asian—species with broad distributions on both continents, (2) North

American-Asian, concentrated in North America—species with primarily North American distributions that also occur in northeastern Siberia, (3) North American-Asian, concentrated in Asia—species with primarily Asian distributions that also occur in Alaska, and (4) Beringian endemic—species limited to Alaska and northeastern Siberia. Walker included species endemic to Alaska and Yukon as western North America, but here it was considered important enough to stand on its own. The remaining categories are equivalent to those defined by Walker (1985a).

Species Diversity Indices

The Shannon-Wiener (Shannon and Weaver 1949) index of species diversity was calculated for each plot. This is the most commonly used diversity index that considers species richness and evenness (Pielou 1975). This formula is:

$$H' = -\sum p_i \log p_i \quad (3)$$

where H' is the index value, and p_i is the fraction of total number of individual belonging to the i th species. Fraction percent cover was used here rather than number of individuals. The actual biological meaning of H' has been questioned (Hurlbert 1971), but in this case no specific interpretation is being applied to it, other than a relative measure of diversity that includes evenness within it. The number of species was used as a simple measure of richness.

Definition of Morphological Classes

Some measure of pingo age is needed in order to characterize the successional sequences. At this time, however, there is no known way of getting this value. Geomorphic development of pingos, and the relationships with the surrounding landscape, are reasonably well understood (Mackay 1979; Walker 1985a), and this information was used to define four morphological classes.

While the processes that define the classes are time-dependent, these classes are not defined by age, as we have no firm idea what the lengths of time involved are. Also, pingos may develop at different rates depending on the particular circumstances under which they formed. Thus, there may be overlap in the actual ages between different morphological classes.

CHAPTER IV

VEGETATION AND ENVIRONMENTAL GRADIENTS

This chapter addresses the first two goals of the study: (1) to characterize the vegetation and associated soils of the pingos, and (2) to describe the primary environmental gradients controlling the vegetation. The basic morphology of the study pingos is also described in this chapter. Besides the basic goal of describing this vegetation, which has never been done, there are two secondary objectives. The first is to determine how it relates to the regional vegetation and to the circumpolar vegetation. This is done in a qualitative way, by comparing association tables and stand descriptions. The other secondary objective is to determine if there are communities present on the pingos that are related to steppe types described from isolated areas in north-eastern Siberia (Yurtsev 1962, 1963, 1968, 1972a,b, 1974a, 1978, 1982), interior Alaska (Young 1982, Murray et al. 1983), and the Brooks Range (Cooper 1986, 1989).

Because there is no uniform system for classifying vegetation in North America, comparison with other studies is difficult, and can only be done in a general way. Gjaerevoll (1954, 1968, 1980), Lambert (1968), and Cooper (1986) have applied a floristic classification to alpine tundra, comparison with other studies is difficult, and can only be done in a general way. Gjaerevoll (1954, 1968, 1980), Lambert (1968), and Cooper (1986) have applied a floristic classification to alpine vegetation, which is helpful, as much of the pingo vegetation is allied to alpine types. Viereck and Dyrness' (1980; Viereck et al. 1986) statewide classification is of limited use in making inter-site comparisons. This classification is based primarily on growth form, so that the dwarf shrub tundras of the pingos are related to other shrub types rather than the herbaceous types with which they

intergrade. The goal here was to produce summary tables and descriptions of floristically defined vegetation units so that these types can be integrated into future classification systems.

The second part of the chapter relates to the environmental gradients. There are two questions asked. The first, "Are temperature and soil chemistry gradients major controls of pingo vegetation?" stems from the work of Walker (1985a) who illustrated that these are important gradients in controlling the vegetation at Prudhoe Bay. That study concentrated on individual species response, however, and not on the vegetation as a unit, and it also did not consider the relative importance of the two gradients. Thus, the second question is, "Do these gradients act independently, and if so, which is most important in determining vegetation distribution?" This question is considered for the entire flora, and for the vascular and cryptogam floras separately.

Physical Description of Study Pingos

The physical character of the pingos sampled varies considerably between pingos, and there are also differences

Physical Description of Study Pingos

The physical character of the pingos sampled varies considerably between pingos, and there are also differences among the study areas (Table 15). Mean size is generally larger in both the Kadleroshilik and Toolik River areas, primarily due to one very large pingo in each of those areas. Nine of the 41 pingos were considered to be the broad-based morphological type.

An important difference that has major ecological implications is in mean soil pH values. Mean pH is highest at

Table 15. Description of morphological and environmental variables in each study area. Values are mean plus or minus standard error. Definitions of the variables are in Chapter III.

Variable	Prudhoe Bay	Kuparuk	Kadleroshilik	Toolik River
Height (m)	7.1 ± 1.0	7.3 ± 0.9	27.1 ± 7.0	11.6 ± 2.2
Minimum diameter (m)	91 ± 14	161 ± 19	251 ± 93	119 ± 19
Maximum diameter (m)	117 ± 23	258 ± 38	335 ± 156	195 ± 34
Minimum area (ha)	.84 ± .26	1.7 ± 0.4	9.8 ± 6.5	1.8 ± 0.5
Maximum area (ha)	0.96 ± .26	2.8 ± 0.6	15.4 ± 11.0	3.5 ± 1.4
Distance to coast (km)	9.8 ± 1.1	13.6 ± 1.7	31.8 ± 2.4	61.8 ± 2.9
pH	7.06 ± .32	6.56 ± .10	5.51 ± .33	6.88 ± .28

Prudhoe Bay (7.1), while at Kadleroshilik it is only 5.5. This is due to the deposition of calcareous loess downwind from the Sagavanirktok River (Parkinson 1978; Walker 1985a). A newly-formed pingo will presumably have equivalent pH values across its surface. In all the study areas this initial pH would be approximately neutral or slightly alkaline, due to high calcium carbonate content in the parent material (Parkinson 1978). Over time, however, have equivalent pH values across its surface. In all the study areas this initial pH would be approximately neutral or slightly alkaline, due to high calcium carbonate content in the parent material (Parkinson 1978). Over time, however, the driest sites should accumulate carbonates, and pH should approach 8.0, while in areas where organics accumulate or the soils are flushed occasionally, as in a snowbank, pH should decrease. If there is further eolian input of calcareous materials, however, most sites will continue to remain around neutral. This is il-

lustrated by a negative correlation between pH and standard deviation of pH (Fig. 14), which would not be expected based on random factors or statistical artifact.

While the sediments in which a pingo ice core forms are generally limited to sands and gravels, the overlying sediments are not so limited. These sediments may range in thickness from perhaps as little as 1 m to over 14 m (on Ibyuk Pingo near Tuktoyaktuk, N.W.T. ice core forms are generally limited to sands and gravels, the overlying sediments are not so limited. These sediments may range in thickness from perhaps as little as 1 m to over 14 m (on Ibyuk Pingo near Tuktoyaktuk, N.W.T. Müller [1962]) or more. Most of the Prudhoe Bay pingos have sandy gravels or gravelly sands on their surface, which are the predominant surficial materials in this region. The exception is a strip of land near the coast, where a silt of probable marine origin forms the upper-most layer (Rawlinson 1986c,d,e). Pingos

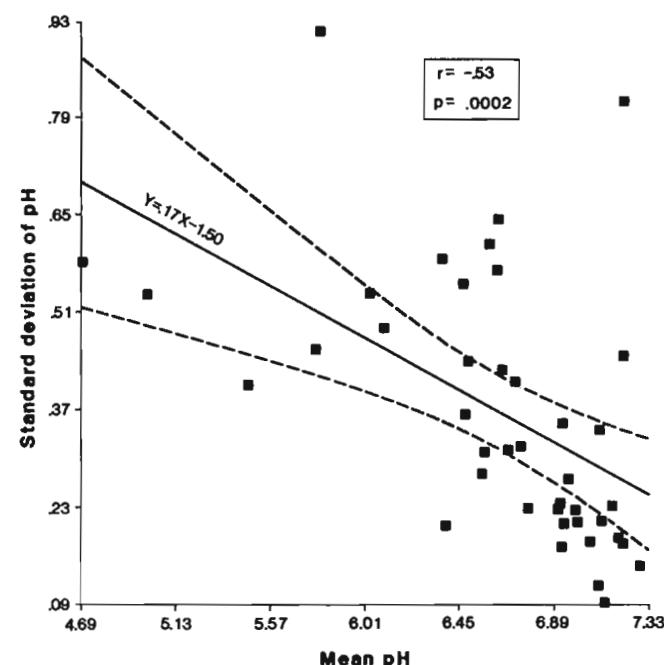


Figure 14. Correlation between mean pH for a given pingo and standard deviation of the mean.

number 3, 5, and 16 were drilled by the U.S. Army Cold Regions Research and Engineering Laboratory (CRREL) in 1982 (Fig. 15) (Brockett 1982). Pingo 3 had 1.1 m of gravel overlying 12.1 m of ice, and Pingo 5 had 2.2 m of gravel overlying 9.1 m of ice. Pingo 16 had 7 m of ice-rich coarse alluvium overlying more than 21 m of ice with gravel. The Tuktoyaktuk pingos, in western Canada, had 1.1 m of gravel overlying 12.1 m of ice, and Pingo 5 had 2.2 m of gravel overlying 9.1 m of ice. Pingo 16 had 7 m of ice-rich coarse alluvium overlying more than 21 m of ice with gravel. The Tuktoyaktuk pingos, in western Canada, have either sand (on the eastern part of the Peninsula) or stony clay (in the west) on their surface (Mackay 1979).

Microclimate

Surface temperature data collected from the north and south slopes of pingo

no. 1 in August of 1986 indicate considerable slope and aspect effects on microclimate (Figs. 16 to 18, Table 16). Average mean temperature between these two sites varies by only 3.3°C, but the average difference in maximum temperature is 5.8°C, and was as great as 16.7°C (on 7 August). The lowest minimum temperatures occur on the south slopes, which is probably because this area is in shadow during the coolest part of the day. These low minimum temperatures on the south slope dampen differences in mean temperatures compared to other sites, and indicate that the south slope has not only the warmest temperatures but also the greatest range of temperatures. An early fall storm

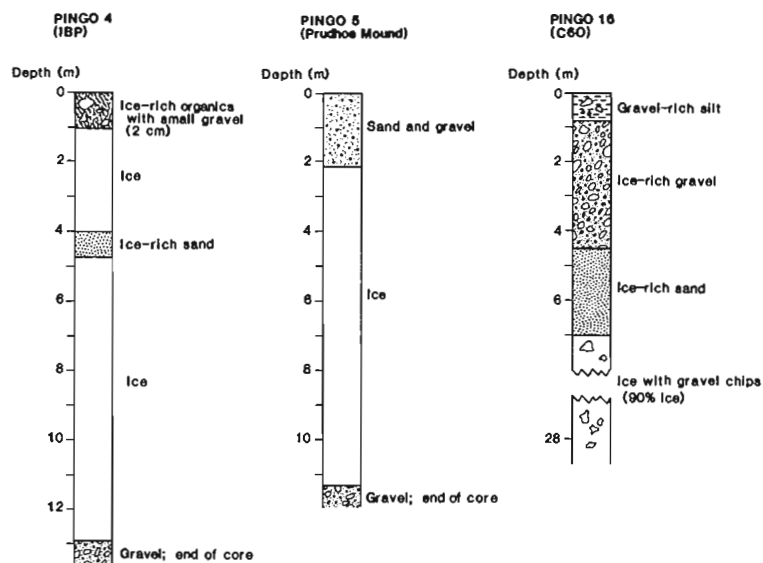


Figure 15. Cores drilled from pingo nos. 4, 5, and 16 by CRREL (redrawn from Brockett 1982).

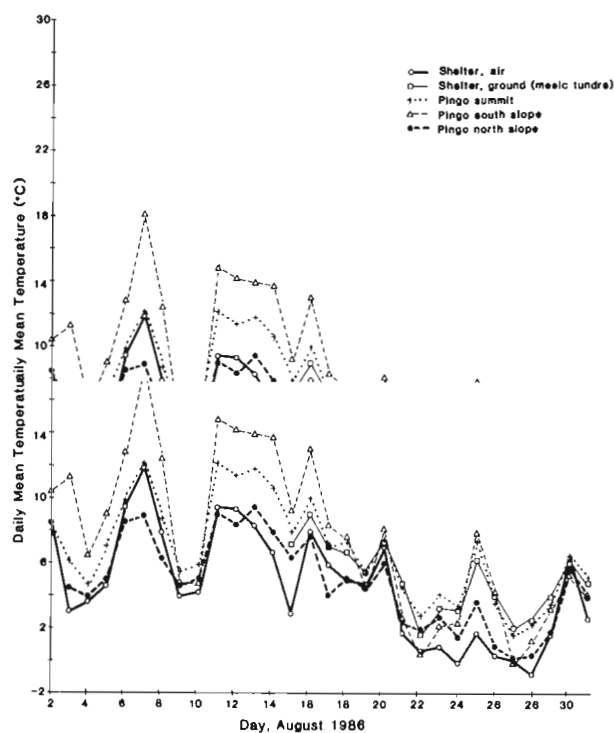


Figure 16. Mean daily temperature during August 1986.

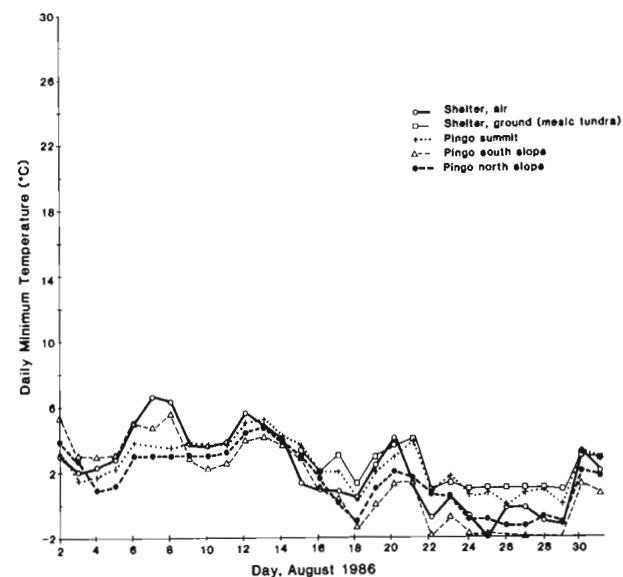


Figure 17. Minimum daily temperature during August 1986.

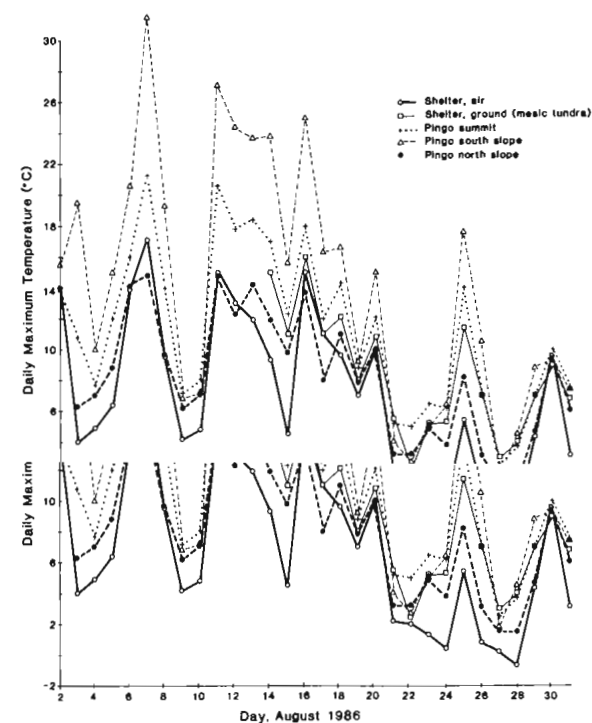


Figure 18. Maximum daily temperature during August 1986.

passed through the area on 22 August, and temperatures were at or near freezing for over a week after this, which

minimized the differences between the two slopes. Solar radiation data were not calibrated, and there were many days of

Table 16. Mean temperature, August 1986, for standard height shelter, ground next to shelter, and pingo summit, south slope, and north slope. Second figure is standard error of the mean. Because some stations had missing data, the number of data points for each is given as *n*.

	MEAN	MINIMUM	MAXIMUM
Standard height shelter	4.6 ± .63 n=30	2.1 ± .42 n=30	7.1 ± .94 n=30
Ground next to shelter (mesic tundra)	5.1 ± .49 n=18	2.2 ± .27 n=20	9.0 ± .82 n=22
Pingo summit	6.8 ± .56 n=30	2.4 ± .27 n=30	11.2 ± .94 n=30
Pingo south slope	7.7 ± .90 n=30	1.4 ± .46 n=30	14.0 ± 1.5 n=30
Pingo north slope	4.8 ± .50 n=29	1.6 ± .34 n=30	8.2 ± .75 n=29

missing data due to instrument failure, so there is no way to correlate these with temperature. Examination of one week of complete data, however, indicates that there is a relationship between incoming solar radiation and surface temperature differences on the north and south slopes (Fig. 19).

Ground temperatures are all highly correlated with air temperature at the solar radiation and surface temperature differences on the north and south slopes (Fig. 19).

Ground temperatures are all highly correlated with air temperature at the standard height shelter (Table 17). Since the calculated equivalent latitude of the north slope at this site is 80°N, it is expected to be colder than the flat mesic tundra (ground temperature at shelter). The mean difference in daily maximum temperature between these two sites is 1.9°C, considerably less than would be expected for a 10°N change in latitude.

The drier soils on the pingo, as compared to the mesic tundra, partially explain this minimal difference. The pingo summit, which has zero slope, had higher temperatures than the flat mesic tundra, because the soils are dry on the pingo summit, and therefore warm up more quickly than do the mesic tundra soils. The south slope, as expected, had higher ground temperatures than any other site. because the soils are dry on the pingo summit, and therefore warm up more quickly than do the mesic tundra soils. The south slope, as expected, had higher ground temperatures than any other site.

Snow

Results of the May, 1986 snow surveys indicate that there is a consistent drift pattern on the pingos (Figs. 20 to 23). Within the Prudhoe Bay region generally, drifting results in an annual snow cover that varies from 0 to 2 m, with an

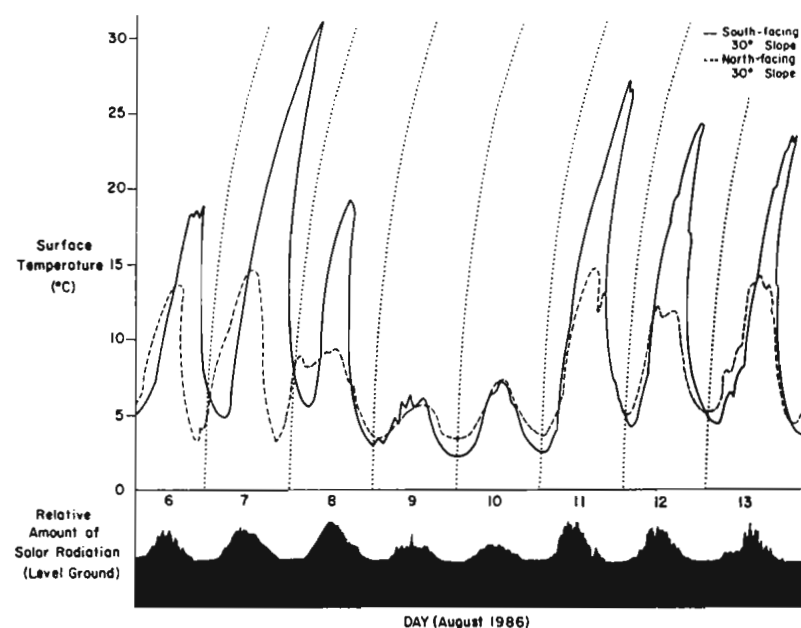


Figure 19. One week of data showing ground surface temperature on a 30° south-facing slope, a 30° north-facing slope, and relative amount of solar radiation at a standard height shelter next to the pingo.

Table 17. Pearson product-moment correlation coefficients between air temperature at standard height shelter and ground temperature next to the shelter, on the pingo summit, south slope, and north slope. Significance in all cases is $p \leq .001$. Because some stations have missing data, the number of data points (*n*) is also given.

SHELTER (AIR)			
GROUND	MEAN	MINIMUM	MAXIMUM
Mesic tundra	.8726 n=18	.8741 n=20	.8210 n=22
SHELTER (AIR)			
GROUND	MEAN	MINIMUM	MAXIMUM
Mesic tundra	.8726 n=18	.8741 n=20	.8210 n=22
Pingo summit	.9136 n=30	.8198 n=30	.9078 n=30
Pingo south slope	.8310 n=30	.8892 n=30	.8517 n=30
Pingo north slope	.9336 n=29	.8454 n=30	.9437 n=30

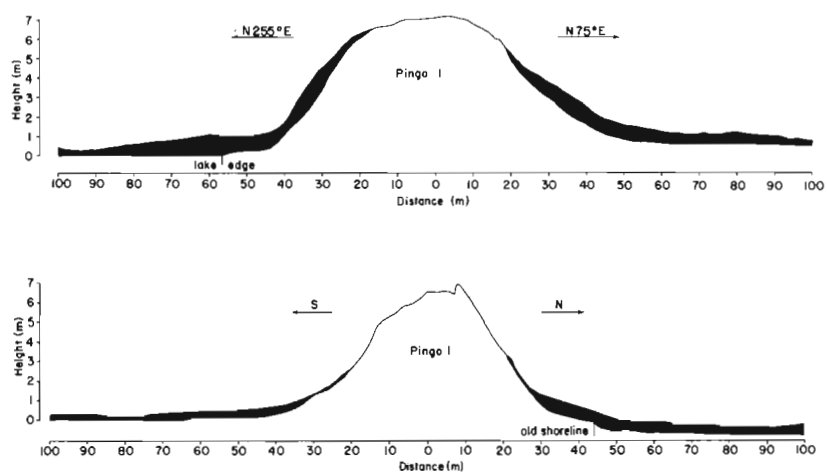


Figure 20. Snow cover (in black) on Pingo 1, on May 17, 1986, with 5x vertical exaggeration.

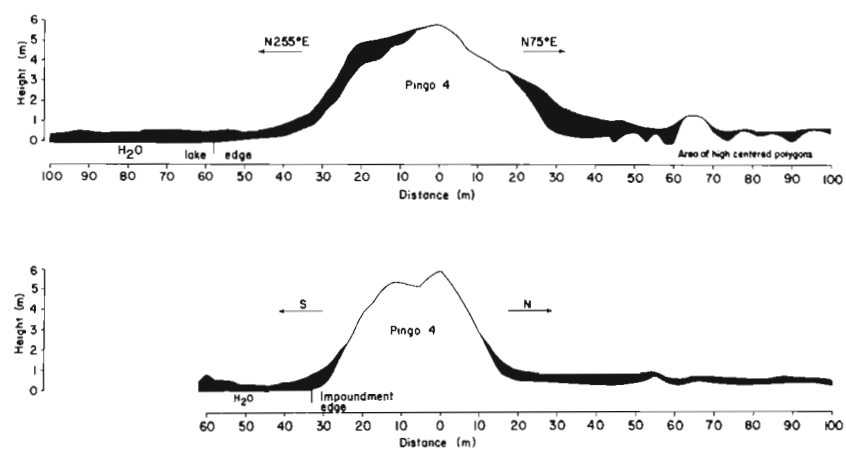


Figure 22. Snow cover (in black) on Pingo 4, on May 17, 1986, with 5x vertical exaggeration.

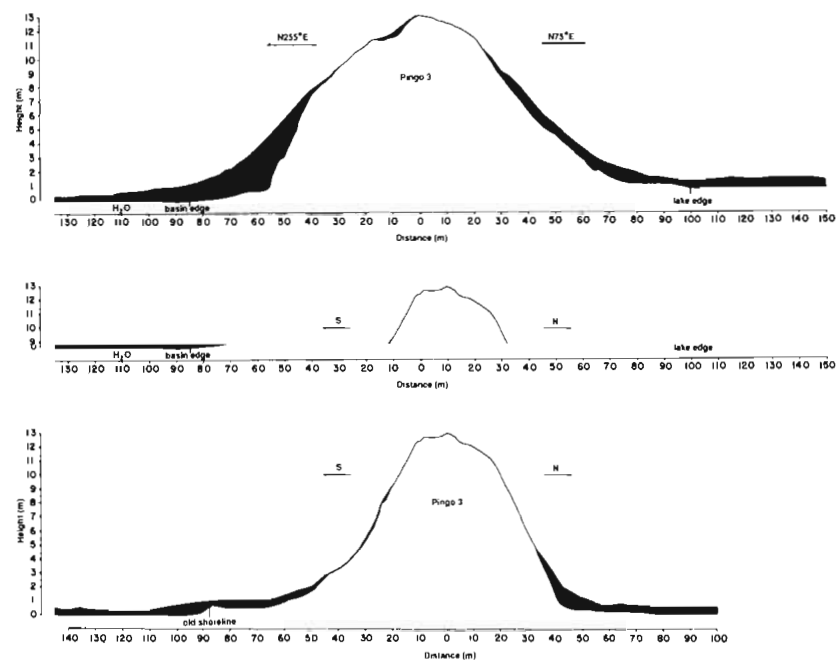


Figure 21. Snow cover (in black) on Pingo 3, on May 17, 1986, with 5x vertical exaggeration.

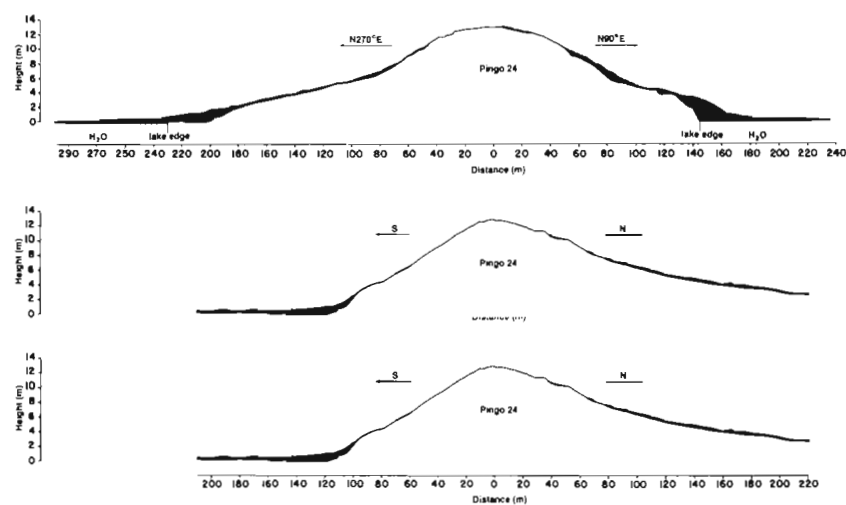


Figure 23. Snow cover (in black) on Pingo 24, a broad-based pingo, on May 17, 1986, with 5x vertical exaggeration.



Figure 24. Pingo 4 (IBP) in mid-May, 1986. Although it snowed several hours each day in the several days preceding this photograph, the upper slopes remain free of snow.

average around 30-40 cm on flat surfaces. Most snowfall comes from westerly storms, but prevailing winds are from the east and cause most of the drifting (Benson et al. 1975). This results in the constant pattern of drifts associated with the pingos. The summits and north and south upper slopes are often snow-free, and a deep drift forms on the WSW side (leeward to prevailing winds) (Fig. 24). There is a small drift on the ENE side limited to the very base of the pingo. The upper ENE slope, facing associated with the pingos. The summits and north and south upper slopes are often snow-free, and a deep drift forms on the WSW side (leeward to prevailing winds) (Fig. 24). There is a small drift on the ENE side limited to the very base of the pingo. The upper ENE slope, facing into prevailing winds, is snow-free.

A comparison of Figs. 20 to 22 with Fig. 23 illustrates the difference in snow cover patterns between steep-sided and broad-based pingos. Pingo no. 24 (Fig. 23), which is a typical broad-based type, has much more uniform snow cover over

Soils

Soils are a product of the interaction between parent materials and environmental conditions, integrated over the time during which a soil at a particular site has been forming. The primary environmental conditions that shape all soils include climate, drainage, and organisms. Other secondary factors, such as eolian inputs or deflation, may also be important. Jenny (1941, 1961) developed a model of soil formation factors that is equally applicable to vegetation (Major 1951). This model was an attempt at a concise expression of the factors contributing to soil formation, with regional climate, parent material, topography or relief, organisms, and duration of soil formation as the primary controlling factors.

The U.S. *Soil Taxonomy* (Soil Survey Staff 1975) is based solely on genetic factors; it includes soil moisture and temperature as soil properties. This hierarchical system has six levels (great order, suborder, great group, subgroup, family, and series), and soil temperature is a primary factor at the suborder and great group levels. Thus, soils of cold regions are recognized within this taxonomy as being distinct at a high level. This system represents a compromise between a purely ecological and a purely genetic system, and thus represents both of these components less than perfectly (Rieger 1983).

The U.S.S.R. soil classification scheme is based on an entirely different concept than either the U.S. or Canadian systems. It relies heavily on the concept of zones and their corresponding zonal soils (Tedrow 1977, Rieger 1983). This concept was first developed by Dokuchaev (1899), who developed small scale maps of Russian soils based on climatic zones. Sibirtsev (1895, in Afanasiev 1927) defined a zonal soil as "...lying on the continental surface in a definite sequence, in zones according to the physiographic conditions of soil formation." Using this concept, only well-drained sites can support zonal soils. Thus, the pingo soils may be considered zonal soils on the coastal plain (Everett 1980c), although their spatial extent is quite limited.

Soils of the Pingos

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Thirteen soil subgroups in seven great groups and four orders were described from the sample plots. The orders are Mollisol, Inceptisol, Entisol, and Histosol. Distribution of the soil types is related to microsite gradients and re-

gional gradients. The variables slope, exposure, thaw depth, moisture, snow cover, stability, cryoturbation, pH, and distance to coast all showed significant differences between the subgroups (using one-way ANOVA, $p < .01$ in all cases). Both moisture and pH are important factors in the taxonomy, and so by definition would be different between these groups. Height of microrelief and equivalent latitude showed no difference between the soil types. Distribution of the soil types among the microsites is shown in Table 18.

Mollisols. This was by far the most common order, with 63% (173) of all plots classified belonging to this group. The concept of a Mollisol is a "...very dark colored, base-rich soil of the steppes" (Soil Survey Staff 1975). These soils have an epipedon with well developed color, at least 50% base saturation, and are at least 0.6% organic carbon by weight. Fifty-one percent (89) of the Mollisols were classified as Pergelic Cryoborolls, 25% (43) as Calcic Pergelic Cryoborolls, 9% (15) as Pachic Pergelic Cryoborolls, 0.6% (1) as Cumulic Pergelic Cryoboroll, and 14% (25) as Pergelic Cryaquolls. The concept of a grassland soil is fitting here, as these soils support the grass and forb vegetation of the pingo slopes.

The Pergelic Cryoborolls in particular have more in common with prairie soils than they do with more typical coastal plain soils, although they represent a grassland soil is fitting here, as these soils support the grass and forb vegetation of the pingo slopes.

The Pergelic Cryoborolls in particular have more in common with prairie soils than they do with more typical coastal plain soils, although they represent the best expression of regional climate on well-drained sites (Everett 1980c). They are differentiated from other Borolls solely on the basis of temperature, but may be very similar in all other respects. Pergelic Cryoborolls are found in all microsites, but are most

Table 18. Distribution of the 13 soil types among the microsites. The upper number is the total occurrences, the second is the percent of each soil type in the given microsite.

	Microsite ¹							
Soil Type	1	2	3	4	5	6	7	Total
MOLLISOLS								
Pergelic Cryoboroll	7 7.9	15 16.9	20 22.5	14 15.7	3 3.4	19 21.3	11 12.4	89 31.4
Calcic Pergelic Cryoboroll	10 23.3	3 7.0	4 9.3	2 4.7	0 0	10 23.3	14 32.6	43 15.2
Pachic Pergelic Cryoboroll	1 6.7	10 66.7	0 0	0 0	0 0	3 20.0	1 6.7	15 5.3
Cumulic Pergelic Cryoboroll	0 0	0 0	0 0	0 0	1 100.0	0 0	0 0	1 .04
Pergelic Cryaquoll	0 0	0 0	2 8.0	7 28.0	13 52.0	1 4.0	2 8.0	25 8.8
INCEPTISOLS								
Pergelic Cryochrept	6 30.0	2 10.0	4 20.0	1 5.0	1 5.0	2 10.0	4 20.0	20 7.1
Calcic Pergelic Cryochrept	2 16.7	1 8.3	2 16.7	2 16.7	0 0	1 8.3	14 33.3	22 7.8
Pergelic Cryumbrept	3 20.0	4 26.7	1 6.7	4 26.7	2 13.3	1 6.7	0 0	15 5.3
Pachic Pergelic Cryumbrept	0 0	1 100.0	0 0	0 0	0 0	0 0	0 0	1 .04
Pergelic Cryaquept	0 0	0 0	0 0	3 37.5	5 62.5	0 0	0 0	8 2.8
Histic Pergelic Cryaquept	3 17.6	1 5.9	3 17.6	2 11.8	7 41.2	0 0	1 5.9	17 6.0
ENTISOLS								
Pergelic Cryorthent	3 17.6	2 11.8	2 11.8	2 11.8	3 17.6	3 17.6	2 5.1	17 6.0
Pergelic Cryaquept	0 0	0 0	0 0	0 37.5	0 62.5	0 0	0 0	0 2.8
Histic Pergelic Cryaquept	3 17.6	1 5.9	3 17.6	2 11.8	7 41.2	0 0	1 5.9	17 6.0
ENTISOLS								
Pergelic Cryorthent	3 17.6	2 11.8	2 11.8	2 11.8	3 17.6	3 17.6	2 5.1	17 6.0
HISTOSOLS								
Pergelic Cryosaprist	0 0	1 10.0	0 0	5 50.0	4 40.0	0 0	0 0	10 3.5

¹1) ENE wind-exposed side, 2) summit, 3) dry leeward side (WSW), 4) middle snowbank 5) lower snowbank 6) south slope, 7) north slope

common on south slopes, WSW shoulders, and summits (microsites 6, 3, and 2). Frequent disturbance by animals prohibits development of a calcic horizon at these sites that would otherwise accumulate carbonates. Mean pH for this type is $6.8 \pm .04$, but the range of values is from 5.6 to 7.5. Soils with a pH below 5.5 were presumed to be less than 50% base saturated, and thus could not be classified as Mollisols.

Comparison of profiles from steep-sided and broad-based pingos indicates a different genesis for the same soil on these two pingo types. On the steep-sided pingos, soil genesis is related to the origin of the pingos as lakes. Most of the organics in these soils were present in the lake basin at the time of drainage, and they subsequently became the A horizon that represents most of the mollic epipedon (Fig. 25). These horizons darken rapidly, probably in less than 100 years following drainage. The reddish color (hue of 7.5 YR) of the A is related to oxidation of the organics. The platy structure is typical of a lake sediment. The uppermost (A) horizon on a broad-based pingo profile, however, indicates an origin for this horizon due to *in situ* accumulation of organics following pingo formation (Fig. 26). This horizon has a subangular blocky structure and a localized strong granular structure. Thus, it shows no relationship to a former lake. The gravelly subhorizons on the broad-based pingo show development of color and structure down to 114 cm. The high percentage of carbonates in the steep-sided pingo profile reflects the importance of calcareous loess in this soil. The broad-based pingos are all outside the zone of loess influence. The combination of color, structure, and *in situ* organ-

ism period for soils on the broad-based pingos. The amount of time necessary to form a 15 cm thick A horizon on the pingos is unknown, but this amount of organics seems unlikely under present vegetation and climate conditions. If these organics did form in place, it was probably under warmer summer temperatures and a grassland type of vegetation.

All of the Pergelic Cryoborolls have free carbonates present, and when these accumulate in the A or B horizon the soil is classified as a Calcic Pergelic Cryoboroll. This subgroup was first described at Prudhoe Bay by Everett and Parkinson (1977); it is not listed in *Soil Taxonomy* and thus far has only been described on these pingos. It is most common on north slopes, and is the most common soil type for this microsite and for the ENE wind-exposed side. It is also frequent on south slopes, and is the second most common type for that microsite. Mean pH is 7.0, the highest for any type.

Pachic Pergelic Cryoborolls are not recognized in *Soil Taxonomy*, but these soils are distinct enough to be separated from typical Pergelic Cryoborolls. They primarily occur on summits, and are characterized by a mollic epipedon greater than 40 cm thick. Summits of pingos are often den sites, heavily used by arctic fox, arctic ground squirrel, and occasionally collared lemming. Digging leads to mixing of the lake organics with underlying mineral material, and a thick, usually fairly uniform mollic epipedon greater than 40 cm thick. Summits of pingos are often den sites, heavily used by arctic fox, arctic ground squirrel, and occasionally collared lemming. Digging leads to mixing of the lake organics with underlying mineral material, and a thick, usually fairly uniform mollic epipedon is the result. Grasses establish quickly on these den sites, and roots may extend down over 50 cm. These are the most deeply thawed sites, with a mean thaw depth of 68 ± 5.3 cm. Mean pH is high, $6.8 \pm .10$, with a range from 6.2 to

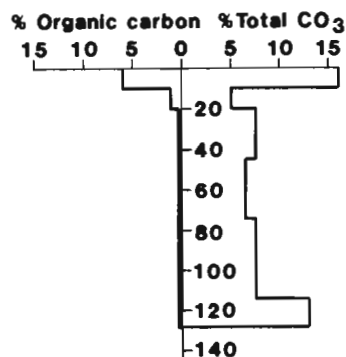
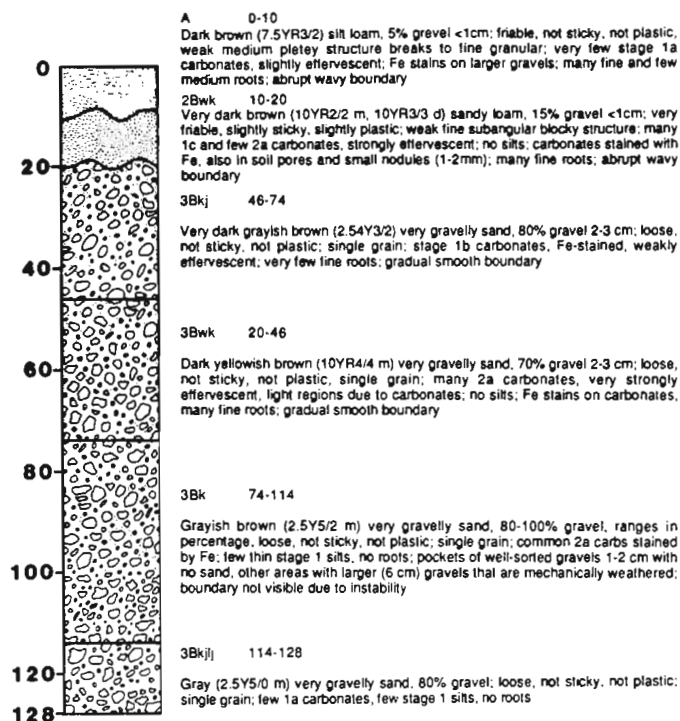


Figure 25. A Pergelic Cryoboroll on the south-facing shoulder of a steep-sided pingo

(IBP, no. 4). These sites have the best developed soils. Silt and carbonate stages are according to Forman and Miller (1984). An "I" subhorizon indicates secondary silt morphology.

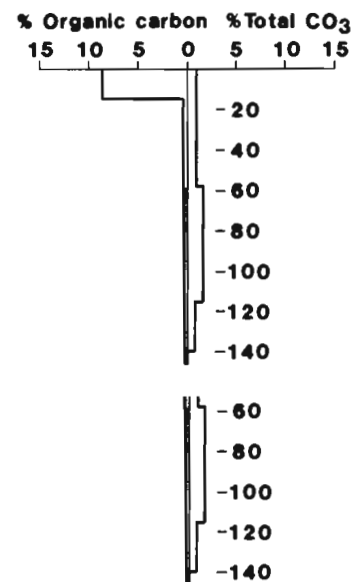
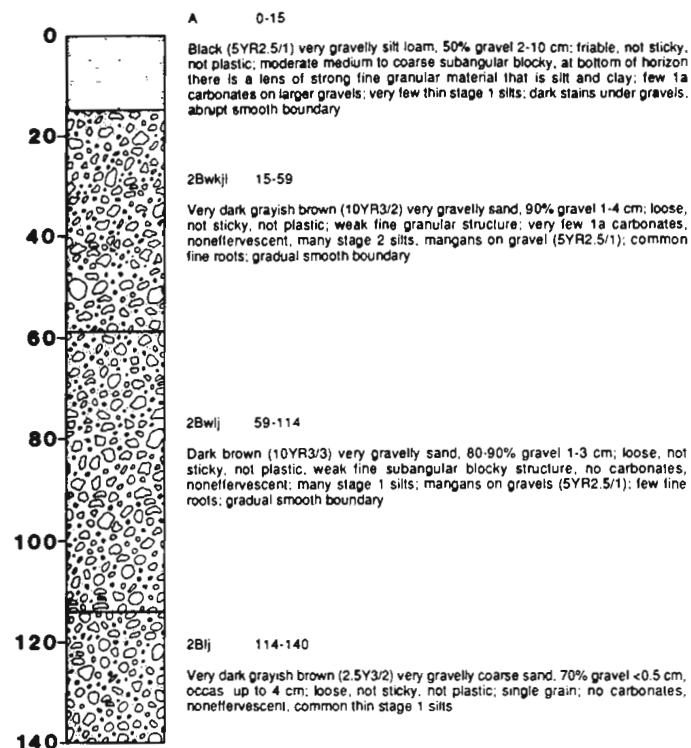


Figure 26. A Pergelic Cryoboroll on the south-facing shoulder of a broad-based pingo. Silt and carbonate stages are according to Forman and Miller (1984). An "I" subhorizon indicates secondary silt morphology.

Cumulic Pergelic Cryoboroll is also not recognized by the official U.S. taxonomy, again because temperature is weighted more heavily than other factors. A cumulic mollic epipedon is also over 40 cm thick, and has the additional property of having a decreasing percentage of organic matter down the profile. The concept is based on overthickening of the epipedon due to downslope movement of material. Only one plot was classified as this type, microsite 5 (lower snowbed), pingo 23. This is a broad-based pingo, and the plot is not at the base of the slope, but in the lower back-slope area. Thus, it is well-drained and dry, and typical of a cumulic site.

Pergelic Cryaquolls are cold, wet Mollisols, occurring primarily in snowbeds. They are often gleyed, mottled, or both. In a few cases this type was found on upper (north and south) slopes where there was sufficient moisture. Thaw depths are intermediate, with a mean of 47 ± 18 cm. The mollic epipedon in these sites is very organic, and these grade into the Pergelic Cryaquepts and Histic Pergelic Cryaquepts.

Inceptisols. The basic concept of an Inceptisol is a mineral soil that does not have characteristic subhorizons, but does have some indication of development, such as a cambic horizon. Soils with a histic (organic) epipedon, but with mineral subhorizons, are placed here also. Sixty-two (23%) of the soils were placed in this order. Twenty-seven percent (17) of the Inceptisols were classified as Pergelic Cryochrepts, 13% (8) as Calcic Pergelic Cryochrepts, 19% (12) as Pergelic Cryumbrepts, 2% (1) as Pachic Pergelic Cryumbrept, 13% (8) as Pergelic Cryaquepts, and 26% (16) as Histic

The Pergelic Cryochrepts are characterized primarily by the presence of an ochric epipedon. This epipedon is either too thin or too low in organics, or has too high a color value to be mollic. This soil occurred at least once at each microsite type, but was most common on the ENE side, where wind erosion precludes much organic accumulation. These are very dry soils with variable pH, as a thin epipedon characterizes this type, and pH ranges from 5.3 to 7.5.

The concept of a Calcic Pergelic Cryochrept is not recognized in the U.S. taxonomy, again because temperature is given more weight than the presence of a calcic horizon. Nonetheless, there were a number of sites that fit the concept of a Pergelic Cryochrept and that also had a calcic horizon. These are classified here as Calcic Pergelic Cryochrepts, and they are very similar to the Calcic Pergelic Cryoborolls, but with a thinner epipedon or little color development. The calcic horizon is generally very close to or at the surface in these soils, and the carbonate may be great enough to cause an increase in color value. These soils are deeply thawed (64 ± 10 cm), but are generally very gravelly and show little development other than some change in color.

The Pergelic Cryumbrepts are similar to the Pergelic Cryoborolls, but have an umbric epipedon. This meets all the requirements of a mollic epipedon, but it is not base saturated. Thus, these soils all have pH 5.5 or lower, with a mean of $5.1 \pm .57$, and a minimum of 4.3. This type was found in all microsites except the north slope, and was found only once on a south slope. It was not common anywhere, and is limited to sites well away from the influence of calcareous loess,

The Pergelic Cryumbrepts are similar to the Pergelic Cryoborolls, but have an umbric epipedon. This meets all the requirements of a mollic epipedon, but it is not base saturated. Thus, these soils all have pH 5.5 or lower, with a mean of $5.1 \pm .57$, and a minimum of 4.3. This type was found in all microsites except the north slope, and was found only once on a south slope. It was not common anywhere, and is limited to sites well away from the influence of calcareous loess,

Pachic Pergelic Cryumbrept is another type not recognized by the U.S. taxonomy, but which is the non-base saturated equivalent of the Pachic Pergelic Cryoboroll. There was only one occurrence of this type, on the summit of pingo 11 in the Kadleroshilik study area.

The Pergelic Cryaquepts are the cold, wet Inceptisols, and are closely related to the Cryaquolls, but without a mollic epipedon. On the pingos, they generally have a highly organic surface horizon that sits directly on a gleyed mineral horizon. Mottles are common. These soils are moderately deeply thawed, with a mean depth of 48 ± 15 cm. Everett's (1980c) concept of this soil at Prudhoe Bay is a moist to wet soil that appears organic, but which remains mineral due to eolian inputs.

When these soils become sufficiently organic, they are classified as Histic Pergelic Cryaquepts. The primary difference between these two is the presence or absence of a histic epipedon. A histic epipedon has a complex description, but in this case it is basically greater than 18% organic carbon by weight, and is between 20 and 40 cm thick. Thaw depths are shallow, ranging from 12 to 43 cm.

Entisols. The concept of an Entisol is "...little or no evidence of development of pedogenic horizons" (Soil Survey Staff 1975). Seventeen soils (6%) were classified as Pergelic Cryorthents. Orthents are generally associated with

Entisols. The concept of an Entisol is "...little or no evidence of development of pedogenic horizons" (Soil Survey Staff 1975). Seventeen soils (6%) were classified as Pergelic Cryorthents. Orthents are generally associated with erosional surfaces, and are common in rocky, mountainous areas. Here they are associated with pingos that are young enough that pedogenesis is not yet evident. They are equally distributed among the microsites, as the environment at a

given site has not yet affected soil development. These are shallowly thawed soils, 33 ± 6.1 cm, and pH is quite variable, from 5.1 to 7.9. These are most common near the coast where temperatures are lowest, and soil-forming processes are likely to be slowed.

Histosols. If there is no mineral horizon within 40 cm of the surface, then the soil is classified as a Histosol; all soils within this order on the pingos belong to the Pergelic Cryosapists subgroup. Ten soils were classified thus, primarily in snowbeds. These grade into the Histic Pergelic Cryaquepts, and are separated by the thickness of the organic horizon. Histosols are considered organic soils; all other orders are mineral soils, although they may have a histic epipedon.

Vegetation

The vegetation of the pingos is primarily dominated by *Dryas integrifolia*, although it is not universally present in all of the stand types. There are also grass-forb dominated types as well as fellfield and blockfield types. In the most acidic sites an ericaceous heath is present. The classification resulted in three groups, 11 stand types, 1 subtype, and 20 facies. The summary tables are in Appendix B. Group *Dryas integrifolia* - *Lecanora epibryon* contains the plots from ENE wind-exposed sides and north slopes (microsites 1 and 7, Table 19). present. The classification resulted in three groups, 11 stand types, 1 subtype, and 20 facies. The summary tables are in Appendix B. Group *Dryas integrifolia* - *Lecanora epibryon* contains the plots from ENE wind-exposed sides and north slopes (microsites 1 and 7, Table 19). Group *Dryas integrifolia* - *Tortula ruralis* represents the summits and south slopes (microsites 2 and 6, Table 20). Group *Dryas integrifolia* - *Tomenthypnum nitens* represents all of the snowbed microsites (microsites 3, 4, and 5,

Table 19. Classification used for north slopes and wind-exposed ENE-facing sides (microsites 1 and 7). The abbreviation for each classification entity is given in parentheses following the full name, these are used in other tables and figures.

GROUP *Dryas integrifolia* - *Lecanora epibryon* (G DRYINT-LECEPI)

STAND TYPE *Saxifraga bronchialis* - *Sphaerophorus globosus* (ST SAXBRO-SPHGLO)

FACIES *Rhacomitrium lanuginosum* - *Polytrichum piliferum* (F RHALAN-POLPIL)

STAND TYPE *Cerastium beeringianum* - *Minuartia rubella* (ST CERBEE-MINRUB)

STAND TYPE *Dryas integrifolia* - *Oxytropis nigrescens* (ST DRYINT-OXYNIG)

FACIES *Carex nardina* - *Calamagrostis purpurascens* (F CARNAR-CALPUR)

STAND TYPE *Dryas integrifolia* - *Astragalus umbellatus* (ST DRYINT-ASTUMB)

FACIES *Kobresia myosuroides* - *Pedicularis capitata* (F KOBMYO-PEDCAP)

FACIES *Carex bigelowii* - *Cassiope tetragona* (F CARBIG-CASTET)

Table 21), with the exception of four plots that were in wet, late-lying snowbeds. These are in Stand Type *Phippsia alga* - *Saxifraga rivularis*, which is not

Table 21), with the exception of four plots that were in wet, late-lying snowbeds. These are in Stand Type *Phippsia alga* - *Saxifraga rivularis*, which is not placed in any group.

ENE sides and north slopes

These sites are represented by Group *Dryas integrifolia* - *Lecanora epibryon*, which is the most homogeneous of the

groups. It is subdivided into four stand types and four facies. Stands in this group have a fairly high cover percentage of *D. integrifolia* up to 50% and most of

groups. It is subdivided into four stand types and four facies. Stands in this group have a fairly high cover percentage of *D. integrifolia*, up to 50%, and most of the other differentiating species are lichens. There is often a high percentage of bare ground. Other important ubiquitous species include *Thamnolia subuliformis*, *Cetraria nivalis*, *Hypogymnia subobscura*, and *Cetraria cucullata*.

Table 20. Classification used for plots on south slopes and summits (microsites 2 and 6).

GROUP *Dryas integrifolia* - *Tortula ruralis* (G DRYINT-TORRUR)

STAND TYPE *Cerastium beeringianum* - *Ranunculus pedatifidus* (ST CERBEE-RANPED)

FACIES *Festuca baffinensis* - *Luzula confusa* (F FESBAF-LUZCON)

FACIES *Trisetum spicatum* - *Potentilla uniflora* (F TRISPI-POTUNI)

STAND TYPE *Poa glauca* - *Bromus pumpellianus* (ST POAGLA-BROPUM)

FACIES *Potentilla hookeriana* - *Polemonium acutiflorum* (F POTHOO-POLACU)

FACIES *Artemisia glomerata* (F ARTGLO)

FACIES *Carex obtusata* - *Saxifraga tricuspidata* (F CAROBT-SAXTRI)

FACIES *Kobresia myosuroides* - *Salix glauca* (F KOBMYO-SALGLA)

STAND TYPE *Carex rupestris* - *Saxifraga oppositifolia* (ST CARRUP-SAXOPP)

FACIES *Carex petricosa* - *Carex nardina* (F CARPET-CARNAR)

FACIES *Carex franklinii* - *Salix brachycarpa* ssp. *niphoclada* (F CARFRA-SALBRANIP)
SAXOPP)

FACIES *Carex petricosa* - *Carex nardina* (F CARPET-CARNAR)

FACIES *Carex franklinii* - *Salix brachycarpa* ssp. *niphoclada* (F CARFRA-SALBRANIP)

FACIES *Carex rupestris* - *Saxifraga oppositifolia* (F CARRUP-SAXOPP)

Table 21. Classification used for snowbed plots (microsites 3, 4 and 5).

STAND TYPE <i>Phippsia algida</i> - <i>Saxifraga rivularis</i> (STPHIALG-SAXRIV)
GROUP <i>Dryas integrifolia</i> - <i>Tomenthypnum nitens</i> (G DRYINT-TOMNIT)
STAND TYPE <i>Salix rotundifolia</i> - <i>Dryas integrifolia</i> (ST SALROT-DRYINT)
FACIES <i>Salix rotundifolia</i> - <i>Oxyria digyna</i> (F SALROT-OXYDIG)
FACIES <i>Salix rotundifolia</i> - <i>Eriophorum triste</i> (F SALROT-ERITRI)
STAND TYPE <i>Cassiope tetragona</i> - <i>Dryas integrifolia</i> (ST CASTET-DRYINT)
SUBTYPE <i>Vaccinium uliginosum</i> - <i>Salix glauca</i> (SB VACULI-SALGLA)
FACIES <i>Ledum decumbens</i> - <i>Betula nana</i> (F LEDDEC-BETNAN)
FACIES <i>Arctous rubra</i> - <i>Rhododendron lapponicum</i> (F ARCRUB-RHOLAP)
FACIES <i>Cassiope tetragona</i> - <i>Dryas integrifolia</i> (F CASTET-DRYINT)
STAND TYPE <i>Dryas integrifolia</i> - <i>Astragalus umbellatus</i> - <i>Carex rupestris</i> (ST DRYINT-ASTUMB-CARRUP)
FACIES <i>Dryas integrifolia</i> - <i>Astragalus umbellatus</i> - <i>Kobresia myosuroides</i> (F DRYINT-ASTUMB-KOBMYO)
FACIES <i>Carex rupestris</i> - <i>Oxytropis nigrescens</i> (F CARRUP-OXYNIG)
FACIES <i>Dryas integrifolia</i> - <i>Astragalus umbellatus</i> - <i>Kobresia myosuroides</i> (F DRYINT-ASTUMB-KOBMYO)
FACIES <i>Carex rupestris</i> - <i>Oxytropis nigrescens</i> (F CARRUP-OXYNIG)

Stand Type *Saxifraga bronchialis* - *Sphaerophorus globosus*. This stand type is found on steep slopes with gravelly, acidic soils on pingos 9 and 41 in the Kadleroshilik area (Fig. 27). Lichens are

the most abundant growth form. Important species include *Psoroma hypnorum*, *Luzula confusa*, *Salix phlebophylla*, *Polytrichum alpinum*, *Pertusaria dactylina*, and *Saxifraga tricuspidata*. There



Figure 27. Stand Type *Saxifraga bronchialis*-*Sphaerophorus globosus*.

is minimal microrelief (3.6 ± 0.2 cm), and pH is the lowest of any stand type (5.2 ± 0.1). *Dryas integrifolia* was not present in 3 of the 5 stands, but was abundant in the other two. Soils are Pergelic Cryochrepts or Pergelic Cryum-brepts, depending on the thickness of the epipedon.

Plant cover in these sites is open, and they generally have a fellfield appearance, but they have little else in common with fellfield types described by Cooper (1986) in the Brooks Range. This is probably a relatively rare type that may be limited to the pingos. It has some connection to south slope communities, but they have little else in common with fellfield types described by Cooper (1986) in the Brooks Range. This is probably a relatively rare type that may be limited to the pingos. It has some connection to south slope communities dominated by *Saxifraga tricuspidata*, but differs considerably in general appearance and associated species. These north slope and ENE-facing stands have much less plant cover and lower vascular species diversity than related south slope types. Batten (1977) described the habi-

tat of *Saxifraga bronchialis* in the northern Brooks Range as "[s]table taluses, coarse alluvium, and well-drained slopes." It is uncommon on the pingos in these relatively acidic sites.

Facies *Racomitrium lanuginosum* - *Polytrichum piliferum* is represented by only a single stand on Kadleroshilik pingo (no. 41) (Fig. 28). The site has the appearance of an alpine fellfield or block-field; it is in a 'valley' on the top of this very large pingo, where river boulders up to 40 cm across have eroded out of the pingo side. This is a very unusual site, as it is essentially an alluvial deposit on top of appearance of an alpine fellfield or block-field; it is in a 'valley' on the top of this very large pingo, where river boulders up to 40 cm across have eroded out of the pingo side. This is a very unusual site, as it is essentially an alluvial deposit on top of a mountain. The rocks are covered by *Rhizocarpon geographicum* and *Umbilicaria* spp., and the thin soil between them is dominated by *Saxifraga tricuspidata*, *Racomitrium lanuginosum*, and *Polytrichum piliferum*. The site faces due north, and pH is 5.2.

a



b



b

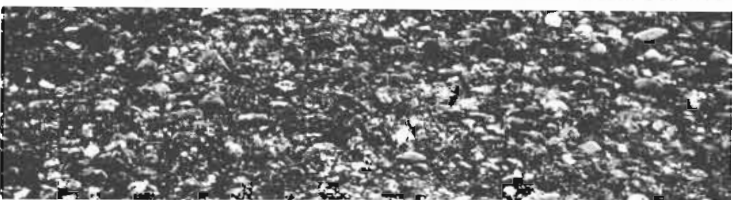


Figure 28. *Facies Rhacomitrium lanuginosum - Polytrichum piliferum*. The site faces north on Kadleroshilik pingo (no. 41). View (a) is the general appearance of the site, and (b) is a close-up of the vegetation.



Figure 29. Stand Type *Cerastium beeringianum - Minuartia rubella*.

Cooper (1986) described *Umbilicario hyperboreae - Rhizocarpon geographicum* from the southern Brooks Range, and this type seems to fit into his concept of that alliance. Walker et al. (1987) also described a similar type from block-fields in the Brooks Range northern foothills.

Stand Type *Cerastium beeringianum - Minuartia rubella*. This stand type is also found on extremely exposed sites, but is primarily near the coast on alkaline soils (Fig. 29). Four plots are assigned to this type. Other important species include *Melandrium affine*, *Cerastium beeringianum*, and *Minuartia rubella*.

This stand type is also found on extremely exposed sites, but is primarily near the coast on alkaline soils (Fig. 29). Four plots are assigned to this type. Other important species include *Melandrium affine*, *Draba corymbosa*, and *Papaver lapponicum*. Lichens are not as important in this stand type as in others within this group, and this type grades into Stand Type *Cerastium beeringianum - Ranunculus pedatifidus* in Group *Dryas integrifolia - Tortular ruralis*. Slopes are fairly gentle (5.5 to 12°), and the soil is 7.4 to 8.2 pH.

highest of any stand type. Soils are Pergelic Cryoborolls or Calcic Pergelic Cryoborolls.

This type is similar to vegetation on beach terraces near Barrow (Wiggins and Thomas 1962) and in several areas of Greenland and northeastern Canada (Tedrow et al. 1968; Aleksandrova 1980), and has some relation to the polar deserts described by Svoboda (1972).

Stand Type *Dryas integrifolia - Oxytropis nigrescens*. This is a widespread and fairly varied type to which 37 plots were assigned (Fig. 30). These stands have a moderate coverage of *Dryas integrifolia* (mean of 25%), and *Oxytropis nigrescens* is always present. *Thamnia subuliformis* and *Cetraria nivalis* are present in all of the samples. This stand type represents the best expression of a typical stand for these microsites throughout the study region. This type is similar to the vegetation described by Svoboda (1972).

Stand Type *Dryas integrifolia - Oxytropis nigrescens*. This is a widespread and fairly varied type to which 37 plots were assigned (Fig. 30). These stands have a moderate coverage of *Dryas integrifolia* (mean of 25%), and *Oxytropis nigrescens* is always present. *Thamnia subuliformis* and *Cetraria nivalis* are present in all of the samples. This stand type represents the best expression of a typical stand for these microsites throughout the study region. This type is similar to the vegetation described by Svoboda (1972).



Figure 30. Stand Type *Dryas integrifolia* - *Oxytropis nigrescens*.

(1985a) Dry *Dryas integrifolia*, *Carex rupestris*, *Oxytropis nigrescens*, *Lecanora epibryon* dwarf shrub, crustose lichen tundra vegetation type, but is somewhat more narrowly defined here. *Carex rupestris* is common throughout Group *Dryas integrifolia* - *Lecanora epibryon*, but *Oxytropis nigrescens* is generally not found in other stand types within this group. It is the presence of *Oxytropis nigrescens*, often in association with either *Encalypta raptocarpa*, *Distichium inclinatum*, or both, that separates this as a distinct type. Slopes are relatively steep ($11 \pm 1.3^\circ$), and very exposed to winds (3.9 ± 0.1 using a 4 point scalar system). They are extremely well-drained, and therefore deeply thawed, 64 ± 4 cm. Estimated percentage of cryoturbation was $10.5 \pm 2.2\%$, which was the highest of any stand type, but some of this may have been due to wind erosion, resulting in deflated areas

that are often difficult to distinguish from cryoturbation surfaces. Microrelief height is low, only 5.8 ± 0.5 cm, but this was typical for the group as a whole. Mean pH is 6.9 ± 0.1 . Calcic Pergelic Cryoboroll is the most common soil type (22 out of 37 samples); other types include Pergelic Cryochrept (4 samples), Calcic Pergelic Cryochrept (4 samples), and Pergelic Cryumbrept (2 samples).

Oxytropis nigrescens is a Beringian endemic restricted primarily to Aleksandrova's (1980) subarctic region of the arctic tundras, and Young's (1971) Pergelic Cryumbrept (2 samples).

Oxytropis nigrescens is a Beringian endemic restricted primarily to Aleksandrova's (1980) subarctic region of the arctic tundras, and Young's (1971) zone 2, and is absent from the highest arctic. It is abundant on the pingos in alkaline sites, particularly on north slopes. This particular stand type is probably limited to dry sites around Prudhoe Bay, and regionally it is restricted to these dry, gravelly sites. In the Arrigetch Creek Valley of the Brooks Range, *Oxytropis*



Figure 31. Facies *Carex nardina* - *Calamagrostis purpurascens*.

nigrescens is found on xeric limestone bedrock (Cooper 1986, *Oxytropis nigrescens* - *Salicetum dodgeanae*).

Facies *Carex nardina* - *Calamagrostis purpurascens* is the only facies recognized within this stand type. Two plots on pingo no. 26 within the Toolik River study area are separated into this facies, which represents a gradation into the steppe types more commonly found on the south slopes and summits (Fig. 31). Both *Carex nardina* and *Calamagrostis purpurascens* have been recognized as steppe-tundra species by numerous authors. Cooper (1986, 1989) lists both of these species as members of steppe associations in the Arrigetch Peaks of the Brooks Range, and Yurtsev (1982) classifies dry meadows with calcic soils, dominated by *Carex rupestris*, *C. nardina*, and *C. glacialis*, all of which are found within this type, as being the best

representation in Siberia of herbaceous-cryoxerophyte vegetation. He considers this to be essentially an alpine type with the general characteristics of steppe vegetation. *Calamagrostis purpurascens* is also listed by Yurtsev as typical of a number of Siberian steppe types and steppe areas in northern Canada and Greenland, and by Young (1982) as a species that was probably typical of the open steppes of central Alaska during the Duvanny Yar. The other differentiating species (found in both of the stands but rare elsewhere within the group) are *Buellia punctata*, *Cetraria tilesii*, *Senecio resedifolius*, *Tofieldia pusilla*, and *Oxytropis maydelliana*. Soils on both sites are Calcic Pergelic Cryoborolls, which is the best expression of a steppe soil within this region. These are stable sites with minimal cryoturbation or expression of microrelief, and pH is high, 7.2 at both sites.



Figure 32. Stand Type *Dryas integrifolia* - *Astragalus umbellatus*.

Stand Type *Dryas integrifolia* - *Astragalus umbellatus*. This is the second most common stand type within the group (31 occurrences), and is found in somewhat more moist sites that are less exposed to wind than Stand Type *Dryas integrifolia* - *Oxytropis nigrescens*. It is characterized by high coverage of *Dryas integrifolia* (from 15 to 50%), with *Astragalus umbellatus* as a conspicuous subdominant (Fig. 32). *Saxifraga oppositifolia*, which is common throughout Group *Dryas integrifolia* - *Lecanora epibryon*, is most common and has the highest cover percentages within this stand type. Other important species include *Papaver macounii*, *Parrya nudicaulis*, *Oxytropis jordallii*, and *Carex scirpoidea*, illustrating the link between this type and communities on more protected sites. Slopes are gentle ($6 \pm 0.8^\circ$), and relatively highly cryoturbated ($7.6 \pm 1.9\%$ cover). Microrelief is most highly

expressed in this type within the group, with a height of 12 ± 3 cm. The pH is very slightly acidic, 6.7 ± 0.1 . Soils are varied, and include Pergelic Cryoborolls, Calcic Pergelic Cryoborolls, Pachic Pergelic Cryoborolls, Pergelic Cryochrepts, Calcic Pergelic Cryochrepts, Pergelic Cryaquepts, Histic Pergelic Cryaquepts, and Pergelic Cryorthents. This stand type is most common in the Kuparuk area (19 occurrences), somewhat so in the Toolik River area (10 occurrences), rare at Prudhoe Bay (1 occurrence), and not present in the Ynd'stand type is most common in the Kuparuk area (19 occurrences), somewhat so in the Toolik River area (10 occurrences), rare at Prudhoe Bay (1 occurrence), and not present in the Kadleroshilik area.

Facies *Kobresia myosuroides* - *Pedicularis capitata* is another example of a steppe-related type (Fig. 33). This facies is represented by nine samples, and other important species include *Tomenthypnum nitens* and *Solorina saccata*. It is limited to the Toolik River



Figure 33. Facies *Kobresia myosuroides* - *Pedicularis capitata*.

area. It is not a true steppe type as it is dominated by *Dryas integrifolia*, but it does have a relationship to the cold tundra steppes. *Kobresia myosuroides* is found in arctic and alpine steppes in other parts of the world including Greenland (Böcher 1959). Yurtsev (1982) speculated that it was important in Beringia during the Duvanny Yar in the most northern steppe associations, just south of the cold deserts that were believed to have predominated in farthest north areas. Soils in this facies are Pergelic Cryoborolls, Calcic Pergelic Cryoborolls, Calcic Pergelic Cryochrepts, or Histic Pergelic Cryaquepts.

Facies *Carex bigelowii* - *Cassiope tetragona* is the other division of this stand type, and represents stands that are closely related to snowbed types and are probably in ecotonal areas (Fig. 34).

They may also possibly be from young pingos where the vegetation is not well defined by microsite. *Carex bigelowii* is a typical species of moist tundra, and appears to be most abundant in areas of solifluction or otherwise unstable soils. Batten (1977) described *Carex bigelowii* as generally associated with hummocky areas in the northern Brooks Range. This facies was included within this group and stand type because it was found in the appropriate microsites, but it is an outlier that is not typical of either the group or stand type. These stands are on gentle slopes, $4 \pm 2.4^\circ$, with very high microrelief in some sites (40 ± 30 cm) probably indicating solifluction, and slightly acidic soils (pH 6.4 ± 0.2). Each of the three sites represented by this type has a different soil type, including Pergelic Cryaquept, Histic Pergelic Cryaquept, and Pergelic Cryochrept.



Figure 34. *Facies Carex bigelowii - Cassiope tetragona*.

Summits and South Slopes

These stands are placed in Group *Dryas integrifolia - Tortula ruralis*. The group is subdivided into three stand types and nine facies. These are the warmest and driest sites on the pingos, and many sites have experienced chronic disturbance by arctic ground squirrel, arctic fox, and perching birds. These animal-disturbed sites are deeply thawed (one site was thawed to 230 cm) and rich in nutrients. The type includes many ubiquitous cryptogams including *Cetraria cucullata*, *Lecanora epibryon*, *Cetraria nivalis*, and *Thamnolia subuliformis*. Stand types are differentiated based on the relative importance of *Dryas integrifolia* and on differentiating vascular species.

Stand Type *Cerastium beeringianum - Ranunculus pedatifidus*. This is the largest type within this group; 35

stands are assigned to it. All but four stands are additionally assigned to one of two facies. Coverage of *Dryas integrifolia* is variable, and ranges from absent to 50%, but with a fairly low mean value of 11%. *Tortula ruralis* is present in all but two stands. Differentiating species, other than *Cerastium beeringianum* and *Ranunculus pedatifidus*, are *Papaver lapponicum* and *Draba cinerea*. Forbs and grasses are dominant overall (Fig. 35), and this would be considered a steppe type. It is most common on the highly animal-disturbed summits, but is also found on south slopes near the coast, primarily in the Prudhoe Bay and Kuparuk River areas. It is roughly equivalent to the Moist *Festuca baffinensis*, *Papaver macounii*, *Ranunculus pedatifidus* forb, grass tundra type described by Walker (1985a) at Prudhoe Bay, which he associated with areas of high animal use.



Figure 35. *Stand Type Cerastium beeringianum - Ranunculus pedatifidus*.

Soils are generally sandy, so that species associated with other sandy sites, such as the coast and rivers, are common. Examples include *Potentilla pulchella*, *Antennaria friesiana*, and *Alopecurus alpinus*. Most sites are flat, as these are generally summits. Cryoturbation effects are minimal, but microrelief height is 11 ± 2.8 cm, due primarily to animal activity. These sites are also the most disturbed by people. Disturbances are concentrated in the oil field areas, where many pingos have benchmarks present, or have been used to place survey markers or even radio towers. Soils are mainly Pergelic Cryoborolls (13 occurrences), Pachic Pergelic Cryoborolls (10 occurrences), and Calcic Pergelic Cryoborolls (5 occurrences), with scattered occurrences of Calcic Pergelic Cryochrepts, Pergelic Cryumbrepts, Pachic Pergelic Cryumbrepts, Histic Pergelic Cryaquepts, and Pergelic Cryorthents.

Facies *Festuca baffinensis - Luzula confusa* is found only on summits (Fig. 36). Other differentiating species include *Poa arctica*, *Rinodina turfacea*, *Melandrium affine*, *Saxifraga caespitosa*, *Timmia austriaca*, and *Polytrichastrum alpinum*. The flora of this facies has a distinct alpine character. Three of the species common here, *Saxifraga caespitosa*, *Festuca brachyphylla*, and *Papaver lapponicum*, are listed by Cooper (1989) as present in only the most exposed sites in the Arrigetch Peaks of the Brooks Range. Seven of the ten differentiating and associated vascular species are listed by Cooper as present in the Arrigetch flora. These sites are moderately thawed, 43 ± 5 cm, and there is no evidence of cryoturbation. The pH is slightly acidic, 6.3 ± 0.2 . Soils are primarily Pergelic Cryoborolls and Pachic Pergelic Cryoborolls.



Figure 36. *Facies Festuca baffinensis - Luzula confusa*.

Facies *Trisetum spicatum - Potentilla uniflora* is also primarily on the summits but was also found on five south slopes within the Prudhoe Bay area. These sites are highly disturbed by animals, with high use estimates for arctic fox, arctic ground squirrel, and birds. Like the previous facies, these sites have a distinctly alpine character, and are dominated by grasses and forbs (Fig. 37). Other differentiating species are *Lloydia serotina*, *Androsace septentrionalis*, *Campanula uniflora*, and *Taraxacum phymatocarpum*. There are no cryptogams that are either differentiating or associated, although the ubiquitous cryptogam species associated with this group are generally present. Cover of *Dryas integrifolia* is fairly low, with a mean value of only 8%. *Oxytropis nigrescens* is important in some sites, with cover as high as 15%. *Androsace chamaejasme* is found at most sites, as well as *Poa glauca*, which may have cover

values as high as 85%. This facies grades into the next type, Stand Type *Poa glauca - Bromus pumpellianus*. Soils are deeply thawed, 73 ± 8 cm, and there was no evidence of cryoturbation. The pH is high, 6.9 ± 0.1 . Soils are Pergelic Cryoborolls, Calcic Pergelic Cryoborolls, and Pachic Pergelic Cryoborolls.

Stand Type *Poa glauca - Bromus pumpellianus*. This stand type contains within it the best examples of steppe-tundra types found on the pingos. It is fairly varied, and includes four facies. *Dryas integrifolia* is of minimal importance. The stand type is found only in the warmer Kadleroshilik and Toolik River study areas, and is characterized by high coverage of both *Poa glauca* and *Bromus pumpellianus* (Fig. 38). *Bupleurum triradiatum* is also a differentiating species; this is an arctic-alpine species that has been associated with the herb zone pollen stratum that is hypothesized by some



Figure 37. *Facies Trisetum spicatum - Potentilla uniflora*.



Figure 38. *Stand Type Poa glauca - Bromus pumpellianus*.

to have represented a steppe-tundra type of vegetation (Ritchie and Cwynar 1982; Matthews 1982). The type is equally

slopes. There is no evidence of cryoturbation, but solifluction (on the south slope sites) and animal disturbance are



Figure 39. *Facies* *Potentilla hookeriana* - *Polemonium acutiflorum*.

evidence of disturbance by both squirrels and bears. The pH is fairly low, 6.3 ± 0.2 . Soils are variable, and include Pergelic Cryoborolls, Calcic Pergelic Cryoborolls, Pachic Pergelic Cryoborolls, Pergelic Cryochrepts, Calcic Pergelic Cryochrepts, Pergelic Cryumbrepts, Pergelic Cryosaprists, and Pergelic Cryorthents.

Facies* *Potentilla hookeriana* - *Polemonium acutiflorum was described from the summits of three pingos and also the south slope of one of the same three (Fig. 39). Other differentiating

Facies* *Potentilla hookeriana* - *Polemonium acutiflorum was described from the summits of three pingos and also the south slope of one of the same three (Fig. 39). Other differentiating species are *Agropyron boreale* ssp. *hyperarcticum*, *Draba glabella*, and *Oxytropis maydelliana*. Mean pH is 6.6 ± 0.4 . Fox disturbance estimates are higher in this facies than in any other. These are sandy, gravelly sites, and soils are classified as Pergelic Cryoboroll, Calcic Pergelic Cryoboroll, or Pergelic

Cryorthent. Although the species composition is different, this community has a striking physiognomic similarity to *Acomastylis rossii* - *Polemonium viscosum* associated with gophers in the Colorado alpine (Zwinger and Willard 1972).

Facies* *Artemisia glomerata is an outlier represented by only a single stand on pingo no. 15 at the northern tip of the Toolik River area (Fig. 40). This facies may represent a more widespread type, but this could not be documented with the present data. It is poor in species, outlier represented by only a single stand on pingo no. 15 at the northern tip of the Toolik River area (Fig. 40). This facies may represent a more widespread type, but this could not be documented with the present data. It is poor in species, dominated by *Artemisia glomerata*, with *Poa glauca*, *Bromus pumpellianus*, and *Bupleurum triradiatum* also conspicuous. It has few species in common with other facies. *Dryas integrifolia* was not present, and the lichen species associated with Group *Dryas integrifolia* - *Tortula ruralis* were mostly missing.



Figure 40. *Facies* *Artemisia glomerata*.

Because Stand Type *Poa glauca* - *Bromus pumpellianus* is a steppe type, and because the presence of *Artemisia* species has been emphasized in the definition of steppe tundra, primarily due to its abundance in the pollen record, it is separated as a unique type for now. More descriptive work is needed to verify if this will hold up as a valid type. Soil was not classified at this site, but it was gravelly with minimal organics.

Facies* *Carex obtusata* - *Saxifraga tricuspidata was found in eight sites, all but one (on pingo no. 7 at Toolik River) classified at this site, but it was gravelly with minimal organics.

Facies* *Carex obtusata* - *Saxifraga tricuspidata was found in eight sites, all but one (on pingo no. 7 at Toolik River) in the Kadleroshilik study area. These are the most well-developed examples of steppe-tundra vegetation on the pingos, and probably represent the northernmost examples of steppe tundra in North America today (Fig. 41). *Dryas integrifolia* has less than 1% cover or is absent entirely. Other vascular differen-

tiating species are *Anemone drummondii*, *Phlox sibirica*, *Polemonium boreale*, *Minuartia arctica*, *Astragalus aboriginum*, and *Saxifraga reflexa*. Several fairly significant range disjunctions are found here, including *Saxifraga reflexa*, *Pulsatilla patens*, and *Eritrichum aretioides*. *Erigeron muirii*, a north slope endemic found primarily in the foothills of the Brooks Range, was found only in this facies. *Carex obtusata* and *Pulsatilla patens* are listed by Yurtsev (1982) as important in many modern analogs of Pleistocene steppe vegetation. These are generally considered as the foothills of the Brooks Range, was found only in this facies. *Carex obtusata* and *Pulsatilla patens* are listed by Yurtsev (1982) as important in many modern analogs of Pleistocene steppe vegetation. These are generally considered as characteristic of meadow steppe types (Aleksandrova 1980). No exact measurements are available, but snow cover is probably thin to absent in most sites. Slopes may be very steep (up to 30°), and soils are sandy gravel. There is no evidence of cryoturbation, little microrelief, and pH is low, 6.0 ± 0.3 .



Figure 41. Facies *Carex obtusata* - *Saxifraga tricuspidata*.

All of the south slope types would be considered calcareous when compared to other arctic areas, but within this calcareous area there is a gradient related to pH, carbonates, and other soil chemical factors. Within the range of pHs present on the pingos, the best examples of steppe types are present on sites with the lowest pH. This is somewhat surprising, as steppe-tundra types have generally been associated with the most calcareous soils in any given region.

Facies *Kobresia myosuroides* - *Salix glauca* is found mainly on summits in steppe-tundra types have generally been associated with the most calcareous soils in any given region.

Facies *Kobresia myosuroides* - *Salix glauca* is found mainly on summits in the Toolik River area; it was also described from the south slope of pingo no. 10 in the Kadleroshilik study area. This type is characterized by the presence of erect shrubs in the genus *Salix* (Fig. 42). *Salix lanata* may be present, as well as the dwarf shrub *Arctous rubra*. *Dryas integrifolia* is present, and may have

cover values as high as 25%, although generally less. This is not a steppe type, but it does have a relationship to the steppes. *Calamagrostis purpurascens* is an associated species. These sites are very heavily disturbed by digging squirrels, and the ground is generally complex, with multiple burrow openings. Estimated disturbance by squirrels was 3.0 ± 0.5 on a 4 point scale. No cryoturbation was noted in any of the samples, and microrelief is high but variable, 27 ± 10 cm. Soil pH is moderate, 6.5 ± 0.3 . Soils are variable and include Pergelic Cryoborolls, Pergelic Cryochrepts, 3.0 ± 0.5 on a 4 point scale. No cryoturbation was noted in any of the samples, and microrelief is high but variable, 27 ± 10 cm. Soil pH is moderate, 6.5 ± 0.3 . Soils are variable and include Pergelic Cryoborolls, Pergelic Cryochrepts, Pergelic Cryumbrepts, Pergelic Cryosaprists, and Pergelic Cryorthents.

Vegetation dominated by *Kobresia myosuroides* and *Salix* spp. has been described from the Brooks Range (Salicidodgeanae - Kobresion myosuroidis of Cooper 1986) and Iceland (*Kobresia myosuroides* - *Salix lanata* community



Figure 42. Facies *Kobresia myosuroides* - *Salix glauca*.

of Gunnlaugsdóttir 1985). *Kobresia myosuroides* dominated associations are uncommon in Alaska. Its presence is not uncommon, but it is generally a rather minor component (Spetzman 1959; Drew and Shanks 1965; Johnson et al. 1966). Hanson (1951) described it in association with *Dryas octopetala* and *Hedysarum alpinum* ssp. *americanum*. Batten (1977) reported it as common on dry, calcareous alluvial fans often in association with *Carex misandra*, *C. rupestris*, and *C. scirpoidea* in the northern Brooks Range. *Dryas integrifolia*, *Arctous rubra*, and *Salix reticulata* Batten (1977) reported it as common on dry, calcareous alluvial fans often in association with *Carex misandra*, *C. rupestris*, and *C. scirpoidea* in the northern Brooks Range. *Dryas integrifolia*, *Arctous rubra*, and *Salix reticulata* dominate these Brooks Range sites. In the northern foothills, *Kobresia myosuroides* is associated with *Dryas octopetala*, *Selaginella sibirica* and *Minuartia obtusiloba* on snow-free sandstone outcrops (Walker et al. 1987a). *Kobresia myosuroides* has a circumpolar distribution (Hultén 1968). Komárková

(1981) discussed the problems of placing *Kobresia myosuroides* communities into higher levels of classification; she divided them into three broad groups: (1) zonal alpine, (2) nonzonal alpine, and (3) arctic. Thus, despite the similar ecology of *Kobresia myosuroides* throughout its range, its syntaxonomy is complex.

Stand Type *Carex rupestris* - *Saxifraga oppositifolia*. This is the best expression of the south slope vegetation that has been only minimally disturbed by animals in the Prudhoe Bay and Kuparuk study areas (Fig. 43). It is relatively common in the Toolik River area, but is not found at Kadleroshilik, and is subdivided into three facies. It is characterized by cover values of *Carex rupestris* as high as 40%, and also by high cover of *Dryas integrifolia*, ranging from 10 to 70%. Other differentiating species are *Oxytropis jordalii*, *Carex*



Figure 43. Stand Type *Carex rupestris* - *Saxifraga oppositifolia*.

scirpoidea, and *Lecanora luteovernalis*. Walker (1985a) described Dry, *Dryas integrifolia*, *Saxifraga oppositifolia*, *Lecanora epibryon* dwarf shrub, crustose lichen tundra from dry sites with evidence of cryoturbation at Prudhoe Bay. On the pingos, however, there was little evidence for cryoturbation. These are relatively stable sites with little microrelief. The pH is high, 6.9 ± 0.1 . Soils are primarily Pergelic Cryoborolls, but also include Calcic Pergelic Cryoborolls, Pachic Pergelic Cryoborolls, Pergelic Cryochrepts, Pergelic Cryaquept, and Pergelic Cryorthent. pH is high, 6.9 ± 0.1 . Soils are primarily Pergelic Cryoborolls, but also include Calcic Pergelic Cryoborolls, Pachic Pergelic Cryoborolls, Pergelic Cryochrepts, Pergelic Cryaquept, and Pergelic Cryorthent.

Both *Carex rupestris* and *Saxifraga oppositifolia* are arctic-alpine, circum-polar species; both are also components of the polar deserts (Hultén 1968; Aleksandrova 1980). *Carex rupestris* is an important component of alpine vegetation in southern areas as well (Komárková 1979). Cooper's (1986)

Caricetum *scirpoideo* - *rupestris* in the Brooks Range is very similar to this, the major difference being the abundance of *Dryas octopetala* in the alpine types and *Dryas integrifolia* on the pingos. Cooper (1986) allied the Brooks Range types to the southern Rocky Mountain types (Cox 1933; Curry 1962; Michener 1964; Kiener 1967; Marr 1967; Bamberg and Major 1968; Komárková 1979; Willard 1979). He felt that the primary difference between these sites and the Brooks Range sites was that the Brooks Range sites were often snow-covered in winter. The pingo communities of this type are Major 1968; Komárková 1979; Willard 1979). He felt that the primary difference between these sites and the Brooks Range sites was that the Brooks Range sites were often snow-covered in winter. The pingo communities of this type are snow-free throughout the year.

Facies *Carex petricosa* - *Carex nardina* is found mainly in the Toolik River area; one stand was described from Prudhoe Bay. These stands are related to the herbaceous-cryophyte vegetation that Yurtsev (1982) states has the general



Figure 44. Facies *Carex petricosa* - *Carex nardina*.

aspect of a steppe but is characterized by arctic-alpine species (Fig. 44). Other vascular differentiating species are *Hedysarum alpinum* ssp. *americanum* and *Braya glabella*. *Thalictrum alpinum* is associated. *Kobresia myosuroides* is present in all but one of the stands. These are some of the most calcic sites, with pH of 7.2 ± 0.1 . Soils are Pergelic Cryoborolls or Calcic Pergelic Cryoborolls.

Carex nardina is a dominant species in high alpine areas south of Alaska (Douglas and Bliss 1977; Komárková 1979). Its status within Alaska, however, is uncertain, and surveys of many areas have failed to locate it (Batten 1977; Kassler 1980). Cooper (1986) described it from exposed limestone bedrock outcrops in the Arrigetch Creek Valley of the Brooks Range (*Cetrario tilesii* - Caricetum *nardinae*), but the association generally does not match

Carex nardina is a dominant species in high alpine areas south of Alaska (Douglas and Bliss 1977; Komárková 1979). Its status within Alaska, however, is uncertain, and surveys of many areas have failed to locate it (Batten 1977; Kassler 1980). Cooper (1986) described it from exposed limestone bedrock outcrops in the Arrigetch Creek Valley of the Brooks Range (*Cetrario tilesii* - Caricetum *nardinae*), but the association generally does not match

well. It is possible that *Carex nardina* is more widespread in Alaska, as it is easily confused with *Kobresia myosuroides*, which has a similar ecology. *Carex nardina* is found in some of the most exposed, calcareous sites in Siberia (Yurtsev 1982), Greenland (Böcher 1954), and Spitsbergen (Acock 1940; Rønning 1965).

Facies *Carex franklinii* - *Salix brachycarpa* ssp. *niphoclada* is an outlier that was present on the summit and south slope of pingo no. 27 in the Toolik River area (Fig. 45). There are no other differ-

Facies *Carex franklinii* - *Salix brachycarpa* ssp. *niphoclada* is an outlier that was present on the summit and south slope of pingo no. 27 in the Toolik River area (Fig. 45). There are no other differentiating or associated species. Overall it is similar to Facies *C. petricosa* - *C. nardina*, but neither of these species is present in this type. *Kobresia myosuroides* is present in both of the stands. These are also very calcic sites, with pH of 7.1, and the soils are classified as Pergelic Cryoboroll and Pergelic Cryochrept.

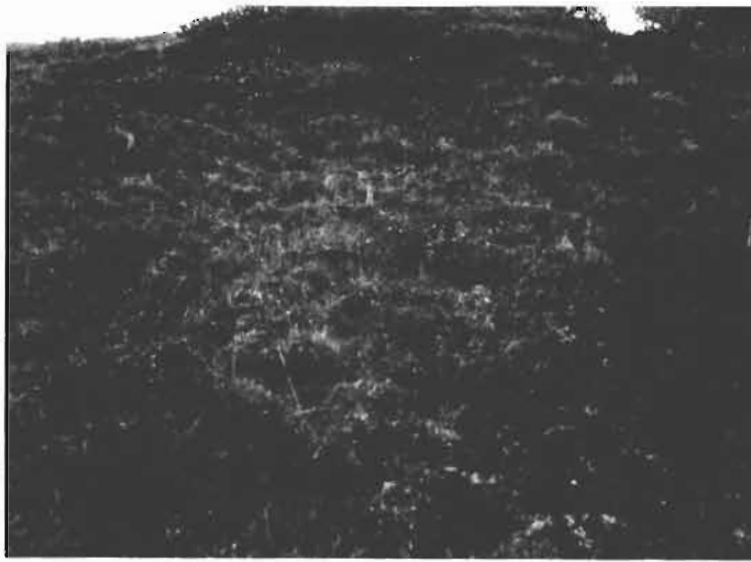


Figure 45. *Facies Carex franklinii - Salix brachycarpa ssp. niphoclada*.

Facies *Carex rupestris - Saxifraga oppositifolia* is differentiated from others within this stand type by a group of eight species, primarily lichens (Fig. 46). The two most important differentiating species are *Dactylina arctica* and *Fistulariella almqvistii*. This type is most common in the Kuparuk study area, but has a few occurrences at Prudhoe Bay and Toolik River. It has minimal animal disturbance and occurs on more gentle slopes than the more typical south slope communities at Prudhoe Bay. Slope is only $7 \pm 1^\circ$, and there is little evidence of cryoturbation or animal disturbance. Mean pH is 6.9 ± 0.02 . Soils are mainly Pergelic Cryoborolls, but also include Calcic Pergelic Cryoborolls. Pachic Pergelic Cryoborolls. Pachic Pergelic Cryoborolls, Pergelic Cryochrepts, Pergelic Cryaquepts, and Per-

Snowbeds

These sites are included in Group *Dryas integrifolia - Tomenthypnum nitens*, with the exception of Stand Type *Phippsia algida - Saxifraga rivularis*, which is not included in any higher class. The snowbeds show the most clear relations to other arctic and alpine types described from the circumpolar region (Aleksandrova 1980).

Stand Type *Phippsia algida - Saxifraga rivularis*. This type is present on the leeward base of pingo no. 13 in the Kuparuk area and below a permanent snowbank at the base of pingo no. 41 in the Kadleroshilik area (Fig. 47). These are both large pingos with steep slopes at their leeward base. Pingo no. 13 does not

Stand Type *Phippsia algida - Saxifraga rivularis*. This type is present on the leeward base of pingo no. 13 in the Kuparuk area and below a permanent snowbank at the base of pingo no. 41 in the Kadleroshilik area (Fig. 47). These are both large pingos with steep slopes at their leeward base. Pingo no. 13 does not

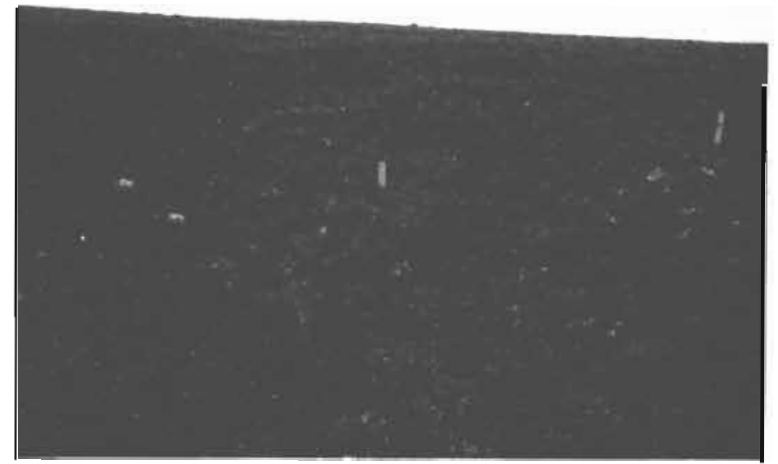


Figure 46. *Facies Carex rupestris - Saxifraga oppositifolia*.



Figure 47. *Stand Type Phippsia algida - Saxifraga rivularis*.

undoubtedly very late-lying. *Phippsia algida* was observed just putting out leaves at this site in late August, when most of the tundra had begun to senesce.

These are rather unusual sites that have not been described elsewhere on the coastal plain. They are more closely related to alpine snowbed types than to most of the snowbeds found associated with the pingos. One species found at Kadleroshilik pingo, *Stellaria umbellata*, is not known elsewhere on the coastal plain, and is generally rare and limited to specific alpine habitats (Hultén 1968). It is infrequent in the southern Rockies (Little 1941; Scott 1966; Weber 1976; Komárková 1979). *Koenigia islandica*, which was also found at Kadleroshilik, is an alpine snowbed plant that is also fairly common in barren areas near the coast. This is the only annual known from this region. It is also present but rare in the Colorado Rockies, where its ecology is similar in similar sites (Weber 1976; Komárková 1979). *Phippsia algida*, which is known only from these deep snowbeds within the study region, is a characteristic plant of the very high latitude polar deserts (Korotkevich 1958; Aleksandrova 1980). These pingo sites have very few species in common with Group *Dryas integrifolia* - *Toment-hypnum nitens*. They are wet sites with some standing water and very shallow thaw. There is some gradation with Stand Type *Salix rotundifolia* - *Dryas integrifolia*. Microrelief is minimal, and pH is low, 5.4 ± 0.3 . Soils are Pergelic have very few species in common with Group *Dryas integrifolia* - *Toment-hypnum nitens*. They are wet sites with some standing water and very shallow thaw. There is some gradation with Stand Type *Salix rotundifolia* - *Dryas integrifolia*. Microrelief is minimal, and pH is low, 5.4 ± 0.3 . Soils are Pergelic Cryosaprists.

Group *Dryas integrifolia* - *Toment-hypnum nitens*

within it. There are 22 ubiquitous species associated with the group, and 9 associated species. Some of the more important ubiquitous species are *Salix reticulata*, *Cetraria nivalis*, *Cetraria islandica* ssp. *islandica*, *Cetraria cucullata*, and *Pedicularis capitata*. Stand types within the group range from late-lying snowbed sites with some relationship to Stand Type *Phippsia algida* - *Saxifraga rivularis* to dry sites related to stand types described from the north and south slopes.

Stand Type *Salix rotundifolia* - *Dryas integrifolia*. This type is found at the leeward base of pingos and is characterized by dominance of *S. rotundifolia*, with cover values as high as 90% (Fig. 48). These sites are sometimes fairly poor in species compared to other stand types. They are under deep snow and are poorly drained, and snow cover probably lasts at least several weeks after regional meltout. Other differentiating species are *Arctagrostis latifolia* and *Carex bigelowii*, both common in ground disturbed by solifluction. *Stereocaulon alpinum* is frequent in these sites and may be a subdominant. There are two facies within Stand Type *Salix rotundifolia* - *Dryas integrifolia*, related to moisture and disturbance gradients. Thaw is shallow, with a depth of 39 ± 2 cm, and pH is moderate, 6.5 ± 0.1 . There is no evidence of cryoturbation, and microrelief is moderate, with a height of 13 ± 3 cm. Soils are mainly Pergelic facies within Stand Type *Salix rotundifolia* - *Dryas integrifolia*, related to moisture and disturbance gradients. Thaw is shallow, with a depth of 39 ± 2 cm, and pH is moderate, 6.5 ± 0.1 . There is no evidence of cryoturbation, and microrelief is moderate, with a height of 13 ± 3 cm. Soils are mainly Pergelic Cryaquolls, but Pergelic Cryoborolls, Calcic Pergelic Cryoborolls, Cumulic Pergelic Cryoborolls, Pergelic Cryochrepts, Pergelic Cryumbrepts, Pergelic Cryaquepts, Histic Pergelic Cryaquepts,



Figure 48. Stand Type *Salix rotundifolia* - *Dryas integrifolia*.

This stand type appears to fit within Cooper's (1986) provisional Polygono vivipari - Salicion rotundifoliae. It is equivalent to Walker's (1985) Moist *Salix rotundifolia*, *Equisetum scirpoides* dwarf shrub tundra. *Salix rotundifolia* types have been described from many sites in Alaska (Clebsch 1957; Shacklette 1969; Anderson 1974; Komárková and Webber 1976; Webber 1978; Racine and Anderson 1979; Viereck et al. 1986). *Salix rotundifolia* is a Beringian endemic limited primarily to Alaska; it is known from only a few localities in eastern Siberia, including Wrangel Island (Petrovsky 1967; Hultén 1968; Aleksandrova 1980). *Salix rotundifolia* types are related to Salicetalia herbacea (Nordhagen 1943) in Scandinavia, which has a similar growth habit.

Facies *Salix rotundifolia* - *Oxycia*

mineral soils that are disturbed by solifluction and lemming burrows (Fig. 49). Other important species in this facies include *Trisetum spicatum*, *Lloydia serotina*, and *Petasites frigidus*. Slopes are fairly steep, $19 \pm 2^\circ$, and since they are also leeward, these sites are some of the most protected from wind, and probably the most deeply covered by snow. Thaw is moderately deep (52 ± 12 cm) due to the well-drained mineral soils. Instability values were the highest of any group (3 ± 0.2 on a 4 point scale), but soils were not cryoturbated. The importance of solifluction is reflected by a great amount of microrelief, 24 ± 13 cm. Soil pH is low, 6.3 ± 0.4 . Soil type is variable, depending on the exact site, and includes Pergelic Cryoboroll, Calcic Pergelic Cryoboroll, Pergelic Cryaquoll, Pergelic Cryumbrept, and Pergelic Cryaquept.

***Oxycia diurna* is a circumpolar ar-**

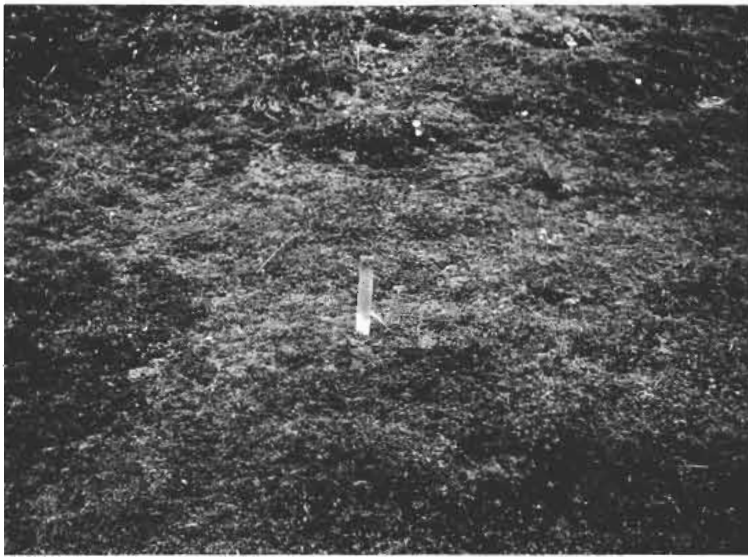


Figure 49. *Facies Salix rotundifolia - Oxyria digyna*.

1968; Aleksandrova 1980). On the pingos, and in the Prudhoe Bay region generally (Walker 1985a), it is limited to these unstable sites on mineral soil. Batten (1977) describes its habitat in the northern Brooks Range as "...gravelly seepy areas on slopes." Cooper (1986) lists it as diagnostic for Polygono vivipari - Salicion rotundifoliae. It is associated with late-melting snow patches on mineral soils in many arctic and alpine areas of the world (Komárková 1979; Aleksandrova 1980).

Facies *Salix rotundifolia* - *Eriophorum triste* is on more stable sites with gentle slopes, less drainage, and more part - Salicion rotundifoliae. It is associated with late-melting snow patches on mineral soils in many arctic and alpine areas of the world (Komárková 1979; Aleksandrova 1980).

Facies *Salix rotundifolia* - *Eriophorum triste* is on more stable sites with gentle slopes, less drainage, and more wet, organic-rich (but still mineral) soils (Fig. 50). Other important vascular species include *Equisetum scirpoides*, *Equisetum variegatum*, *Pedicularis*

few places where hepatics are regularly found, and some of the common ones are *Anastrophyllum minutum*, *Blepharostoma trichophyllum*, and *Ptilidium ciliare*. *Eriophorum vaginatum*, which is dominant over most acidic areas of the coastal plain, may be found in this facies in the more acidic areas. These are some of the least deeply thawed sites, only 37 ± 2 cm. They are not cryoturbated, and micro-relief is only moderate, 9 ± 0.8 cm. The pH is fairly alkaline, 6.6 ± 0.1 . Soils are primarily Pergelic Cryaquolls, Histic Pergelic Cryaquepts, and Pergelic Cryaquepts, but there are scattered occurrences of Pergelic Cryoborolls, Cumulic Pergelic Cryoborolls, Pergelic of the least deeply thawed sites, only 37 ± 2 cm. They are not cryoturbated, and micro-relief is only moderate, 9 ± 0.8 cm. The pH is fairly alkaline, 6.6 ± 0.1 . Soils are primarily Pergelic Cryaquolls, Histic Pergelic Cryaquepts, and Pergelic Cryaquepts, but there are scattered occurrences of Pergelic Cryoborolls, Cumulic Pergelic Cryoborolls, Pergelic Cryochrepts, Pergelic Cryumbrepts, and Pergelic Cryorthents.

This facies represents the best expression of Walker's (1985a) Moist *Salix*

a



b



b



Figure 50. *Facies Salix rotundifolia - Eriophorum triste*. General site aspect (a) and close-up of vegetation (b).



Figure 51. Stand Type *Cassiope tetragona* - *Dryas integrifolia*.

Eriophorum angustifolium (includes *E. triste* and *E. angustifolium* ssp. *subarcticum*), *Dryas integrifolia*, *Tomenthypnum nitens*, *Thamnolia subuliformis* sedge, dwarf shrub tundra. *Eriophorum triste* is abundant in mesic upland tundra at Prudhoe Bay; it is a high arctic species that extends south into the boreal forest, and it is not found in the alpine.

Stand Type *Cassiope tetragona* - *Dryas integrifolia*. This is the most complex stand type, and it contains considerable floristic and microsite variability (Fig. 51). It contains 55 stands boreal forest, and it is not found in the alpine.

Stand Type *Cassiope tetragona* - *Dryas integrifolia*. This is the most complex stand type, and it contains considerable floristic and microsite variability (Fig. 51). It contains 55 stands united as a single type by the presence of both type species. Other differentiating species for this stand type are *Hylocomium splendens*, *Peltigera aphthosa*, and *Minuartia arctica*. There are 25

nation of a temperature and acidity gradient within the stand type. Compared to the circumpolar vegetation, this would be a calcareous type, as evidenced by the importance of *Dryas integrifolia*. Slopes are moderate to steep, $12 \pm 1^\circ$, and microrelief is well developed, with a height of 21 ± 2 cm. Microrelief is expressed as a series of evenly-spaced, relatively homogeneous hummocks. *Dryas integrifolia* is mainly on the hummocks, and *Cassiope tetragona* is on both hummock and inter-hummock areas. Foliose lichens, mainly *Cetraria* spp. and *Dactylina* spp., are in the inter-hummock sites. as a series of evenly-spaced, relatively homogeneous hummocks. *Dryas integrifolia* is mainly on the hummocks, and *Cassiope tetragona* is on both hummock and inter-hummock areas. Foliose lichens, mainly *Cetraria* spp. and *Dactylina* spp., are in the inter-hummock sites.

The origin of these hummocks is not well understood. Everett (1980a) attributed them to erosion following snow melt, a rapid event that would be difficult to observe and document. Their origin is

about 1 to 3 m across are common as these slopes steepen during the first phases of pingo formation. These subsequently break up into smaller pieces, and shrubs, such as *Dryas integrifolia*, *Cassiope tetragona*, and *Salix* spp., persist on the colluviated ground. Subsequent erosion between these shrubs intensifies the hummocky terrain. Soils are generally fairly organic on the hummocks, but are mineral between hummocks. The most common type is Pergelic Cryoboroll, but all except three of the soil types described from the pingos may be associated with this stand type.

Vegetation dominated by *Dryas* and *Cassiope* has been described from snowbeds throughout the arctic (Sochava 1934; Gorodkov 1944; Polunin 1948; Porsild 1951; Böcher 1954; Churchill 1955; Holmen 1957; Svoboda 1972, 1973, 1977; Pospelova 1974; Aleksandrova 1980). *Cassiope* tundras are particularly well developed on Spitsbergen (Summerhayes and Elton 1923), although there is no *Dryas integrifolia* there, only *Dryas octopetala*. On the pingos, *Cassiope tetragona* reaches its peak in the more alkaline sites, although these microsites are acidic when compared with the drier pingo microsites.

Cooper (1986) proposed the provisional alliance *Cassiope tetragonae* - *Dryadion alaskensis* in a provisional order of the same name. The diagnostic species for the alliance are all found within this stand type as it is defined here (with the exception of *Campylium halleri*, the other pingo microsites).

Cooper (1986) proposed the provisional alliance *Cassiope tetragonae* - *Dryadion alaskensis* in a provisional order of the same name. The diagnostic species for the alliance are all found within this stand type as it is defined here (with the exception of *Campylium halleri*, which was not found in this study). The major difference is again the presence of *Dryas octopetala* rather than *Dryas integrifolia*. Others have classified *Dryas* - *Cassiope* tundras somewhat differently.

tain associations into Kobresieto - *Dryadion*, while Rønning (1965) placed the Spitsbergen association *Tetragona Dryadetum* in *Dryadion*.

Subtype *Vaccinium uliginosum* - *Salix glauca*. This subtype is found only in the Toolik River and Kadleroshilik study areas, and is dependent on the warm temperatures present in those sites. It is characterized by the presence of *Vaccinium uliginosum* and usually also *Salix glauca* (Fig. 52). *Salix glauca* is generally not dominant in most stands, and is often less than 20 cm high. In a few stands, however, it is erect and over 50 cm tall. There is only one additional differentiating species, *Aulacomnium acuminatum*, and the two facies within the type are distinct and related to soil acidity. Slopes are moderate, $11 \pm 1^\circ$, and microrelief height is typical for this stand type, 23 ± 4 cm. Mean pH is 6.0 ± 0.2 . Eight different soil types were recognized, and the most common are Pergelic Cryosaprist and Histic Pergelic Cryaquept.

Vaccinium uliginosum is a characteristic species of the ericaceous tundras often associated with snow patches throughout the circumpolar region (Aleksandrova 1980). It is rare at Prudhoe Bay (Walker 1985a), but quite common south of there (Walker and Acevedo 1987). This subgroup has many similarities to Cooper's Carici scirpoideae - *Vaccinietum uliginosi*, again with the major difference being the *Dryas* spe- throughout the circumpolar region (Aleksandrova 1980). It is rare at Prudhoe Bay (Walker 1985a), but quite common south of there (Walker and Acevedo 1987). This subgroup has many similarities to Cooper's Carici scirpoideae - *Vaccinietum uliginosi*, again with the major difference being the *Dryas* species.

Facies *Ledum decumbens* - *Betula nana* is the more acidic of the two facies within this subtype (Fig. 53). It is found



Figure 52. Subtype *Vaccinium uliginosum* - *Salix glauca*.

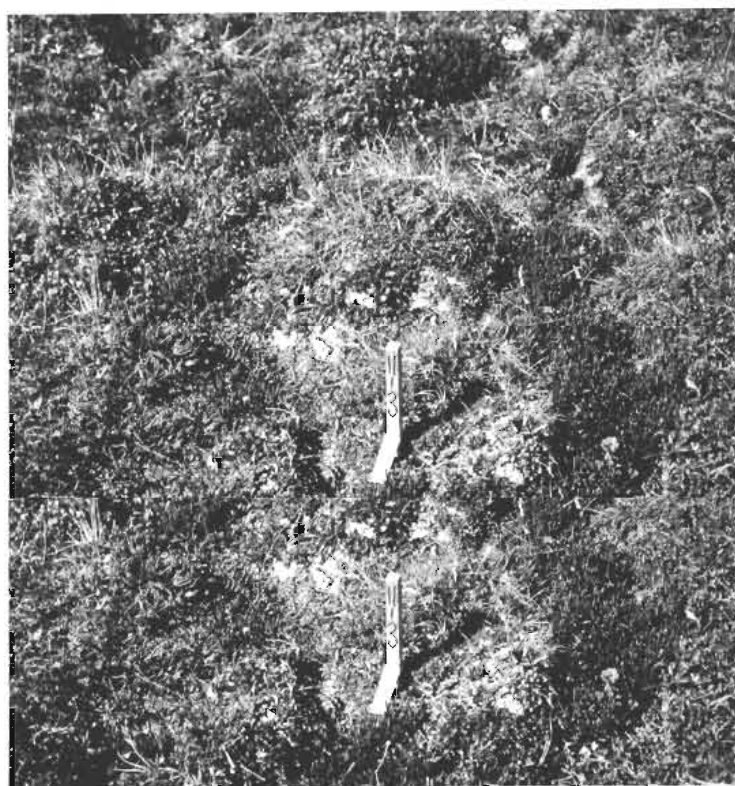


Figure 53. Facies *Ledum decumbens* - *Betula nana*.

Dryas integrifolia is of minimal importance, but was present in all stands surveyed. Other differentiating species include *Saxifragapunctata*, *Pyrola grandiflora*, and *Polytrichum juniperinum*. In the most acidic sites *Vaccinium vitis-idaea* and *Empetrum nigrum* are present. At a few sites, none of which were sampled, *Sphagnum warnstorffii* was the dominant moss species. Two sites included within this facies are actually from south slopes rather than leeward sides. These were the areas with the tallest *Salix glauca* individuals; they were on the lower part of the slope, and are probably covered by snow all winter. This combination of winter snow protection combined with warm summer temperatures allows for the very robust and upright growth of these shrubs. Mean slope is $16 \pm 3^\circ$. These areas often had relatively high amounts of cryoturbation evident, with as much as 45% coverage of cryoturbated ground. Microrelief is very well developed, with a height of 38 ± 8 cm. Mean pH is 4.8 ± 0.3 , and the lowest pH measured, 3.8, was within this type. Soils are Histic Pergelic Cryaquepts, Pergelic Cryaquepts, Pergelic Cryorthents, or Pergelic Cryumbrept.

This type is similar to Walker et al.'s (1987) Community Type *Betula nana* - *Rubus chamaemorus*, and Cooper's (1986) *Betulo glandulosae* - *Alnetum crispae*, but in both cases differs with one or more dominant species. Lambert's (1968) *Betulo* - *Ledetum decumbentis* is

This type is similar to Walker et al.'s (1987) Community Type *Betula nana* - *Rubus chamaemorus*, and Cooper's (1986) *Betulo glandulosae* - *Alnetum crispae*, but in both cases differs with one or more dominant species. Lambert's (1968) *Betulo* - *Ledetum decumbentis* is also similar, but is a much taller shrub type than on the pingos, and is dominated by *Betula glandulosa* rather than *B. nana*.

with *Vaccinium uliginosum* and *Salix glauca* in the more alkaline Toolik River area (Fig. 54). Coverage by *Arctous rubra* is variable, but may be as high as 40%. *Dryas integrifolia* is a codominant, with cover values ranging from 10 to 35%. Other differentiating species are *Anemone parviflora* and *Hedysarum alpinum* ssp. *americanum*. *Lupinus arcticus* is frequently present and very conspicuous. Slopes are gentle ($8 \pm 1^\circ$) and appear stable. Microrelief height is 15 ± 2 cm, and mean pH is 6.6 ± 0.1 , which is high for a snowbed site.

This type is similar to Walker et al.'s (1987) community type *Vaccinium uliginosum* - *Arctous alpina*, the primary difference being the presence of *Arctous alpina* rather than *Arctous rubra* on the pingos. Generally, *Arctous rubra* is more of a coastal plain species, while *Arctous alpina* is more common in alpine areas (Hultén 1968), although they may occur together (Batten 1977). This community has connections to Lambert's (1968) *Lupino* - *Dryadetum alaskensis* and Cooper's (1968) *Carici scirpoidae* - *Vaccinietum uliginosi*. Porsild (1951) described communities in northwestern Canada with *Betula glandulosa*, *Ledum decumbens*, *Rhododendron lapponicum*, *Arctous alpina*, *Cassiope tetragona*, *Vaccinium uliginosum*, and *Vaccinium vitis-idaea*, and Polunin (1948) described similar types in Labrador. The separation of *Betula* sp. and *Ledum decumbens* from *Arctous* sp. and *Rhododendron lapponicum* was not evident in those sites. Sørensen (1937) described a *Vaccinium uliginosum*, *Rhododendron lapponicum*, *Salix arctica* community from Greenland.



Figure 54. *Facies* Arctous rubra - *Rhododendron lapponicum*.

Vaccinium uliginosum - *Salix glauca*. It is found primarily at the Prudhoe Bay and Kuparuk study areas, although two stands from Kadleroshilik were also assigned to it. There are three differentiating species, *Polytrichastrum alpinum*, *Hypnum procerrimum*, and *Cetraria laevigata*, but the *facies* is defined primarily by the absence of *Vaccinium uliginosum* and the increased importance of *Cassiope tetragona* (Fig. 55). Coverage of *Cassiope tetragona* may be as high as 40% in this type, and is always at least 10%, whereas its range in other *facies* within this stand type is only 0.3 to 35%. Coverage of *Dryas integrifolia* ranges from 10 to 55%. This *facies* is the equivalent of Walker's (1985a) Dry *Dryas integrifolia*, *Cassiope tetragona*, *Cetraria nivalis* dwarf shrub,

$\pm 2^\circ$, and thaw is fairly deep, 52 ± 5 cm. Hummocks are always present, and their mean height is 18 ± 4 cm. Mean pH is 6.4 ± 0.2 . Soils are mainly Pergelic Cryoborolls, although Calcic Pergelic Cryoborolls, Pergelic Cryaquolls, Pergelic Cryumbrepts, Pergelic Cryaquepts, and Pergelic Cryorthents were also noted.

Stand Type *Dryas integrifolia* - *Astragalus umbellatus* - *Carex rupestris*. This type is included within this group as a snowbed type, but it includes some sites that may be above the snowbank and snow-free most of the year (Fig. 56). *Dryas integrifolia* is dominant in all cases, with cover ranging from 30 to 75%, but *Tomenthypnum nitens* is of less impor-

Stand Type *Dryas integrifolia* - *Astragalus umbellatus* - *Carex rupestris*. This type is included within this group as a snowbed type, but it includes some sites that may be above the snowbank and snow-free most of the year (Fig. 56). *Dryas integrifolia* is dominant in all cases, with cover ranging from 30 to 75%, but *Tomenthypnum nitens* is of less importance in these sites, usually with only a few percent cover. *Astragalus umbella-*

a



b



b



Figure 55. *Facies* Cassiope tetragona - *Dryas integrifolia*. General site aspect (a) and close-up of vegetation (b).



Figure 56. Stand Type *Dryas integrifolia* - *Astragalus umbellatus* - *Carex rupestris*.

common. Of the four differentiating species, three are lichens: *Hypogymnia subobscura*, *Ochrolechia frigida*, and *Cornicularia divergens*. There is minimal cryoturbation, and microrelief height is variable, with a mean of 21 ± 2 cm. Mean pH is alkaline, $6.9 \pm .05$. Soils are mainly Pergelic Cryoborolls, but Calcic Pergelic Cryoborolls, Pergelic Cryaquolls, Pergelic Cryochrept, Calcic Pergelic Cryochrepts, Histic Pergelic Cryaquepts, and Pergelic Cryorthents were also present.

A similar type is also known from Point Barrow (Wiggins and Thomas 1962), where it is found on beach terraces. The brightly colored *Astragalus* gives the community its distinctive appearance, but when this is not flowering it has a similar appearance to *Dryas octopetala* ssp. *hookeriana* - *Carex*

Komárková 1979). It is also related to Cooper's (1986) *Pedicularis kanei* - *Dryadion octopetalae*.

Facies *Dryas integrifolia* - *Astragalus umbellatus* - *Kobresia myosuroides* is limited to the Toolik River area and to a single pingo in the Kuparuk area. Differentiating species other than *Kobresia myosuroides* are *Oxytropis jordallii*, *Alectoria nigricans*, and *Ochrolechia upsaliensis* (Fig. 57). There are no associated species. These sites appear to be slightly more moist and have somewhat more organic soils than other sites within the stand type. Mean slope is $12 \pm 1^\circ$, and soils are stable, with little evidence of cryoturbation or movement. Microrelief is moderate, 16 ± 2 cm. The pH is high, $7.0 \pm .05$. Soils are variable, and include all types found within the stand



Figure 57. Facies *Dryas integrifolia* - *Astragalus umbellatus* - *Kobresia myosuroides*.



Figure 58. Facies *Carex rupestris* - *Oxytropis nigrescens*.

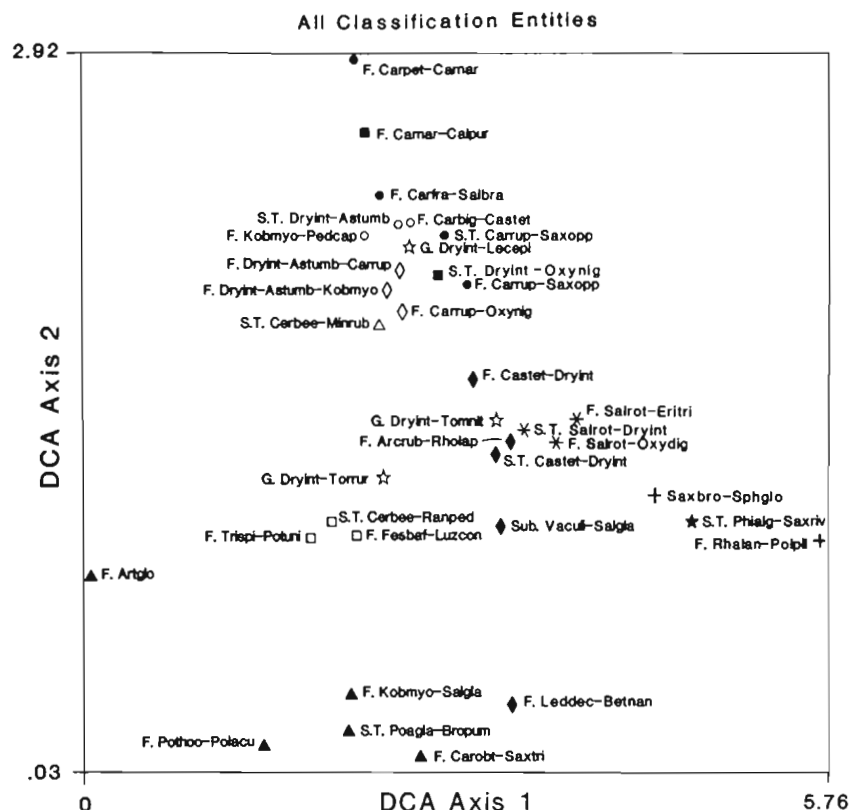


Figure 59. Simultaneous ordination of all groups, stand types, and facies. Input was mean percent cover for all species that occurred anywhere in an entity. Stand types and their associated facies are given the same symbol. Group positions are represented by an empty star. See tables 19 to 21 for abbreviations.

Other differentiating species are *Fistulariella almqvistii* and *Dicranum elongatum*. This type grades into Stand Type *Dryas integrifolia* - *Oxytropis nigrescens*, but has more coverage by *Carex rupestris* and *Dryas integrifolia*.

Other differentiating species are *Fistulariella almqvistii* and *Dicranum elongatum*. This type grades into Stand Type *Dryas integrifolia* - *Oxytropis nigrescens*, but has more coverage by *Carex rupestris* and *Dryas integrifolia* than that type, and less coverage by *Oxytropis nigrescens*. Slopes are gentle, $8 \pm 1^\circ$, and microrelief is often well developed, with a height of 22 ± 5 cm. Mean pH is 6.8 ± 0.1 . Soils are primarily Pergelic Cryoborolls, but include the other types found within the stand type.

Relationships Between Classification Entities

When all of the entities are ordinated simultaneously, there is a considerable amount of gradation between the classi-

Relationships Between Classification Entities

When all of the entities are ordinated simultaneously, there is a considerable amount of gradation between the classification units at the level of stand type and facies (Fig. 59). Nevertheless, three major groups appear. There are several outliers including Facies *Carex petri-cosa* - *Carex nardina*, Facies *Artemisia glomerata*, Stand Type *Saxifraga bronchialis* - *Sphaerophorus globosus*, and

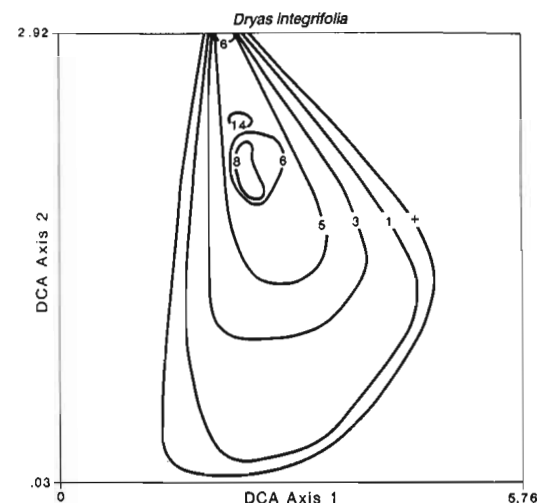


Figure 60. Isoline diagram of the coverage of *Dryas integrifolia* within the ordination of the groups, stand types, and facies.

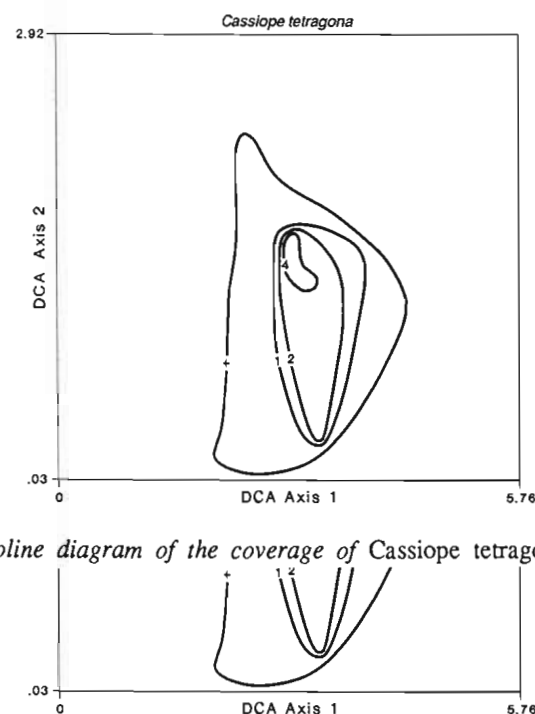


Figure 61. Isoline diagram of the coverage of *Cassiope tetragona* within the

Figure 61. Isoline diagram of the coverage of *Cassiope tetragona* within the ordination of the groups, stand types, and facies.

Stand Type *Phippsia algida* - *Saxifraga rivularis*. Isoline diagrams of the coverage of *Dryas integrifolia*, *Cassiope tetragona*, and *Tomenthypnum nitens* within this ordination space illustrate the

role of these three species in the ordination (Figs. 60 to 62, respectively). Outlying plots are primarily outside the range of *Dryas integrifolia*. *Cassiope tetragona* and *Tomenthypnum nitens* have similar

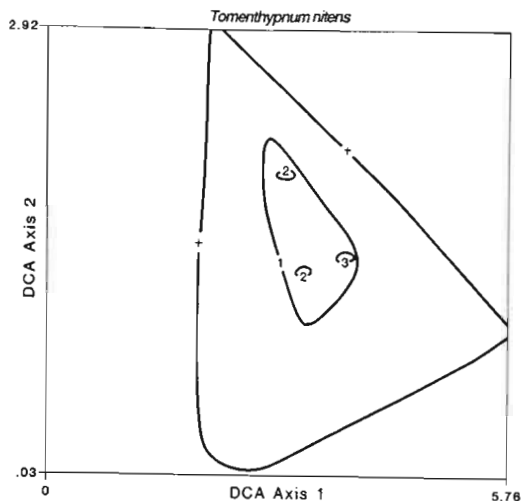


Figure 62. Isoline diagram of the coverage of *Tomenthypnum nitens* within the ordination of the groups, stand types, and facies.

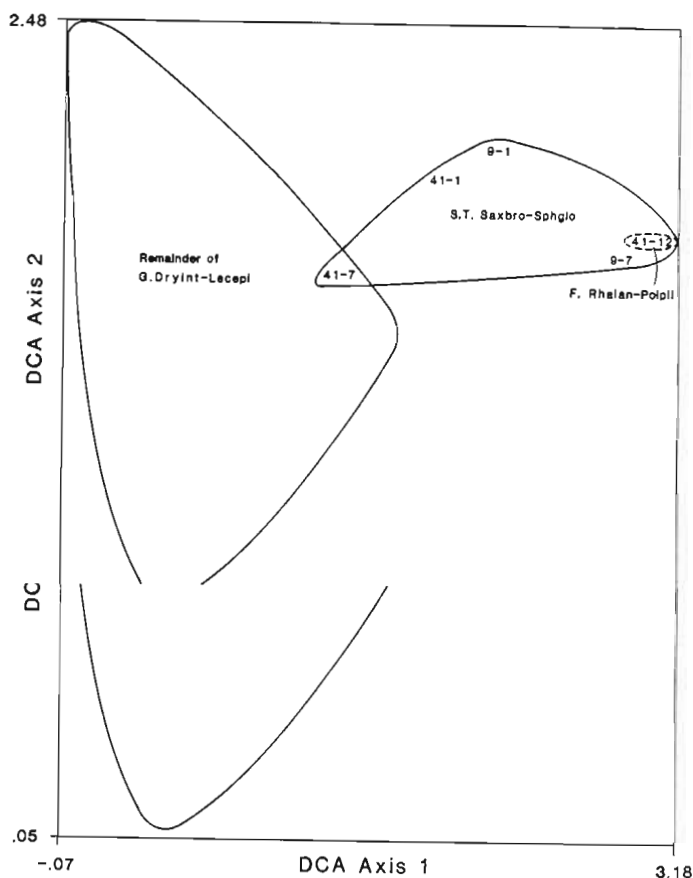


Figure 63. Ordination of Group *Dryas integrifolia* - *Lecanora epibryon* showing the position of Stand Type *Saxifraga bronchialis* - *Sphaerophorus globosus* relative to the rest of the group. Facies *Rhacomitrium lanuginosum* - *Polytrichum piliferum* is

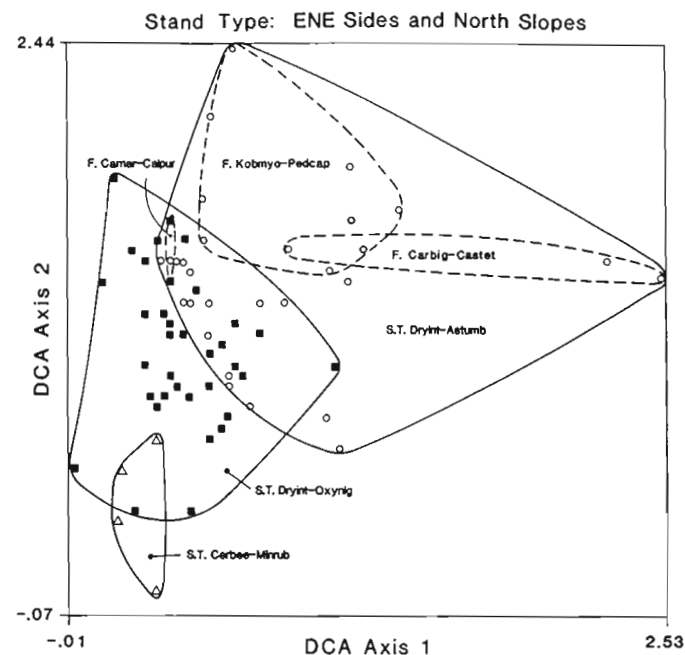


Figure 64. Ordination of stand types and facies within Group *Dryas integrifolia* - *Lecanora epibryon* without Stand Type *Saxifraga bronchialis* - *Sphaerophorus globosus*. Plots within stand types are enclosed by a solid line, within facies by a dashed line. Each stand type is represented by a unique symbol.

distributions, as both are primarily found in snowbeds, but *T. nitens* has a broader amplitude than *C. tetragona*.

Within Group *Dryas integrifolia* - *Lecanora epibryon*, Stand Type *Saxifraga bronchialis* - *Sphaerophorus globosus* is sufficiently different that when these stands and facies are ordinated, this stand type has as much floristic variation within it as the remaining stand types and facies within this group have

Lecanora epibryon, Stand Type *Saxifraga bronchialis* - *Sphaerophorus globosus* is sufficiently different that when these stands and facies are ordinated, this stand type has as much floristic variation within it as the remaining stand types and facies within this group have between them (Fig. 63). The stand types are best separated along the first two axes in all cases, so here and in the following examples only the first two axes are shown. The first ordination gradient is relatively long (3.2 SDs). In

order to demonstrate better the relationships between the remaining stand types in this group, a second ordination was done without Stand Type *Saxifraga bronchialis* - *Sphaerophorus globosus* (Fig. 64). The stand types are fairly well-defined, although there are gradations between them, which is expected. Stand Type *Cerastium beeringianum* - *Minuartia rubella*, which is mainly an extreme coastal type, grades into Stand Type *Dryas integrifolia* - *Oxytropis nigrescens*, which is common in dry tundra in the Prudhoe Bay region generally. Facies *Carex nardina* - *Calamagrostis purpurascens*, which is mainly found at Toolik River, is related to Facies

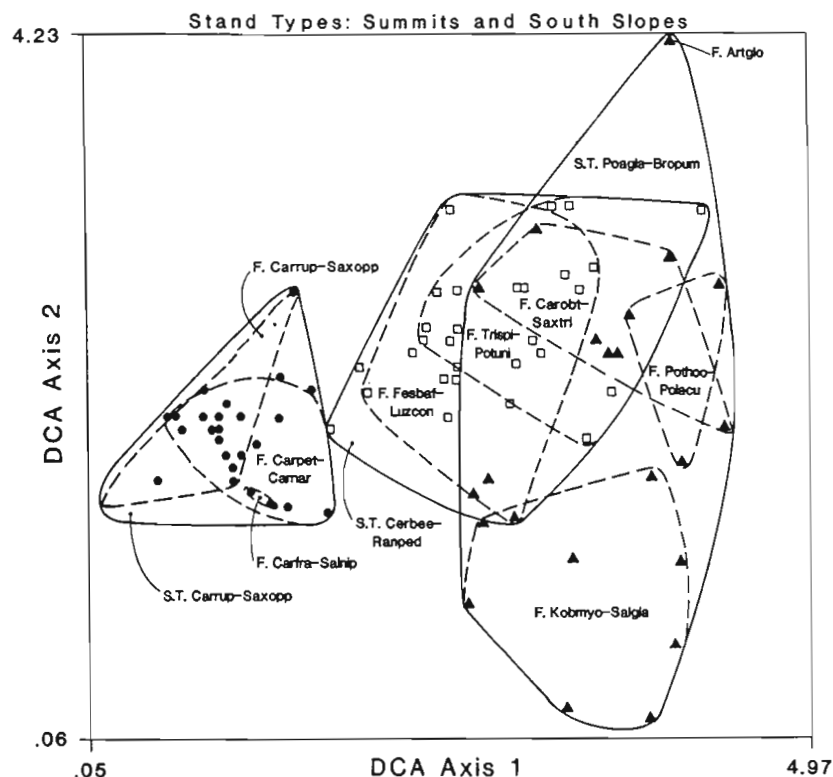


Figure 65. Ordination of stand types and facies within Group *Dryas integrifolia* - *Tortula ruralis*. Plots within stand types are enclosed by a solid line, within facies by a dashed line. Each stand type is marked by a unique symbol.

Kobresia myosuroides - *Pedicularis capitata* in Stand Type *Dryas integrifolia* - *Astragalus umbellatus*. Facies *Carex bigelowii* - *Cassiope tetragona*, which is probably ecotonal with snowbed types, is an outlier.

Group *Dryas integrifolia* - *Tortula ruralis* has much more complex relationships between the stand types (Fig. 65). This group has more floristic variation within it (first ordination axis of 5.0 SDs) than does Group *Dryas integrifolia* - *Lecanora epibryon*. Stand Type *Carex*

not intergrade with other stand types at all. Stand Type *Cerastium beeringianum* - *Ranunculus pedatifidus* and Stand Type *Poa glauca* - *Bromus pumpellianus*, however, have considerable overlap, and there is a gradual gradation between them. The various steppe types do not form a recognizable grouping. not intergrade with other stand types at all. Stand Type *Cerastium beeringianum* - *Ranunculus pedatifidus* and Stand Type *Poa glauca* - *Bromus pumpellianus*, however, have considerable overlap, and there is a gradual gradation between them. The various steppe types do not form a recognizable grouping.

Stand Type *Phippsia algida* - *Saxifraga rivularis* is sufficiently different from stands in Group *Dryas integrifolia* - *Tomenthypnum nitens* that the DECO-RANA program was unable to construct

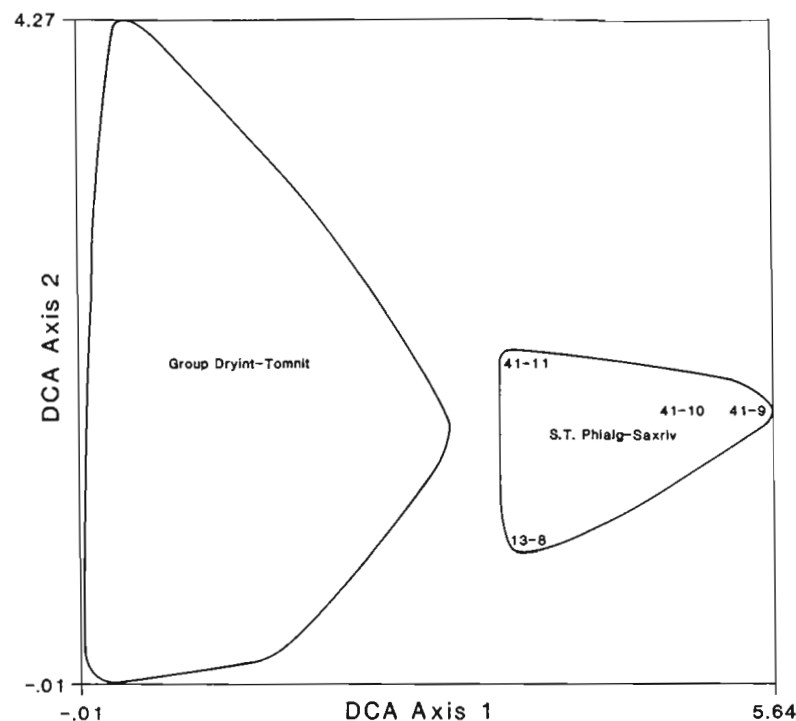


Figure 66. Ordination of Group *Dryas integrifolia* - *Tomenthypnum nitens* relative to Stand Type *Phippsia algida* - *Saxifraga rivularis*.

is a gap within the ordination (Fig. 66). This gap supports the separation of this stand type as separate from the group.

Ordination of the remaining snowbed plots shows the three stand types are well-defined, with minimal overlap (Fig. 67). Within Stand Type *Cassiope tetragona* - *Dryas integrifolia* the facies are well-defined, and may represent good associations. Facies *Ledum decumbens* - *Betula nana* and Facies *Arctous rubra*

Ordination of the remaining snowbed plots shows the three stand types are well-defined, with minimal overlap (Fig. 67). Within Stand Type *Cassiope tetragona* - *Dryas integrifolia* the facies are well-defined, and may represent good associations. Facies *Ledum decumbens* - *Betula nana* and Facies *Arctous rubra* - *Rhododendron lapponicum* do not overlap at all. Nevertheless, they have been retained as a subgroup because many of their differentiating species occur together in other arctic areas

Wildlife on Pingos

Because there are no data available on the use of pingos by wildlife, and because animals may have a profound influence on the vegetation and soils of the pingos, notes of vertebrate animal observations were kept (Table 22). These were in addition to the scalar estimates of use within each relevé. Twelve species of birds, eight mammals, and one fish, in a small pond on top of pingo no. 33 in the Kuparuk area, were observed. The pingos are used by wildlife throughout the year, although in winter the number of species using these areas is

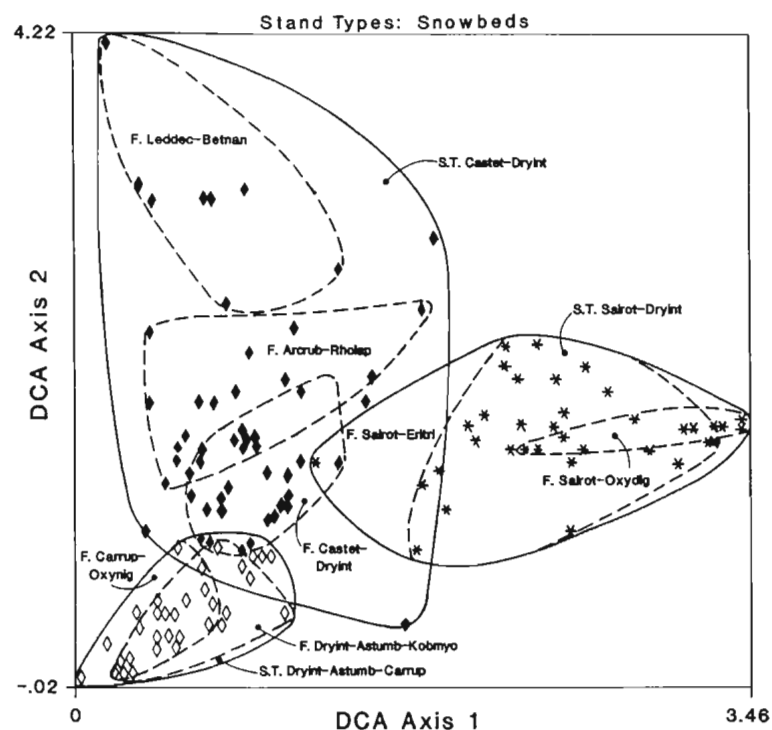


Figure 67. Ordination of stand types and facies within Group *Dryas integrifolia* - *Tomenthypnum nitens*. Stand types are enclosed within solid lines, facies within dashed lines. Each stand type is represented by a unique symbol.

1986, when snow measurements were made on the pingos, several groups of caribou were observed feeding in snow-free areas on the pingos. Snow depths at that time were approximately 40 cm over much of the landscape, and pingos were the only snow-free areas. It is likely they caribou were observed feeding in snow-free areas on the pingos. Snow depths at that time were approximately 40 cm over much of the landscape, and pingos were the only snow-free areas. It is likely they are important winter habitat for the small herd of caribou that remains in the region all year.

Pingos are frequent den sites for arctic ground squirrel (*Spermophilus parryi*), arctic fox (*Alopex lagopus*), and collared lemming (*Dicrostonyx groenlandicus*) (Feist 1975; Underwood 1975; personal

observation). Most pingos at least 3 to 4 m high have one or more arctic ground squirrel colonies on them; most also have a fox den. The lower snowbank areas have abundant lemming nests; a brief search of these areas often reveals multiple nests spaced 1 to 4 m apart. There is also abundant sign of ptarmigan (*Lagopus lagopus*) in these sites. The interaction of the wildlife with the pingo soils and vegetation has a profound effect on the ecology of these sites. The Pacific Pergelic Cryoborolls described from the pingo summits apparently have a genesis due to the animals' presence.

Table 22. Number of animal observations and sign on 30 pingos in July and August, 1984.¹

Species	Direct Observation ²	MAMMALS			
		Active Den or Nest	Scat	Bones or Antlers	Other
Arctic Fox (<i>Alopex lagopus</i>)	3	5	20	5	-
Arctic ground squirrel (<i>Spermophilus parryi</i>)	9	28	28	4	1 ³
Caribou (<i>Rangifer tarandus granti</i>)	5	-	29	4	-
Grizzly bear (<i>Ursus horribilis</i>)	-	-	2	-	15 ⁴
Collared lemming (<i>Dicrostonyx groenlandicus</i>)	1	8	28	-	28 ⁵
Least weasel (<i>Mustela rixosa</i>)	-	-	-	1 ⁶	-
Wolf (<i>Canis lupus</i>)	-	-	2	-	-
BIRDS					
Common Redpoll (<i>Acanthis hornemanni</i>)	2	-	-	-	-
Golden eagle (<i>Aquila chrysaetos</i>)	1	-	-	-	6 ⁷
Golden plover (<i>Pluvialis dominica</i>)	5	1	-	-	-
Goose (<i>Branta</i> sp.)	-	1	5	-	-
Lapland longspur (<i>Calcarius lapponicus</i>)	18	-	-	-	-
Long-tailed jaeger (<i>Stercorarius longicaudus</i>)	4	-	-	-	-
Parasitic jaeger (<i>S. parasiticus</i>)	1	-	-	-	-
Ptarmigan (<i>Lagopus</i> sp.)	2	-	22	-	-
Raptors ⁸	-	-	1	-	14 ⁹
Tree sparrow (<i>Spizella arborea</i>)	2	-	-	-	-
Northern wheatear (<i>Oenanthe oenanthe</i>)	1	-	-	-	-
Yellow wagtail (<i>Motacilla flava</i>)	2	-	-	-	-
FISH					
Fourhorn sculpin ¹⁰ (<i>Myoxocephalus quadricornis</i>)	1	-	-	-	-
FISH					
Fourhorn sculpin ¹⁰ (<i>Myoxocephalus quadricornis</i>)	1	-	-	-	-

¹ (*Motacilla flava*)
² Indicates number of pingos on which observations were made, not necessarily number of animals present.
³ Inactive den.
⁴ Craters from squirrel burrow excavations.
⁵ Burrows and runways.
⁶ Skull.
⁷ Feathers or excrement.
⁸ May include species of eagle, hawk, falcon, and owl.
⁹ Regurgitated pellets in all cases, also feathers in some.
¹⁰ In a small pond on top of pingo no. 33, near Oliktok Pt.



Figure 68. Mammals and birds that use pingos in winter. (Illustrations are from Burt and Grossenheider [1976] and Robbins et al. [1983].)

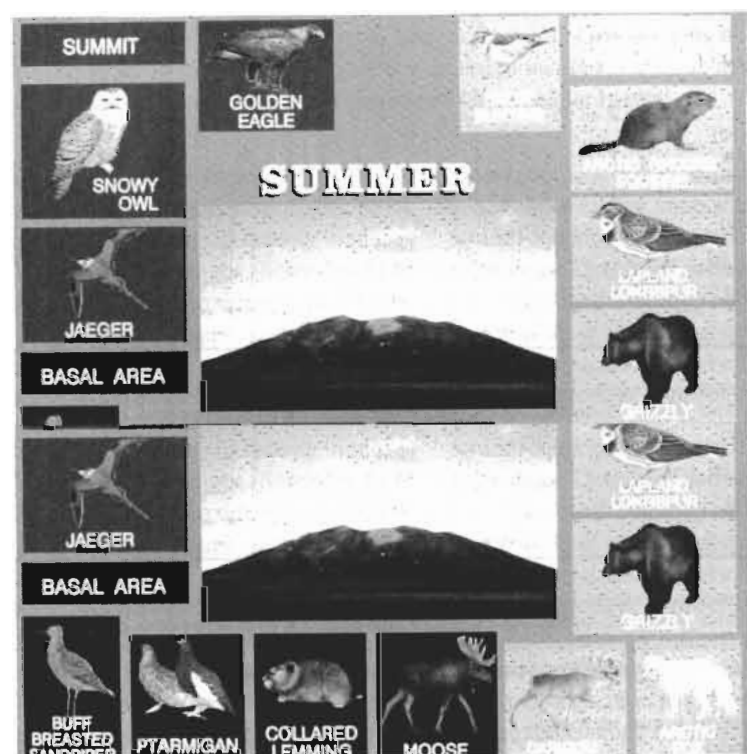


Figure 69. Mammals and birds that use pingos in summer. (Illustrations are from Burt and Grossenheider [1976] and Robbins et al. [1983].)



Figure 70. Crater left by grizzly bear (*Ursus horribilis*) on pingo no. 7 (Beny). Bears were particularly active in this area which is less than a kilometer from the Toolik River, a major corridor for bear movement. (Photograph by D.A. Walker.)

Many years of digging by squirrels and foxes mixes organics that were present in the lake basin into the soil subhorizons, and the result is an overthickened mollic epipedon with a zoogenic origin. The small mammals and birds attract predators to the pingos. Grizzly bears (*Ursus horribilis*) leave large craters in the pingos where they dig for squirrels (Fig. 70). Several fairly significant bear disturbances involving areas as large as 12 to 15 m² were observed in 1986. While this is not a great extent, the cumulative effect of downslope soil movement by bears over centuries or millennia is likely significant.

The high amount of interaction between wildlife and the pingo landscape, as well as the interactions between wildlife species, led to the development of the term 'landscape focal points'. Walker and Walker (1987) defined a landscape

focal point as an environmental resource patch (in the sense of Forman and Godron 1986) characterized by high species richness and interaction, with this interaction critical to landscape function. A landscape focal point is a concentrated center of species diversity, and may also attract frequent human attention. The exact role of the pingos in landscape function has never been studied. These are only preliminary data based on observation, but they suggest high enough concentrations of wildlife on pingos to merit further study. The invertebrates have not been studied at all, and this could potentially be an important aspect of the pingo ecosystem. The Coleopteran, Hymenopteran, and soil invertebrate faunas, in particular, would be important aspects of the steppe-tundra ecosystem that has been proposed.

Environmental Gradients

This section describes the primary gradient complexes that relate to the vegetation and flora of the pingos on two levels: (1) the landscape level, looking at changes in flora, and (2) the microsite level, looking at how more important gradients may change between the various microsites. The term environmental gradient is a shortening of Whittaker's (1970) term complex-environmental-gradient, which conveys the idea that the environmental factors on which species are dependent are not independent of one another, but covary, and that species response can be related to this complex of interacting factors. Dependence on any single factor is difficult or impossible to demonstrate unless controlled experiments are designed specifically for that purpose. An example of this on the Arctic Coastal Plain is the soil moisture gradient, where minor changes in soil moisture lead to major changes in species composition (Peterson 1978; Walker 1985a). Soil moisture is highly correlated with soil organic content and nutrient availability. The species composition changes associated with soil moisture are a reflection of the entire complex of gradients. The indirect gradient analyses presented here are based on correlations of environmental variables with the ordination axes. It is necessary to realize that while these complex of gradients. The indirect gradient analyses presented here are based on correlations of environmental variables with the ordination axes. It is necessary to realize that while these gradients are referred to be the name of the most highly correlated environmental variable, they are in fact complex gradients.

Landscape-Level Gradients

Floras of the pingos show distinct regional trends, with the Kadleroshilik

area being the most distinct (Fig. 71). There is some overlap between the Prudhoe Bay and Kuparuk regions, which are the closest spatially. The first ordination axis is 1.37 SD units long, indicating considerable floristic similarity between the regions. Distance to coast (a complex gradient related mainly to temperature) and pH are both correlated with the ordination axes, and temperature is the strongest correlation with both of the first two axes (distance to coast Spearman $r = .748$, $p < .001$ axis 1, $r = .520$, $p < .001$ axis 2; pH Spearman $r = -.564$, $p < .001$ axis 1, $r = -.503$, $p < .001$ axis 2). Distance to coast is also weakly rank correlated with the fourth axis ($r = .300$, $p < .05$) but not the third, and pH is correlated with the third axis ($r = .520$, $p < .001$) but not the fourth. Eigenvalues for the ordination axes indicate that a relatively small amount of the floristic variation is explained by the ordination. Only presence/absence data were used to construct this ordination, which may make two sites appear more similar than they actually are. The four axes account for 16.7, 9.6, 7.5, and 4.9% of the variation in the data, respectively¹.

When the vascular flora is considered separately, Kadleroshilik and Toolik River are still distinct, but there is almost 100% overlap of Prudhoe Bay onto Kuparuk, and the three Kuparuk plots outside of this overlap zone are coastal sites, indicating some floristic and likely River are still distinct, but there is almost 100% overlap of Prudhoe Bay onto Kuparuk, and the three Kuparuk plots outside of this overlap zone are coastal sites, indicating some floristic and likely

¹The percent of variance explained by an ordination axis is indicated by its eigenvalue. DCA is an eigenanalysis technique, and thus allows for an exact mathematical definition of variance.

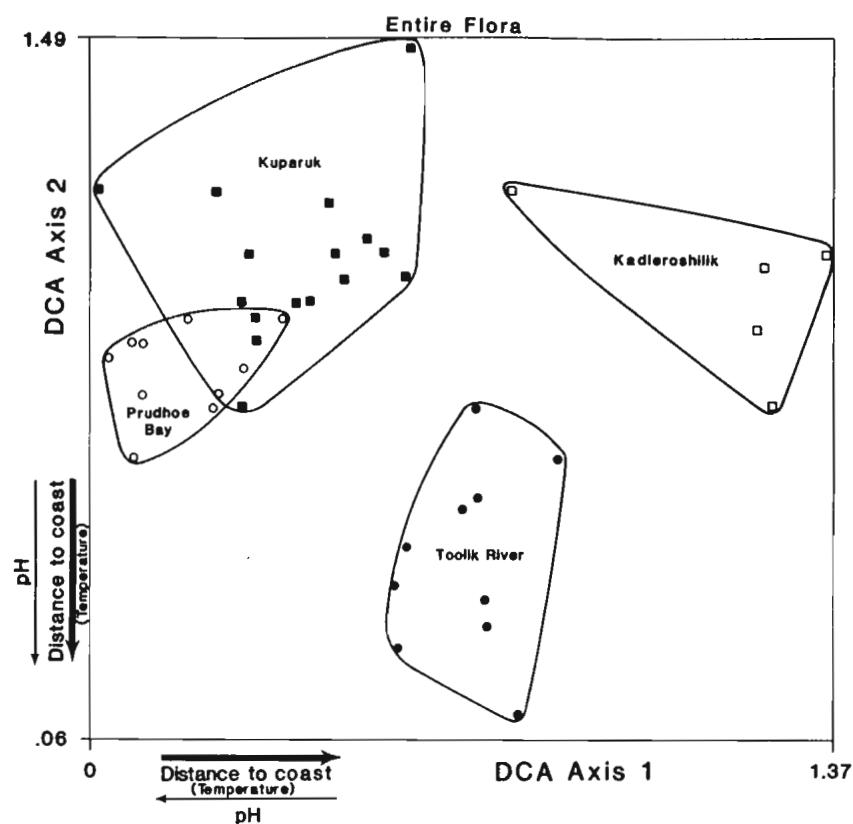


Figure 71. Ordination of the 41 sample plots based on total flora and grouped according to study area. Arrows represent Spearman rank correlations with the axes; heavier arrows are the stronger relationship. Correlation coefficients are in the text.

Prudhoe Bay region (Fig. 72). The floristic gradient constructed by the DECORANA program is 1.95 SDs long for the first axis, and the four DCA axes account for 22.5, 18.2, 7.5, and 5.9% of the variance, respectively. Thus, the vascular gradients are more clearly defined than the overall floristic gradient. The first two axes of this ordination are more strongly correlated with distance to coast (Spearman $r = .802$, $p < .001$ for axis 1; $r = -.467$, $p < .01$ for axis 2), and the third

and fourth axes are not correlated with this variable. Soil pH is correlated with the second, third, and fourth axes (Spearman $r = -.463$, $p < .01$ for axis 2; $r = .359$, $p < .05$ for axis 3; $r = -.674$, $p < .001$ for axis 4). Although the rank correlation coefficient for axis 4 is very significant, there is a rather small amount of variance explained by that axis.

Ordination of the cryptogam flora indicates a very different relationship between the study areas than for the

and fourth axes are not correlated with this variable. Soil pH is correlated with the second, third, and fourth axes (Spearman $r = -.463$, $p < .01$ for axis 2; $r = .359$, $p < .05$ for axis 3; $r = -.674$, $p < .001$ for axis 4). Although the rank correlation coefficient for axis 4 is very significant, there is a rather small amount of variance explained by that axis.

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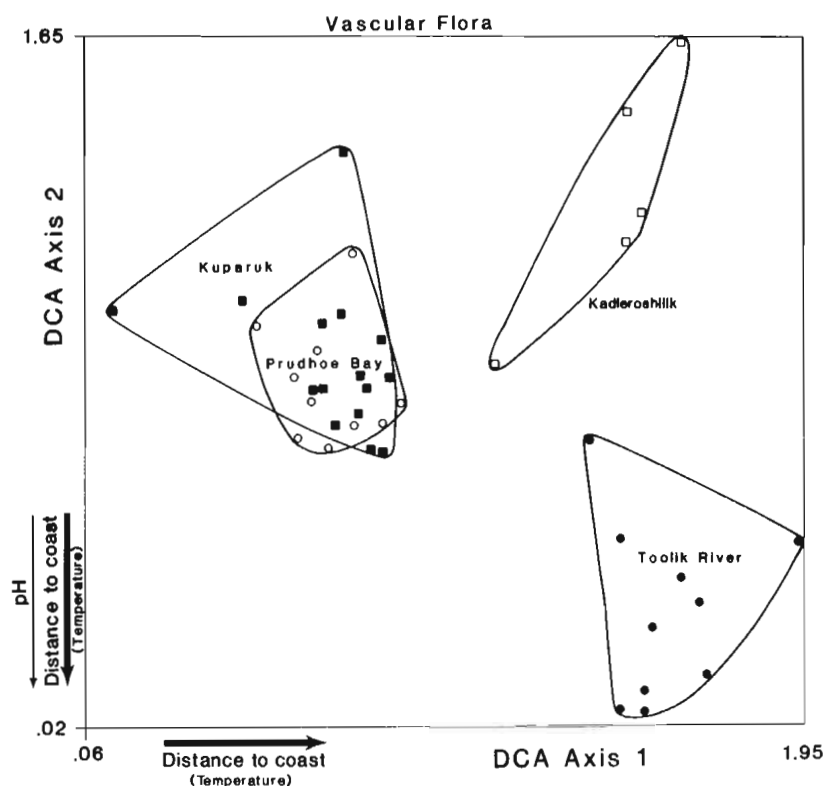


Figure 72. Ordination of the 41 sample pingos based on total vascular flora and grouped according to the study area. Arrows represent Spearman rank correlations with the axes; heavier arrows are the stronger relationship. Correlation coefficients are in the text.

Figure 72. Ordination of the 41 sample pingos based on total vascular flora and grouped according to the study area. Arrows represent Spearman rank correlations with the axes; heavier arrows are the stronger relationship. Correlation coefficients are in the text.

vascular flora (Fig. 73). The Prudhoe Bay and Toolik River areas both have some overlap with Kuparuk, which is closer to the Kadleroshilik area in this ordination space than in the other. The gradient is relatively short, 1.33 SDs for the first axis, and the variance explained

by the ordination axes is therefore fairly low (13.0, 8.7, 6.2, and 5.2% respectively). In this case it is pH, rather than distance to coast, that most strongly correlates with the axes, but distance to coast is still a significant factor. The Spearman rank correlation coefficient

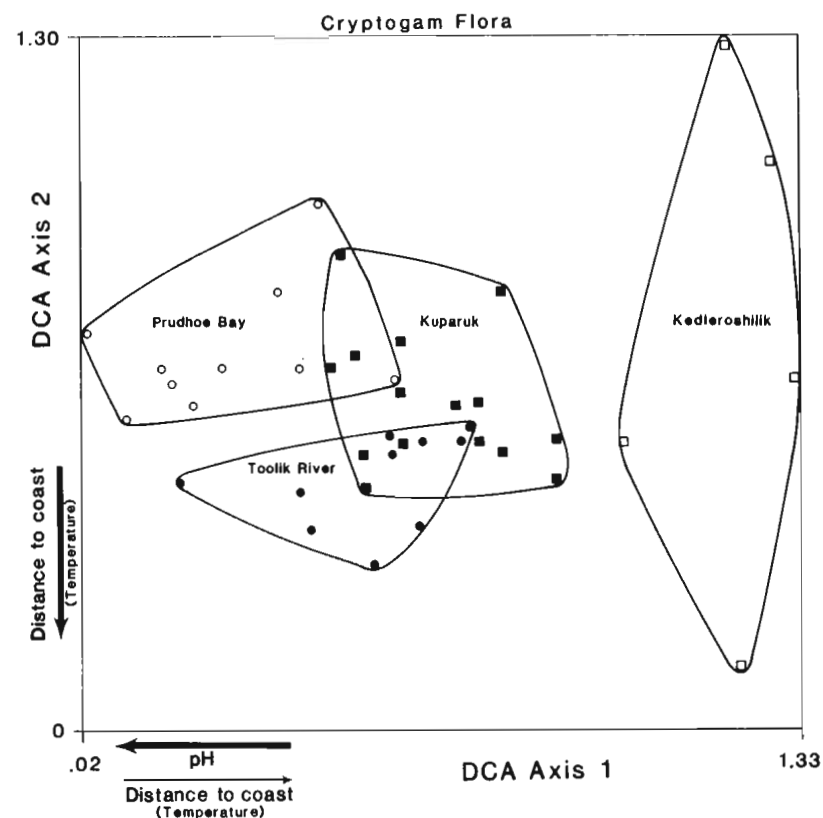


Figure 73. Ordination of the 41 sample pingos according to total cryptogam flora and grouped according to study area. Arrows represent Spearman rank correlations with the axis; heavier arrows are the stronger relationship. Correlation coefficients are in the text.

Figure 73. Ordination of the 41 sample pingos according to total cryptogam flora and grouped according to study area. Arrows represent Spearman rank correlations with the axis; heavier arrows are the stronger relationship. Correlation coefficients are in the text.

for pH with axis 1 is -0.796 ($p < .001$), and for axis 4 it is 0.474 ($p < .001$). Soil pH is not correlated with axis 2 or 3. Distance to coast is significantly correlated with the first three axes (Spearman $r = .209$, $p < .05$ for axis 1; $r = -.485$, $p < .001$

for axis 2; $r = .406$, $p < .01$ for axis 3). These data indicate that the vascular flora are most strongly related to a temperature gradient and the cryptogam flora to a complex soil gradient.

Table 23. Spearman rank correlation coefficients with the DCA ordination axes, based on all sample plots. Order of the environmental factors is according to the strength of their relationship with the first axis. Only variables with at least one significant correlation are shown.

Factor	Axis 1	Axis 2	Axis 3	Axis 4
Snow (scalar)	0.733***	0.268***	-0.022	-0.164**
Soil Moisture (scalar)	0.730***	0.345***	0.077	-0.190
Exposure (scalar)	-0.672***	-0.206***	0.018	0.155**
Lemming disturbance	0.434***	0.089	0.046	-0.061
Microrelief height (cm)	0.424***	0.211***	0.187***	0.022
Squirrel disturbance	-0.411***	0.175**	0.197***	-0.098*
Thaw Depth (cm)	-0.325***	-0.248***	-0.090	-0.035
Stability (scalar)	-0.280***	0.078	0.085	-0.092
Human disturbance	-0.257***	-0.063	-0.010	-0.227***
Cryoturbation (% cover)	-0.223***	-0.471***	-0.015	0.142
pH	-0.195***	-0.268	0.124*	-0.227***
Slope (°)	0.164**	-0.225***	-0.058	-0.035
Fox disturbance	-0.161	0.116	0.043	-0.323***
Equivalent latitude	-0.116*	-0.082	-0.008	0.003
Distance to coast	0.077	0.171	0.168**	0.372***
Bird disturbance	-0.073	0.272***	0.075	0.016
Equivalent latitude	-0.116*	-0.082	-0.008	0.003
Distance to coast	0.077	0.171	0.168**	0.372***
Bird disturbance	-0.073	0.272***	0.075	0.016
Bear disturbance	-0.028	0.172**	0.072	0.025

* $p < .05$; ** $p < .01$; *** $p < .001$.

Disturbance includes any evidence of use and does not imply destruction.

Microsite-Level Gradients

Simultaneous ordination of the 293 sample plots resulted in the construction of a continuous gradient with no major breaks in it, and the variance explained by the ordination is high (66.7, 56.0, 47.0, and 40.2% for axes 1 to 4, respectively). The high eigenvalues for all of the axes indicate there is some amount of redundancy between them, and correlations of the environmental variables with the ordination axes support this (Table 23). The redundancy is not complete, however, and each axis contains different information. The redundancy relates primarily to the covariance between the environmental variables. The number of correlations is some indication of the ecological meaning of the axis, and using this value it appears that axes 1, 2, and 4 contain the most information. Because the sampling scheme was along gradients of snow cover, moisture, exposure to winds, animal use, and other gradients associated with these, it is not surprising that there are so many significant correlations. The environmental variables are highly intercorrelated, although often weakly (Table 24), and stepwise discriminant analysis of the non-disturbance variables indicates that all of them contribute significantly to the discrimination between the microsites (Table 25). Of the 18 environmental variables measured at each relevé, only one, caribou use, is not significantly correlated with any ordination axis. In this case, the gradients within microsites and between microsites are all shown in one space, making interpretation difficult.

Individual ordinations of each microsite are a better indication of what gradients are controlling within a given

microsite type. Each microsite has a different set of variables that are correlated with the vegetation (as indicated by the ordinations) (Table 26), and all resulted in the construction of a continuous gradient with no major gaps. There are considerable differences between the microsites regarding the variance explained by the ordinations and the length of gradient constructed (Table 27). Microsite 1, the ENE side, is a snow-free site that is exposed to winds at all times. Within this microsite, temperature and soil chemistry gradients are most important (Table 28). In this instance, distance to coast may be a combination wind and temperature gradient, as wind speeds are also higher near the coast (Everett 1980d). Use by birds also shows up as a factor, which may be due to winter use by ptarmigan in some regions. Equivalent latitude, a measure of microclimate, appears to be less important than regional temperature gradients. The first axis has a much higher eigenvalue than the other three, but all appear to have some significance. The second axis has little redundancy with the first, and is related to moisture, microrelief, and slope angle. The third axis is apparently related to disturbance, and the fourth to a somewhat complex combination of gradients, most strongly to microrelief.

In microsite 2, the summit, temperature gradients are most important (Table 29). Although equivalent latitude, rather than distance to coast, is the strongest what complex combination of gradients, most strongly to microrelief.

In microsite 2, the summit, temperature gradients are most important (Table 29). Although equivalent latitude, rather than distance to coast, is the strongest correlation, these sites have little or no slope angle, so that equivalent latitude and actual latitude are the same, and equivalent latitude is therefore simply a crude measure of distance to coast. Disturbance gradients generally are important here. Summits are frequently used both as bird perches and mammal

Table 24. Pearson product-moment correlation matrix of the environmental variables.

	Slope	Aspect	Exp	Aspect	Exposure	Thaw Depth	Soil Moisture	Snow Cover	Stability	Cryoturbation	Micro-relief	Human
Slope	1.0000	.2490 (.291) p = .001	-.15 (.2) p = .001	.2490 (.291) p = .001	-.1539 (.291) p = .009	.2765 (.236) p = .001	-.1288 (.290) p = .028	.1688 (.290) p = .004	.2221 (.289) p = .001	-.0037 (.287) p = .951	.1196 (.291) p = .041	-.2342 (.291) p = .001
Aspect	.2490 (.291) p = .001	1.0000	-.41 (.2) p = .001	1.0000	-.4163 (.291) p = .001	-.1358 (.236) p = .037	.2856 (.290) p = .001	.3709 (.290) p = .001	-.1920 (.289) p = .001	-.0353 (.288) p = .551	.0683 (.292) p = .244	-.1342 (.292) p = .022
Exposure	-.1539 (.291) p = .009	-.4163 (.291) p = .001	1.00	-.4163 (.291) p = .001	1.0000	.1039 (.237) p = .111	-.7405 (.291) p = .001	-.9060 (.291) p = .001	.1930 (.290) p = .001	.2494 (.288) p = .001	-.2073 (.292) p = .001	.2069 (.292) p = .001
Thaw Depth	.2765 (.236) p = .001	-.1358 (.236) p = .037	.103	-.1358 (.236) p = .037	.1039 (.237) p = .111	1.0000	-.2726 (.237) p = .001	-.1183 (.237) p = .069	.2780 (.236) p = .001	.0909 (.234) p = .166	-.0887 (.237) p = .173	.1157 (.237) p = .075
Moisture	-.1288 (.290) p = .028	.2856 (.290) p = .001	-.74 (.2) p = .001	.2856 (.290) p = .001	-.7405 (.291) p = .001	-.2726 (.237) p = .001	1.0000	.7992 (.291) p = .001	.2519 (.289) p = .001	-.2778 (.287) p = .001	.1751 (.291) p = .003	-.1353 (.291) p = .021
Snow Cover	.1688 (.290) p = .004	.3709 (.290) p = .001	-.90 (.2) p = .001	.3709 (.290) p = .001	-.9060 (.291) p = .001	-.1183 (.237) p = .069	.7992 (.291) p = .001	1.0000	-.1363 (.289) p = .020	-.2553 (.287) p = .001	.2235 (.291) p = .001	-.2467 (.291) p = .001
Stability	.2221 (.289) p = .001	-.1920 (.289) p = .001	.193 (.2) p = .001	-.1920 (.289) p = .001	.1930 (.290) p = .001	.2780 (.236) p = .001	-.2519 (.289) p = .001	-.1363 (.289) p = .020	1.0000	.0878 (.287) p = .138	.1274 (.290) p = .030	.0278 (.290) p = .637

Table 24. (continued)

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	Slope	Aspect	Exp	Aspect	Exposure	Thaw Depth	Soil Moisture	Snow Cover	Stability	Cryoturbation	Micro-relief	Human
Cryoturbation	.0037 (.287) p = .951	-.0353 (.288) p = .551	.249 (.2) p = .001	-.0353 (.288) p = .551	.2494 (.288) p = .001	.0909 (.234) p = .166	-.2778 (.287) p = .001	-.2553 (.287) p = .001	.0878 (.287) p = .138	1.0000	.1279 (.289) p = .030	-.0054 (.288) p = .927
Micro-relief	.1196 (.291) p = .041	.0683 (.292) p = .244	-.20 (.2) p = .001	.0683 (.292) p = .244	-.2073 (.292) p = .001	-.0887 (.237) p = .173	.1751 (.291) p = .003	.2235 (.291) p = .001	.1274 (.290) p = .030	.1279 (.289) p = .030	1.0000	-.0561 (.292) p = .340
Human	-.2342 (.291) p = .001	-.1342 (.291) p = .022	.206 (.2) p = .001	-.1342 (.291) p = .022	.2069 (.292) p = .001	.1157 (.237) p = .075	-.1353 (.291) p = .021	-.2467 (.291) p = .001	.0278 (.290) p = .637	-.0054 (.288) p = .927	1.0000	
Caribou	.0203 (.291) p = .730	.0481 (.291) p = .414	.016 (.2) p = .001	.0481 (.291) p = .414	.0161 (.292) p = .784	.0047 (.237) p = .942	.0870 (.291) p = .139	.0853 (.291) p = .147	.1370 (.290) p = .020	-.0200 (.288) p = .735	.0184 (.292) p = .754	-.0281 (.292) p = .633
Fox	-.1131 (.291) p = .054	-.2183 (.291) p = .001	.050 (.2) p = .001	-.2183 (.291) p = .001	.0500 (.292) p = .395	.0684 (.237) p = .294	-.0540 (.291) p = .359	-.0584 (.291) p = .321	.1946 (.290) p = .001	-.1062 (.288) p = .072	.0956 (.292) p = .103	.1409 (.292) p = .016
Squirrel	-.1638 (.291) p = .005	-.3313 (.291) p = .001	.262 (.2) p = .001	-.3313 (.291) p = .001	.2623 (.292) p = .001	.1108 (.237) p = .089	-.2085 (.291) p = .001	-.2258 (.291) p = .001	.3051 (.290) p = .001	-.1712 (.288) p = .004	-.0080 (.292) p = .892	.1849 (.292) p = .002
Bear	.0448 (.291) p = .446	-.0337 (.291) p = .566	.015 (.2) p = .001	-.0337 (.291) p = .566	.0154 (.292) p = .793	-.0355 (.237) p = .587	-.0122 (.291) p = .836	.0249 (.291) p = .672	.2168 (.290) p = .001	-.1057 (.288) p = .073	.0107 (.292) p = .856	-.0277 (.292) p = .638

Table 24. (continued)

1)

	Slope	Aspect	Exl	Aspect	Exposure	Thaw Depth	Soil Moisture	Snow Cover	Stability	Cryoturbation	Micro-relief	Human
Lemming	.1025 (.291) p = .081	.1928 (.291) p = .001	-.3 (.291) p = .001	.1928 (.291) p = .001	-.3934 (.292) p = .001	-.1350 (.237) p = .038	.2586 (.291) p = .001	.4039 (.291) p = .001	.0355 (.290) p = .547	-.1625 (.288) p = .006	.2154 (.292) p = .001	-.1735 (.292) p = .003
Bird	.0126 (.291) p = .831	-.1038 (.291) p = .077	.05 (.291) p = .001	-.1038 (.291) p = .077	.0512 (.292) p = .384	.0941 (.237) p = .149	.0296 (.291) p = .615	.0181 (.291) p = .758	.3251 (.290) p = .001	-.2050 (.288) p = .001	.1259 (.292) p = .031	.0401 (.292) p = .494
pH	-.1291 (.286) p = .029	-.0086 (.286) p = .885	.07 (.291) p = .001	-.0086 (.286) p = .885	.0726 (.287) p = .220	.0724 (.232) p = .272	-.1877 (.286) p = .001	-.2053 (.286) p = .001	.0028 (.285) p = .962	.1695 (.283) p = .004	-.1460 (.287) p = .013	.0935 (.287) p = .114
Distance to coast	.0730 (.291) p = .214	.0768 (.292) p = .191	-.0 (.291) p = .001	.0768 (.292) p = .191	-.0460 (.292) p = .434	-.1363 (.237) p = .036	.0345 (.291) p = .557	.0274 (.291) p = .641	.0759 (.290) p = .198	-.0907 (.289) p = .124	.0884 (.293) p = .131	-.2911 (.292) p = .001
Distance to nearest pingo	.0510 (.291) p = .386	.0089 (.292) p = .880	.01 (.291) p = .001	.0089 (.292) p = .880	.0107 (.292) p = .855	-.1345 (.237) p = .039	.0692 (.291) p = .240	.0471 (.291) p = .423	-.0441 (.290) p = .454	-.0107 (.289) p = .856	-.0750 (.293) p = .200	.0892 (.292) p = .128
Distance to nearest river	.1259 (.291) p = .032	.0031 (.292) p = .957	-.0 (.291) p = .001	.0031 (.292) p = .957	-.0111 (.292) p = .850	.0422 (.237) p = .518	-.0785 (.291) p = .182	.0568 (.291) p = .335	.2193 (.290) p = .001	.0831 (.289) p = .159	.0319 (.293) p = .587	-.0942 (.292) p = .108
Equivalent latitude	-.4198 (.291) p = .001	.0181 (.291) p = .758	.34 (.291) p = .001	.0181 (.291) p = .758	.3442 (.291) p = .001	-.2554 (.236) p = .001	-.1154 (.290) p = .050	-.2895 (.290) p = .001	-.1877 (.289) p = .001	.2286 (.287) p = .001	-.1419 (.291) p = .015	.1083 (.291) p = .065

Table 24. (continued)

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	Caribou	Fox	Squ	Fox	Squirrel	Bear	Lemming	Bird	pH	Distance to coast	Distance to nearest pingo	Distance to nearest river
Caribou	1.0000	.1546 (.292) p = .008	.03 (.291) p = .001	.1546 (.292) p = .008	.0312 (.292) p = .596	.1572 (.292) p = .007	.0808 (.292) p = .168	.1081 (.292) p = .065	-.1017 (.287) p = .085	-.1154 (.292) p = .049	.1860 (.292) p = .001	.0831 (.292) p = .157
Fox	.1546 (.292) p = .008	1.0000	.14 (.291) p = .001	1.0000	.1418 (.292) p = .015	.1198 (.292) p = .041	-.0824 (.292) p = .160	.0946 (.292) p = .107	.0760 (.287) p = .199	-.1742 (.292) p = .003	.0159 (.292) p = .786	.0120 (.292) p = .838
Squirrel	.0312 (.292) p = .596	.1418 (.292) p = .015	1.00	.1418 (.292) p = .015	1.0000	.2086 (.292) p = .001	-.0712 (.292) p = .225	.2664 (.292) p = .001	.0301 (.287) p = .611	.0969 (.292) p = .098	-.0426 (.292) p = .468	.1919 (.292) p = .001
Bear	.1572 (.292) p = .007	.1198 (.292) p = .041	.201 (.291) p = .001	.1198 (.292) p = .041	.2086 (.292) p = .001	1.0000	.0593 (.292) p = .312	.1506 (.292) p = .010	-.0565 (.287) p = .340	.1506 (.292) p = .010	-.0134 (.292) p = .819	.0094 (.292) p = .873
Lemming	.0808 (.292) p = .168	-.0824 (.292) p = .160	-.07 (.291) p = .001	-.0824 (.292) p = .160	-.0712 (.292) p = .225	.0593 (.292) p = .312	1.0000	.0380 (.292) p = .518	-.0582 (.287) p = .326	.2712 (.292) p = .001	-.0863 (.292) p = .141	-.0417 (.292) p = .478
Bird	.1081 (.292) p = .065	.0946 (.292) p = .107	.266 (.291) p = .001	.0946 (.292) p = .107	.2664 (.292) p = .001	.1506 (.292) p = .010	.0380 (.292) p = .518	1.0000	-.1791 (.287) p = .002	.1970 (.292) p = .001	.1025 (.292) p = .080	.1090 (.292) p = .063
pH	-.1017 (.287) p = .085	.0760 (.287) p = .199	.030 (.291) p = .001	.0760 (.287) p = .199	.0301 (.287) p = .611	-.0565 (.287) p = .340	-.0582 (.287) p = .326	-.1791 (.287) p = .002	1.0000	-.0587 (.287) p = .322	-.0524 (.287) p = .377	-.1430 (.287) p = .015

Table 24. (concluded)

	Caribou	Fox	S	Fox	Squirrel	Bear	Lemming	Bird	pH	Distance to coast	Distance to nearest pingo	Distance to nearest river
Distance to coast	-.1154 (.292) p=.049	-.1742 (.292) p=.003	-.1742 (.292) p=.003	-.1742 (.292) p=.003	.0969 (.292) p=.098	.1506 (.292) p=.010	.2712 (.292) p=.001	.1970 (.292) p=.001	-.0587 (.287) p=.322	1.0000	-.2898 (.293) p=.001	-.0292 (.293) p=.619
Distance to nearest pingo	.1860 (.292) p=.001	.0159 (.292) p=.786	.0159 (.292) p=.786	.0159 (.292) p=.786	-.0426 (.292) p=.468	-.0134 (.292) p=.819	-.0863 (.292) p=.141	.1025 (.292) p=.080	-.0524 (.287) p=.377	-.2898 (.293) p=.001	1.0000	-.1994 (.293) p=.001
Distance to nearest river	.0831 (.292) p=.157	.0120 (.292) p=.838	.0120 (.292) p=.838	.0120 (.292) p=.838	.1919 (.292) p=.001	.0094 (.292) p=.873	-.0417 (.292) p=.478	.1090 (.292) p=.063	-.1430 (.287) p=.015	-.0292 (.293) p=.619	-.1994 (.293) p=.001	1.0000
Equivalent latitude	.0271 (.291) p=.645	-.0272 (.291) p=.644	-.0272 (.291) p=.644	-.0272 (.291) p=.644	-.0878 (.291) p=.135	-.1737 (.291) p=.003	-.1324 (.291) p=.024	-.1413 (.291) p=.016	.0852 (.286) p=.151	-.0047 (.291) p=.936	-.0355 (.291) p=.547	-.0495 (.291) p=.401

Table 25. Variables that discriminate between microsites, in order of their entry in a stepwise discriminant analysis.

Variable	Wilks Lambda	Significance	1st Discriminant Function Coefficient
Exposure	.141	.000	0.621
Moisture	.189	.000	-0.114
Equivalent latitude	.064	.000	-0.020
Slope	.044	.000	-0.257
Snow	.034	.000	-0.451
Cryoturbation	.024	.000	-0.007
Stability	.020	.000	0.199
Microrelief	.018	.000	0.061
Thaw	.018	.000	0.193

den sites, and this use by animals affects vegetation patterns on these sites, as indicated by the number of animal species groups correlated with vegetation patterns in these sites. The second ordination axis is related to microrelief height, and the third to snow (or lack of it, as indicated by a correlation with both snow and exposure). The fourth axis, in spite of a relatively high eigenvalue (.288), does not appear to have any ecological significance.

Microsite 3, the dry leeward side above the snowbank, has the lowest eigenvalues and shortest floristic gradients of all the microsites, yet even with this high amount of floristic similarity there are recognizable gradients (Table 30). Slope angle has the highest correlation with axis 1. It is likely that steeper slopes lead to an increased leeward effect, and this is supported by the snow data, which show less of a leeward effect (*i.e.* fewer

differences in snow cover) on the gently sloping broad-based pingos. The second axis is related to regional temperature and exposure, and to several other factors to a lesser degree. The third axis is very similar to the second, and the fourth axis, which has an eigenvalue of only .081, has only one correlation that did not appear in the first three axes, with equivalent latitude.

The first ordination axis of microsite 4, the middle snowbank, is correlated with four variables (Table 31). These sites are generally dominated by ericaceous shrubs, which are sensitive to equivalent latitude.

The first ordination axis of microsite 4, the middle snowbank, is correlated with four variables (Table 31). These sites are generally dominated by ericaceous shrubs, which are sensitive to pH differences. Both regional temperature and microclimate effects are important on the second axis, as well as a number of animal disturbances. Lemming nests are often found in these sites, and this variable shows up on this axis. The third axis is related to stability, snow cover, and temperature, and the fourth only weakly to fox disturbance and snow

Table 26. Summary table of factors core of factors correlating with the first DCA ordination axis for each of the microsite ordinations (in order of strength of the relationship).¹

ENE Side	Summit	mit	WSW Side	Middle Snowbank	Lower Snowbank	South Slope	North Slope
Distance to coast (temperature)	Distance to coast (temperature)	Distance to coast (temperature)	Slope	pH (-)	Distance to coast (-) (temperature)	Equivalent latitude (-)	Moisture (-)
Bird	Fox		Microrelief	Thaw (-)	Moisture (-)	Slope	Slope
pH (-)	Human (-)	Human (-)	Cryoturbation (-)	Exposure	Caribou	Stability	Equivalent latitude
Equivalent latitude (-)	Bear	Bear	Exposure	Caribou	Slope	pH (-)	pH (-)
Caribou	Bird	Bird	Squirrel		Bear	Squirrel	Microrelief (-)
Bear	Caribou	bou	pH			Cryoturbation (-)	
Moisture							

¹Factors above the first line are correlated with $p < .001$, those below the first line have $p < .01$, and those below the second line have $p < .05$.

Table 27. Eigenvalues and DCA ordination axis lengths for the individual microsite ordinations. Eigenvalues represent the proportion of variance explained by the ordination axes. (The top number is the eigenvalue; length of the gradient in SD units is listed under that.)

Microsite	Axis 1	Axis 2	Axis 3	Axis 4
1) ENE wind-exposed side	.699 4.0	.326 3.0	.179 1.93	.111 1.50
2) summit	.550 3.83	.388 3.88	.267 2.64	.288 2.77
3) WSW side above snowbank	.282 2.16	.160 1.58	.106 1.33	.081 1.28
4) middle snowbank	.509 3.31	.295 2.88	.216 2.43	.145 1.45
5) lower snowbank	.723 5.26	.351 3.24	.244 2.80	.155 1.80
6) south slope	.800 5.15	.488 4.13	.380 2.51	.265 2.34
7) north slope	.651 3.74	.235 2.18	.138 1.54	.155 1.51

cover. This fourth axis has little meaning, but it does indicate that use by foxes is weakly related to the vegetation in these sites.

Microsite 5, the lower snowbank. cover. This fourth axis has little meaning, but it does indicate that use by foxes is weakly related to the vegetation in these sites.

Microsite 5, the lower snowbank, has the longest floristic gradient, 5.3 SD units long, indicating a high amount of beta diversity within this type. Eigenvalues are also relatively high, but this microsite has the fewest correlations (Table 32). The first axis is related primarily to regional temperature and soil moisture. This microsite probably has more variability in soil moisture than

any other, as it intergrades into the mesic tundra surrounding the pingo. The second axis is highly correlated with thaw depth (Spearman $r = .700$, $p < .001$). Thaw depths are most shallow in this any other, as it intergrades into the mesic tundra surrounding the pingo. The second axis is highly correlated with thaw depth (Spearman $r = .700$, $p < .001$). Thaw depths are most shallow in this microsite compared to the rest of the pingo. Over most of the pingo surface they are probably deep enough that they would have minimal effect on plant growth. In these sites, however, thaw depth may be as shallow as 15 to 20 cm. This variable will covary with many other factors, including soil moisture, soil temperature, and organic matter. The

Table 28. Spearman rank correlation coefficients of environmental factors with the DCA ordination axes for microsite no. 1, the ENE side. Order of the environmental factors is according to the strength of their relationship with the first axis. Only variables with at least one significant correlation are included.

Factor	Axis 1	Axis 2	Axis 3	Axis 4
Distance to coast (km)	0.613***	-0.061	-0.023	-0.192
pH	-0.477**	-0.177	0.060	-0.325*
Bird disturbance	0.474**	0.171	0.010	-0.150
Equivalent latitude (°)	-0.401**	-0.152	-0.162	-0.056
Caribou disturbance	0.298*	0.018	-0.256	-0.287*
Bear disturbance	0.285*	-0.155	0.203	-0.041
Soil Moisture (scalar)	0.281*	-0.353*	0.175	-0.422**
Human disturbance	-0.278	0.212	-0.170	0.314*
Microrelief height	0.251	-0.421**	0.272	-0.572***
Fox disturbance	-0.108	0.006	0.303*	-0.061
Cryoturbation (% cover)	-0.090	-0.167	-0.478**	-0.087
Slope (°)	0.058	0.336*	-0.216	0.081
Thaw depth (cm)	0.036	0.332*	-0.354*	0.284

* $p < .05$; ** $p < .01$; *** $p < .001$.

Table 29. Spearman rank correlation coefficients of environmental factors with the DCA ordination axes for microsite no. 2, summit. Order of the environmental factors is according to the strength of their relationship with the first axis. Only variables with at least one significant correlation are included.

Factor	Axis 1	Axis 2	Axis 3	Axis 4
Equivalent latitude (°)	-0.727***	0.113	-0.075	0.108
Distance to coast (km)	0.674***	-0.122	0.318*	0.138
Fox disturbance	-0.487***	0.214	0.077	0.005
Human disturbance	-0.454**	0.139	0.025	-0.090
Bear disturbance	0.401**	-0.169	0.152	0.185
Bird disturbance	0.397**	0.194	0.084	-0.157
Caribou disturbance	-0.327*	-0.247	0.322*	0.082
Distance to coast (km)	0.674***	-0.122	0.318*	0.138
Fox disturbance	-0.487***	0.214	0.077	0.005
Human disturbance	-0.454**	0.139	0.025	-0.090
Bear disturbance	0.401**	-0.169	0.152	0.185
Bird disturbance	0.397**	0.194	0.084	-0.157
Caribou disturbance	-0.327*	-0.247	0.322*	0.082
Microrelief height (cm)	0.259	-0.341*	0.069	-0.047
Exposure (scalar)	-0.134	-0.098	0.397**	0.105
Thaw depth (cm)	-0.059	0.022	-0.371**	-0.002
Snow cover (scalar)	0.017	0.157	-0.423**	-0.152

Equivalent latitude and actual latitude are the same in these microsites, because they have no slope. For this reason, distance to coast, rather than equivalent latitude, is listed in the summary table as being most highly correlated with this microsite.

Table 30. Spearman rank correlation coefficients of environmental factors with the DCA ordination axes for microsite no. 3, WSW side above snowbank. Order of the environmental factors is according to the strength of their relationship with the first axis. Only variables with at least one significant correlation are included.

Factor	Axis 1	Axis 2	Axis 3	Axis 4
Slope (°)	0.509***	0.225	-0.116	0.350**
Microrelief height (cm)	0.467**	0.208	-0.028	0.156
Cryoturbation (% cover)	-0.416**	0.038	0.189	-0.418**
Exposure (scalar)	-0.363*	-0.513***	0.069	-0.309*
Squirrel disturbance	0.326*	0.259	-0.322*	0.118
pH	0.289*	0.161	-0.109	0.217
Fox disturbance	0.182	0.349*	-0.336*	0.194
Snow cover (scalar)	0.151	0.324*	-0.069	0.257
Equivalent latitude (°)	-0.112	-0.270	0.008	-0.287*
Stability (scalar)	0.112	0.244	-0.372*	-0.127
Distance to coast (km)	0.058	-0.593***	-0.382**	0.055
Soil moisture (scalar)	0.058	0.391**	0.164	0.062

* $p < .05$; ** $p < .01$; *** $p < .001$.

third axis is related mainly to slope angle, and the fourth to fox disturbance.

The south slope, (microsite 6), which had the most complex and varied community types, also has a long floristic gradient. This microsite has some of the steepest slopes, and also shows the most variability in slope angle, which is most highly correlated with the first axis (Table 33). Although other microsites show temperature effects that are most strongly related to regional temperature, equivalent latitude is most important here. These microsites face due south and so (along with the north slopes) will have the greatest equivalent latitude differences. Slope and equivalent latitude should covary, as equivalent latitude is directly dependent on slope when aspect is held constant.

Stability is also a function of slope to some degree. The second axis is related only to soil chemistry (pH), which is also correlated with the first and third axes. The third axis reflects regional temperature gradients, and microclimate is a secondary effect. The fourth axis is again related to microclimate, and also to moisture and exposure.

Microsite 7, the north slope, has moisture as the most important factor, and slope and equivalent latitude are also the gradients, and microclimate is a secondary effect. The fourth axis is again related to microclimate, and also to moisture and exposure.

Microsite 7, the north slope, has moisture as the most important factor, and slope and equivalent latitude are also correlated with the first axis (Table 34). This microsite is similar to the south slope in that slopes are steep and variable between pingos, and it is in these two microsites that the strongest effects from microclimate are expected. One difference between this microsite and all of the

Table 31. Spearman rank correlation coefficients of environmental factors with the DCA ordination axes for microsite no. 4, middle snowbank on leeward side. Order of the environmental factors is according to the strength of their relationship with the first axis. Only variables with at least one significant correlation are included.

Factor	Axis 1	Axis 2	Axis 3	Axis 4
pH	-0.635***	0.001	-0.136	-0.077
Thaw depth (cm)	-0.372**	-0.273*	-0.208	-0.023
Exposure (scalar)	0.326*	0.083	-0.022	0.004
Caribou disturbance	0.257*	-0.024	0.340*	0.014
Human disturbance	-0.217	0.304*	-0.202	0.040
Distance to coast (km)	0.247	-0.624***	0.328**	-0.073
Cryoturbation (% cover)	-0.233	0.184	-0.249*	-0.080
Equivalent latitude (°)	0.231	0.252*	0.154	0.117
Bear disturbance	0.186	-0.354**	0.148	-0.118
Soil moisture (scalar)	0.184	-0.292*	0.254*	-0.012
Slope (°)	-0.160	-0.010	0.274*	-0.039
Fox disturbance	-0.117	0.201	0.125	-0.299*
Bird disturbance	0.098	-0.056	0.291*	-0.052
Stability (scalar)	-0.097	-0.080	0.380**	-0.010
Snow cover (scalar)	0.062	-0.178	0.457***	-0.252*
Lemming disturbance	0.015	-0.414**	0.204	0.001

* $p < .05$; ** $p < .01$; *** $p < .001$.

others is that there are no variables correlated with the first axis at more than the 99% significance level, indicating a somewhat more random arrangement of vegetation in relation to environmental gradients in these sites. The second axis is most strongly correlated with regional temperature gradients, and also with a number of other factors, mostly related to disturbance. The third axis has four significant correlations, and only one of these, stability, is not redundant with the first two axes. The fourth axis has no variables correlated with it.

Discussion and Conclusions

The pingo vegetation is primarily related to the circumpolar vegetation; however, there are several facies and stand types that have not been described elsewhere. It also has many ties to arctic-alpine types, primarily in the Rocky

The pingo vegetation is primarily related to the circumpolar vegetation; however, there are several facies and stand types that have not been described elsewhere. It also has many ties to arctic-alpine types, primarily in the Rocky Mountains. The abundance of *Dryas integrifolia* on most sites links it with other calcareous arctic and alpine sites. The snowbed types, dominated by *Dryas integrifolia* with either *Salix rotundifolia* or *Cassiope tetragona*, are also closely

Table 32. Spearman rank correlation coefficients of environmental factors with the DCA ordination axes for microsite no. 5, lower snowbank on leeward side. Order of the environmental factors is according to the strength of their relationship with the first axis. Only variables with at least one significant correlation are included.

Factor	Axis 1	Axis 2	Axis 3	Axis 4
Distance to coast (km)	-0.471***	-0.024	0.170	-0.034
Soil moisture (scalar)	-0.372**	-0.277*	0.247	0.117
Caribou disturbance	0.344*	-0.099	-0.377**	-0.002
Slope (°)	0.317*	0.451**	-0.465**	-0.136
Bear disturbance	0.314*	0.188	-0.280*	0.036
pH	0.251	0.237	0.195	0.350*
Stability (scalar)	0.140	0.391**	-0.165	0.023
Equivalent latitude (°)	-0.113	-0.362**	0.059	0.270*
Thaw depth (cm)	0.089	0.700***	0.052	0.072
Fox disturbance	0.010	-0.008	-0.060	0.451**

* $p < .05$; ** $p < .01$; *** $p < .001$.

Table 33. Spearman rank correlation coefficients of environmental factors with the DCA ordination axes for microsite no. 6, south slope. Order of the environmental factors is according to the strength of their relationship with the first axis. Only variables with at least one significant correlation are included.

Factor	Axis 1	Axis 2	Axis 3	Axis 4
Equivalent latitude (°)	-0.534***	-0.031	-0.305*	-0.564***
Slope (°)	0.572***	0.071	0.329*	0.534***
Stability (scalar)	0.446**	-0.049	0.266*	0.374**
pH	-0.376**	-0.333*	-0.274*	0.234
Squirrel disturbance	0.376**	0.022	0.186	0.382**
Cryoturbation (% cover)	-0.352**	-0.236	-0.332*	-0.167
Bird disturbance	0.230	-0.067	0.230	0.502***
Equivalent latitude (°)	-0.534***	-0.031	-0.305*	-0.564***
Slope (°)	0.572***	0.071	0.329*	0.534***
Stability (scalar)	0.446**	-0.049	0.266*	0.374**
pH	-0.376**	-0.333*	-0.274*	0.234
Squirrel disturbance	0.376**	0.022	0.186	0.382**
Cryoturbation (% cover)	-0.352**	-0.236	-0.332*	-0.167
Bird disturbance	0.230	-0.067	0.230	0.502***
Lemming disturbance	-0.204	0.172	0.363**	-0.040
Snow cover (scalar)	0.156	-0.040	0.348*	-0.249
Distance to coast (km)	0.149	0.188	0.638***	0.078
Microrelief height (cm)	0.052	-0.152	0.307*	-0.327*
Soil moisture (scalar)	-0.048	-0.033	0.135	-0.600***
Exposure (scalar)	0.007	0.138	-0.117	0.494***

* $p < .05$; ** $p < .01$; *** $p < .001$.

Table 34. Spearman Rank correlation coefficients of environmental factors with the DCA ordination axes for microsite no. 7, north slope. Order of the environmental factors is according to the strength of their relationship with the first axis. Only variables with at least one significant correlation are included.

Factor	Axis 1	Axis 2	Axis 3	Axis 4
Soil moisture	-0.439**	-0.034	-0.224	-0.010
Slope (°)	0.423**	0.064	-0.052	0.192
Equivalent latitude (°)	0.395**	0.126	-0.189	0.123
pH	-0.346*	0.056	-0.046	0.076
Microrelief height (cm)	-0.285*	-0.326*	-0.203	0.154
Human disturbance	-0.251	0.350*	-0.056	0.050
Fox disturbance	-0.238	0.324*	0.343*	-0.042
Lemming disturbance	-0.214	-0.321*	0.120	0.137
Squirrel disturbance	-0.175	-0.261*	0.226	0.193
Distance to coast (km)	0.111	-0.614***	-0.109	0.109
Caribou disturbance	-0.048	0.155	-0.324*	-0.106
Bird disturbance	-0.046	-0.368**	-0.266*	0.008
Stability (scalar)	0.041	-0.038	0.333*	-0.197

* $p < .05$; ** $p < .01$.

related to types described from many circumpolar areas. Many of the north slope and ENE side types (microsites 7 and 1) have a fellfield character. These cold sites are physiognomically and ecologically similar to high arctic vegetation in the Brooks Range, but they do not contain any high arctic species unique to these sites. It is important to note here that it is the vegetation that shows these links to the alpine, and not necessarily the flora. The pingos have many communities that are related to alpine types, but frequently only at the genus level. The classification system used here is

were often made based on physiognomy or growth form.

A problem with floristic classification systems is that many of the species that differ are closely related pairs that may hybridize in certain areas of their ranges (e.g. *Dryas integrifolia* vs. *D. octopetala*, *Betula nana* vs. *B. glandulosa*, and others), and this relationship cannot be defined precisely. This problem is especially noticeable in the Arctic where the flora is relatively young. Floristic classification systems is that many of the species that differ are closely related pairs that may hybridize in certain areas of their ranges (e.g. *Dryas integrifolia* vs. *D. octopetala*, *Betula nana* vs. *B. glandulosa*, and others), and this relationship cannot be defined precisely. This problem is especially noticeable in the Arctic, where the flora is relatively young (Löve 1959). In such a situation, there will be many closely related species that often hybridize. In this study, one or more species in the genera *Dryas*, *Bet.*

Potentilla, and *Oxytropis* have taxonomic problems related to species pairs. The genus *Dryas* is a good example. *Dryas octopetala* is often considered a calciphile (e.g. Komárková 1979). Many of the comparisons of the pingo vegetation with that of the southern Brooks Range vegetation (Cooper 1986) indicate that the two species have similar ecology in these two areas. Yet in the areas where its range overlaps with *Dryas integrifolia*, *D. octopetala* is limited to slightly more acidic sites, and this difference is consistent (Walker et al. 1987a). In some of the more alpine-like, and also, perhaps coincidentally, more acidic, sites on the pingos, the *Dryas integrifolia* looked very much like typical *D. octopetala*, but lacked certain key characteristics of that species, and may well have been a hybrid (Hultén 1968).

The other problem encountered is a result of the steep north-south temperature gradient that is present within the region (Fig. 74) (Walker and Webber 1979; Haugen and Brown 1980). The gradient is so steep that the estimated number of thaw degree days at pingo 12, the most coastal, is 400, and at pingo 37, the most inland, is 764. Several authors (Young 1971; Rannie 1987) have shown a correlation between number of species and summer warmth. Walker (1985a) demonstrated that even within the relatively small Prudhoe Bay region, the temperature gradient is steep enough that there is a loss of species in more northern areas. This influence within the present study is illustrated in Table 35. The trend (Young 1971; Rannie 1987) have shown a correlation between number of species and summer warmth. Walker (1985a) demonstrated that even within the relatively small Prudhoe Bay region, the temperature gradient is steep enough that there is a loss of species in more northern areas. This influence within the present study is illustrated in Table 35. The trend is not perfect, as Toolik River, with the highest estimated average thaw degree days, has fewer species than Kadleroshilik, but it illustrates the differences

effect on the classification that is illustrated by Stand Type *Cassiope tetragona* - *Dryas integrifolia*. This type is consistently found in the backslope area of the leeward side, where there is snow accumulation combined with good drainage. In the Prudhoe Bay and Kuparuk areas, communities in these sites primarily have only these two shrubs, and also occasionally the dwarf willows *Salix reticulata* and *S. arctica*. In the Toolik River and Kadleroshilik areas, however, all of these species are present as well as a number of other ericaceous shrubs, occasionally *Betula nana*, and also low but erect willows. This link is shown by the hierarchical classification scheme, where the stand type is essentially the lowest common denominator.

Another problem encountered was uncertainty in the designation of steppe types. Steppe and tundra are both physiognomic terms. Steppe is defined by Daubenmire (1968) as "grassland in regions too dry for natural forest on the uplands". He further divides this into meadow steppe, shrub steppe, and true steppe. Yurtsev (1963) has emphasized a floristic-ecological interpretation in his definition of steppes, including steppe tundras, and he separates steppe tundra from true steppe, which is herb-grass vegetation with origins in a continental climate. Ritchie (1984) claims that the term steppe-tundra is improperly used unless some specific ecological or floristic relationship to the modern steppes is demonstrated. Freitag (1977) also noted that there has been confusion associated with this term, and that steppe should only be used when it applies to temperate grasslands.

The term steppe tundra is useful for

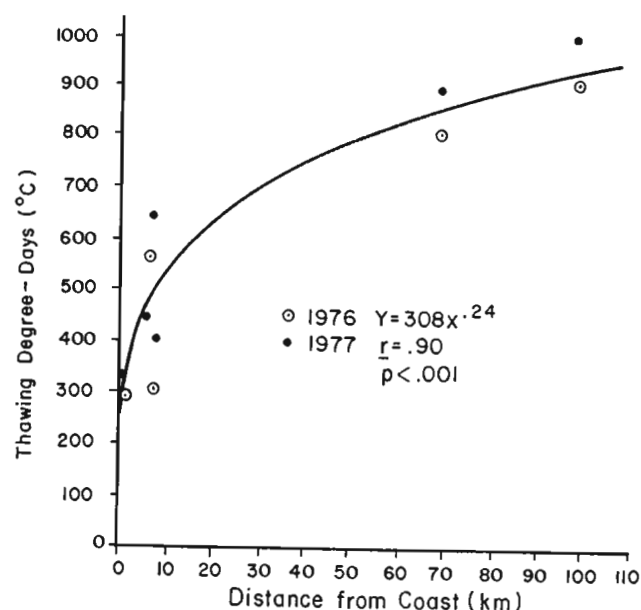


Figure 74. Correlation of thaw-degree days with distance to coast.
Source: Walker, D.A. 1985. *Vegetation and environmental gradients of the Prudhoe Bay region, Alaska*. Hanover, NH: U.S. Army Cold Regions Research and Engineering Laboratory, CRREL Report 80-14, p. 10-13.

Table 35. Number of vascular species and estimated thaw degree days in each of the study areas. (Thaw degree days estimate is from Haugen and Brown [1980]).

Study Area	Number of Species	Mean Regressed Thaw Degree Days
Prudhoe Bay	121	483 ± 16
Kuparuk	139	502 ± 31
Toolik River	154	735 ± 53
Kadleroshilik	167	580 ± 47

TDD = 434.54 + 4.915DC, where TDD = thaw degree days and DC = distance to coast due south (Haugen and Brown 1980).

tundra areas that is dominated by grasses and forbs. This does not necessarily imply that the origin of this vegetation was a true steppe. Unfortunately, this term, which is quite useful, evolved in a somewhat backwards manner. It was proposed to describe hypothesized Pleistocene vegetation types, and then there was a search for types that could fit the name. Defining the term based on physiognomy and growth form alleviates the problem inherent in naming a vegetation type based on an implied origin. The vegetation should be named according to its current position, and based on this an origin for the vegetation can be considered. For this study, steppe-tundra is defined in this manner, and it is properly applied according to this definition. Yurtsev (1982), Young (1982), Murray et al. (1983) and Cooper (1986) have also described modern plant assemblages fitting this definition. The climatic conditions under which this vegetation formed have not yet been fully elucidated, and in any case topographic and microclimatic gradients of the past can never be recovered fully (Barry 1982). Young (1982) is one of many who have taken the moderate middle ground and suggested that the full glacial vegetation was likely a complex mosaic, although large areas were probably similar physiognomically, much as the coastal plain is basically one physiognomic type today over the majority of its surface.

The types described here as steppe was likely a complex mosaic, although large areas were probably similar physiognomically, much as the coastal plain is basically one physiognomic type today over the majority of its surface.

The types described here as steppe tundra are ecologically related to true steppes, as they have steppe-like soils, and the likely origin of these soils, at least on the broad-based pingos, is such that a steppe-like vegetation would have been almost necessary. There is also abundant floristic evidence to relate them

to other steppe-tundra vegetation, as the term has been used by Yurtsev (1982), Murray et al. (1983), and Cooper (1986). More work is needed in Alaska looking at transitions between these isolated Coastal Plain stands, the Brooks Range vegetation, and interior Alaska to determine how these are related ecologically and floristically.

The ordinations of the pingo floras indicate that although there is a general regional character to the flora, with a high amount of similarity in all areas, each of the four study areas has a different flora associated with it. These differences are related to complex temperature and soil chemistry gradients, with vascular species appearing to be most strongly related to temperature, cryptogams to soil chemistry. Although there were no measurements taken on soil chemical factors other than pH, Walker (1985a) demonstrated that there is a very complex soil chemistry gradient within the Prudhoe Bay region that is related to pH changes. Thus, some species may be responding to pH and others to related factors. Recognizing the pH gradient as a complex soil gradient indicated by pH and not necessarily a direct pH gradient is therefore appropriate.

Temperature and pH are both important gradients within the Prudhoe Bay area (Walker 1985a). The pH gradient is due to deposition of calcareous loess downwind of the Sagavanirktok River, which affects both vegetation and soils

Temperature and pH are both important gradients within the Prudhoe Bay area (Walker 1985a). The pH gradient is due to deposition of calcareous loess downwind of the Sagavanirktok River, which affects both vegetation and soils (Everett and Parkinson 1977; Walker 1985a). The data presented here extend earlier findings to a broader area and relate them specifically to the pingos. These are also the first data indicating that the vascular plants and cryptogams respond somewhat differently to the two

gradients, which do act independently of one another. The greater sensitivity of cryptogam species to soil chemistry has been indirectly implicated in studies of road dust effects, where cryptogams are some of the first species to show visible signs of deterioration due to dust (Walker and Everett 1987).

The microsite ordinations indicate that each microsite has a different set of gradients associated with it, but all of the microsites are correlated with most of the measured environmental variables at some level. Many of the environmental variables covary, so there are actually a few major complexes associated with each microsite. The north slope sites have no variables that are highly correlated with the first axis. Savile (1960) observed that in high arctic regions, vegetation communities may have a high degree of overlap and be poorly defined compared to low arctic or temperate vegetation. In high arctic regions, most species are at or near their northern limit of distribution, and are likely controlled by environmental stress rather than competition. Peterson (1978) and Webber (1978) both noted that arctic vegetation often is controlled more by allogenic (environmental) rather than autogenic (biotic) factors.

The apparently more random arrangement of the north-slope vegetation on the pingos is related to this same principle. For simplicity of argument, imagine that temperature is the only difference between the north and south slopes of a pingo. At this northern lati-

tude, there will be many species near their northern limit of distribution, but few or none near their southern limit. If temperature is what ultimately controls this northern limit, then there will be fewer species available that can tolerate the coldest sites regionally, compared to the warmest sites. With a smaller pool of species available, more overlap in distribution is expected, and consequently species distributions are less highly correlated with environmental factors.

Species become more widespread as they are released from competition, and their compressed niche expands into their realized niche (Hutchinson 1959; MacArthur and Wilson 1967). The importance of microclimatic temperature to vegetation on both the north and south slopes supports this hypothesis of species distributions on the pingos. Essentially, the north slopes appear to be more arctic in nature than the south slopes. Boyko's (1947) geocological law of distribution states, "The specific topographic distribution (micro-distribution) of an ecotypic plant species or of a plant community is a parallel function of its general geographical distribution (macro-distribution), since both are determined by the same ecological amplitudes." Thus, the north and south slopes of pingos offer an opportunity to examine the equivalent of a latitudinal gradient within a controlled setting that would be difficult to find along an actual gradient. Principles of arctic vegetation that have been implied in other studies can be demonstrated with this model system.

The apparently more random arrangement of the north-slope vegetation on the pingos is related to this same principle. For simplicity of argument, imagine that temperature is the only difference between the north and south slope of a pingo. At this northern lati-

CHAPTER V

FLORISTICS AND BIOGEOGRAPHY

Whereas Chapter IV examined the relationships between species assemblages, this chapter concentrates on the species themselves and their potential origin. A key consideration is how the pingo flora is related to Asian floras and floras of other areas where steppe-tundra has been described. One of the main questions considered here is whether or not steppe-tundra assemblages represent relicts, or are just unusual combinations of species that are well-adapted to their environment that arrived there through a combination of short and long-distance dispersal. Although the classification of a given type as steppe does not imply a relationship to any past vegetation, if there is evidence these are relict then it would be further evidence for the presence of these types in the past. Many of the species important in these assemblages are not limited to them, but a number represent fairly significant range disjunctions.

There are two ways in which biogeography and species-area correlations can contribute to the determination of whether or not these are relicts. The suggestion made by Koranda (1970) and Walker (1985a) that the pingos are island-like may have consequences beyond the pingos being unusual natural features; by being islands they could contribute to the determination of whether or not these are relicts. The suggestion made by Koranda (1970) and Walker (1985a) that the pingos are island-like may have consequences beyond the pingos being unusual natural features; by being islands they could have maintained relicts of past environments and may hold clues to what those environments might have been like. If there are relicts on the pingos, then they should have non-equilibrium biogeography, with extinction rates exceeding colonization rates. This would lead to a

high value of z , the slope of the species-area curve, because smaller pingos will lose species to extinction more quickly than larger pingos due to smaller population sizes on smaller pingos. The second application of biogeography is to examine relationships between number of species and distance to other pingos and rivers that could be sources for these plants. A high correlation with distance to rivers would be indirect evidence that the species may have dispersed onto the pingos from the river corridors, which could have happened recently. A correlation with distance to other pingos would indicate that these species are actively dispersing between the pingos today, but would not rule out the possibility that they are in the region primarily because the pingos are there.

Besides their direct application to the steppe-tundra question, the pingos allow for a unique application of equilibrium biogeography in the Arctic. An important underlying assumption of island biogeography theory that is not often discussed is that there is available, somewhere on the planet, a pool of species capable of colonizing a given site, and that these species are limited only by their ability to disperse and to find resources that satisfy their niche requirement (in the sense of Hutchinson 1959). There are two reasons why this basic assumption may not be met in the Arctic. To a colonizing plant species, newly arrived at any environment where some type of long-distance dispersal was necessary, the presence or absence of

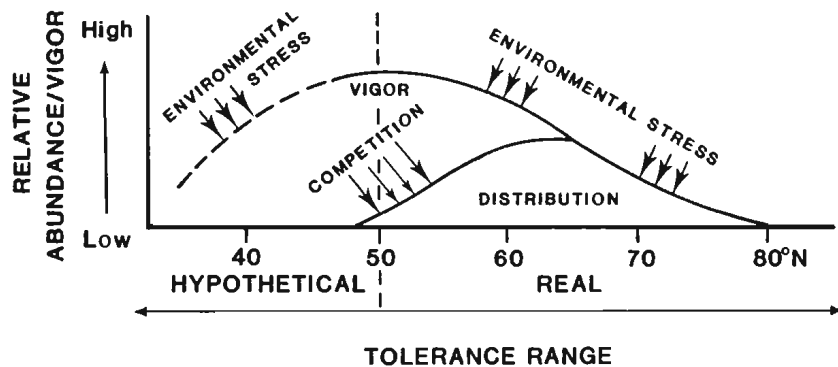


Figure 75. Distribution of *Dryas integrifolia* along a latitudinal gradient. The peak of the abundance curve is north of the peak for vigor of individual plants. This is hypothesized on the basis of increased competitive pressure at lower latitudes (adapted from Svoboda and Henry 1987).

establishment can occur, is the first obstacle that a plant must overcome in order to establish a population (Harper 1977). At the northernmost limits of plant growth, there are relatively few species capable of survival; those that are present are extremely minute and may not even be noticed without some effort (Svoboda and Henry 1987). In these polar desert regions, the absence of safe sites, and perhaps competition for the few safe sites available, severely limits the number of species regionally. In such sites the concept of an equilibrium becomes almost meaningless. The same effort (Svoboda and Henry 1987). In these polar desert regions, the absence of safe sites, and perhaps competition for the few safe sites available, severely limits the number of species regionally. In such sites the concept of an equilibrium becomes almost meaningless. The same assemblages are found in all areas where plants are able to colonize at all (Savile 1960), and the species-area curve would have a slope of zero. In the Low Arctic, however, there is complete plant cover in most sea-level areas, so presumably it

competition for available sites that is limiting. At some unknown point on a north to south gradient, the importance of competition, rather than environmental stress, controls plant distribution (Svoboda and Henry 1987; Fig. 75). North of this point, species-area curves should all have slopes less than the predicted value of .12 for a mainland site in equilibrium (or less than .20 for an island).

The other reason why the theory may not hold in the Arctic is because the flora is depauperate. The Arctic flora is relatively young; it is believed to have been predicted value of .12 for a mainland site in equilibrium (or less than .20 for an island).

The other reason why the theory may not hold in the Arctic is because the flora is depauperate. The Arctic flora is relatively young; it is believed to have been formed mainly by the end of the Tertiary, at which time there were approximately 1500 circumpolar species. The Plio-Pleistocene glaciations left few refugia in the north; thus, the flora of this region today is a depauperate remnant of its

Table 36. Species that are primarily restricted to pingos within the study region. Asterisks mark species that are likely disjuncts. Other species may be more common, particularly along rivers, but have probably been overlooked. They are included here for now.

<i>Anemone drummondii</i>	<i>Festuca altaica</i>
<i>Aster sibiricus</i>	<i>Luzula arcuata</i> *
<i>Braya humilis</i>	<i>Oxytropis campestris</i> ssp. <i>varians</i>
<i>Carex franklinii</i> *	<i>Oxytropis jordalii</i>
<i>Carex glacialis</i> *	<i>Phlox sibirica</i>
<i>Carex nardina</i> *	<i>Potentilla nivea</i>
<i>Carex obtusata</i> *	<i>Pulsatilla patens</i> *
<i>Carex petricosa</i> *	<i>Pyrola asarifolia</i>
<i>Carex supina</i> ssp. <i>spaniocarpa</i> *	<i>Pyrola secunda</i> ssp. <i>obtusata</i>
<i>Cnidium cnidifolium</i> *	<i>Ranunculus pygmaeus</i>
<i>Cystopteris fragilis</i>	<i>Saxifraga davurica</i>
<i>Delphinium brachycentrum</i>	<i>Saxifraga reflexa</i> *
<i>Draba fladnizensis</i>	<i>Selaginella sibirica</i> *
<i>Draba subcapitata</i> *	<i>Senecio hyperborealis</i> *
<i>Elymus innovatus</i>	<i>Stellaria umbellata</i> *
<i>Erigeron muirii</i> *	<i>Thalictrum alpinum</i>
<i>Erysimum pallassii</i>	<i>Zygadenus elegans</i>
<i>Eritrichum aretioides</i> *	

1974). It becomes more depauperate in the more northern regions, until eventually there are no species at all (Svoboda and Henry 1987). The effect of this depauperate flora would be the same as the last example. Slopes of species-area curves will be diminished whenever there is less than a full complement of species available. Because Beringia was a major refugium, it is an excellent area in which and Henry 1987). The effect of this depauperate flora would be the same as the last example. Slopes of species-area curves will be diminished whenever there is less than a full complement of species available. Because Beringia was a major refugium, it is an excellent area in which to apply these ideas.

Floristics

There were 232 vascular taxa in 218 species, 113 genera, and 32 families, 104 lichens, and 50 bryophytes documented

on pingos from the region of this study. The most common vascular families are the Graminae, with 27 taxa and 23 species, the Compositae, with 24 taxa and 23 species, the Cyperaceae, with 24 taxa and 23 species, and the Cruciferae, with 22 species. Of the vascular species, 35 are known regionally more or less only from the pingos, although this does not imply rarity elsewhere (Table 36). Some of these species have also been collected occasionally along rivers in this area, but they are not known elsewhere. Steep river bluffs and gravel river bars have similar habitats to those found on the pingos, and potentially the rivers could serve as migration corridors for alpine

Restricted Species

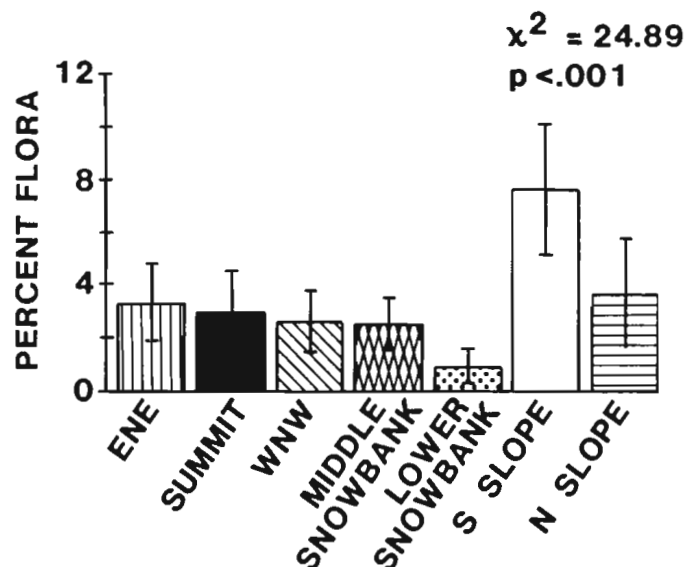


Figure 76. Distribution of restricted species within the seven microsites.

species from the Brooks Range to disperse onto the coastal plain. Because the river floras are rather poorly known at this time, several species that have been collected along rivers but are thought to be uncommon in those areas are included in this list for now, although future work may indicate they are more common.

The pingo flora of the study region consists primarily of circumpolar (100 species) and North American-Asian (including Beringian endemic) elements (87 species) with fewer North American species (15), Western North American-in this list for now, although future work may indicate they are more common.

The pingo flora of the study region consists primarily of circumpolar (100 species) and North American-Asian (including Beringian endemic) elements (87 species) with fewer North American species (15), Western North American-Asian-European species (12), and Alaskan-Yukon endemics (10). The 35 species that are regionally restricted to pingos (which will be referred to as restricted species) are mainly on the south

has a slightly higher proportion of arctic-alpine species and a lower proportion of arctic species than do the regionally more widespread species (Fig. 77). There are no coastal species restricted to pingos. The restricted species have a strikingly different pattern from the widespread species with regard to northern limit types (Fig. 78); the widespread species are primarily zone 2 and zone 3, the restricted species are mostly zone 4, and there is an upward trend from zone 1 to zone 4 in the latter group (northern limit zones are according to Young [1971], different pattern from the widespread species with regard to northern limit types (Fig. 78); the widespread species are primarily zone 2 and zone 3, the restricted species are mostly zone 4, and there is an upward trend from zone 1 to zone 4 in the latter group (northern limit zones are according to Young [1971], zone 1 is the most northern, zone 4 the most southern). Geographic range also shows noticeable differences between the restricted and widespread group (Fig. 79). Whereas nearly half the widespread

Environmental Regions

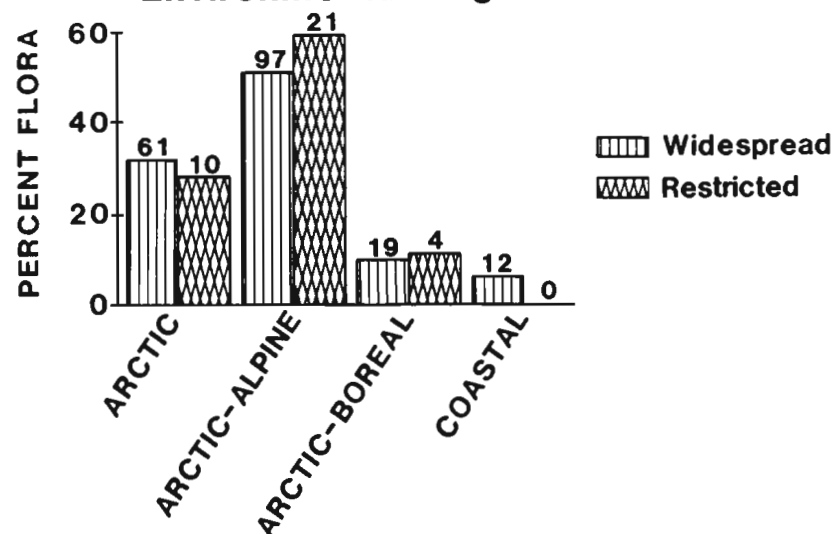


Figure 77. Distribution of species among the environmental regions types. Number of species is on top of each bar.

Northern Limit

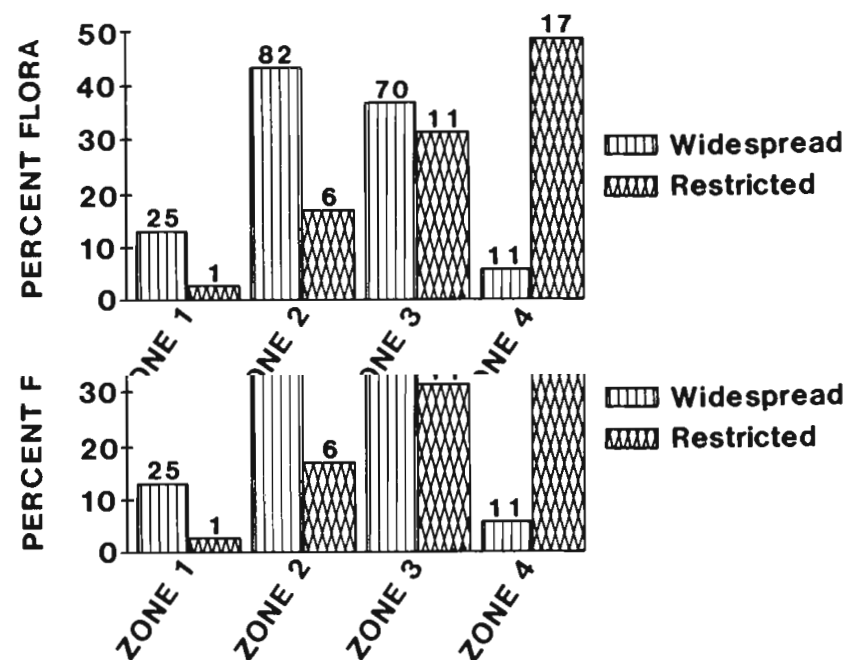


Figure 78. Distribution of species among the northern limit types. Number of species is on top of each bar.

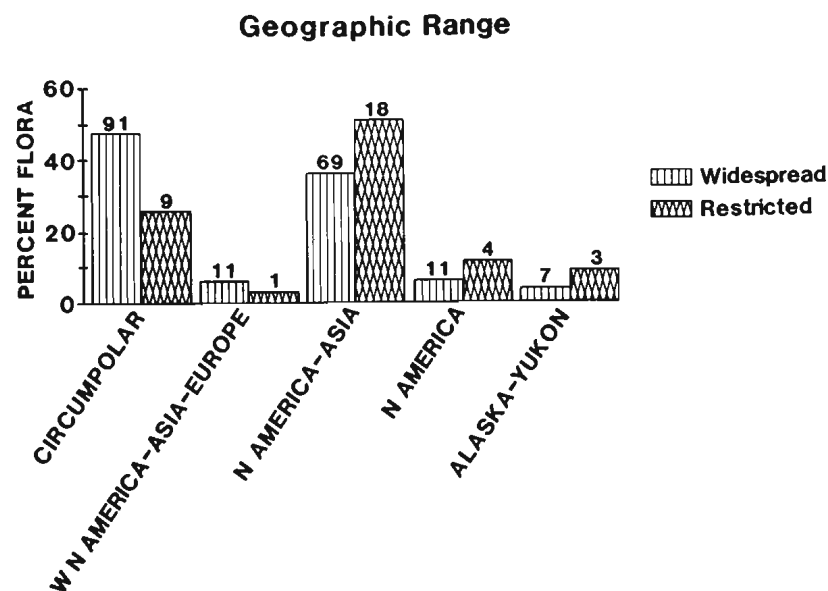


Figure 79. Distribution of species among the geographic range categories. All North American categories are combined, as are all North American-Asian categories, including Beringian endemics. Number of species is on top of each bar.

restricted species are North American-Asian (all of the North American-Asian categories, including Beringian endemics, are combined in this figure). There is also a slightly higher proportion of North American species and Alaskan-Yukon endemics here.

Landscape Level Effects

The study areas represent different landscapes, and are used here as the basis for examining trends at this level. There are only minimal differences between the study area floras with regard to environmental regions (Fig. 80). The

Landscape Level Effects

The study areas represent different landscapes, and are used here as the basis for examining trends at this level. There are only minimal differences between the study area floras with regard to environmental regions (Fig. 80). The Kadleroshilik area, which has more species than the other study areas, has most of this increase in the arctic-alpine category. The Toolik River area also shows most of its additional species

(compared to the other areas) in this category. These are warmer areas, with a few more arctic-boreal plants. Coastal species are minimal in all areas, but the Kugaruk, which has a few pingos within a kilometer of the coast, has the most.

The geographic elements also differ in their importance between the four study areas (Fig. 81). The circumpolar species are the largest category, and this shows only minimal differences. The Kadleroshilik area is relatively rich in North American-Asian species. Beringian endemics, and Alaskan-Yukon endemics. The Toolik River area has a greater number of North American-Asian species concentrated in North America than the other study areas. The other categories show only minimal differences between the study areas.

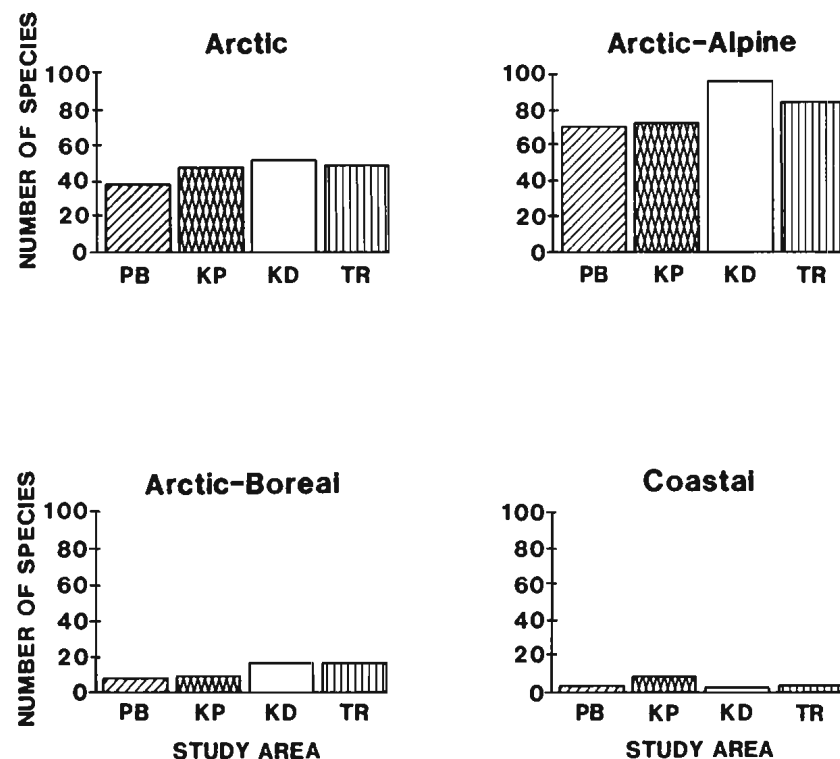


Figure 80. Number of species in each of the environmental regions categories within each study area.

The northern limit categories show some rather striking differences related to distance of the study areas from the coast (Fig. 82). The mean distance to coast increases from Prudhoe Bay to Kugaruk to Kadleroshilik to Toolik River, but Kugaruk has more extreme coastal sites than Prudhoe Bay. The greatest number of zone 1 and 2 species are in the Kugaruk area, while there are nearly twice as many zone 3 species and over four times as many zone 4 species in the Kadleroshilik and Toolik River areas as in the Kugaruk and Prudhoe Bay areas.

Microsite-Level Effects

There are significant differences in the relative importance of the environmental regions elements among the microsites (Kruskal-Wallis test, $p < .001$ in all cases; Fig. 83). These data represent the proportion of the species

present at a given site; a value of 70% indicates that all plots in that microsite have an average of 70% of their species in that particular floristic element. The rather small error bars, representing the 95% confidence interval for the mean,

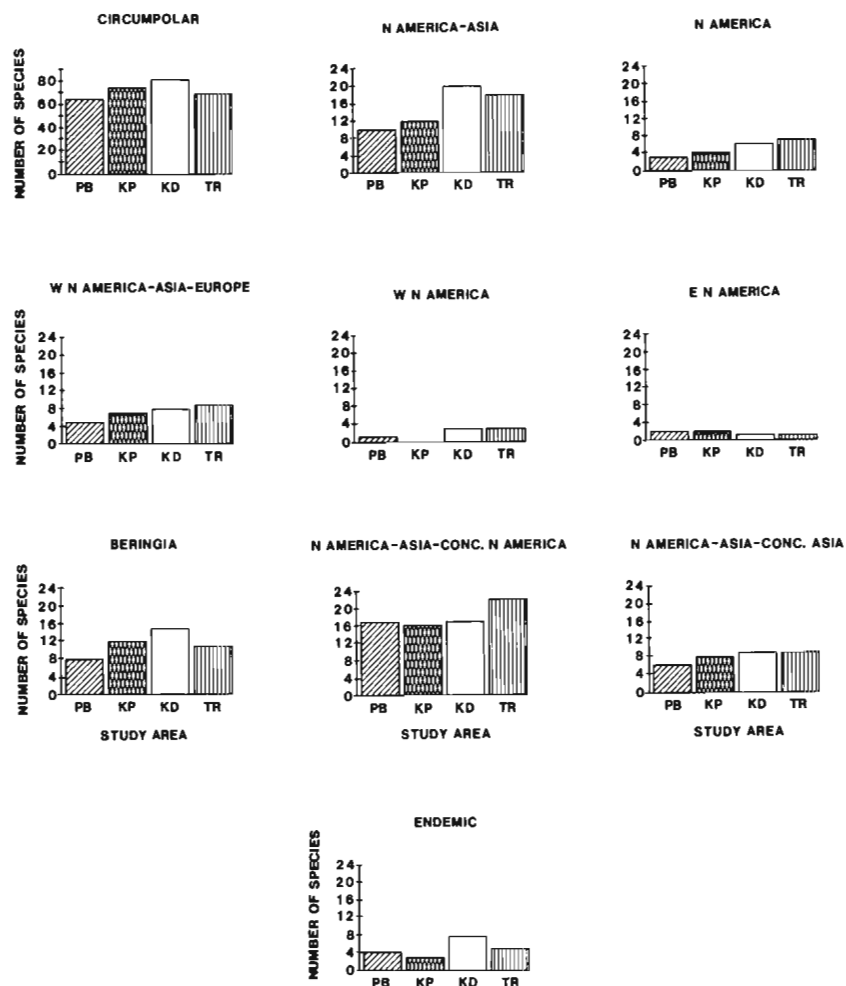


Figure 81. Number of species within each of the geographic range categories in each study area.



Figure 81. Number of species within each of the geographic range categories in each study area.

indicate high consistency in types represented within the various microsites.

Arctic species are least common in the most exposed sites and most common in the snowbeds, while arctic-alpine species show the opposite trend,

and make up the greatest part of the flora on the north slope, south slope, and ENE side. Arctic-boreal species are not particularly important in any microsite, but they are a significantly greater portion of the species in the lower snowbanks

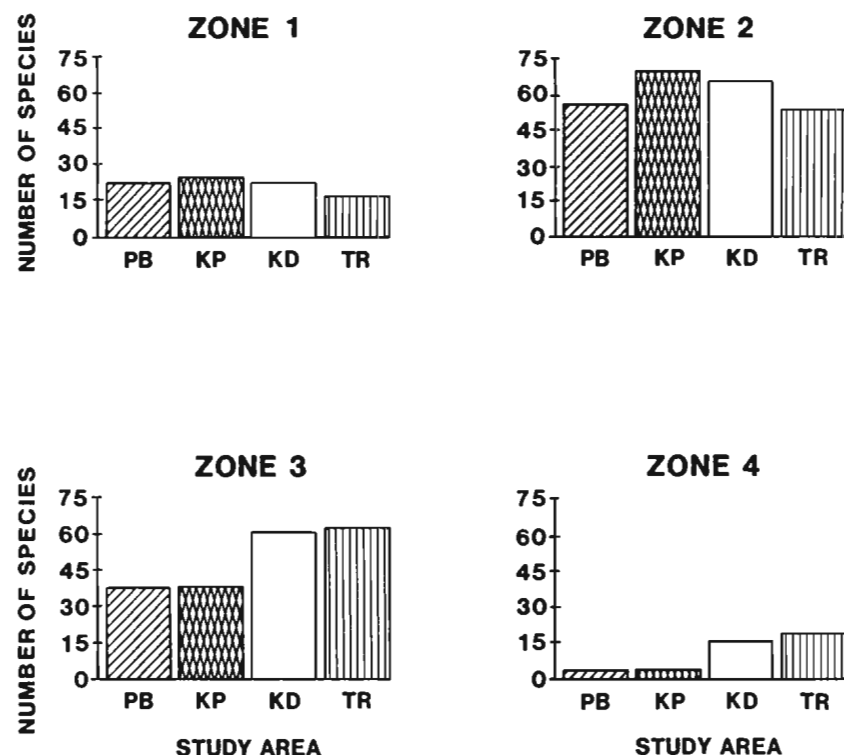


Figure 82. Number of species within each of the northern limit categories in each of the study areas.

(microsite 5), and to a lesser degree in the middle snowbank (microsite 4). Coastal species are never more than 2% of the total flora found in any microsite. The relatively high numbers of arctic and arctic-boreal species in the snowbed sites are somewhat puzzling, because these categories would seem to have very different characteristics. Because these species are never more than 2% of the total flora found in any microsite. The relatively high numbers of arctic and arctic-boreal species in the snowbed sites are somewhat puzzling, because these categories would seem to have very different characteristics. Because these are based on proportions, the categories are not independent. A decrease in one category will lead necessarily to an increase in another. These relatively high numbers of arctic and arctic-boreal species could be, therefore, merely a reflection of the low numbers of arctic-alpine

species in these sites. The arctic-alpine species are primarily in the snow-free sites.

Abundance of the circumpolar types is significantly higher on the summits (microsite 2) than in the other microsites (Fig. 84; Kruskal-Wallis test $\chi^2 = 60.66$, $p < .0001$). The circumpolar species are found throughout the arctic and there-sites.

Abundance of the circumpolar types is significantly higher on the summits (microsite 2) than in the other microsites (Fig. 84; Kruskal-Wallis test $\chi^2 = 60.66$, $p < .0001$). The circumpolar species are found throughout the arctic and therefore should be widely adapted to many conditions. Their presence on these disturbed sites suggests this is the case. Cooper (1989) also found circumpolar species to be most abundant on unstable sites in the Arrigetch Valley of the Brooks Range. They are the majority of the flora

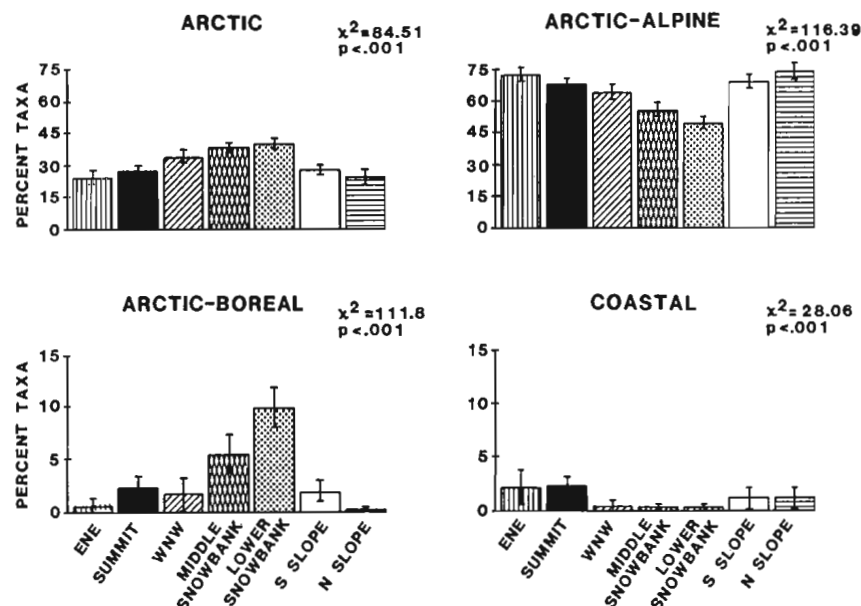


Figure 83. Distribution of the environmental region categories within each of the microsites. Chi-square values are based on Kruskal-Wallis test. Error bars represent the 95% confidence interval.

in all of the microsites. North American-Asian species show a corresponding decrease in importance in microsite 2, but are not particularly different between the other sites. The Beringian endemics are included in this figure, which includes all North American-Asian categories. The south slopes (microsite 6), which are where the restricted species are most common, do not show striking differences from the other microsites with regard to geographic range types.

There are differences in the distribution of all North American-Asian categories. The south slopes (microsite 6), which are where the restricted species are most common, do not show striking differences from the other microsites with regard to geographic range types.

There are differences in the distribution of northern limit types by microsite, except in the most common category, zone 2 (Fig. 85). The differences within the zone 1, 3, and 4 species do make sense in terms of warmth. This is expected because of the definition of the

northernmost, are most common on the ENE side and north slope, which are the coldest sites, probably both in winter and summer. Summer ground temperatures on north slopes are colder than temperatures on flat mesic tundra. In winter these sites are mostly snow-free, and so have little protection from winds and low air temperatures. Zone 3 species are least common in these same sites, and most common in the snowbank and south slope sites. There are no temperature data available for the snowbanks, but the these sites are mostly snow-free, and so have little protection from winds and low air temperatures. Zone 3 species are least common in these same sites, and most common in the snowbank and south slope sites. There are no temperature data available for the snowbanks, but the deep drifts that form there probably stabilize winter temperatures, and these sites likely have temperatures close to flat surfaces in summer, as they face nearly due west. The south slopes are warmer than other microsites in the summer.

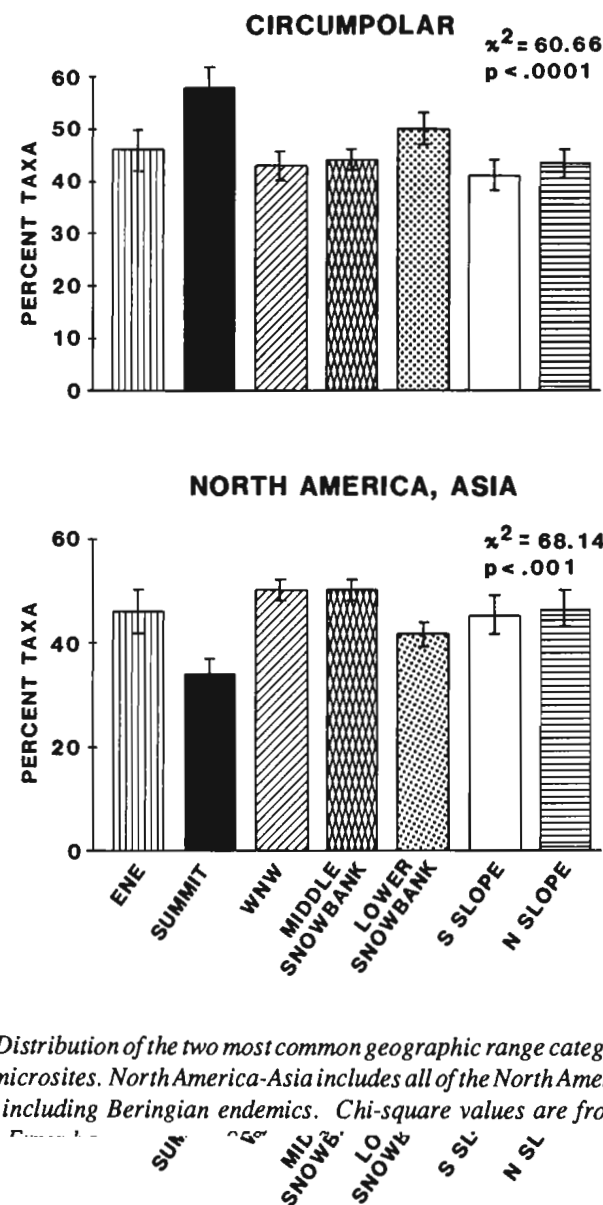


Figure 84. Distribution of the two most common geographic range categories within each of the microsites. North America-Asia includes all of the North American-Asian categories, including Beringian endemics. Chi-square values are from Kruskal-Wallis test. Error bars represent 95% confidence interval.

Figure 84. Distribution of the two most common geographic range categories within each of the microsites. North America-Asia includes all of the North American-Asian categories, including Beringian endemics. Chi-square values are from Kruskal-Wallis test. Error bars represent 95% confidence interval.

region, as defined by the oil field boundaries, is north of the zone 4 line (Young 1971), but there are a few zone 4 species at Prudhoe Bay (Walker 1985a). On the

pingos they are never very abundant, but they are significantly more important on summits and south slopes, which are the warmest sites.

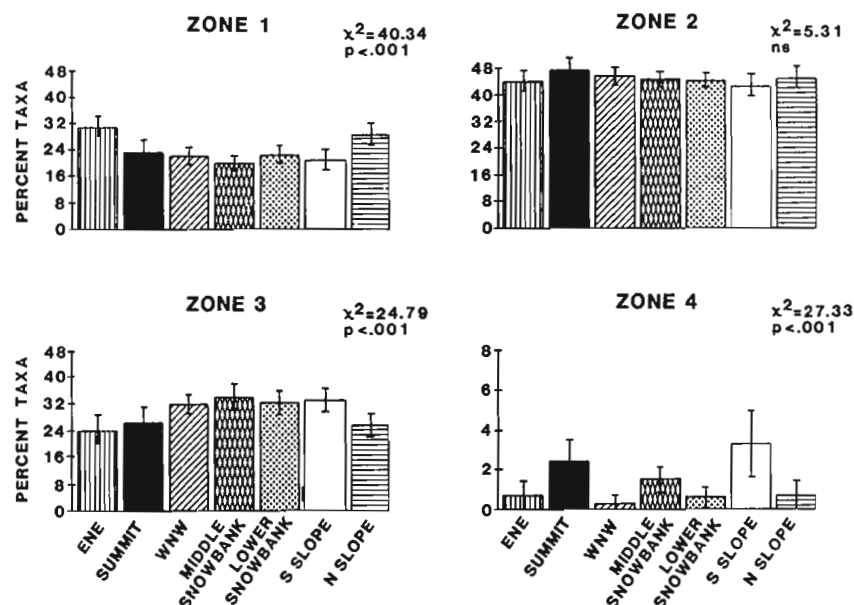


Figure 85. Distribution of the northern limit categories within the seven microsites. Chi-square values are from Kruskal-Wallis test. Error bars represent the 95% confidence interval.

Community Patterns

The stand types and facies do not differ greatly with respect to environmental region types (Table 37). All stand types and facies have arctic-alpine species the most common, and arctic the second most common. The few differences that show up are in the relative percentages of coastal and arctic-boreal species. Stand Types *Phippsia algida* - *Saxifraga rivularis*, *Salix rotundifolia* - stand types and facies have arctic-alpine species the most common, and arctic the second most common. The few differences that show up are in the relative percentages of coastal and arctic-boreal species. Stand Types *Phippsia algida* - *Saxifraga rivularis*, *Salix rotundifolia* - *Dryas integrifolia*, and *Cassiope tetragona* - *Dryas integrifolia* have high numbers of arctic-boreal species compared to the other types, with Facies *Ledum decumbens* - *Betula nana* the highest at 16%. Most of the types within

epibryon have no arctic-boreal species and generally no coastal species. The exception is Stand Type *Cerastium beer- ingianum* - *Minuartia rubella*, which is a coastal type, with 10% coastal species, much higher than the mean of 1% for all stand types. The highest amounts of arctic-alpine species are in the most exposed sites, primarily within Group *Dryas integrifolia* - *Lecanora epibryon*, which supports the idea that these sites are similar to alpine fellfields.

Distribution of geographic types within the stand types and facies reflects their general distribution (Table 38). Circumpolar species are most important in the great majority of stands. The exceptions are Stand Type *Dryas integrifolia* - *Oxytropis nigrescens*, its asso-

Table 37. Percentages of each of the four environmental regions within the stand types and facies. The highest percentage in each row is in bold type. Abbreviations are in Tables 19-21.

Stand Type/ Facies	ENVIRONMENTAL REGIONS			
	Arctic	Arctic-Alpine	Arctic-Boreal	Coastal
ST Saxbro-Sphglo	17.2 ± 2.9	80.1 ± 4.4	2.7 ± 1.8	0
F Rhalan-Polpil	16.7 ¹	83.0	0	0
ST Cerbee-Minrub	27.0 ± 5.5	63.0 ± 4.7	0	10.0 ± 2.1
ST Dryint-Oxynig	19.5 ± 1.8	78.5 ± 1.9	.16 ± .16	1.8 ± .74
F Carnar-Calpur	12.9 ± 4.5	87.1 ± 4.5	0	0
ST Dryint-Astumb	31.3 ± 1.3	68.2 ± 1.5	0	.48 ± .34
F Kobmyo-Pedcap	30.9 ± 2.0	69.1 ± 2.0	0	0
F Carbig-Castet	30.0 ± 4.7	70.1 ± 4.7	0	0
ST Cerbee-Ranped	26.9 ± .86	68.4 ± 1.3	1.7 ± .41	3.1 ± .71
F Fesfab-Luzcon	27.5 ± 1.1	68.9 ± 1.4	1.2 ± .48	2.3 ± .72
F Trispi-Luzcon	25.6 ± 1.2	70.3 ± 1.7	1.7 ± .59	2.4 ± .78
ST Poagla-Bropum	28.4 ± 2.0	67.0 ± 2.4	4.1 ± .97	.54 ± .39
F Pothoo-Polacu	30.2 ± 7.6	62.5 ± 9.6	7.3 ± 2.6	0
F Artglo	16.7 ¹	83.3	0	0
F Carobt-Saxtri	25.8 ± 2.6	72.5 ± 2.7	1.7 ± .69	0
F Kobmyo-Salgla	31.6 ± 2.2	61.6 ± 1.2	5.3 ± 1.8	1.4 ± .97
ST Carrup-Saxopp	28.8 ± 1.5	70.0 ± 1.7	.53 ± .30	.64 ± .36
F Carpet-Camar	22.7 ± 2.5	76.4 ± 3.4	.93 ± .93	0
F Carfra-Salnip	26.7 ± 6.7	73.3 ± 6.7	0	0
F Carrup-Saxopp	30.8 ± 1.7	67.8 ± 2.0	.46 ± .32	.89 ± .49
ST Phialg-Saxriv	41.9 ± 2.7	42.0 ± 3.7	9.2 ± 3.9	6.9 ± 3.5
ST Salrot-Dryint	41.2 ± 1.6	48.8 ± 1.5	9.6 ± 1.0	.36 ± .20
F Salrot-Oxydig	31.2 ± 3.3	57.7 ± 2.0	9.2 ± 2.8	1.8 ± .90
F Salrot-Eritri	43.3 ± 1.6	46.0 ± 1.6	10.7 ± 1.1	0
ST Castet-Dryint	37.2 ± 1.2	56.1 ± 1.4	6.6 ± .87	.09 ± .09
F Leddec-Betnan	34.9 ± 3.3	49.5 ± 3.6	15.6 ± 2.2	0
F Arcrub-Rholap	33.8 ± 2.2	60.8 ± 2.0	5.5 ± 1.6	0
F Castet-Dryint	39.9 ± 2.4	55.7 ± 2.5	4.2 ± .90	.23 ± .23
ST Salrot-Dryint	41.2 ± 1.6	48.8 ± 1.5	9.6 ± 1.0	.36 ± .20
F Salrot-Oxydig	31.2 ± 3.3	57.7 ± 2.0	9.2 ± 2.8	1.8 ± .90
F Salrot-Eritri	43.3 ± 1.6	46.0 ± 1.6	10.7 ± 1.1	0
ST Castet-Dryint	37.2 ± 1.2	56.1 ± 1.4	6.6 ± .87	.09 ± .09
F Leddec-Betnan	34.9 ± 3.3	49.5 ± 3.6	15.6 ± 2.2	0
F Arcrub-Rholap	33.8 ± 2.2	60.8 ± 2.0	5.5 ± 1.6	0
F Castet-Dryint	39.9 ± 2.4	55.7 ± 2.5	4.2 ± .90	.23 ± .23
ST Dryint-Astumb-Carrup	34.0 ± 1.7	65.1 ± 1.6	.56 ± .27	.40 ± .22
F Dryint-Astumb-Kobmyo	31.8 ± 3.3	66.4 ± 3.2	.86 ± .58	.87 ± .58
F Carrup-Oxynig	34.9 ± 2.1	64.6 ± 2.1	.50 ± .34	.22 ± .22

Table 38. Percentages of each of the geographic types within the stand types and facies. The North American types are combined here, as are all of the North America, Asia types, including Beringian endemics. The highest value in each row is in bold type; abbreviations are in Tables 19-21.

Stand Type/ Facies	GEOGRAPHIC RANGE				
	Circumpolar	N Amer, Asia Europe	N Amer, Asia	N America	Alaska-Yukon Endemic
ST Saxbro-Sphglo	53.4 ± 4.5	6.1 ± 2.8	32.0 ± 6.6	5.9 ± 3.1	2.7 ± 1.7
F Rhalan-Polpil	41.7 ¹	8.3	25	16.7	8.3
ST Cerbee-Minrub	59.5 ± 5.9	7.3 ± 2.5	27.5 ± 4.0	4.5 ± 2.6	1.4 ± 1.4
ST Dryint-Oxynig	43.4 ± 1.4	3.9 ± .71	47.6 ± 9.5	4.1 ± .77	1.4 ± .49
F Camar-Calpur	40.4 ± 1.3	4.4 ± 4.4	48.9 ± 1.1	6.4 ± 2.0	0
ST Dryint-Astumb	42.6 ± 1.6	3.4 ± .75	49.5 ± 8.6	3.3 ± .72	1.2 ± .47
F Kobmyo-Pedcap	39.9 ± 1.6	4.8 ± 1.1	51.1 ± 2.0	2.7 ± 1.2	1.4 ± .97
F Carbig-Castet	56.6 ± 3.4	1.5 ± 1.5	38.8 ± 1.4	1.5 ± 1.5	1.5 ± 1.5
ST Cerbee-Ranped	59.6 ± 3.4	4.7 ± .75	33.0 ± 9.0	1.8 ± .50	.88 ± .31
F Feshaf-Luzcon	64.3 ± 2.7	2.8 ± .91	31.5 ± 2.6	.55 ± .37	.84 ± .46
F Trispi-Potuni	56.4 ± 2.0	7.0 ± 1.1	33.2 ± 2.1	2.3 ± .61	1.1 ± .53
ST Poagla-Bropum	46.3 ± 2.2	7.2 ± 1.1	39.3 ± 6.6	4.9 ± 1.0	2.3 ± .74
F Pothoo-Polacu	50.2 ± 5.4	7.4 ± 2.0	38.6 ± 3.8	3.8 ± 2.2	0
F Artglo	41.7 ¹	16.7	41.7	0	0
F Carobt-Saxtri	37.1 ± 1.8	10.6 ± .99	40.7 ± 2.4	7.8 ± 1.6	3.8 ± 1.4
F Kobmyo-Salgla	54.1 ± 2.3	2.5 ± 1.1	37.8 ± 2.5	3.2 ± 1.3	2.4 ± 1.2
ST Carrup-Saxopp	39.0 ± 2.0	3.7 ± .80	49.5 ± 10.3	6.6 ± 1.2	1.3 ± .55
F Carpet-Camar	34.5 ± 1.9	5.6 ± 1.3	44.8 ± 3.3	12.1 ± 3.2	3.0 ± 2.0
F Carfra-Salnip	40.0 ± 0	6.7 ± 0	46.7 ± .00	0	6.7 ± 0
F Carrup-Saxopp	40.1 ± 2.6	2.8 ± 1.0	51.1 ± 2.4	5.6 ± 1.1	.26 ± .26
ST Phialg-Saxriv	72.6 ± 10.4	4.2 ± 2.7	21.8 ± 15.8	0	1.4 ± 1.4
ST Salrot-Dryint	50.5 ± 1.6	2.9 ± .61	42.0 ± 8.6	1.7 ± .51	2.9 ± .48
F Salrot-Oxydig	53.0 ± 5.8	7.5 ± 1.5	33.9 ± 3.4	3.3 ± 1.7	2.2 ± .81
F Salrot-Eritri	49.2 ± 1.5	2.1 ± .54	43.8 ± 1.5	1.5 ± .52	3.4 ± .59

Table 38 Continued

F Leddec-Beman	51.1 ± 2.0	1.8 ± .93	45.2 ± 2.6	1.5 ± 1.2	.38 ± .38
F Arcrub-Rholap	43.2 ± 2.2	2.4 ± 1.0	48.2 ± 2.7	2.9 ± .78	3.3 ± .95
F Castet-Dryint	42.7 ± 1.5	1.4 ± .52	50.7 ± 1.4	3.7 ± .64	1.4 ± 5.0
ST Dryint-Astumb-Carrup	42.3 ± 1.4	2.4 ± .61	50.4 ± 7.8	3.8 ± .50	1.1 ± .38
F Dryint-Astumb-Kobmyo	42.0 ± 1.7	3.6 ± 1.1	48.8 ± 1.2	4.6 ± .86	.98 ± .66
F Carrup-Oxynig	42.4 ± 1.8	1.5 ± .77	51.4 ± 1.8	3.9 ± .63	.73 ± .41

¹n=1.

folia - *Astragalus umbellatus* and Facies *Kobresia myosuroides* - *Pedicularis capitata* within it, Facies *Carex obtusata* - *Saxifraga tricuspidata*, Stand Type *Carex rupestris* - *Saxifraga oppositifolia* and its facies, Stand Type *Cassiope tetragona* - *Dryas integrifolia* and Facies *Arctous rubra* - *Rhododendron lapponicum* and *Cassiope tetragona* - *Dryas integrifolia* within it, and Stand Type *Dryas integrifolia* - *Astragalus umbellatus* - *Carex rupestris* and the facies within it, all of which have more North American-Asian than circumpolar species.

Distribution of northern limit types varies considerably between the classifications (Table 39). Most stand types and facies have zone 2 the most common, followed by zone 3, which is the overall pattern. There are quite a few that do not follow this pattern, however. Facies

Distribution of northern limit types varies considerably between the classifications (Table 39). Most stand types and facies have zone 2 the most common, followed by zone 3, which is the overall pattern. There are quite a few that do not follow this pattern, however. Facies *Rhacomitrium lanuginosum* - *Polytrichum piliferum* is equally divided between zone 1 and zone 2, and the ENE side and north slope types in general have higher percentages of zone 1 species.

the steppe-tundra types have higher percentages of zone 3 than zone 2 species: Stand Type *Poa glauca* - *Bromus pumellianus* and all of its facies, Facies *Carex franklinii* - *Salix brachycarpa* ssp. *niphoclada*, and Facies *Arctous rubra* - *Rhododendron lapponicum*. Zone 4 species are of minimal importance to almost all types. An important exception is Facies *Carex obtusata* - *Saxifraga tricuspidata*, which is the best example of a steppe-tundra type.

Distribution of restricted species indicates that they are not randomly distributed, but are most common in the steppe types (Table 40). Although the mean number of restricted species for a given sample plot is only 1.2 ± .06, within Stand Type *Carex obtusata* - *Saxifraga obtusata* the mean is 4.2 ± .88.

Comparison with Other Regions

distributed, but are most common in the steppe types (Table 40). Although the mean number of restricted species for a given sample plot is only 1.2 ± .06, within Stand Type *Carex obtusata* - *Saxifraga obtusata* the mean is 4.2 ± .88.

Comparison with Other Regions

Comparison of the pingo flora to four other selected floras is shown in Table 41. The two figures represent Sørensen's (1948) index of similarity

Table 39. Percentages of each of the four northern limit types (Young 1971) within the stand types and facies. The highest values in each row are in bold type; abbreviations are in Tables 19-21.

Stand Type/ Facies	NORTHERN LIMIT ZONES			
	Zone 1	Zone 2	Zone 3	Zone 4
ST Saxbro-Sphglo	26.2 ± 5.4	44.7 ± 3.3	25.4 ± 3.8	3.7 ± 2.3
F Rhalan-Polpil	33.3 ¹	33.3	25.0	8.3
ST Cerbee-Minrub	36.5 ± 4.8	55.9 ± 2.2	7.6 ± 3.6	0
ST Dryint-Oxynig	31.3 ± 1.5	46.0 ± 1.6	22.3 ± 1.8	.32 ± .32
F Carnar-Calpur	23.2 ± 10.1	51.3 ± 9.6	25.5 ± .54	0
ST Dryint-Astumb	27.5 ± 1.8	41.9 ± 2.0	30.0 ± 2.1	.64 ± .30
F Kobmyo-Pedcap	17.0 ± 2.3	43.7 ± 4.2	37.2 ± 3.4	2.1 ± .84
F Carbig-Castet	28.8 ± 6.0	43.1 ± 6.1	28.1 ± 11.0	0
ST Cerbee-Ranped	25.4 ± 1.8	54.3 ± 1.4	18.8 ± 1.5	1.5 ± .43
F Fesbaf-Luzcon	31.7 ± 2.9	49.1 ± 2.4	18.4 ± 2.7	.80 ± .43
F Trispi-Potuni	18.6 ± 1.7	58.9 ± 1.3	20.8 ± 1.7	1.7 ± .68
ST Poagla-Bropum	13.1 ± 1.4	37.2 ± 1.7	43.4 ± 2.0	6.3 ± 1.3
F Pothoo-Polacu	17.0 ± 1.9	32.3 ± 4.9	48.8 ± 4.9	1.9 ± 1.1
F Artglo	0	50.0 ¹	50.0	0
F Carobt-Saxtri	12.4 ± 2.1	37.6 ± 2.6	37.7 ± 3.6	12.3 ± .98
F Kobmyo-Salgla	13.4 ± 2.3	37.6 ± 2.2	45.7 ± 1.9	3.3 ± 1.7
ST Carrup-Saxopp	24.8 ± 1.6	41.0 ± 1.8	32.3 ± 1.7	2.0 ± .86
F Carpet-Carnar	15.9 ± 1.2	45.4 ± 5.2	31.0 ± 5.7	7.6 ± 3.1
F Carfra-Salnip	16.7 ± 3.3	33.3 ± 6.7	43.4 ± 3.3	6.7 ± 0
F Carrup-Saxopp	28.1 ± 1.8	40.4 ± 1.9	31.4 ± 1.7	0
ST Phialg-Saxriv	34.2 ± 11.4	46.9 ± 4.8	16.2 ± 6.8	2.8 ± 2.8
ST Salrot-Dryint	24.5 ± 1.3	45.7 ± 1.2	29.4 ± 1.7	.35 ± .20
F Salrot-Oxydig	25.1 ± 4.1	46.2 ± 3.2	27.7 ± 4.8	1.0 ± .65
F Salrot-Eritri	23.8 ± 1.4	45.5 ± 1.4	30.5 ± 1.9	.21 ± .21
ST Castet-Dryint	18.3 ± 1.1	43.4 ± 1.1	36.7 ± 1.8	1.5 ± .31
F Leddec-Betnan	14.3 ± 1.5	43.3 ± 3.1	39.8 ± 3.6	2.6 ± .87
F Arcrub-Rholap	11.9 ± .65	36.1 ± 1.7	50.5 ± 1.7	1.5 ± .68
F Castet-Dryint	23.1 ± 1.6	47.8 ± 1.4	27.8 ± 2.0	1.3 ± .48
ST Salrot-Dryint	24.5 ± 1.3	45.7 ± 1.2	29.4 ± 1.7	.35 ± .20
F Salrot-Oxydig	25.1 ± 4.1	46.2 ± 3.2	27.7 ± 4.8	1.0 ± .65
F Salrot-Eritri	23.8 ± 1.4	45.5 ± 1.4	30.5 ± 1.9	.21 ± .21
ST Castet-Dryint	18.3 ± 1.1	43.4 ± 1.1	36.7 ± 1.8	1.5 ± .31
F Leddec-Betnan	14.3 ± 1.5	43.3 ± 3.1	39.8 ± 3.6	2.6 ± .87
F Arcrub-Rholap	11.9 ± .65	36.1 ± 1.7	50.5 ± 1.7	1.5 ± .68
F Castet-Dryint	23.1 ± 1.6	47.8 ± 1.4	27.8 ± 2.0	1.3 ± .48
ST Dryint-Astumb-Carrup	22.7 ± 1.4	45.9 ± 1.4	31.0 ± 1.7	.36 ± .20
F Dryint-Astumb-Kobmyo	17.4 ± 1.7	44.0 ± 2.6	37.5 ± 3.3	.86 ± .58
F Carrup-Oxynig	25.7 ± 1.6	46.5 ± 1.8	27.7 ± 1.8	.16 ± .16

Table 40. Mean number of restricted species within the stand types and facies. Values greater than one are bold faced.

Stand Type/Facies	Number of Species	Stand Type/Facies	Number of Species
S Saxbro-Sphglo	.60 ± .40	S Carrup-Saxopp	1.3 ± .31
F Rhalan-Polpil	1.0	F Carpet-Carnar	3.5 ± .99
S Cerbee-Minrub	.25 ± .25	F Carfra-Salnip	2.0 ± 0
S Dryint-Oxynig	.38 ± .18	F Carrup-Saxopp	.57 ± .11
F Carnar-Calpur	2.0 ± 1.0	S Phialg-Saxriv	1.2 ± .63
S Dryint-Astumb	.80 ± .15	S Salrot-Dryint	.17 ± .07
F Kobmyo-Pedcap	1.6 ± .29	F Salrot-Oxydig	.57 ± .30
F Carbig-Castet	.33 ± .33	F Salrot-Eritri	.04 ± .04
S Cerbee-Ranped	.37 ± .09	S Castet-Dryint	.57 ± .09
F Fesbaf-Luzcon	.27 ± .12	F Leddec-Betnan	.67 ± .24
F Trispi-Potuni	.44 ± .16	F Arcrub-Rholap	.93 ± .27
S Poagla-Bropum	2.0 ± .53	F Castet-Dryint	.29 ± .10
F Pothoo-Polacu	.50 ± .29	S Dryint-Astumb-Carrup	.56 ± .73
F Artglo	0	F Dryint-Astumb-Kobmyo	1.3 ± .20
F Carobt-Saxtri	4.2 ± .88	F Carrup-Oxynig	.27 ± .12
F Kobmyo-Salgla	.75 ± .31		

Table 41. Comparison of the pingo flora with four other floras. Index of similarity is according to Sørensen (1948). Percent of pingo flora is the percentage of the pingo flora present in the other area.

Area	Number of Species in Common	Index of Similarity	Percent of Pingo Flora
Prudhoe Bay (D.A. Walker 1985)	167	70.0	72.0
Lake Peters, northern Brooks Range (Batten 1977)	175	67.4	75.4
Arrigetch Creek Valley, southern Brooks Range	145	62.2	62.5
Prudhoe Bay (D.A. Walker 1985)	167	70.0	72.0
Lake Peters, northern Brooks Range (Batten 1977)	175	67.4	75.4
Arrigetch Creek Valley, southern Brooks Range (Cooper 1987)	145	62.2	62.5
Indian Peaks, Colorado (Komárková 1979)	53	21.9	22.8

$IS_s = 2c/A+B$, where c is the total number of species in common, and A and B are the total number of species at each of the two areas.

in the other area. These are slightly different statistics. The index of similarity indicates similarity between the two floras, but in this case we are interested also in how much of the pingo flora is shared with that area. This is related again to the increasingly depauperate nature of the flora as one goes north. A High Arctic area with only 10 species could have 100% of those present in another area, and yet might have a rather low similarity to that area if it had a much larger flora. In this case the two figures are very similar, although the second generally indicates more similarity than the indices do. The pingo flora is not a complete regional flora, and in this sense the second figure may have more meaning.

The pingo flora is a partial subset of the Prudhoe Bay region, but this study covered a broader area. Within the Prudhoe Bay region, there are 245 vascular plant taxa (Walker 1985a). At the family level, the two floras are quite similar (Table 42), but only 72% (167) of the pingo flora is within the Prudhoe Bay flora, including those species that are probably only at Prudhoe Bay because the pingos are there. The greater number of restricted species on the south slopes of pingos suggests that these habitats are probably not found elsewhere on the coastal plain. The steep temperature gradient in this region, combined with the extension of this study further to the south and the increased temperatures on the south slopes, results in a unique flora of pingos suggests that these habitats are probably not found elsewhere on the coastal plain. The steep temperature gradient in this region, combined with the extension of this study further to the south and the increased temperatures on the south slopes, results in a unique flora that contains elements not common in the Prudhoe Bay mesic tundra. Also, many species that are common within the Prudhoe Bay region are not found on the pingos because the appropriate habitats are not present, primarily species

common in wet and aquatic habitats or in specialized habitats, such as frost scars and sand dunes.

While the similarity index between the pingos and the Lake Peters area in the northern Brooks Range (Batten 1977) is somewhat lower than between the pingos and Prudhoe Bay, the number of species in common is actually higher. This indicates the alpine character of the pingo vegetation and its links to the Brooks Range. The pingos share a number of vegetation elements with the Arrigetch Creek area described by Cooper (1986), and the floras of the two areas also share nearly two-thirds of their species. Comparison to the Indian Peaks region is shown as an example of a well-known region in the Colorado Rockies. Twenty-two percent of the pingo flora is in common with this region.

The somewhat higher numbers of North American and Alaskan-Yukon endemics within the species restricted to the pingos, along with the high numbers of zone 3 and 4 species in this group, suggests a possible link to interior Alaska. Young (1982) has suggested that if there was an extensive full-glacial steppe in Beringia, it was probably best developed in the interior region. The climate of these areas would have been more continental than today, although mean temperatures were undoubtedly colder (Barry 1982). If this were the case, then this region is perhaps the best place to look for modern analogs.

... Murray et al. (1983) examined species assemblages that they hypothesized are relicts along steep, south-facing bluffs of the Yukon, Copper, and Tanana Rivers in the interior region of Alaska. A number of the vascular species restricted to the sites within the interior boreal

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Table 42. Number of vascular taxa in plant families recorded in this study and in the Prudhoe Bay region (Walker 1985a).

Family	PINGOS		PRUDHOE BAY REGION	
	Number	Percent	Number	Percent
Graminae	27	11.6	31	13.0
Compositae	24	10.3	22	9.2
Cyperaceae	24	10.3	29	12.2
Cruciferae	22	9.5	21	8.8
Saxifragaceae	15	6.5	15	6.3
Leguminosae	14	6.0	13	5.5
Salicaceae	13	5.6	12	5.0
Caryophyllaceae	12	5.2	15	6.3
Rosaceae	11	4.7	8	3.4
Ranunculaceae	10	4.3	11	4.6
Ericaceae	8	3.4	5	2.1
Papaveraceae	6	2.6	2	0.8
Juncaceae	5	2.2	9	3.8
Polygonaceae	5	2.2	4	1.7
Scrophulariaceae	5	2.2	10	4.2
Liliaceae	4	1.7	2	0.8
Primulaceae	4	1.7	4	1.7
Equisetaceae	3	1.3	3	1.3
Polemoniaceae	3	1.3	3	1.3
Pyrolaceae	3	1.3	2	0.8
Onagraceae	2	0.9	2	0.8
Umbelliferae	2	0.9	1	0.4
Betulaceae	1	0.4	0	0
Boraginaceae	1	0.4	2	0.8
Campanulaceae	1	0.4	1	0.4
Gentianaceae	1	0.4	2	0.8
Halorgaceae	1	0.4	2	0.8
Lycopodiaceae	1	0.4	1	0.4
Plumbaginaceae	1	0.4	2	0.8
Polypodiaceae	1	0.4	0	0
Boraginaceae	1	0.4	2	0.8
Campanulaceae	1	0.4	1	0.4
Gentianaceae	1	0.4	2	0.8
Halorgaceae	1	0.4	2	0.8
Lycopodiaceae	1	0.4	1	0.4
Plumbaginaceae	1	0.4	2	0.8
Polypodiaceae	1	0.4	0	0
Valerianaceae	1	0.4	1	0.4
Selaginellaceae	1	0.4	0	0
Crassulaceae	0	0	1	0.4
Lentibulariaceae	0	0	1	0.4
Sparganiaceae	0	0	1	0.4
TOTAL	232	100	238	100

Table 43. Species found on pingos that were listed by Murray *et al.* (1983) as restricted in subarctic (interior) Alaska and Yukon to steep, south-facing river bluffs. An asterisk indicates the species is thought to be restricted to pingos within the region of this study.

VASCULAR SPECIES

Carex supina ssp. *spaniocarpa**
Lesquerella arctica
Potentilla hookeriana
*Pulsatilla patens**
*Selaginella sibirica**

MOSSES

Encalypta rhabdocarpa
Hylocomium splendens
Polytrichum piliferum
Rhytidium rugosum
Thuidium abietinum
Tortella fragilis
Tortula ruralis

LICHENS

Caloplaca stillicidiorum
Cetraria nivalis
Cladonia pyxidata
Cornicularia aculeata
Peltigera aphthosa
*P. lepidophora*¹
*Phaeophyscia constipata**
Physconia muscigena
Rinodina roscida
Toninia caeruleonigricans

¹A new record for this region, probably overlooked.

forest are plants of the true steppes, such as *Carex filifolia*, *Linum lewisii*, *Phlox hoodii*, and *Townsendia hookeri*. Other species, such as *Selaginella sibirica*, are considered steppe-tundra plants. These areas, therefore, may represent a critical link between the steppe-tundras and the true steppes. Table 43 lists the species that Murray *et al.* listed as restricted to these bluffs within that region and that are also found on pingos. There are only five vascular species on the list, but three of them are restricted primarily to the pingos, and all of them are primarily found on south slopes (*Potentilla hookeriana* is also common on summits).

Table 43 lists the species that Murray *et al.* listed as restricted to these bluffs within that region and that are also found on pingos. There are only five vascular species on the list, but three of them are restricted primarily to the pingos, and all of them are primarily found on south slopes (*Potentilla hookeriana* is also common on summits). The bryophytes listed are all common on the pingos, as are almost all of the lichens. The exception is *Phaeophyscia constipata*, which is listed by Thomson (1984) as "very rare arctic-alpine."

locality is only the third in Alaska; the other is in the Aleutian Islands. Its ecological importance to the steppe question is uncertain, but its rarity, combined with its presence in two very distant sites, both of which are believed to represent possible relicts, is difficult to explain based on long-distance dispersal. It was found in only two plots, both on the same pingo, in Stand Type *Carex obtusata* - *Saxifraga tricuspidata* and Stand Type *Trisetum spicatum* - *Potentilla uniflora*, both of which are considered steppe tundras here.

explain based on long-distance dispersal. It was found in only two plots, both on the same pingo, in Stand Type *Carex obtusata* - *Saxifraga tricuspidata* and Stand Type *Trisetum spicatum* - *Potentilla uniflora*, both of which are considered steppe tundras here.

Biogeography

Species-Area Correlations

Number of species is significantly correlated with pingo area for all species

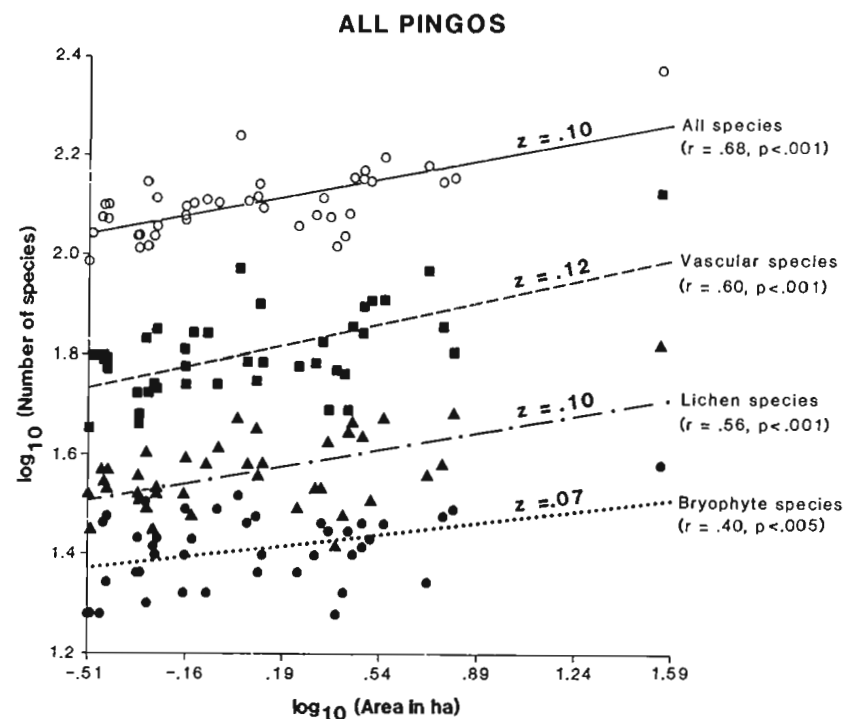


Figure 86. Correlation of number of species with pingo area. The z symbol represents the slope of the line.

subgroups (Fig. 86). The value of z for vascular species (.10) is at the lower limit of the expected range for a mainland site (MacArthur and Wilson 1967), and for all other groups it is below this value. The intercepts of these lines reflect the relative richness of the three subgroups. Both the slope and the correlation coefficient increase as the relative richness of the subgroups increases. The intercept of the line for vascular species (.10) is at the lower limit of the expected range for a mainland site (MacArthur and Wilson 1967), and for all other groups it is below this value. The intercepts of these lines reflect the relative richness of the three subgroups. Both the slope and the correlation coefficient increase as the relative number of species increases, going from bryophytes to lichens to vascular plants. The low slopes for the cryptogams suggest a non-equilibrium condition where colonization rates are high compared to extinction rates. Colonization rate is

area than on island size. Cryptogams reproduce by spores and are therefore more efficient at dispersal than vascular species. Habitat may not be limiting for cryptogams when measured at this scale.

When Koranda (1970) and Walker (1985a) made the suggestion that pingos are islands, they were certainly referring to steep-sided types. The broad-based pingos are generally similar to other mesic uplands present in the gently rolling thaw-lake plains; until an ice core was confirmed in one of them (pingo 16; Brockett 1982), there was considerable doubt that they were pingos at all. When

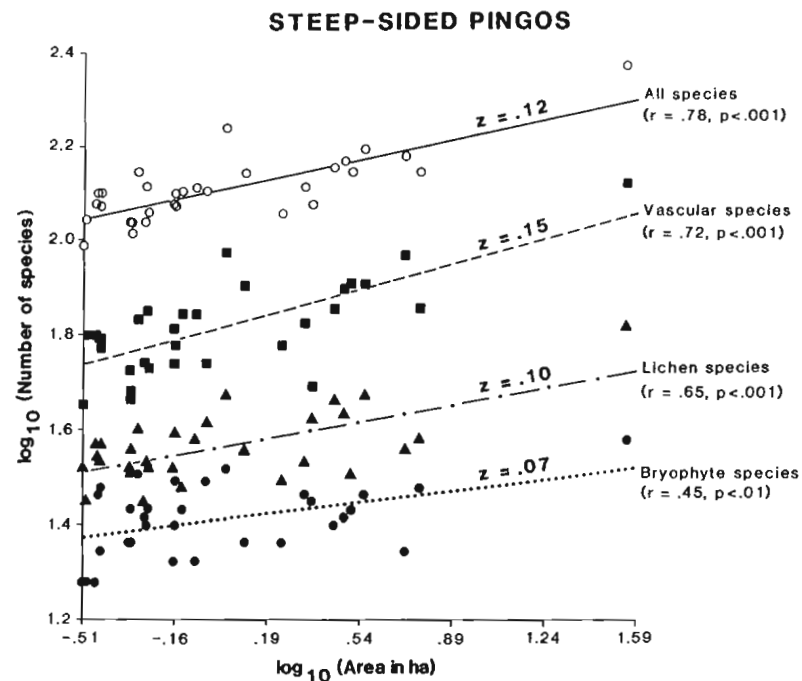


Figure 87. Correlations of number of species with steep-sided pingo area.

the analyses, the slope of the vascular species increases to .15, and all of the correlations increase in strength (Fig. 87), so it appears that the steep-sided pingos are more island-like than the broad-based forms, but the slopes of their species-area curves are still well within the range expected for a mainland site. Thus, the pingos do not function as isolated islands.

If the vascular species that are regionally restricted to pingos are analyzed separately, however, a different picture emerges (Fig. 88). While the correlation with area is not as strong for this group as it is when all vascular species are considered ($r = .49$, $p < .05$), it is significant, and the z value of .24 is within the range of .20 to .35 expected

for an oceanic island (MacArthur and Wilson 1967). There are two possible interpretations for this. One is that all of these species really are restricted to certain sites on the pingos within this region, but they are moving about between sites, and thus this value represents an island type of equilibrium. The other possibility is that some of these species are more common than they are thought to be based on current collections, and this group of species can freely colonize the pingo by short-distance dispersal. The remainder of the species in this scenario, however, would not be in equilibrium, and thus would be relict and not actively dispersing today. In this case the value of z is midway between the value expected for a non-equilibrium

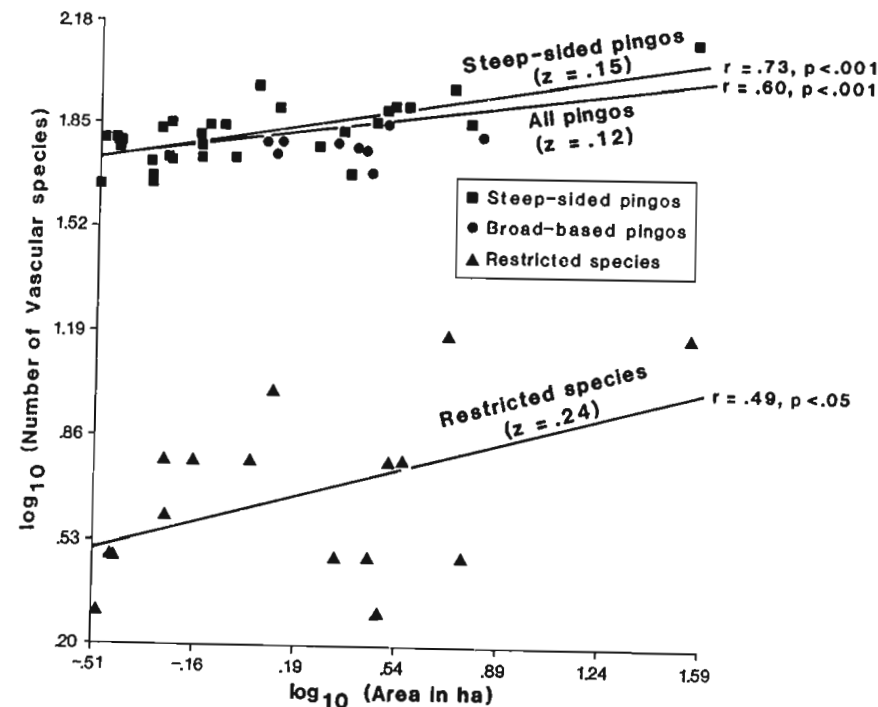


Figure 88. Correlations of vascular species with pingo area, comparing steep-sided pingos, broad-based pingos, and restricted species.

island (above .35) and an equilibrium mainland (below .17). The two scenarios are not mutually exclusive and cannot really be separated. This is not a particular problem for this study, however, as they both support the idea that at least some of these species are relict. In the first instance they are all relict regionally but able to colonize new sites where habitats are appropriate. In the second instance some are not relict at all, particular problem for this study, however, as they both support the idea that at least some of these species are relict. In the first instance they are all relict regionally but able to colonize new sites where habitats are appropriate. In the second instance some are not relict at all, and the remainder are truly relict in the sense that they are not able to disperse to new sites. The actual situation is likely somewhere in between, and data to be presented in Chapter 6 suggest these species are mostly capable of dispersal.

Correlations with Other Factors

Stepwise multiple regressions were run to determine if variables other than area were related to number of species. For vascular species, height of the pingos, rather than area, best explains number of species (Table 44). A total of five variables entered into the regression equation, and the most variation is explained by having all five variables in the area were related to number of species. For vascular species, height of the pingos, rather than area, best explains number of species (Table 44). A total of five variables entered into the regression equation, and the most variation is explained by having all five variables in the equation. Once height, which accounts for nearly 60% of the variance in number of species, is in the equation, however, the contribution of the other variables is not significant. Temperature (distance to coast), which is the second variable to

Table 44. Multiple regression summary table of number of vascular species (\log_{10}) against environmental and morphological variables.

Step	Variable	Significance	R ²	Significance of Regression
1	Height	.000	.558	<.0001
2	Distance to coast (temp.)	.082	.592	<.0001
3	S.D. of pH	.059	.630	<.0001
4	Area (log)	.593	.633	<.0001
5	Nearest river	.688	.634	<.0001

enter, was shown in Chapter 4 to be closely related to vascular species distribution. It is also correlated with number of vascular species ($r = .352$, $p < .05$), and its contribution to the multiple regression is almost significant.

One variable in Table 44 that requires explanation is the standard deviation of pH. In Chapter 4, pH was shown to be the factor most strongly related to the distribution of cryptogams, and the second most important to the distribution of vascular plants. A significant negative correlation between pH and standard deviation of pH was also demonstrated. Number of species correlates with both pH and standard deviation of pH, and the strength of the correlations is similar. Because pH has been demonstrated to relate to species distributions, standard deviation of pH is an indirect measure of habitat variability. Thus, standard deviation of pH rather than pH was used in the analyses.

The correlation of height with number of vascular species is also likely related to habitat variability, which MacArthur and Wilson (1967) specu-

lated is likely the ultimate factor controlling number of species. Taller pingos have longer, more complex slopes and are therefore likely to have a greater variability of habitats present on them. The direct measurement of habitat variability is difficult, as different species will have different habitat requirements. These data do suggest a correlation between habitat and number of species. The final variable to enter the equation is distance to the nearest river. This variable does not make a significant contribution to the multiple regression, and it is not correlated with number of vascular species ($r = .078$) or with number of bryophytes or lichens. Thus, most of the species on pingos probably did not get there by dispersal from rivers.

The vascular species restricted to pingos show a somewhat different pattern than the other vascular plants (Table 45). In this case temperature (distance to coast) is most important, but height also makes a significant contribution to the regression. Adding standard deviation of pH increases the total variance explained but not significantly, and area

The vascular species restricted to pingos show a somewhat different pattern than the other vascular plants (Table 45). In this case temperature (distance to coast) is most important, but height also makes a significant contribution to the regression. Adding standard deviation of pH increases the total variance explained but not significantly, and area

Table 45. Multiple regression summary table of number of vascular species (\log_{10}) restricted regionally to pingos against environmental and morphological variables.

Step	Variable	Significance	R ²	Significance of Regression
1	Distance to coast (temp.)	.0000	.542	<.0000
2	Height	.000	.794	<.0001
3	S.D. of pH	.152	.806	<.0000
4	Area (log)	.917	.806	<.0001

Table 46. Multiple regression summary table of \log_{10} number of lichen species against environmental and morphological variables.

Step	Variable	Significance	R ²	Significance of Regression
1	Area (log)	.000	.317	.000
2	S.D. of pH	.218	.344	.000
3	Distance to coast (temp.)	.242	.369	.001
4	Height	.144	.405	.001
5	Distance to nearest pingo	.153	.440	.001
6	Distance to nearest river	.621	.444	.002

does not add anything. The restricted species are mainly zone 3 and zone 4

5 Distance to nearest pingo .153 .440 .001

6 Distance to nearest river .621 .444 .002

does not add anything. The restricted species are mainly zone 3 and zone 4 plants; they are most common in the warmer inland areas. These species are not correlated with distance to rivers at any level.

Multiple regression of number of lichen (Table 46) and bryophyte (Table

47) species indicates that these two

groups are controlled by fairly similar factors. The bryophytes are most strongly related to standard deviation of pH, again suggesting that habitat variability is likely very important in determining number of species. Five additional variables also entered the equation, but none

Table 47. Multiple regression summary table of \log_{10} number of bryophyte species against environmental and morphological variables.

Step	Variable	Significance	R ²	Significance of Regression
1	S.D. of pH	.002	.218	.002
2	Area (log)	.180	.255	.004
3	Distance to coast (temp.)	.658	.259	.011
4	Distance to nearest pingo	.700	.262	.024
5	Height	.857	.262	.050
6	Distance to nearest river	.864	.263	.090

significant contribution, and the significance of the regression actually decreases rather than increases when any other variables are included. The lichens are most strongly correlated with area, and standard deviation of pH is the second variable to enter. It does not make an additional significant contribution to the total variance explained, but the maximum amount of information is explained when these two variables are included. Addition of other variables again decreases the regression significance.

Discussion and Conclusions

Boyko's (1947) law of geoeological when these two variables are included. Addition of other variables again decreases the regression significance.

Discussion and Conclusions

Boyko's (1947) law of geoeological distribution, discussed in the last chapter, is applicable here. This law states that the regional and also specific habitat distribution of a species is a reflection of its broader (in this case worldwide) distribution. There are more southerly

more high arctic species in the coldest sites. All the floristic evidence presented supports this law, and again, the pingos are shown to be useful systems to test ideas that are often to difficult to support with direct evidence.

The floristic and biogeographic evidence supports the concept of relict elements on the pingos. The floristic relationships of the restricted species indicate that they are southerly, arctic-alpine species with links to Asia and also to North America. The high percentage of North American-Asian species links these plants to Siberia; the arctic-alpine and zone 3 and 4 species link them to the Brooks Range, and the North American and zone 3 and 4 species link them to interior Alaska. These species are not randomly distributed, but are most common on south slopes, particularly in the steppe-tundra types. Additionally, the species-area analyses indicate that at

relict, and an absence of a link to the rivers, which would be the only plausible modern point of dispersal, further supports this concept. These species are often found together, and the odds of an assemblage of rare species randomly dispersing to the same site are likely less than the odds of their representing a vegetation that was once more widespread and is now limited to a few sites (Murray et al. 1983).

Many of the problems with steppe vegetation were discussed in Chapter IV. These will be briefly reviewed here in order to evaluate all of the evidence simultaneously. There are actually two quite different problems. The first is the classification of present day arctic and alpine types that have a steppe-like character; that is, those that are well-drained and dominated by grasses and forbs. The second and more controversial problem is the hypothesized link between these modern types and the Pleistocene Beringian vegetation. If the modern types are defined by physiognomy and growth form, which was done here, then there is no classification problem. It is still useful, however, to demonstrate floristic and ecological relationships between the various steppe types, including possible links between true steppes and steppe tundras. On the pingos, the primary ecological links are the occurrence of these types on sites with the greatest daily temperature variation (south slopes), and possibly the greatest annual variation, making them more continental than other sites (although certainly still arctic by Köppen's [1936] definition), and the soils on these sites, which are very closely related to the Mollisols of the Great Plains.

It is the link to the past that has been

Pollen is only a crude tool for estimation of past environments, and unless very careful work is done, often utilizing electron microscopy, identification to the species or even the genus level is difficult or impossible. The Graminae, which are an important part of the herb zone pollen strata believed by many to represent a steppe type, are a particularly difficult group. *Artemisia*, which has also been very important in these profiles, cannot be identified to species level (Ritchie 1984). This leads to a variety of possible interpretations based on the same evidence. Nevertheless, it is agreed that the Pleistocene North Slope vegetation was very different than it is today. The climate was probably much drier, and there was a greater importance of grasses and herbaceous species present in the vegetation. There was little or no accumulation of peat during the full glacial approximately 10,000 to 24,000 BP. Between about 8,000 and 10,000 BP there was a catastrophic change, which shows up in the pollen record as an influx of birch (Ager 1982; Giterman et al. 1982; Ritchie and Cwynar 1982; Schweger 1982; and others). This birch influx has been documented as far north as the modern northern coast (Wilson 1984). The birch began to retreat somewhere between 7,000 and 4,000 BP, and this is when the modern vegetation is believed to have become established.

Ritchie (1984; Ritchie and Cwynar 1982) has been a major proponent of the idea that the pollen evidence perhaps fits the modern northern coast (Wilson 1984). The birch began to retreat somewhere between 7,000 and 4,000 BP, and this is when the modern vegetation is believed to have become established.

Ritchie (1984; Ritchie and Cwynar 1982) has been a major proponent of the idea that the pollen evidence perhaps fits the concept of fellfield type of vegetation rather than a steppe. Both steppe and fellfield are herbaceous and grass-dominated, and could be interpreted from the pollen records. Ritchie has cited low pollen influx rates as other evidence for

(1982), who described the Pleistocene vegetation as most likely a mosaic, feels that fellfield types were probably more common in the northern areas of Beringia, grading into steppes in the interior. The pingo plant communities consist of some types that are very much like alpine fellfields, with well-spaced cushion and mat plants and gravelly soils. Many of the dominant species in these areas, such as *Oxytropis nigrescens*, are arctic-alpine Beringian endemics. There are also steppe-like communities, which have much higher coverage by vascular plants and which are primarily dominated by grasses. Murray et al. (1983) have made the important point that "...the abundance of arctic-alpine cryophytes in ... pollen spectra is not fatal to the idea of a steppe-like vegetation, ...with the lowering of tree line during cooler times ... the mountain and steppe types would mingle."

With the present evidence, there is no way to make a completely firm link between the pingo vegetation today and types that would have existed in the past. Pingos are not completely isolated, and if we imagine one that has existed for 10,000 years or so, its vegetation represents an integration of past events with present climate, environment, and flora. There is indirect evidence, based primarily on soils and geomorphology, that at least some pingos have been in existence that long or longer (Walker et al. 1985; also see Chapter 6). Young (1982) stressed the need for multiple lines of evidence in dealing with such a represents an integration of past events with present climate, environment, and flora. There is indirect evidence, based primarily on soils and geomorphology, that at least some pingos have been in existence that long or longer (Walker et al. 1985; also see Chapter 6). Young (1982) stressed the need for multiple lines of evidence in dealing with such a complex problem. Floristic and ecological evidence is needed from modern sites that are most likely to represent analogs of possible past

region that may have analogs include the sand dunes associated with the Sagavanirktok and Kuparuk river deltas (Walker 1985a) and the steep banks of rivers. More careful work is needed, particularly along the rivers, to determine if they support other steppe types.

The other question considered here was the more general problem of an equilibrium in the Arctic. Both the lichen and bryophyte species-area curves have slopes below the level predicted by MacArthur and Wilson (1967) for mainland areas, and the vascular species are at the lower end of the expected range of values. There is a consistent relationship between the total size of a flora for a given taxonomic group and both the slope and strength of the species-area correlation for that group. Thus, the bryophytes, with the smallest flora on the pingos, also have the lowest slope and weakest correlation with pingo size. These data suggest that the vascular species are in equilibrium, but that the bryophytes and lichens have too few species available for an equilibrium in the sense of MacArthur and Wilson (1967). This is supported by the position of most of these species within the plant communities. They are generally ubiquitous and common in several stand types. If this is true, then the vascular species should show a similar trend on a northward gradient in the Arctic, as species are lost due to their inability to exist at high latitudes.

While the lowered values of z can be explained based on a lowered number of communities. They are generally ubiquitous and common in several stand types. If this is true, then the vascular species should show a similar trend on a northward gradient in the Arctic, as species are lost due to their inability to exist at high latitudes.

While the lowered values of z can be explained based on a lowered number of colonizing species, the reduced strength of the correlations was not expected. Habitat variability appears to be important in determining numbers of species.

suitable habitats on pingos for the majority of the regional bryophyte flora. They are most common in moist and wet tundra. On the pingos, it is likely that appropriate habitats are not necessarily well correlated with pingo size, nor are they particularly well defined by standard deviation of pH. Total amount of moisture available may well determine the number of bryophyte species. Other

equilibrium studies have not considered cryptogamic species, as they are a minor component in most environments, and their taxonomy is difficult. Other studies that consider cryptogams, preferably in arctic environments, are needed to corroborate this interpretation and to determine if the vascular species show a similar trend as they diminish in number to the north.

CHAPTER VI

SUCCESSION

This chapter has two purposes. The first is to describe a series of four geomorphic classes of pingos and to propose that these represent a time series. The second purpose is to analyze vegetation and floristic patterns in relation to these four classes in light of the three succession hypotheses outlined in Chapter I.

Geomorphic Classes

Walker et al. (1985) first described the broad-based mounds that are abundant on the gently rolling thaw-lake plains surfaces and hypothesized that they were a form of pingo. Other possible explanations for the origin of these mounds include erosional surfaces and sand dunes, but their almost perfectly round shape in plan view makes both of these explanations unlikely. They have sandy gravel soils with up to 90% gravel, which would be impossible in a dune. The discovery of an ice core over 21 m thick (Brockett 1982) in one of these features is at least partial confirmation of their correct classification as pingos. There are three likely explanations for their difference in shape compared to the steep-sided types: 1) they are approximately the same age as the steep-sided pingos, but either because of some difference in sediment type or mode of formation, is at least partial confirmation of their correct classification as pingos. There are three likely explanations for their difference in shape compared to the steep-sided types: 1) they are approximately the same age as the steep-sided pingos, but either because of some difference in sediment type or mode of formation, they have taken a different shape, 2) they are old steep-sided pingos that have gained their broad shape from the combined actions of mass-wasting and permafrost creep (as discussed by Mackay

like the steep-sided pingos. Until there is independent evidence based on dating of sediment or carbon, the exact age of the broad-based and steep-sided pingos will remain a mystery. The existing evidence, however, is almost all in support of the last two hypotheses, that these are older types, and these two hypotheses are difficult to separate. If they are in fact old, their former shape can only be inferred from existing evidence. If an intermediate type was found, however, this would be indirect evidence in support of the second hypothesis.

The differences between the steep-sided and broad-based types outlined by Walker et al. (1985) must first be reviewed before any additional evidence can be presented. They described these pingos as having gentler slopes and broader basal diameters, but not greater or lesser heights than the steep-sided types. Thus, they also have greater volumes than the steep-sided types. As an example, we can construct two average pingos that each have height and diameter equivalent to the regional mean for that morphological type, and are each shaped as a perfect spherical sector. The volume of this average steep-sided pingo, with a height of 4.1 m and a diameter of 72 m, is 8,400 m³, whereas that of a broad-based pingo 5.0 m high and 242 m in diameter is 115,000 m³. This is over a thirteen fold increase in volume. Additionally, broad-based pingos are restricted to older surfaces and are generally not present in recognizable lake

The greater volume of the broad-based pingos is not particularly relevant to the question of their age, although according to Mackay (1986) it would take at least several thousand years to reach this size. Their position on the landscape, however, is pertinent. The broad-based pingos are limited to the gently rolling thaw-lake plains landscape type, while the steep-sided pingos are found on both thaw-lake plains surfaces. This essentially rules out hypothesis one proposed above, that the shape of the broad-based types is due to a difference in sediment type. If this were the case there should be no steep-sided types within the same geologic and geomorphic units as the broad-based types. The relative densities of pingos on these two surfaces also indicates a long period of formation. Walker et al. (1985) calculated the total pingo density on the flat thaw-lake plains to be 0.096 • km⁻², while on the gently-rolling thaw-lake plains it is 0.286 • km⁻², or nearly three times as great. Sixty percent of the pingos on the gently rolling thaw-lake plains are broad-based.

The modern surface peat layer began to accumulate on both thaw-lake plains surfaces approximately 8 ka, based on radiocarbon dating at the peat-mineral interface (Everett 1980a; Walker et al. 1981; Schell and Ziemann 1983; Wilson 1984). This 8,000 year date is thought to represent the beginning of the current thaw-lake cycle on both surfaces and also the likely date when the Putuligayuk surfaces approximately 8 ka, based on radiocarbon dating at the peat-mineral interface (Everett 1980a; Walker et al. 1981; Schell and Ziemann 1983; Wilson 1984). This 8,000 year date is thought to represent the beginning of the current thaw-lake cycle on both surfaces and also the likely date when the Putuligayuk River became restricted to its modern channel (Walker et al. 1985). The Brooks Range glaciations, for which the Sagavanirktok, Putuligayuk, and Kuparuk rivers were outwash channels, were

initiation of pingo formation on the flat thaw-lake plains (it is likely younger by several thousand years, because at least one thaw-lake cycle must be completed before a pingo can form), and if we presume that pingos have formed on the two surfaces at the same rate, then the estimated age for the oldest pingos on the gently rolling thaw-lake plains would be 23,800 years¹. It is very unlikely that conditions have been so uniform. Conditions during the Duvanny Yar interval are believed to have been much drier, with extensive loess and sand deposits present (Black 1951; Carter 1981, 1983). There was little or no peat formation, and there is no evidence for lakes. Thus, it is unlikely that pingos would have formed at the same rate during the Duvanny Yar as they have within the Holocene, if they formed during this time at all. They could have persisted, however, as it was a cold interval and would not have led to melting of the ice cores. Walker et al. (1985) hypothesized that the broad-based pingos may have formed during the Boutellier Interval (65 to 30 ka, Hopkins 1982), which was an interglacial period believed to be warmer and wetter than the Duvanny Yar, but not as wet as the Birch Interval 8 to 14 ka (the period when the pollen record reflects an influx of *Betula* pollen).

Walker et al. (1985) also described a third type of pingo that they labeled intermediate. This type has certain characteristics of both the steep-sided and broad-based forms. They are generally Birch Interval 8 to 14 ka (the period when the pollen record reflects an influx of *Betula* pollen).

Walker et al. (1985) also described a third type of pingo that they labeled intermediate. This type has certain characteristics of both the steep-sided and broad-based forms. They are generally very large pingos with relatively steep and gravelly upper slopes, and with a

¹This is based on the ratio of the densities of the two types of pingos, multiplied times the

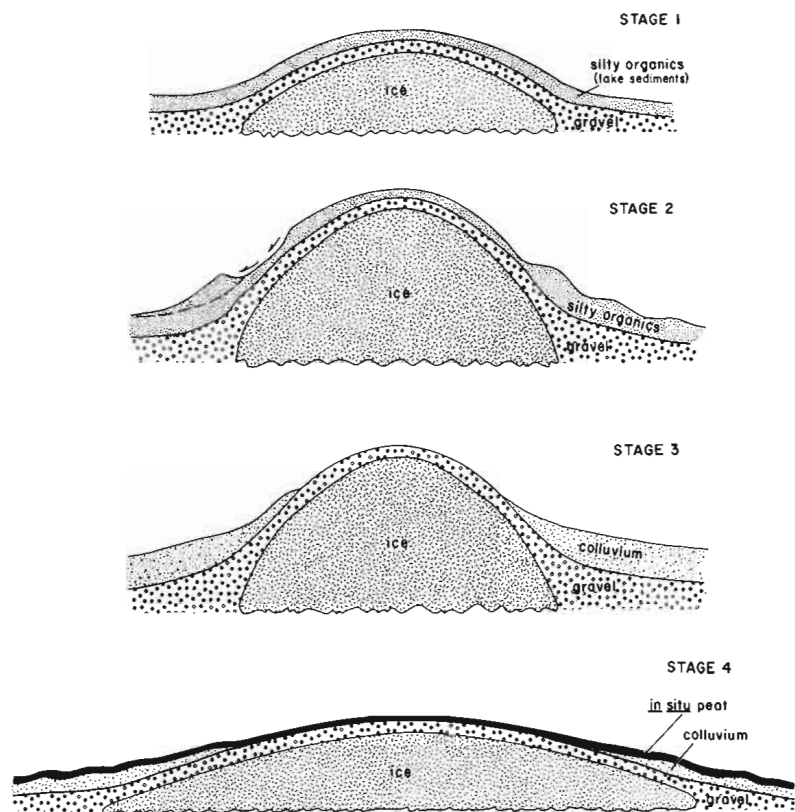


Figure 89. Four morphological types representing a proposed time sequence. Descriptions of the stages are in the text.

large colluvial apron around the base. Like the broad-based pingos, intermediate types are generally not present within recognizable lake basins, although in several instances they are directly on the edge of a basin, and it is difficult to evaluate their exact relationship to the

large colluvial apron around the base. Like the broad-based pingos, intermediate types are generally not present within recognizable lake basins, although in several instances they are directly on the edge of a basin, and it is difficult to evaluate their exact relationship to the basin. Although Walker et al. (1985) concluded that these did not represent a valid category, a possible scheme for development of these pingos is presented here in which the intermediate pingos

sized to represent a time-dependent development sequence (Fig. 89). For now, these are called morphological classes rather than age classes. There is likely overlap in the actual ages between these categories, because the time required for a single pingo to progress

sized to represent a time-dependent development sequence (Fig. 89). For now, these are called morphological classes rather than age classes. There is likely overlap in the actual ages between these categories, because the time required for a single pingo to progress

Descriptions of the Stages

Stage 1 In Stage 1 the pingo is



Figure 90. A stage 1 pingo, no. 39.

slopes are gentle (Fig. 90). Surface sediments are silty organics that accumulated before the lake drained, and there is minimal or no soil development. As these sediments are uplifted they become stretched, and dilation cracks form on the surface, radiating outward from the center, although at Prudhoe Bay these are small and fairly limited in extent. The silty organics are underlain by gravels. Plant cover becomes established during this phase, but the time required to achieve complete cover is unknown. The characteristics used to identify this stage were gentle slopes, often obvious dilation cracks (although these were generally well vegetated), no extent. The silty organics are underlain by gravels. Plant cover becomes established during this phase, but the time required to achieve complete cover is unknown. The characteristics used to identify this stage were gentle slopes, often obvious dilation cracks (although these were generally well vegetated), no real development of ice-wedge polygons in the surrounding lake basin (strangmoor may be present), and little evidence of soil development.

Two pingos were discovered in 1984

photography revealed that the lake drained sometime between 1949 and 1968 (Fig. 91). They represent a matched pair that is useful for examination of the very earliest stages of pingo growth and formation, as the variability in their geomorphic and ecological development can be monitored. The 1949 photograph (Fig. 92a) shows the lake in June. By 1968 (Fig. 92b) the two pingos are clearly in place, and one has a clear pattern of dilation cracks on its surface. In 1979 (Fig. 92c) the outline of the pingos still matches, but the dilation cracks are not as well-defined. Vegetation cover in the surrounding lake basin was much more extensive in 1979 than in 1968, and was dominated by *Eriophorum angustifolium*, *Puccinellia andersonii*, and *Alopecurus alpinus*. Examination of these pingos in 1984 indicated that arctic ground squirrels had colonized both sites,



Figure 91. One of two pingos that formed in a drained lake basin after 1949 and prior to 1968. This photograph was taken in 1984, and shows the south-facing slope. The pingo is approximately 3 m high and 90 m in diameter.

the squirrels may be important agents in the amelioration of these features on the pingo surface.

Plant cover was also limited on the pingos primarily to the small trough formed by the surface cracking (Fig. 93). Species were generally the same as those present in the drier areas of the surrounding basin (Table 48). Wind erosion is significant during this extended period with only minimal vegetation cover.

Stage 2. The next stage is characterized by continuing growth of the ice core. Growth is primarily from the center, which causes the slopes to steepen, present in the drier areas of the surrounding basin (Table 48). Wind erosion is significant during this extended period with only minimal vegetation cover.

Stage 2. The next stage is characterized by continuing growth of the ice core. Growth is primarily from the center, which causes the slopes to steepen, up to 45° or more, although generally ranging from 15° to 30° (Fig. 94). Mass wasting is intense in this phase, and

zons begin to develop in more stable areas, but they are limited in extent and frequently disturbed. Vegetation cover on the upper slopes may still be incomplete, and therefore there is likely to be continued wind erosion, although at a lesser level than in Stage 1. The characteristics used to identify this stage were steep slopes, evidence of soil development initiation (formation of secondary carbonate accumulations was often an indicator of this), evidence of mass wasting, and the presence of fairly well-defined ice-wedge polygon systems in the surrounding basin. Stages 1 and 2 both fall within the steep-sided type of teristics used to identify this stage were steep slopes, evidence of soil development initiation (formation of secondary carbonate accumulations was often an indicator of this), evidence of mass wasting, and the presence of fairly well-defined ice-wedge polygon systems in the surrounding basin. Stages 1 and 2 both fall within the steep-sided type of Walker et al. (1985).

Radiocarbon analysis of organic materials of what is believed to be the

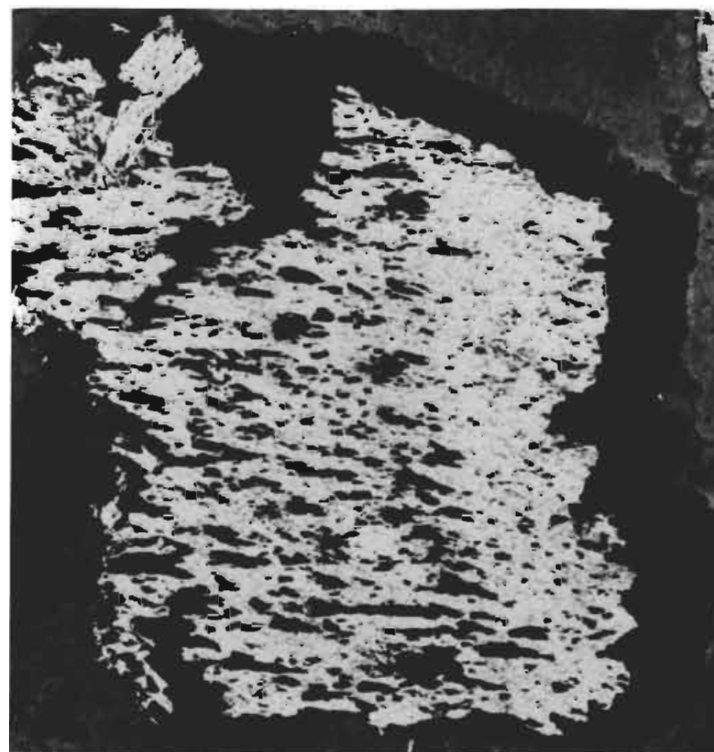


Figure 92 (a). Aerial photograph of a lake in June 1949. This lake, which is about 0.8 km across, drained sometime after 1949 and prior to 1968. The white material is ice.

possible age of 6585 ± 110 years for this pingo (Walker et al., unpubl.). This is reasonable based on the degree of soil development on this pingo. Further analysis and dating of mineral sediments are needed to corroborate this date, but it is presented here as it may represent the first reliable radiocarbon date from a pingo in this region.

possible age of 6585 ± 110 years for this pingo (Walker et al., unpubl.). This is reasonable based on the degree of soil development on this pingo. Further analysis and dating of mineral sediments are needed to corroborate this date, but it is presented here as it may represent the first reliable radiocarbon date from a pingo in this region.

Stage 3. In the third stage, the origi-

ing a gravel surface (Fig. 96). The upper slopes are mostly snow free all winter, and intense winds act in combination with the mass wasting to produce this stage. What is not blown away is redeposited as a colluvial apron that extends around the pingo base. This stage is equivalent to the intermediate type of Walker et al. (1985).

ing a gravel surface (Fig. 96). The upper slopes are mostly snow free all winter, and intense winds act in combination with the mass wasting to produce this stage. What is not blown away is redeposited as a colluvial apron that extends around the pingo base. This stage is equivalent to the intermediate type of Walker et al. (1985).

An important characteristic of these pingos that is necessary to make the link



Figure 92 (b). The same basin in 1968, an unknown period of time following drainage. The two pingos are indicated by arrows. The faint radiating lines on the pingos are dilation cracks. The lake drained through the breach in the upper right corner of the photograph.

any other stage. Walker et al. (1985) reported that the intermediate type was significantly taller than either the steep-sided or broad-based type, which did not have significantly different mean heights. We can envision a scenario where the stage 2 (steep-sided) pingos continue to

between the steep-sided (stage 2) and broad-based (stage 4) type.

Soil characteristics develop during this relatively long and stable period. There is development of structure, B horizons with characteristic accumulations of carbonate, silt, or both, and red

any other stage. Walker et al. (1985) reported that the intermediate type was significantly taller than either the steep-sided or broad-based type, which did not have significantly different mean heights. We can envision a scenario where the stage 2 (steep-sided) pingos continue to grow, very slowly, while permafrost continues to aggrade in the surrounding basin. Once the gravelly slopes develop, they remain relatively stable. The lake

between the steep-sided (stage 2) and broad-based (stage 4) type.

Soil characteristics develop during this relatively long and stable period. There is development of structure, B horizons with characteristic accumulations of carbonate, silt, or both, and red color due to oxidation. Organics on the upper surfaces are primarily those left from the original lake sediments that have been incorporated into the gravels

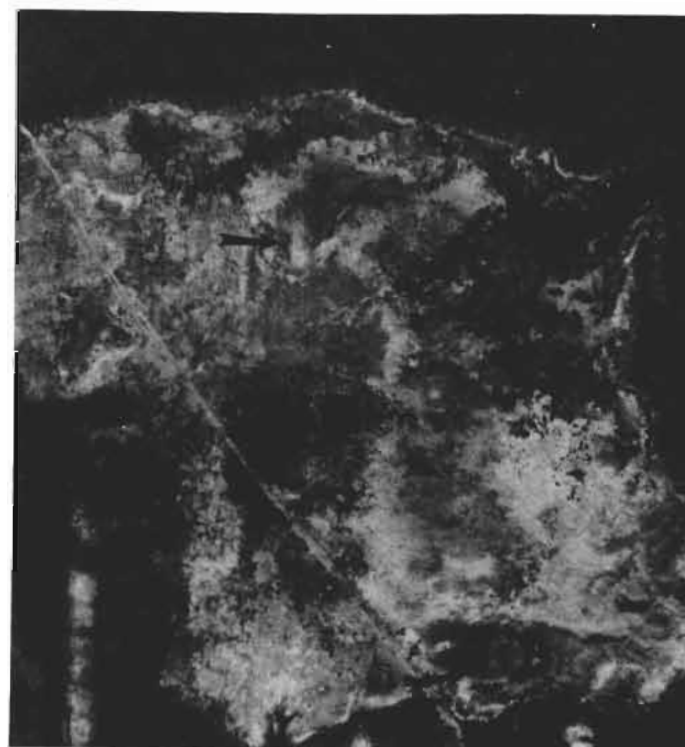


Figure 92 (c). The basin in 1979. The dilation cracks are less evident here.

this stage may be as much as two meters. The main characteristics used to identify this stage were the presence of an extensive colluvial apron around the pingo base, with a well-defined break in slope between this feature and the upper slope area, well-developed soils, a gravel pavement on the shoulder and upper backslope areas, and aggregations of ice. The main characteristics used to identify this stage were the presence of an extensive colluvial apron around the pingo base, with a well-defined break in slope between this feature and the upper slope area, well-developed soils, a gravel pavement on the shoulder and upper backslope areas, and aggregations of ice-wedge polygons in the surrounding basin into small pond complexes.

Stage 4. In Stage 4, which is equivalent to Walker et al.'s (1985) broad-

formed the ice core, and the break between the colluvial apron and upper slopes is less noticeable than in Stage 3 (Fig. 97). A layer of *in situ* organics forms on the surface, and the decreased slopes lead to a decrease in surface temperature and further build-up of peat. These organic horizons begin to form under mats of dwarf shrubs such as *Dryas* between the colluvial apron and upper slopes is less noticeable than in Stage 3 (Fig. 97). A layer of *in situ* organics forms on the surface, and the decreased slopes lead to a decrease in surface temperature and further build-up of peat. These organic horizons begin to form under mats of dwarf shrubs such as *Dryas integrifolia* and *Salix rotundifolia*. *Rhytidium rugosum*, *Thuidium abietinum*, and *Tomenthypnum nitens* colonize these patches, further increasing the



Figure 93. *Puccinellia andersonii* growing alongside dilation cracks on a small pingo that formed between 1949 and 1968.

Table 48. List of species present on two pingos that formed between 1949 and 1968. All species were at one site; an asterisk marks those that were at both sites.

<i>Alopecurus alpinus</i>	<i>Festuca rubra</i>
<i>Arctagrostis latifolia</i>	<i>Melandrium affine</i>
<i>Braya glabella</i> *	<i>Poa arctica</i>
<i>Cerastium beeringianum</i>	<i>Polygonum vivparum</i>
<i>Cochlearia officinalis</i> *	<i>Puccinellia andersonii</i> *
<i>Deschampsia caespitosa</i> *	<i>Salix ovalifolia</i>
<i>Draba</i> sp.	<i>Stellaria longipes</i>
<i>Equisetum arvense</i>	<i>Trisetum spicatum</i>
<i>Equisetum scirpoides</i>	<i>Bryum</i> sp.
<i>Festuca baffinensis</i>	

<i>Cochlearia officinalis</i> *	<i>Puccinellia andersonii</i> *
<i>Deschampsia caespitosa</i> *	<i>Salix ovalifolia</i>
<i>Draba</i> sp.	<i>Stellaria longipes</i>
<i>Equisetum arvense</i>	<i>Trisetum spicatum</i>
<i>Equisetum scirpoides</i>	<i>Bryum</i> sp.
<i>Festuca baffinensis</i>	

surrounding gravels, as little as 15-20 cm. The combination of increased soil organics, decreased depth of thaw, and

colonization by more mesic species. This type is characterized by the gentle slopes and gradual change between the collu-



Figure 94. A stage 2 pingo, pingo no. 10.

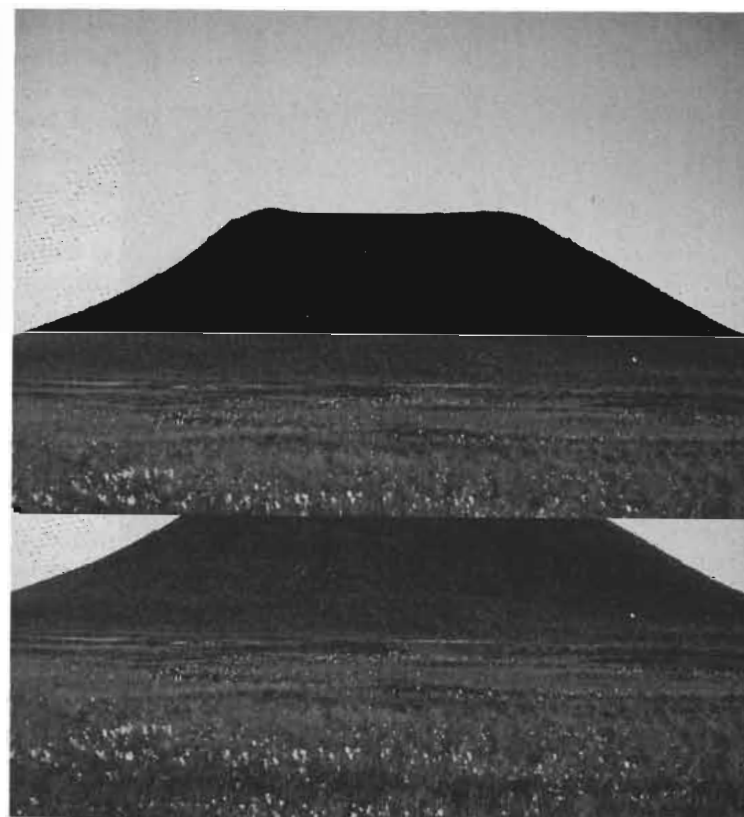


Figure 95. A small scarp on a stage 2 pingo caused by a small landslide.



Figure 96. A stage 3 pingo in the Toolik River area (pingo no. 7). This pingo was called "Toolik Pingo" by Koranda (1970).

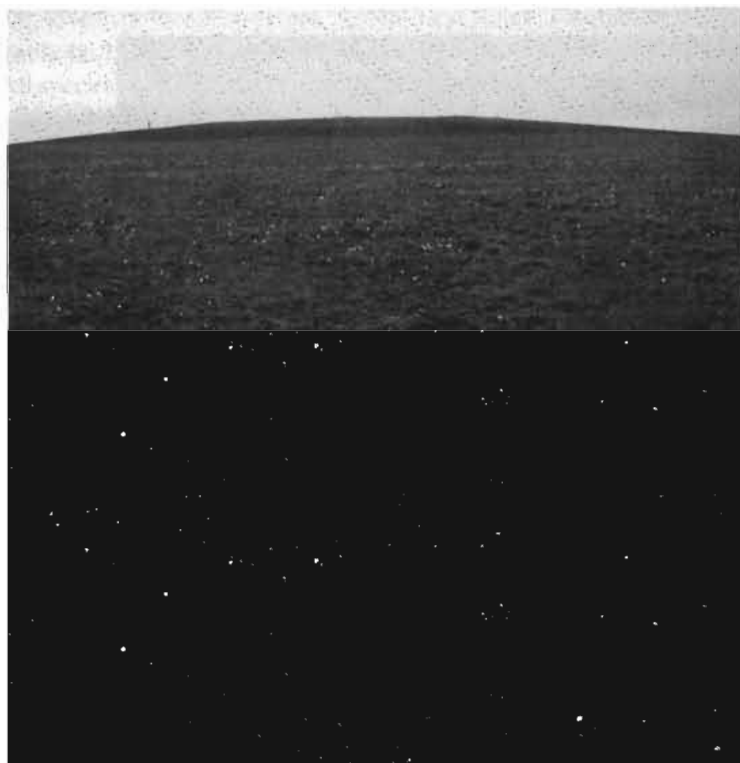


Figure 97. A stage 4 pingo in the Kuparuk area (no. 24).

surrounding the pingo. Soils are very well-developed, and have thick A horizons that appear to have formed *in situ*, similar to those in Fig. 26.

Vegetation Succession

Three succession hypotheses were presented in Chapter 1: (1) because the pingos are in equivalent substrates, environmental gradients will be the same on different pingos, and since vegetation is highly dependent on environmental conditions, there will be a change over time toward a characteristic pingo flora, (2) because initial community composition is a function of chance events, the relationship between species composition and site characteristics or environmental factors is stronger in older pingos compared to younger pingos, and (3) species diversity on cold sites (microsites 1 and 7) will rise more slowly and maintain a lower level than will diversity in warm sites (microsites 2 and 6), which will rise rapidly and maintain a high level, because there is a smaller pool of species capable of colonizing the cold sites. These hypotheses are all based on previous work and current ideas and models of succession. Only the third hypothesis is specific to arctic regions, but it would apply in any situation where the potential pool of colonizers is diminished. In this case there are fewer species on the cold sites because at this latitude many species are limited by cold temperatures and few or none by warm temperatures.

Convergence (Hypothesis 1)

This hypothesis was tested by comparing the amount of floristic variation

classes. Floristic variation between two pingos was measured as the euclidean distance between them in the ordination based on the entire pingo flora. Within each class, mean euclidean distance for each pingo and all other pingos was calculated, as was mean euclidean distance between each pingo and all other pingos within the same morphological class. A value for the entire class was calculated as the mean of all pingos within that class. If the hypothesis is correct, then the pingos within morphological class 4 should have the least amount of floristic variation. That is, the average euclidean distance between them should be the least.

The floras of pingos within morphological class 4 are more similar than within the first three classes (based on the Duncan multiple range test, $p < .05$), supporting the hypothesis that there is convergence toward a characteristic pingo flora (Fig. 98). Over the first three classes, however, it diverges, and this divergence is consistent for the vascular and cryptogam species. The three bar-graphs on the left side of Figure 98 compare the average euclidean distance between all pingos within a morphological class and all other pingos in the study, and on the right hand side, the height of the bar represents average euclidean distance between each pingo in a morphological class and all other pingos within that class. Class 4 shows less variation than class 1.

Each of the microsites was analyzed individually using the ordinations based on the individual microsites. Each of the seven microsites shows a different trend across the four morphological classes (Fig. 99). Four of the microsites, the summit, middle snowbank, lower snow-

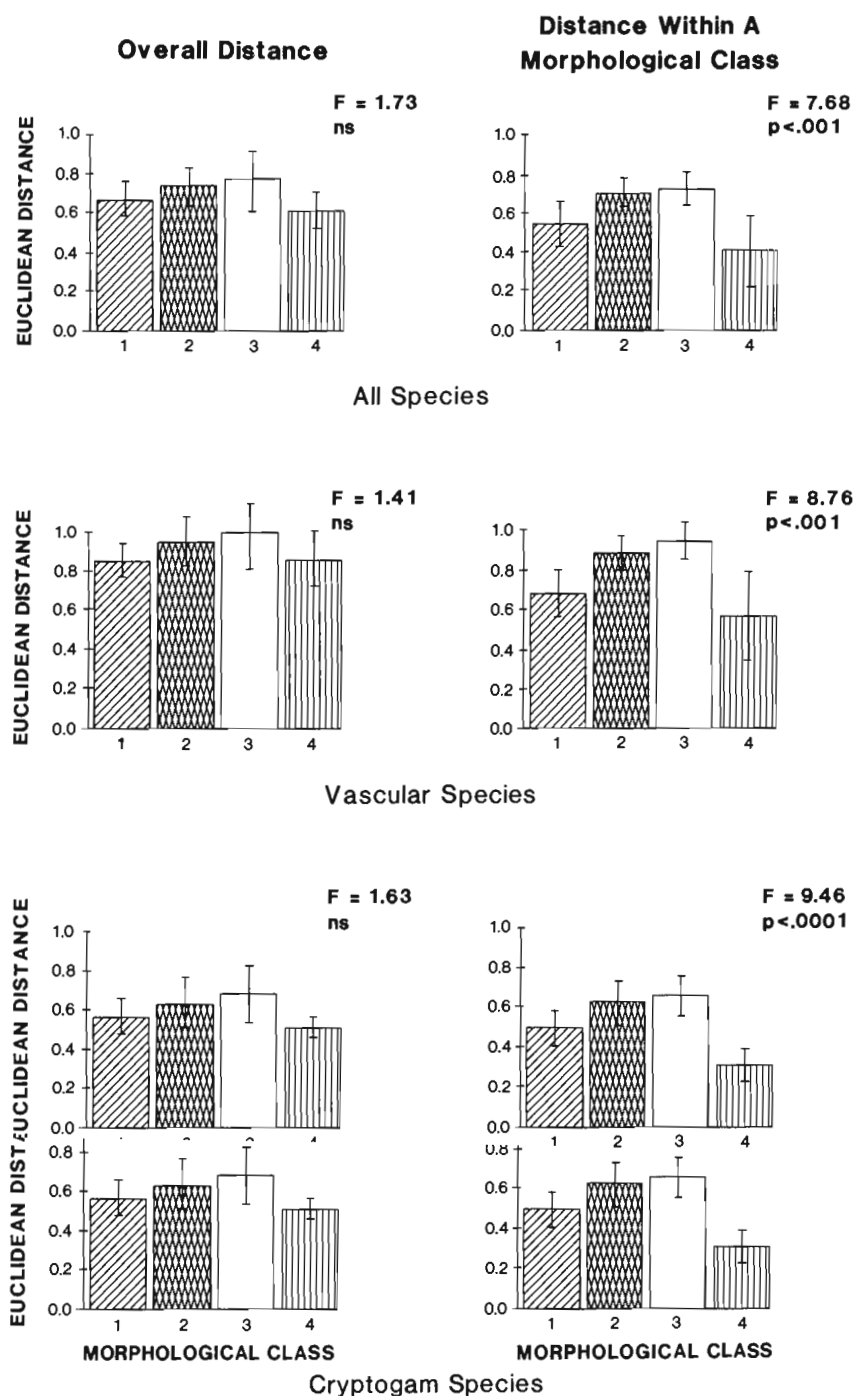


Figure 98. Mean euclidean distance between pingos in each morphological class compared to all other pingos and other pingos within the same morphological class. F values are from one-way ANOVA; error bars represent the 95% confidence interval.

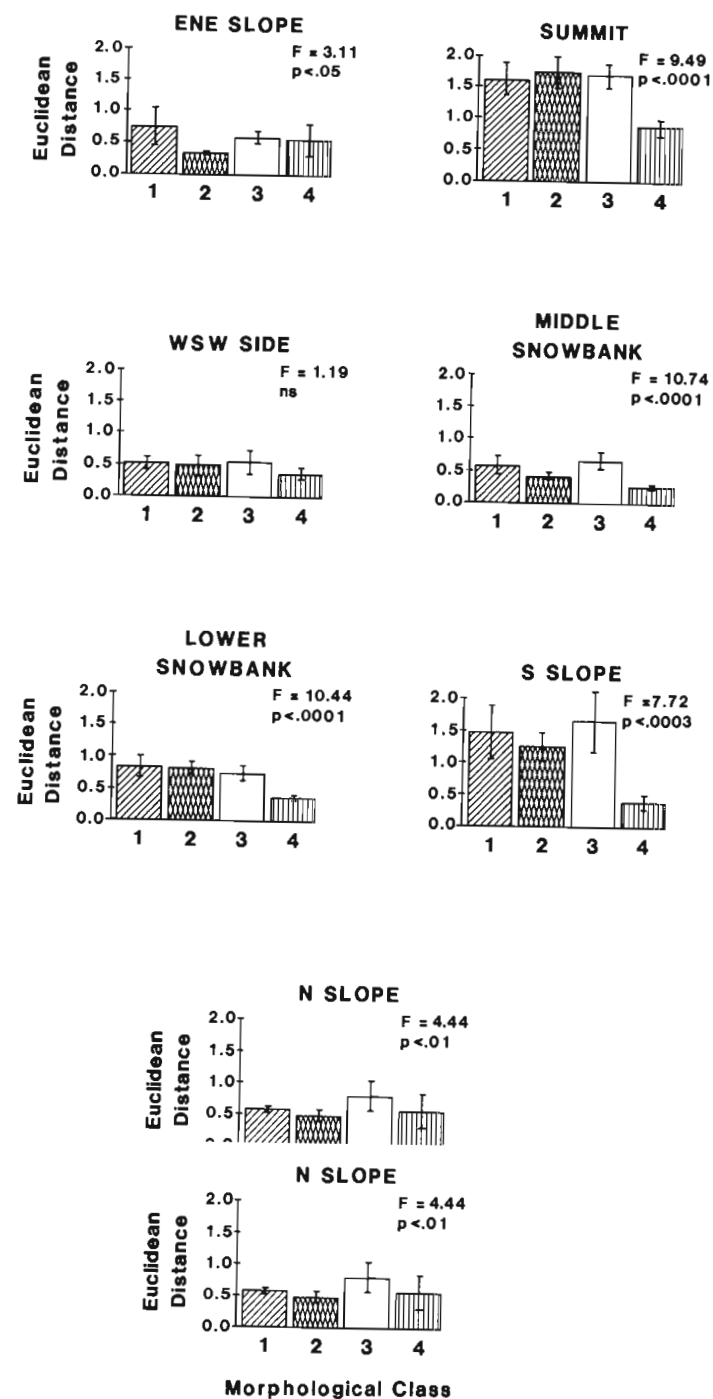


Figure 99. Mean euclidean distance between sample plots within each microsite of each morphological class. F values are from a one-way ANOVA; error bars represent the 95% confidence interval.

decrease in morphological class 4 (based on the Duncan multiple range test, $p < .05$), but none of these mirror the overall trend for divergence in classes 1 through 3 followed by convergence in class 4. The WSW side shows no significant differences in any class, and the ENE slope and N slope show some differences in the first 3 classes, but of a rather low magnitude.

Dependence on Site Factors (Hypothesis 2)

An assumption of this hypothesis that has not been explicitly stated in the literature is that the communities present during different successional stages are all controlled by the same complex environmental gradients. As demonstrated in Chapter 4, each of the microsites has a somewhat different set of environmental gradients associated with it. Individual ordinations were done on each of the morphological classes to determine if the same set of gradients was associated with the various classes. Although the variables correlating with the first ordination axis do differ between the classes, the first three variables are the same in all cases, snow, moisture, and exposure to winds (Table 49). Thus, it appears that this is a valid assumption in this case. The strength of the correlations was not significantly different, and so these data do not support the hypothesis. Class 1 actually has the most variables correlated with it, and class 4 the least. This is the opposite of what is expected should the hypothesis be correct.

Standard bivariate correlations with the ordination axes are not really adequate for hypothesis testing, however,

There are four axes, each of which may have some ecological significance. Also, the mere number of variables correlated with a single axis is only a very crude estimate of dependence on site factors. To avoid this problem, canonical correlation analysis was done between the four ordination axes and all environmental variables simultaneously. This is a measure of the variation in all of the dependent variables (ordination scores) that is explained by the independent variables (environmental factors) as a group (Horst 1961). The results of this analysis indicate that the vegetation patterns within all of the morphological classes are highly correlated with environmental variables (Table 50). Thus, the hypothesis is not supported by these data.

Diversity (Hypothesis 3)

The number of species present at each of the microsites shows no significant changes over the four morphological classes in any case (Fig. 100). The north slope and ENE side have the lowest number of species, and the middle snowbank area the highest number. Differences between total species on a pingo for each morphological class could not be tested, because the classes are not independent of area, and number of species is closely tied to pingo area. Application of the Shannon index to these data also results in no significant differences among the four morphological classes for any of the seven microsites (Fig. 101). Thus, the diversity within each of the microsites appears to be equivalent for all morphological classes.

Table 49. Variables that correlate with the first ordination axis within the individual morphological class ordinations, listed in order of the relative strength of the correlation. Variables at the top have $p \leq .001$, those below the first line have $p \leq .01$, and those below the second line have $p \leq .05$.

Class 1	Class 2	Class 3	Class 4
Snow (-)	Snow (-)	Exposure (-)	Moisture
Moisture (-)	Moisture (-)	Moisture (-)	Snow
Exposure	Exposure	Snow	Exposure (-)
Squirrel	Lemming (-)	Lemming	
Stability	Thaw depth	Microrelief	Stability (-)
Lemming (-)	Squirrel	Squirrel	Lemming
Bird	Microrelief (-)		Cryoturbation (-)
pH	Stability	Fox (-)	
Fox			
Slope			
Caribou (-)			
Microrelief (-)			

Table 50. The first two canonical correlations between ordination axes and environmental variables.

Morphological Class	Canonical Correlation Function	Percent of Variance Explained	Significance
1	1	72	.000
	2	46	.000
2	1	78	.000
Morphological Class	Canonical Correlation Function	Percent of Variance Explained	Significance
1	1	72	.000
	2	46	.000
2	1	78	.000
	2	37	.008
3	1	90	.000
	2	37	.057
4	1	81	.000

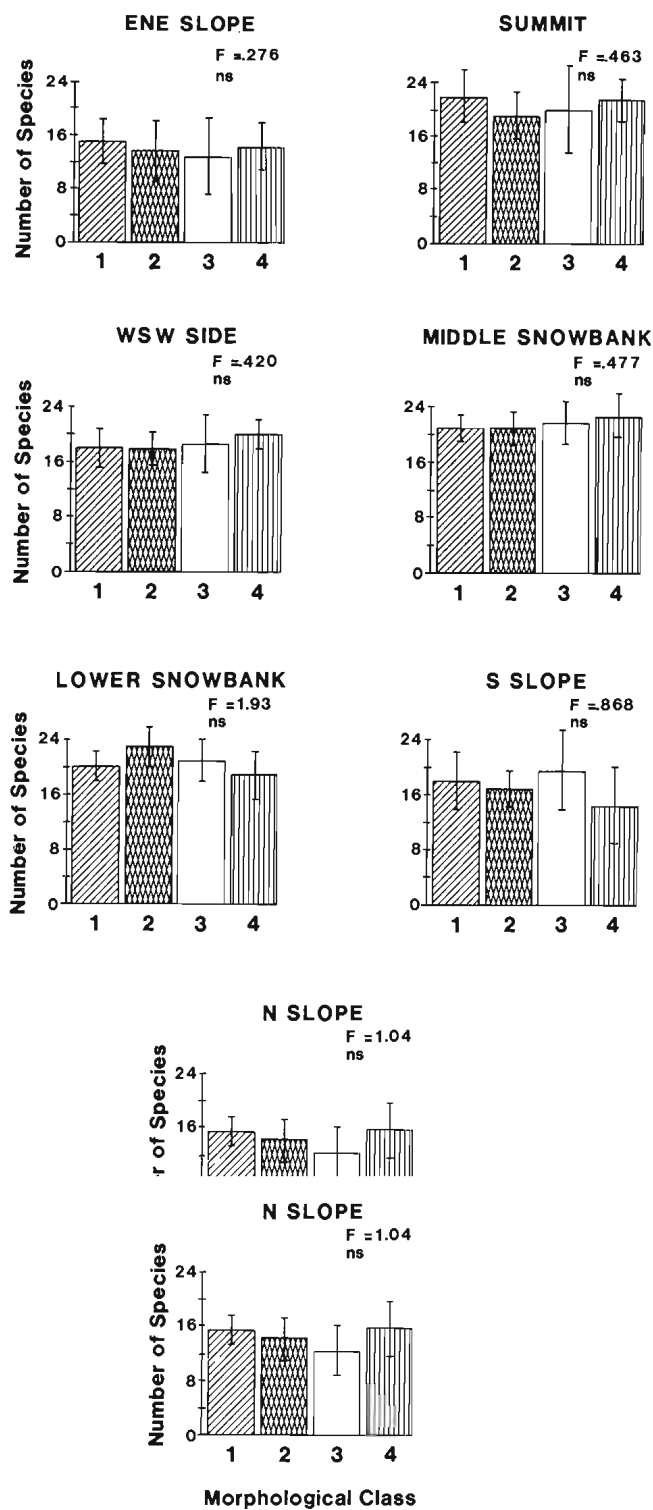


Figure 100. Mean number of species in the sample plots within each microsite within each morphological class. F values are from one-way ANOVA; error bars represent the

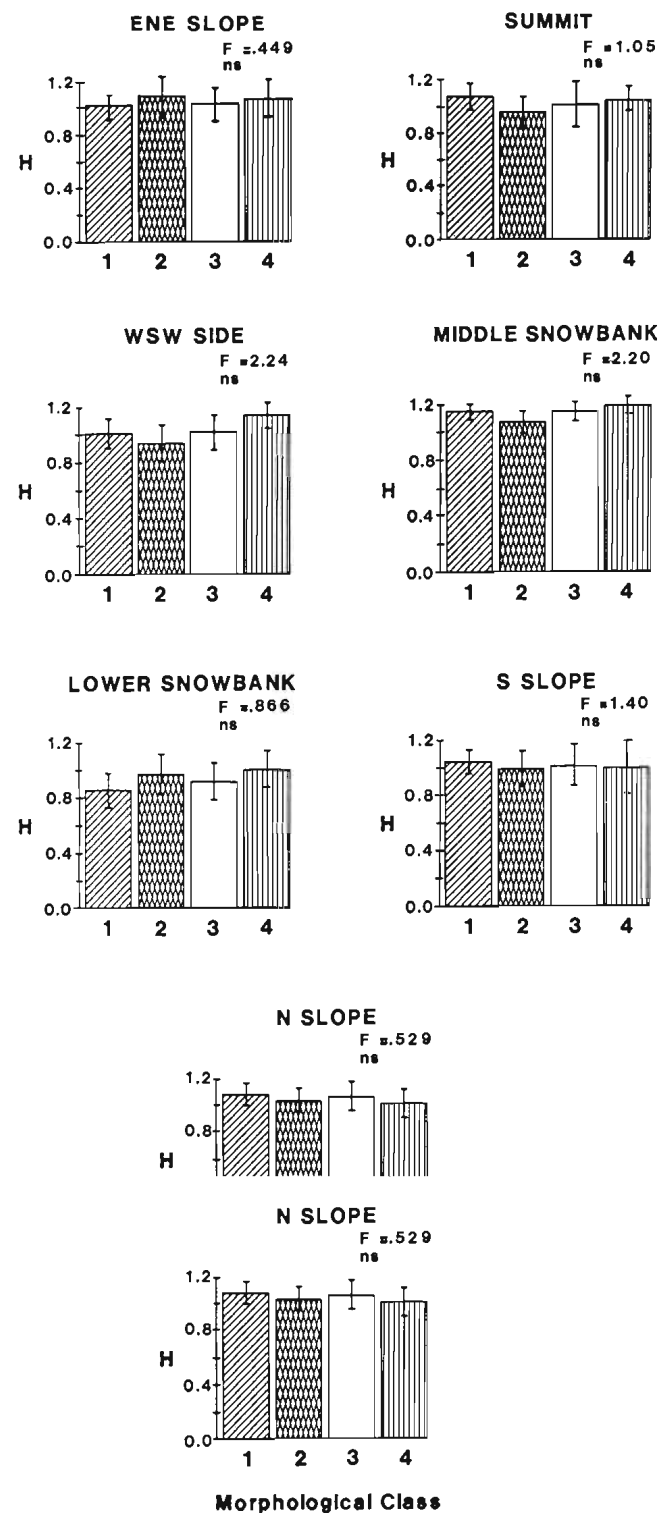


Figure 101. Mean Shannon diversity index (H) for each microsite within each morphological class. F values are from one-way ANOVA; error bars represent the

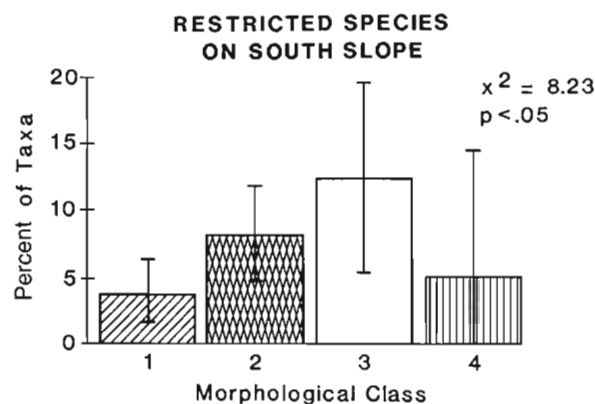


Figure 102. Percentage of restricted species on south slopes within each morphological class. Chi-square is from Kruskal-Wallis test; error bars represent the 95% confidence interval.

Distribution of Restricted Species

Importance of restricted species on south slopes is highest in class 3 (Fig. 102). There are some of these species present even on the class 1 pingos, and they increase in importance from class 1 to class 3. Class 4, which is the oldest, has on the average less of these species than either class 2 or class 3. If the class 4 pingos are in fact older, and if these species are relict, they have likely survived through continual recolonization of new sites, which was proposed in Chapter V.

Discussion and Conclusions

Given the evidence for convergence of new sites, which was proposed in Chapter V.

Discussion and Conclusions

Given the evidence for convergence of the pingo floras in class 4, it is logical to next ask which successional model best fits this situation. Connell and Slatyer (1977) summarized the three primary models of succession that have appeared in the literature. The first model is the *facilitation* model, which is based

on the idea that modification of the environment by early colonizers allows colonization by other species, which may in turn modify the environment for still later stages. The eventual climax community consists of species that are better competitors than the early colonizers. This model is essentially the original one proposed by Clements (1916), and most primary succession is related to this model. Egler (1954) termed this *relay floristics*.

The second model has been called the *tolerance* model, and in this model modification of the environment by early colonizers neither increases nor decreases the ability of other species to colonize the site. All species that disperse to the site are presumed capable of colonizing it. The species that eventually persist are those able to tolerate the modified environment. The final model is the *inhibition* model, which is similar to the tolerance model, but in this case early colonizers modify the environment in such a way that late-arriving species are inhibited

from invading it. Both the tolerance and inhibition models have the ultimate outcome of succession heavily dependent on what species randomly or otherwise initially colonize the site, and were called the *initial floristic composition* model by Egler (1954). Robinson and Dickerson's (1987) experiments with phytoplankton invasion are examples of these last two models.

The data from this study appear to fit the facilitation model most closely, as the evidence for convergence in class 4 indicates that in spite of the large variation among the class 3 pingos, the ultimate community will be a mesic tundra similar to most upland sites on the Coastal Plain. There is some evidence for facilitation processes, in that the deep, organic-rich soils that eventually form on these sites are directly related to the colonization by dwarf shrubs, primarily *Dryas integrifolia*. The status of these classes is uncertain, however, and within classes 1 to 3 there is a divergence, and no evidence for facilitation. Until further confirmation is obtained that these morphological stages represent an actual time sequence, this conclusion will remain tentative. For now, the conclusion is based on the presumption that the class 4 pingos did in fact evolve from the earlier stages.

Is this really facilitation as proposed in the model, however? Although this is considered a succession study, it is on a time scale much different from other successional studies, which generally class 4 pingos did in fact evolve from the earlier stages.

Is this really facilitation as proposed in the model, however? Although this is considered a succession study, it is on a time scale much different from other successional studies, which generally examine structure within the first several hundred years. Vegetation changes on pingos are directly related to geomorphic processes, with a time scale that is in the thousands or perhaps even tens of thousands of years. The processes in-

involved in transforming a barren pingo to a fully vegetated pingo with well-defined plant communities on it, which takes an unknown amount of time, would be comparable to most other studies of succession. On the other hand, this is a cold-climate system, and arctic plants are long-lived perennials. Few successional studies have examined time scales as long as these, but the outcome of succession (as interpreted from data, and not necessarily in reality) is highly dependent on the time scale examined. This problem has plagued interpretation of successional studies and led many investigators to conclude that the climax concept is not valid at all, as eventually there will be a geologic/climatic event that changes the regional climatic climax, and that given a long enough period of time no system is stable. The long time scale of this study could partially explain why the second and third hypotheses, regarding environmental correlations and diversity, were not supported by these data. These questions, particularly the diversity one, deal with the earliest successional stages. Diversity increases rapidly compared to the geomorphic changes that ultimately drive this system.

The importance of appropriate time and space scales have not generally been addressed in most succession studies. There are basically two schools of thought that have been recognized, the population process school and the community process school. Examples of population process models include Egler (1954), Margalef (1963, 1968), Connell and Slatyer (1977), Peet and Christensen (1980), Tilman (1985, 1986), and Cargill and Chapin (1987). Community process examples include Clements

(1916), Robinson and Dickerson (1987), and Svoboda and Henry (1987). There is also a third category, however, based on succession as a geomorphic process. Geomorphic models may include elements from all other models, and often include both linear and cyclic processes. There are fewer examples of this in the literature, as it is mainly limited to dynamic environments where geomorphic processes cycle on a relatively short time scale. Examples of geomorphic succession include Billings and Peterson (1980) and Sterling et al. (1984). Studies related to effects of chronic animal disturbance might also fall in this category (Price 1971; Fox 1985; Smith and Gardner 1985). Dansereau (1954) noted that in cold environments, allogenic processes dominate the control of succession. Webber (1978) and Billings and Peterson (1980) demonstrated this on the Arctic Coastal Plain, particularly in relation to the thaw-lake cycle. In this geomorphically dynamic environment, processes of ice-wedge polygon development, thermokarst, cryoturbation, and other permafrost-related processes prohibit long-term stability as it is understood in most environments. The pingos are a part of the thaw-lake cycle, but the processes driving the succession on pingos, development of slopes and soils and the subsequent mass-wasting of these slopes and accumulation of peat in soils, are more analogous to the building and erosion of mountains than to the thermokarst-related processes on the Coastal Plain. Nevertheless, the result is again the dominance of allogenic over autogenic controls.

The pingos are an example of a geomorphically driven system that includes elements of both the facilitation

the north slopes of the pingos, there is evidence for the tolerance model. It is somewhat modified from Connell and Slatyer's original model, however, because in this case not all species are capable of colonizing these sites. Colonizers on the north slopes will be those species able to withstand the extreme conditions at these sites and to persist. Svoboda and Henry (1987) have stated that in the High Arctic most environments fit this tolerance model. This is the autosuccession of Muller (1952), where the colonizing species remain as the climax community. The environmental resistance is much greater than the driving force of most species. Figure 103 is a generalization of the data from Figure 100. The warm sites are the south slopes and summits; the cold sites are the north slopes and ENE sides. The relative amount of floristic variation in these cold sites supports the idea that there are fewer species capable of colonizing these sites, and that change is slow and minimal there. The warm sites, however, have much higher floristic variation than the cold sites at all stages, and a rapid increase in variation in the earlier stages. Thus, succession on the warm sites appears to follow the facilitation model, while on the cold sites it follows the tolerance model. The overall system, however, is driven geomorphically, and the drop in variation in the class 4 pingos is due to the decreased slopes present in that stage, which would lead to decreased ground surface temperatures. while on the cold sites it follows the tolerance model. The overall system, however, is driven geomorphically, and the drop in variation in the class 4 pingos is due to the decreased slopes present in that stage, which would lead to decreased ground surface temperatures.

Relation to the Steppe-Tundra Question

The data presented in this chapter further support the evidence presented in

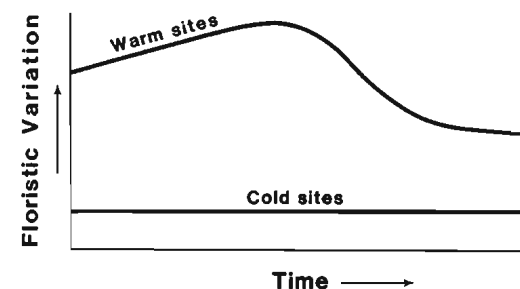


Figure 103. Generalization of the data in Fig. 99. 'Warm sites' are the summits and south slopes; 'cold sites' are the north slopes and ENE sides.

Yar period, or even earlier. If this is the case, then at least some pingos had to be present in the region during that time, and there is rather abundant evidence this was the case. It is not necessary that any given pingo has persisted this long, however. The relict species could have persisted by continual colonization of new sites as they became available. Webber (unpubl.) differentiated regional and stationary persistence. Populations can escape habitats that are unstable in space or time (Wiens 1976; Pickett and White 1985), provided that other appropriate habitats are available and that a species is able to disperse to and colonize these habitats. A population can persist regionally through a climatic change in two ways: (1) by being persistent at a given site (stationary persistence), or (2) by continually escaping into new sites (regional persistence). In the first case, the population or community is truly relict. These communities are perched on the brink of extinction; they cannot be replaced because they are dependent on previous climatic conditions for successful colonization. In the second case, the population or community, although it may be limited to spe-

sites that have the appropriate environmental and microclimatic conditions. These communities are here called remnant, to distinguish them from a truly relict communities, as defined above. In this sense, the pingos may have been a type of nunatak (Ives 1974) on the coastal plain.

Examination of the importance of restricted taxa on the south slopes between the morphological classes (see Fig. 102) supports this idea of remnant species that are regionally but not necessarily locally persistent. These restricted species are primarily arctic-alpine, zone 3 and 4. They are primarily adapted to warm, alpine-like sites, probably with fairly minimal snow cover. The class 3 pingos have the best examples of these habitats. Thus, these species have likely persisted by continually recolonizing new habitats as they became available. They are remnants of a former flora that was warm, alpine-like sites, probably with fairly minimal snow cover. The class 3 pingos have the best examples of these habitats. Thus, these species have likely persisted by continually recolonizing new habitats as they became available. They are remnants of a former flora that was probably more widespread, but are not relict in the strict sense of the word. These data suggest that most of these species will persist in this region as long as there are warm, gravelly, snow-free sites available, that is, as long as there are pingos in the class 2 and 3 stages.

CHAPTER VII

FINAL DISCUSSION AND CONCLUSIONS

Summary

The vegetation of the northern Alaska pingos contains several elements unique to these sites. The region studied here covered a transect from the Prudhoe Bay region, with its High Arctic character, south onto the more central portion of the Arctic Coastal Plain, and thus incorporates elements of the vegetation from both areas. The pingos, with their warm south slopes and cold north slopes, often have mixtures of both elements at a single site.

The abundance of *Dryas integrifolia* in pingo vegetation is a link to the Arctic generally. Each of the three major environments on the pingos (cold, snow-free sites; warm, snow-free sites; and snowbeds) has a relationship to different regions and environments outside the pingos. The snowbed sites in particular are very similar to arctic and alpine snowbed types throughout much of the Arctic. The cold, snow-free sites on pingos are somewhat analogous both to alpine fellfields and to gravelly high arctic areas. The communities on these snow-free pingo sites, which are dominated by *Dryas integrifolia* and *Oxytropis nigrescens*, also occur elsewhere on exposed, calcareous areas of the Alaskan coastal fields and to gravelly high arctic areas. The communities on these snow-free pingo sites, which are dominated by *Dryas integrifolia* and *Oxytropis nigrescens*, also occur elsewhere on exposed, calcareous areas of the Alaskan coastal plain. Nevertheless, they are characteristic of pingos. The south slopes and summits of pingos have a great variety of vegetation, including types related to both alpine and steppe tundra.

The snow and temperature data indicate that the pingos have rather steep environmental gradients, and the corre-

lations of the ordinations with the various environmental variables substantiate these high rates of spatial change. Differences in regional temperature, equivalent latitude, snow cover, and exposure to winds are predominant factors correlating with vegetation. Within each microsite, however, there is a different set of factors that is most important, including animal activity, stability, and moisture. Observations of animal use demonstrate that these are important habitats for many species of wildlife.

The majority of plant species found on pingos are circumpolar, zone 2, arctic-alpine, but within the group of 35 species restricted regionally primarily to pingos there are more zone 3 and 4, North American-Asian species. Although for the entire flora the pingos do not seem to function as biogeographic islands, they do for these restricted species. These restricted species appear to be remnants from a Beringian flora that was once more widespread and is now confined mainly to these sites. The restricted species do not show a correlation with distance to rivers, which would be logical sites for modern dispersal.

Four morphological classes of pingos were described that represent an extension of the two classes proposed by stricted species do not show a correlation with distance to rivers, which would be logical sites for modern dispersal.

Four morphological classes of pingos were described that represent an extension of the two classes proposed by Walker et al. (1985). There is indirect evidence that these can be arranged in a time sequence. The distribution of the restricted species between the four morphological classes suggests that restricted species are not relict but are actively colonizing new sites. There is an increase in their abundance from class 1

(youngest) to class 3 and then a decrease in class 4 (oldest). Using these classes as a basis for a successional study, the pingo flora becomes increasingly variable over the first three stages, and then converges in stage 4. There is no detectable change in species diversity in any microsite over the four stages, and at all stages vegetation is highly correlated with environment.

Significance of the Study

This study has significance on two levels. The first level is simply what the vegetation of pingos indicates about this region, and about pingos themselves. The second level relates to the pingos as a natural ecological experiment. Because they are such ideal sites on which to study development of vegetation and soils, more generalized ecological hypotheses can be developed and tested with the types of data collected here. This study tested four hypotheses and generated several others.

Three factors are most important in characterizing these pingos and their vegetation: (1) their steep environmental gradients, (2) their steep, gravelly, south-facing slopes, and (3) their potential longevity. There are large numbers of gradients that can be related to pingo vegetation, and the various microsites and plant communities differ in their relationships to the gradients. Across much of the coastal plain gradients and longevity. There are large numbers of gradients that can be related to pingo vegetation, and the various microsites and plant communities differ in their relationships to the gradients. Across much of the coastal plain gradients and vegetation change are subtle, and there are vast areas with similar, rather monotonous vegetation. The pingos contrast sharply with their surroundings, and also have rather dramatic changes within them, from the fellfield-like north slopes to the south slopes covered by grasses and brightly colored flowers. It is this

aspect of the pingo vegetation that has been most noticed in the past (Koranda 1970; Walker 1985a).

Beyond this diversity of habitats, however, is another character which sets the pingos out as distinct, and this is their steep, gravelly, south-facing slopes. There are no analogs to these sites elsewhere on the coastal plain, and this is where most of the rare species and communities are found. The presence of these warm, well-drained sites, combined with the potential longevity of the pingos and a calcareous substrate, as well as abundant modern loess, sets the pingos up as the ideal sites on which to look for remnant vegetation from the Duvanny Yar and perhaps even earlier times, when the regional climate was considered to be colder and drier, and when substantial loess deposits (Hopkins 1982) covered much of the coastal plain. Walker (1985a) has suggested that the sand dunes present in the Prudhoe Bay region today are a likely analog to the more extensive dune fields present in northern Alaska during the Duvanny Yar. The pingos are likely another analog, probably more related to sandy and gravelly areas in uplands.

It is not necessary to show a direct connection to the Duvanny Yar vegetation in order for the pingos to be valuable analogs to this period. It is enough to show that the conditions on the pingos today are likely very similar to conditions that were more widespread during connection to the Duvanny Yar vegetation in order for the pingos to be valuable analogs to this period. It is enough to show that the conditions on the pingos today are likely very similar to conditions that were more widespread during that period, and then use the pingos to speculate on what the region might have looked like at that time. The steppe-tundra assemblages present on the pingos today are limited to the south slopes. They may also be found occasionally on summits, where they are in close association with animal dens or burrows.

The steppe-like soils, Pergelic Cryoborolls, are often also found on north slopes.

Why are these steppe-tundra assemblages found on the warmest sites today, when the general consensus is that the full glacial climate was colder than at present? Although the mean annual temperature probably was colder, these data suggest that the climate, at least within the region of this study, was probably also more continental. The coast was further to the north, due to lowered sea level, so the regional climate would have been more continental. A number of climate models support this idea of increased continentality throughout Beringia (Sergin and Shcheglova 1976; Barry 1982). Thus, summer temperatures could actually have been higher than they are today. It is summer temperature that limits plant distribution in the Arctic, not mean annual temperature (Young 1971). Barry (1982) stressed the importance of regional and microclimate variation in the reconstruction of paleoclimates. The temperature data presented here, although limited in extent, are some of the only data available for these effects in northern Alaska today, and demonstrate the magnitude of surface temperature differences for sites with equivalent latitudes of 40° and 80°N.

The final aspect that sets the pingos apart is their potential longevity. This longevity sets them apart not only from most of the coastal plain, which is a dynamic surface that is continually being reworked by the thaw-lake cycle, but also from pingos described from other areas of the world. The general model of pingo growth that has been developed in the literature is based primarily on Mackay's (1979 and others) work in the Tuktoyaktuk Peninsula of northwest

Canada. In this model, the pingo core eventually melts and collapses, leaving a circular lake. There are no known examples of collapsed pingos in the region covered by this study. On the Tuktoyaktuk Peninsula, approximately 3.5% of the pingos are collapsed (Stager 1956). The reason for the apparent stability of the Prudhoe Bay pingos is unknown, although it is probably related to a variety of circumstances. Walker et al. (1985) attributed the difference to the colder temperatures at Prudhoe Bay (as compared to Tuktoyaktuk) and to the presence of gravels as the uppermost sediments at Prudhoe Bay. Another important difference between these two areas is that Tuktoyaktuk was glaciated at some time during the Pleistocene, whereas none of the areas covered by this study were (the flat thaw-lake plains were presumably large floodplains where pingos could not have formed). The gently-rolling thaw-lake plains were probably relatively stable at least throughout the latter part of the Pleistocene, and so there could have been pingos present in this region throughout this entire period. The species now regionally restricted to pingos could have survived by continually recolonizing new pingos as they formed. There are probably few other regions in the arctic that were not ice-covered and that have had stable sites that were present throughout this time.

Continuity of colonization of new pingos as they formed. There are probably few other regions in the arctic that were not ice-covered and that have had stable sites that were present throughout this time.

Future Studies

Additional studies would help to confirm or deny many of the ideas presented here. There is a definite need for firm dates of the pingos. This is particularly true for the broad-based group,

which is hypothesized to represent an old form. Several of the hypotheses concerning biological equilibria along north-south gradients could be tested by examining pingos from other parts of the world. Pingos could be used to examine the effects of gradients on vegetation in other Arctic areas. There are few other opportunities to make these types of comparisons with such good control over other differences, such as substrate. There is also a need for more extensive collection and analysis of microclimatic data from these pingos. Just how different is the climate on the south-facing slopes? Of particular interest would be the annual temperature and moisture regimes in the present-day steppe assemblages. A worldwide survey of pingos would help determine the uniqueness of these central Arctic Coastal Plain pingos.

Importance to Regional Diversity

"This being the only living world we are ever likely to know, let us join to make the most of it." So stated E.O. Wilson (1985, p. 705) in a *BioScience* article on "The Biological Diversity Crisis", in which he made a plea for a complete cataloging of the world's species. The preservation of biological diversity has, in recent years, come to light as an environmental issue of international importance and consequence, and has been called "humankind's most fundamental problem" (Congressman Gus Yalton, quoted in Wenzel 1985). The preservation of biological diversity has, in recent years, come to light as an environmental issue of international importance and consequence, and has been called "humankind's most fundamental problem" (Congressman Gus Yalton, quoted in Wenzel [1985]). This dissertation has been an attempt to describe and understand the floristic diversity of one landform that covers less than 0.1% of the regional landscape, and only a minuscule portion of the world's arctic landscapes as a whole.

The faunal diversity of the pingos has never been studied, and invertebrate species in particular remain unknown and uncataloged. Do the pingos have a particular significance in terms of regional or global diversity?

There are basically two approaches to managing and maintaining diversity. One is essentially a single-species, crisis approach, where attempts are made to protect sufficient habitat to prevent the ultimate destruction of some species. Examples include the grizzly bear in Yellowstone National Park, the whooping crane, and the black-footed ferret. These approaches may take rather staggering amounts of energy and money, and this approach is impractical over the long run. As more and more habitat is destroyed or permanently altered, the number of crises increases until there cannot possibly be enough resources to fight them, and it is now becoming clear that in many cases we have already reached this threshold.

The other approach to maintenance of diversity, which has been more recently heralded, is to preserve whole ecosystems (e.g. Ehrlich and Mooney 1983). Even this approach, however, has been recognized as often leading to fragmented pieces that were originally interconnected and functioned as a unit (Harris 1984). It is now becoming recognized that we must really save *all* of the pieces; that is, we must look at how the entire landscape and even the entire globe functions (Noss 1983; Slobodkin 1984). The International Geosphere/Biosphere Program (IGBP) will be a major effort to examine processes on this scale (Eddy et al. 1986). Processes at the level of landscapes have proven difficult to study using what Naveh (1987) has

called normal science. Much of the value in preserving landscapes is elusive. The science of biocybernetics focuses on positive feedback loops between humans and the landscape (Naveh 1982), with the basic idea that only by taking care of the landscape can we continue to benefit from it.

The pingos are an opportunity to put into practice in the Arctic the knowledge that has been gained in other areas. The difference between the crisis-oriented management approach and the landscape-level approach is most simply one of scale. Noss (1983) formalized this as the maintenance of alpha, beta, and gamma diversity, as defined by Whittaker (1972). Management for alpha diversity concentrates on one or a few species, management for beta diversity concentrates on maximum regional diversity, often through maintenance of early successional stages, and management for gamma diversity concentrates on maintaining large undisturbed areas regionally, and on keeping intact interconnections between habitat patches. How the pingos relate to overall landscape function is unknown. With the great diversity of habitats and species present on pingos, however, it is almost certain that destruction of pingos will have some effect on the regional landscape and its biota.

Geomorphic and ecological events associated with pingos will have some effect on the regional landscape and its biota.

Geomorphic and ecological events may be seen as hierarchical; events at the lowest levels are constrained by those at higher levels, and time and space scales tend to be correlated (Delcourt et al. 1983; Urban et al. 1987). There is interaction between pingos and the surrounding landscape on a daily basis at a small scale, but the formation of pingos is dependent on infrequent geomorphic

events (formation and drainage of a lake deeper than 2 m) (Table 51). The Prudhoe Bay region is a giant experiment on the effects of oil field development on the coastal plain landscape (Walker et al. 1987b). After only fifteen years of development, it already appears that secondary impacts, for which planning cannot be done (for example flooding and thermokarst), are in some areas greater than the primary impacts. The Prudhoe Bay oil field is small in scope when compared to the entire Coastal Plain, but continuing exploration has turned up many other deposits which will likely be developed at some time (see U.S. Fish and Wildlife Service 1987). The ultimate effect of the fragmentation of this landscape, by the building of road networks and pipelines (as investigated by Meehan [1986]), may only be apparent when it is too late. If the recommendations of Noss (1983) and Harris (1984) were to be followed, by leaving focal points such as the pingos intact, and by maintaining natural corridors between various landscape elements, impacts to diversity would likely be lessened.

The northern Alaska pingos represent an uncommon and unusual natural resource that should be protected as part of our national heritage. Their particularly rich floras and faunas, their value as sources of scientific information about geomorphic and ecological processes, or our national heritage. Their particularly rich floras and faunas, their value as sources of scientific information about geomorphic and ecological processes, and their unspecified value as part of the natural landscape would each on its own be reason enough for their protection. The value of maintaining intact ecosystems is generally not specified in environmental assessments, but Barrick (1983) has demonstrated that the majority of citizens do place some value on this. Most of the Toolik River study area

Table 51. Results of scale of natural disturbance events on pingo formation and function. Concepts of patch types and landscape elements are from Forman and Godron (1986).

Event	Frequency (yrs)	Scale (m ²)	Result
Glacial-climatic cycles, glaciation	10 ⁵ - 10 ⁶	10 ¹⁰ - 10 ¹²	Regional landscape types
Formation of permafrost	10 ⁴ - 10 ⁵	10 ⁶ - 10 ¹⁰	Regional landscape elements
Lake drainage	10 ³ - 10 ⁴	10 ⁴ - 10 ⁶	Drained lake basins, pingos
Major colluvial events	10 ² - 10 ³	10 ² - 10 ³	Small environmental resource patches, increased habitat diversity
Colonization by squirrels and foxes	10 ¹ - 10 ²	10 ¹ - 10 ²	Chronic disturbance patches; increased nutrient input, increased attraction to predators
Digging by grizzly bears	10 ⁰ - 10 ¹	10 ⁰ - 10 ¹	Small disturbance patches
Nesting by small mammals and passerines	10 ⁻¹ - 10 ⁰	10 ⁻¹ - 10 ⁰	Movement of nutrients and energy between patches
Nesting by small mammals and passerines	10 ⁻¹ - 10 ⁰	10 ⁻¹ - 10 ⁰	Movement of nutrients and energy between patches within a pingo
Digging and foraging by mammals, perching by birds	10 ⁻² - 10 ⁻¹	10 ⁻² - 10 ⁻¹	Movement of nutrients and energy between pingos and the landscape matrix

and pingo no. 41 (Kadleroshilik Mound) have been recommended for national landmark status (Koranda and Evans 1975; Everett 1983a,b), which would protect the pingos within these areas from further destruction. The Canadian government has taken similar steps toward protection of the Tuktoyaktuk vicinity pingos (Parks Canada 1978). Everett (1983a,b) has recommended that on these national landmark sites there should be no structures, permanent or otherwise, that excavations of any kind be prohibited, and that there should be no vehicle access onto the pingos. No action has yet been taken on these recommendations. For the pingos within areas that have already undergone development (the Prudhoe Bay and Kuparuk areas), protection may be much more difficult to obtain and to enforce. Within developed areas, vehicle access and the placement of permanent structures should be prohibited on all pingos, and tempo-

rary structures, such as survey control points, should be removed immediately after use.

It takes at least several thousand years for a pingo to complete development, and perhaps longer for it to reach a stage of maximum biological diversity. The central Arctic Coastal Plain of Alaska is an unusual situation which has allowed some of these pingos to persist, perhaps from pre-Holocene times. The minimal remains of a 6,000 year old hunting camp on a pingo in the Kuparuk study area (Lobdell 1986) tell us that when people first ventured into the North American Arctic, they encountered some of the pingos that are there today. They have been landmarks, dry camping sites, and observation points for countless generations. It is this generation's responsibility to see that we are not the last people who had the opportunity of knowing and experiencing the pingos.

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APPENDICES

Appendix A - Annotated Species List

Appendix B - Classification Summary Tables

Appendix C - Data

APPENDIX A

Annotated Species List

The purpose of this appendix is to document all species known to occur on pingos within the region considered. There are 232 vascular taxa in 218 species, 113 genera, and 32 families, 104 species of lichens, and 59 species of bryophytes. Recognition of certain subspecies or varieties as valid species is a matter of definition and will never be concrete. Because Hultén (1968) is the standard reference for the Alaskan vascular flora, the names used there are most widely known and accepted. More recent research, however, has often revealed that other names have precedence. In order to be most consistent with other Alaskan work, the names used here are those currently in use by the University of Alaska Herbarium.

Although this was not intended to be a taxonomic study, it did require considerable work with the plants, as many of these represent new records for the region, coastal plain, or north slope. Two types of specimens were collected. The first type, listed as 'Specimens', were collected for the express purpose of deposition in an herbarium. The other type, listed as 'Vouchers', were collected as small samples from individual plots in order to check species identifications in the laboratory. The number following the dash on a voucher number represents the pingo number; thus, one can determine what pingos are represented by looking at these numbers. All specimens and most vouchers have been deposited in either the University of Colorado or University of Alaska herbaria. These were verified or identified by either Dr. David Murray of the University of Alaska or by Dr. William Weber of the University of Colorado. Following each name is a list of the study areas where that species occurred. The abbreviations used are: PB, Prudhoe Bay; KP, Kuparuk; KD, Kadleroshilik; TR, Toolik River; All, all areas. This represents the distribution as documented for pingos only. Some species are more widespread but limited to moist or wet habitats, and therefore rare on pingos.

The list includes species listed by D.A. Walker (1985) as present on pingos or on habitats common on pingos, including animal dens, disturbances, dry sites, and snowbanks. The vascular plant list is probably very nearly complete for the pingos that were sampled, but is likely missing a few species for each study area, as not every pingo within an area could be visited. The cryptogam lists are most certainly incomplete. My inexperience with these groups, particularly with the bryophytes, limited what I was able to accomplish. The majority of bryophytes are pingos that were sampled, but is likely missing a few species for each study area, as not every pingo within an area could be visited. The cryptogam lists are most certainly incomplete. My inexperience with these groups, particularly with the bryophytes, limited what I was able to accomplish. The majority of bryophytes are found in moist to wet habitats, and therefore a great diversity of these taxa is not expected on the pingos. A number of lichen species representing range extensions were verified or identified by Dr. John Thomson of the University of Wisconsin. In spite of my inexperience with these groups, a number of very major range extensions were documented for the lichens. There are likely to be others that I did not recognize. Nomenclature for the cryptogams follows the University of Alaska Herbarium, except for those species listed by Thomson (1984), in which case his treatment is followed.

Vascular Plants

Achillea borealis Bong.

Specimens: 84-142

Vouchers: 1-30

TR

Agropyron boreale (Trucz.) Drobov ssp. *alaskanum* (Scribn. & Merr.) Melderis

Vouchers: 2-29

TR

Agropyron boreale (Trucz.) Drobov ssp. *hyperarcticum* (Polunin) Melderis

Specimens: 83-118

Vouchers: 3-3, 3-21, 3-30, 3-31

All

Alopecurus alpinus Sm. ssp. *alpinus*

Specimens: 83-54, 83-225, 84-31, 84-65

Vouchers: 4-13, 4-19, 4-21, 4-25, 4-33

PB, KP, KD

Alsinarthe rossii (R. Br.) Löve and Löve

See *Minuartia elegans*

Andromeda polifolia L.

New regional record, most coastal locality known.

Specimens: 84-129

KP

Androsace chamaejasme Host ssp. *lehmanniana* (Spreng.) Hult.

Specimens: 83-41, 84-36

Vouchers: 5-1, 5-7, 5-8, 5-12, 5-13, 5-15, 5-17, 5-18, 5-20, 5-21, 5-22, 5-25, 5-26, 5-27, 5-28, 5-29, 5-31, 5-32, 5-33, 5-36, 5-37, 5-39

All

Androsace septentrionalis L.

Specimens: 83-66

Vouchers: 6-1, 6-11, 6-13, 6-15, 6-16, 6-19, 6-21, 6-31, 6-33

All

Anemone drummondii S. Wats.

New coastal plain record.

Specimens: 83-147

Vouchers: 7-7

KD, TR

Anemone parviflora Michx.

Specimens: 83-112

Anemone drummondii S. Wats.

New coastal plain record.

Specimens: 83-147

Vouchers: 7-7

KD, TR

Anemone parviflora Michx.

Specimens: 83-112

Vouchers: 8-3, 8-11, 8-14, 8-15, 8-20, 8-26, 8-27, 8-29, 8-30, 8-31, 8-32, 8-37

All

Antennaria alpina (L.) Gaertn.

(= *Antennaria friesiana* (Trautv.) Ekman ssp. *alaskana* (Malte) Hult.)

Specimens: 83-233, 84-96

Vouchers: 9-11, 9-18, 9-33

PB, KP, KD

Antennaria friesiana (Trautv.) Ekman ssp. *alaskana* (Malte) Hult.

See *Antennaria alpina*

Antiphylla oppositifolia (L.) Fourr.

See *Saxifraga oppositifolia*

Arctagrostis latifolia (R. Br.) Griseb. var. *arundinacea* (Trin.) Griseb.

Fairly common in the southern areas, but generally not distinguished from *A. latifolia* var. *latifolia* in the relevés.

Specimens: 83-162

KD, TR

Arctagrostis latifolia (R. Br.) Griseb. var. *latifolia*

Specimens: 83-116

Vouchers: 10-1, 10-6, 10-8, 10-9, 10-10, 10-13, 10-15, 10-16, 10-17, 10-20, 10-21, 10-22, 10-26, 10-27, 10-28, 10-29, 10-30, 10-31, 30-32, 10-33, 10-34, 10-35, 10-36, 10-37, 10-38, 10-39

All

Arctostaphylos rubra (Rehd. & Wilson) Fern.

See *Arctous rubra*

Arctous rubra (Rehd. & Wilson) Nakai

(= *Arctostaphylos rubra* (Rehd. & Wilson) Fern.)

Specimens: 83-143, 84-154

Vouchers: 11-7, 11-10, 11-20, 11-29, 11-30, 11-31, 11-32

KP, KD, TR

Armeria maritima (Mill.) Willd. ssp. *arctica* (Cham.) Hult.

A coastal species common on the sand dunes at Prudhoe Bay, here occurring inland on a sandy animal den disturbance on Pingo 15. Flower color on this specimen was pink to purple while those at the coast generally have deep pink to red flowers.

Specimens: 84-50

TR

Arnica alpina (L.) Olin ssp. *angustifolia* (M. Vahl) Maguire

Specimens: 83-220, 84-55, 86-41

Vouchers: 12-15, 12-32

KD, TR

Arnica frigida C.A. Mey

Specimens: 83-196, 84-54, 84-66, 86-16

Vouchers: 13-28

KD, TR

Arnica lessingii Greene ssp. *lessingii*

Specimens: 86-40

KD, TR

Arnica frigida C.A. Mey

Specimens: 83-196, 84-54, 84-66, 86-16

Vouchers: 13-28

KD, TR

Arnica lessingii Greene ssp. *lessingii*

Specimens: 86-40

KD, TR

Artemisia arctica Less. ssp. *arctica*

Specimens: 83-81

KP

Artemisia arctica Less. ssp. *comata* (Rydb.) Hult.

Specimens: 84-106

Vouchers: 14-21, 15-21

KP

Artemisia borealis Pall.
(=*Oligosporus groenlandicus* (Homem.) Löve & Löve)
Specimens: 83-114, 84-59
Vouchers: 16-15, 16-33
PB, KP, TR

Artemisia glomerata Ledeb.
Specimens: 83-113, 84-56
Vouchers: 17-15
PB, TR

Aster sibiricus L.
Specimens: 83-117, 83-200
PB, TR

Astragalus aboriginum Richards.
Specimens: 84-53, 86-13
Vouchers: 18-15
KD, TR

Astragalus alpinus L.
Specimens: 83-130, 84-25, 84-20, 84-104, 84-160b
Vouchers: 19-1, 19-20, 19-26, 19-28, 19-30, 19-33, 19-37, 19-40
All

Astragalus umbellatus Bunge
Specimens: 83-70, 84-24
Vouchers: 20-1, 20-2, 20-9, 20-10, 20-13, 20-14, 20-15, 20-16, 20-17, 20-18, 20-19, 20-20, 20-22, 20-23, 20-24, 20-25, 20-26, 20-27, 20-28, 20-29, 20-30, 20-31, 20-32, 20-33, 20-34, 20-35, 20-36, 20-37, 20-38, 20-39, 20-40
All

Betula nana L. ssp. *exilis* (Sukatsch.) Hult.
Vouchers: 21-9, 21-10
KD, TR

Bistorta plumosa (Small) E. Greene
(=*Polygonum bistorta* L. ssp. *plumosum* (Small) Hult.)
Specimens: 83-105, 84-92
Vouchers: 153-10, 153-12, 153-13, 153-16, 153-18, 153-19, 153-23, 153-24, 153-29, 153-34, 153-35, 153-37, 153-38, 153-40
All

Bistorta vivipara (L.) Gray
(=*Polygonum viviparum* L.)
Specimens: 154-1, 154-8, 154-10, 154-12, 154-13, 154-16, 154-17, 154-18
All

Bistorta vivipara (L.) Gray
(=*Polygonum viviparum* L.)
Vouchers: 154-1, 154-8, 154-10, 154-12, 154-13, 154-16, 154-17, 154-18, 154-19, 154-20, 154-21, 154-22, 154-23, 154-24, 154-25, 154-26, 154-27, 154-28, 154-29, 154-30, 154-31, 154-32, 154-33, 154-34, 154-35, 154-36, 154-37, 154-38, 154-39, 154-40
All

Boykinia richardsonii (Hook.) Gray
(=*Theroforon richardsonii* Hook.)
Specimens: 83-139, 83-222, 84-207
Vouchers: 22-13, 22-34, 22-37, 22-38
All

Braya glabella Richards.
Specimens: 83-136, 84-80
Vouchers: 24-14, 24-17, 24-19, 24-20, 24-38, 25-26
PB, KP, TR

Braya humilis (C.A. Mey) Robins.
New regional record.
Specimens: 84-77, 84-218
Vouchers: 23-7, 23-27, 23-31
KP, KD, TR

Braya purpurascens (R. Br.) Bunge
Specimens: 83-135, 84-14, 84-115
Vouchers: 25-5, 25-6, 25-12, 25-13, 25-17, 25-36
PB, KP, TR

Bromus pumpellianus Scribn. var. *arcticus* (Shear) Pors.
Specimens: 83-127, 84-162
PB, TR

Bromus pumpellianus Scribn. var. *pumpellianus*
Specimens: 83-163
Vouchers: 26-7, 27-1, 27-8, 27-9, 27-10, 27-15, 27-30, 27-37, 28-32
PB, KP, TR

Bupleurum triradiatum Adams ssp. *arcticum* (Regel) Hult.
Specimens: 83-175
Vouchers: 29-7, 29-11, 29-15, 29-32
KD, TR

Calamagrostis purpurascens R. Br. ssp. *arctica* (Vasey) Hult.
Specimens: 83-164
TR

Calamagrostis purpurascens R. Br. ssp. *purpurascens*
Specimens: 83-31, 84-176
Vouchers: 30-4, 30-31, 30-32
PB, KP, TR

Caltha palustris L. ssp. *arctica* (R. Br.) Hult.
Specimens: 84-200, 86-33
KP

Campanula uniflora L.
Specimens: 83-49, 84-5a
Vouchers: 31-10, 31-11, 31-14, 31-17, 31-20, 31-21, 31-22
All

Campanula uniflora L.
Specimens: 83-49, 84-5a
Vouchers: 31-10, 31-11, 31-14, 31-17, 31-20, 31-21, 31-22
All

Cardamine digitata Richardson
(=*Cardamine hyperborea* O.E. Schultz)
Specimens: 83-58
Vouchers: 32-9, 32-12, 32-16, 32-18, 32-19, 32-20, 32-21, 32-22, 32-23, 32-24, 32-26, 32-29, 32-30, 32-31, 32-32, 32-33, 32-34, 32-35, 32-37, 32-40
All

Cardamine hyperborea O.E. Schulz
See *C. digitata*

Cardamine pratensis L. ssp. *angustifolia* (Hook.) O.E. Schulz

- Specimens: 84-201
KP, KD
- Carex aquatilis* Wahlenb. ssp. *aquatilis*
Vouchers: 33-19
KP
- Carex aquatilis* Wahlenb. ssp. *stans* (Drej.) Hult.
Specimens: 84-216
Vouchers: 34-1, 34-21, 34-33, 34-38, 34-39
All
- Carex bigelowii* Torr.
Specimens: 83-134
Vouchers: 35-1, 35-2, 35-7, 35-8, 35-9, 35-10, 35-11, 35-13, 35-16, 35-18, 35-19, 35-20, 35-21, 35-22, 35-23, 35-24, 35-25, 35-26, 35-28, 35-29, 35-31, 35-32, 35-34, 35-35, 35-38, 35-39, 35-40, 38-34
All
- Carex capillaris* L.
Specimens: 83-152, 84-138, 84-190
Vouchers: 36-9, 36-10, 39-30
PB, KD, TR
- Carex franklinii* Boott
Second record for the north slope, previously collected along the Firth River (D. Murray, written comm.). The preferred habitat is listed by Hultén (1968) as "[a]lpine slopes, preferably on calcareous soil."
Specimens: 83-153, 84-140, 84-192
Vouchers: 37-27
- Carex glacialis* Mack.
New coastal plain record; generally an alpine plant.
Specimens: 83-150, 84-146, 84-191
Vouchers: 38-7, 42-26
TR
- Carex krausei* Boeck.
Specimens: 84-60, 84-186
TR
- Carex marina* Dew.
Vouchers: 48-11
KD
- Carex maritima* Gunn.
Specimens: 83-63, 84-107
Vouchers: 48-11
KD
- Carex maritima* Gunn.
Specimens: 83-63, 84-107
Vouchers: 40-21, 40-23
PB, KP, TR
- Carex membranacea* Hook.
Specimens: 83-79, 84-69
Vouchers: 41-3, 41-4, 41-8, 41-14, 41-15, 41-16, 41-17, 41-20, 41-23, 41-24, 41-30, 41-32, 41-34, 41-36, 41-37, 41-38, 41-40
All
- Carex misandra* R. Br.
Specimens: 83-88, 84-95

- Vouchers: 42-12, 42-17, 42-19, 42-33, 42-38
All
- Carex nardina* E. Fries
New regional record; probably confused with *Kobresia myosuroides* in earlier studies.
Specimens: 83-122, 84-135, 84-137, 84-180
Vouchers: 43-4, 43-26
PB, KD, TR
- Carex obtusata* Lilj.
New regional record; widespread but easily overlooked.
Specimens: 83-119, 83-155, 84-116, 84-119
Vouchers: 44-3, 44-7, 44-9, 44-10, 44-13, 44-22, 44-24, 44-30, 46-11
All
- Carex petricosa* Dew.
New regional record; previously reported from the northern foothills.
Specimens: 83-124, 84-145, 84-179
Vouchers: 37-7, 37-26, 37-29, 37-31, 37-32
TR
- Carex rupestris* All.
Specimens: 83-91, 84-111
Vouchers: 45-2, 45-3, 45-6, 45-7, 45-12, 45-13, 45-14, 45-15, 45-16, 45-17, 45-18, 45-19, 45-20, 45-22, 45-23, 45-24, 45-25, 45-26, 45-27, 45-29, 45-30, 45-31, 45-32, 45-33, 45-36, 45-37, 45-38, 45-39, 45-40, 46-35
All
- Carex scirpoidea* Michx.
Specimens: 83-33, 84-11
Vouchers: 46-2, 46-3, 46-7, 46-8, 46-10, 46-13, 46-14, 46-15, 46-16, 46-17, 46-18, 46-19, 46-20, 46-21, 46-22, 46-23, 46-24, 46-25, 46-26, 46-27, 46-28, 46-29, 46-30, 46-31, 46-32, 46-34, 46-36, 46-37, 46-38, 46-39, 46-40
All
- Carex supina* Willd. ssp. *spaniocarpa* (Steud.) Hult.
Vouchers: 47-7
TR
- Carex vaginata* Tausch.
Specimens: 84-196
TR
- Cassiope tetragona* (L.) D. Don ssp. *tetragona*
Specimens: 83-170
Vouchers: 48-11, 48-19, 48-20, 48-21, 48-22, 48-23, 48-24, 48-25, 48-26, 48-27, 48-28, 48-29, 48-30, 48-31, 48-32, 48-33, 48-34, 48-35, 48-36, 48-37, 48-38, 48-39, 48-40
All
- Cassiope tetragona* (L.) D. Don ssp. *tetragona*
Specimens: 83-170
Vouchers: 49-1, 49-7, 49-8, 49-9, 49-10, 49-11, 49-12, 49-13, 49-14, 49-15, 49-16, 49-17, 49-18, 49-19, 49-20, 49-22, 49-23, 49-24, 49-25, 49-26, 49-27, 49-28, 49-29, 49-30, 49-31, 49-32, 49-33, 49-34, 49-35, 49-36, 49-37, 49-38, 49-40
All
- Cerastium beeringianum* Cham. & Schlecht. var. *beeringianum*
Specimens: 83-90, 84-19
Vouchers: 50-1, 50-2, 50-3, 50-8, 50-12, 50-13, 50-14, 50-15, 50-16, 50-17, 50-18, 50-19, 50-20, 50-21, 50-22, 50-23, 50-24, 50-25, 50-28, 50-30, 50-33, 50-35, 50-36, 50-38, 50-39, 50-40
All

Cerastium beeringianum Cham. & Schlecht. var. *grandifolium*
Listed by Walker (1985) as the more common variety. Not recognized as distinct from *C. beeringianum* var. *beeringianum* in this study.

Cerastium jenisejense Hult.
Specimens: 83-271
KP

Chamerion latifolium (L.) Holub
See *Epilobium latifolium*

Chrysanthemum integrifolium Richards.

Dendranthemum integrifolium (Richards.) Tsvelev
Specimens: 83-76
Vouchers: 51-12, 51-14, 51-15, 51-17, 51-19, 51-20, 51-22, 51-25, 51-27,
51-28, 51-29, 51-30, 51-31, 51-32, 51-34, 51-35, 51-37, 51-38
All

Chrysosplenium tetrandrum (Lund) T. Fries
Specimens: 84-213
KD,TR

Ciliaria funstonii (Small) Weber
See *Saxifraga bronchialis* ssp. *funstonii*

Ciliaria tricuspidata (Retz.) Weber
See *Saxifraga tricuspidata*

Cnidium cnidifolium (Turcz.) Schischk.
New regional record, northernmost collection.
Specimens: 86-17
KD

Cochlearia officianalis L. ssp. *arctica* (Schlecht.) Hult.
Specimens: 83-249
Vouchers: 52-12
KP

Cystopteris fragilis (L.) Bernh.
Specimens: 83-218
KD

Delphinium brachycentrum Ledeb.
See *D. chamissonis*

Delphinium chamissonis Pritz.
(*D. brachycentrum* Ledeb.)
Delphinium brachycentrum Ledeb.
See *D. chamissonis*

Delphinium chamissonis Pritz.
(*D. brachycentrum* Ledeb.)
New coastal plain record.
Specimens: 83-195, 86-14
KD

Dendranthemum integrifolium (Richards.) Tsvelev
See *Chrysanthemum integrifolium*

Deschampsia caespitosa (L.) Beauv. ssp. *caespitosa*
Specimens: 84-76, 84-144
KD,TR

Descurainia sophioides (Fisch.) O.B. Schulz
Specimens: 83-211, 84-168
KD,TR

Dodecatheon frigidum Cham. & Schlecht.
Specimens: 86-39
Vouchers: 53-25
KD,TR

Draba alpina L.
Listed by Walker (1985) as common on pingos, but not found in this study.
Probably confused with *D. corymbosa* either here or by Walker (1985).

Draba borealis DC.
Specimens: 84-79, 84-108
Vouchers: 55-20, 55-37
TR

Draba cana Adams
Specimens: 84-64
PB,KD

Draba cinerea Adams
Specimens: 83-39, 83-93, 84-4, 84-89, 84-105, 84-122
Vouchers: 56-1, 56-3, 56-8, 56-10, 56-11, 56-13, 56-15, 56-16, 56-17, 56-20, 56-21, 56-33, 56-36, 56-39, 57-1, 57-2, 57-3, 57-4, 57-5, 57-6, 57-9, 57-12, 57-13, 57-14, 57-15, 57-19, 57-20, 57-21, 57-22, 57-24, 57-25, 57-33, 57-35, 57-36, 57-37
All

Draba corymbosa R. Br. ex DC.
(=*Draba macrocarpa* Adams)
Specimens: 84-5, 84-127
Vouchers: 54-5, 54-12, 54-13, 54-14, 54-18, 54-22, 54-23, 54-24, 54-25, 54-36, 54-40, 58-2, 58-6, 58-12, 58-16, 58-17, 58-18, 58-24, 58-26, 58-36, 58-39, 62-14, 66-1, 66-5, 66-16, 66-18, 66-20, 66-25, 66-33, 66-34, 66-35
All

Draba fladnizensis Wulf.
New regional record.
Vouchers: 68-26, 59-11
TR

Draba glabella Pursh
Specimens: 83-197, 83-215, 84-64a, 84-79a, 84-163, 84-217
Vouchers: 55-20, 60-1, 60-8, 60-15, 60-25, 60-28, 60-30, 60-32, 61-1, 62-1, 67-7
TR

Draba glabella Pursh
Specimens: 83-197, 83-215, 84-64a, 84-79a, 84-163, 84-217
Vouchers: 55-20, 60-1, 60-8, 60-15, 60-25, 60-28, 60-30, 60-32, 61-1, 62-1, 67-7
All

Draba lactea Adams
Specimens: 83-68, 84-198
Vouchers: 61-28, 64-16, 65-11, 65-13, 65-16
PB,KP,TR

Draba longipes Raup
Specimens: 83-227
KP

Draba macrocarpa Adams

See *D. corymbosa*

Draba nivalis Liljebl.

New regional record.

Specimens: 86-2

Vouchers: 63-11, 63-24

KP, KD

Draba subcapitata Simm.

New regional record.

Specimens: 83-52, 84-3

Vouchers: 64-2, 64-4

PB

Dryas integrifolia M. Vahl ssp. *integrifolia*

Specimens: 83-72

Vouchers: 69-1, 69-7, 69-8, 69-9, 69-10, 69-11, 69-12, 69-13, 69-14, 69-15, 69-16, 69-17, 69-18, 69-19, 69-20, 69-21, 69-22, 69-23, 69-24, 69-25, 69-26, 69-27, 69-28, 69-29, 69-30, 69-31, 69-32, 69-33, 69-34, 69-35, 69-36, 69-37, 69-38, 69-39, 69-40

All

Dupontia fisheri R. Br. ssp. *fisheri*

Specimens: 83-258

Vouchers: 201-23

KD

Elymus innovatus Beal

(=*Leymus velutinus* (Bowden) Löve & Löve)

Specimens: 83-161, 84-143, 84-52, 84-177

Vouchers: 70-7, 70-15, 70-32

TR

Empetrum hermaphroditum (Lange) Hagerup

(=*Empetrum nigrum* L. ssp. *hermaphroditum* (Lange) Böcher)

Specimens: 83-209

Vouchers: 75-10, 75-11

KD

Empetrum nigrum L. ssp. *hermaphroditum* (Lange) Böcher

See *E. hermaphroditum*

Epilobium davuricum Fisch.

Specimens: 84-73

TR

Epilobium latifolium L.

(=*Chamerion latifolium* (L.) Holub)

See *E. hermaphroditum*

Epilobium davuricum Fisch.

Specimens: 84-73

TR

Epilobium latifolium L.

(=*Chamerion latifolium* (L.) Holub)

Specimens: 83-232

Vouchers: 81-11

PB, KD

Equisetum arvense L.

Specimens: 83-35

Vouchers: 72-1, 72-8, 72-14, 72-15, 72-16, 72-21, 72-24, 72-26, 72-27, 72-28, 72-30, 72-31, 72-34, 72-39

All

Equisetum scirpoides Michx.

(=*Hippochaete scirpoides* (Michx.) Farwell)

Specimens: 83-87

Vouchers: 73-1, 73-6, 73-8, 73-14, 73-15, 73-16, 73-18, 73-19, 73-20, 73-22, 73-24, 73-26, 73-29, 73-32, 73-34, 73-38, 73-40

All

Equisetum variegatum Schleich. ssp. *variegatum*

(=*Hippochaete variegata* (Schleich.) Bruhin)

Specimens: 83-109

Vouchers: 74-2, 74-14, 74-15, 74-17, 74-19, 74-22, 74-23, 74-26, 74-27, 74-32, 74-34, 74-38, 74-39, 74-40

All

Erigeron eriocephalus J. Vahl

Specimens: 83-57, 84-109, 84-203

Vouchers: 75-3, 75-21, 75-33

PB, KP, TR

Erigeron grandiflorus Hook. ssp. *muirii* (Gray) Hult.

See *Erigeron muirii*

Erigeron humilis Graham

Specimens: 84-212, 86-5

Vouchers: 76-33

KP, KD

Erigeron hyperboreus Greene

Specimens: 86-31

Vouchers: 77-11

KD

Erigeron muirii A. Gray

(=*Erigeron grandiflorus* Hook. ssp. *muirii* (Gray) Hult.)

New coastal plain record; a north slope endemic listed by Murray (1980) as threatened.

Specimens: 83-154

TR

Eriophorum angustifolium Honck. ssp. *subarcticum* (Vassiljev.) Hult.

Specimens: 84-161

KP, KD, TR

Eriophorum angustifolium Honck. ssp. *triste* (T. Fries) Hult.

See *E. triste*

Eriophorum scheuchzeri Hoppe var. *scheuchzeri*

Specimens: 84-72, 84-202

KP, KD, TR

Eriophorum angustifolium Honck. ssp. *triste* (T. Fries) Hult.

See *E. triste*

Eriophorum scheuchzeri Hoppe var. *scheuchzeri*

Specimens: 84-72, 84-202

KP

Eriophorum triste (T. Fries) Hadac & A. Löve

(=*Eriophorum angustifolium* Honck. ssp. *triste* (T. Fries) Hult.)

Vouchers: 78-1, 78-4, 78-6, 78-8, 78-14, 78-17, 78-18, 78-19, 78-20, 78-22, 78-29, 78-34, 78-36, 78-37, 78-38

All

Eriophorum vaginatum L.

Vouchers: 79-10, 79-16, 79-22, 79-34

All

Eritrichum aretioides (Cham.) DC.

Specimens: 86-30
KD

Erysimum pallasii (Pursh) Fern.

Specimens: 86-19
KD

Eutrema edwardsii R. Br.

Specimens: 84-114, 84-67, 83-255
Vouchers: 80-13, 80-21
PB, KP, KD

Festuca altaica Trin.

Rare on the coastal plain.
Specimens: 84-165
Vouchers: 27-27, 201-29
TR

Festuca baffinensis Polunin

Specimens: 83-30, 83-89, 84-75
Vouchers: 82-9, 82-10, 82-11, 82-12, 82-15, 82-16, 82-17, 82-18, 82-19,
82-21, 82-22, 82-23, 82-24, 82-25, 82-29, 82-33, 82-34, 82-35, 82-39, 82-40
All

Festuca brachyphylla Schult.

Specimens: 83-104, 83-108, 84-98
Vouchers: 88-8, 88-11, 88-12, 88-13, 88-18, 88-20, 88-21, 88-23, 88-24,
88-25, 88-28, 88-32, 88-33, 88-34, 88-35, 88-38, 88-40
All

Festuca rubra L.

Specimens: 83-166, 83-167, 83-56, 84-194, 84-210
Vouchers: 89-25, 89-29, 89-33, 89-37
All

Gastrolychnis affinis (J. Vahl) Tolm. & Kozh.

(= *Melandrium affine* J. Vahl; *Silene involucrata* (Cham. & Schlecht.) Bocq.)
Specimens: 83-126
Vouchers: 104-1, 104-8, 104-11, 104-12, 104-13, 104-15, 104-16, 104-17,
104-19, 104-20, 104-21, 104-23, 104-24, 104-25, 104-29, 104-30, 104-34,
104-35, 104-36, 104-39, 104-40, 106-10, 106-11, 106-28, 106-39
All

Gastrolychnis affinis (J. Vahl) Tolm. & Kozh.
All

Gastrolychnis apetala (L.) Tolm. & Kozh.

(= *Melandrium apetalum* (L.) Fenzl ssp. *arcticum* (E. Fries) Hult.; *Silene wahlbergella* Chawd. ssp. *arctica* (Fr.) Hult.)
Specimens: 83-132
Vouchers: 105-18, 105-25
All

Gentiana propinqua Richards.

See *Gentianella propinqua*

Gentianella propinqua (Richards.) Gillett.

(= *Gentiana propinqua* Richards.)
Specimens: 83-168
TR

Geum glaciale Adams

See *Novosieversia glacialis*

Hedysarum alpinum L. ssp. *americanum* (Michx.) Fedtsch.

Specimens: 83-46, 83-138
Vouchers: 90-7, 90-15, 90-26, 90-27, 90-29, 90-30, 90-31, 90-32
PB, TR

Hierochloë alpina (Sw.) Roem. & Schult.

Specimens: 83-181, 84-120
Vouchers: 91-10, 91-11
PB, KP, KD

Hippochaete scirpoides (Michx.) Farwell

See *Equisetum scirpoides*

Hippochaete variegata (Schleich.) Bruhin

See *Equisetum variegatum*

Hippuris vulgaris L.

Specimens: 84-214
TR

Hirculus prorepens (Fisch. ex Sternberg) Weber

See *Saxifraga hirculus*

Huperzia selago (L.) C. Martins ssp. *appressa* (Desv.) D. Löve

(= *Lycopodium selago* L. ssp. *appressum* (Desv.) Hult.)
Specimens: 83-212, 84-131, 86-22
KP, KD

Juncus biglumis L.

Specimens: 84-78
Vouchers: 92-8, 92-12, 92-16, 92-18, 92-24, 92-25, 92-32, 92-34, 92-40
All

Kobresia myosuroides (Vill.) Fiori & Paol.

Specimens: 83-34, 84-58, 84-139, 84-170
Vouchers: 43-7, 93-4, 93-7, 93-8, 93-10, 93-11, 93-14, 93-15, 93-19, 93-20,
93-25, 93-26, 93-27, 93-28, 93-29, 93-30, 93-31, 93-32, 93-34, 93-37, 93-39
All

Kobresia sibirica Turcz.

Specimens: 84-70, 84-101, 84-178
Vouchers: 94-8, 94-16, 94-23, 94-25, 94-26, 94-31, 94-34, 94-40
Specimens: 84-70, 84-101, 84-178
Vouchers: 94-8, 94-16, 94-23, 94-25, 94-26, 94-31, 94-34, 94-40
All

Koenigia islandica L.

Specimens: 86-24
KD

Lagotis glauca Gaertn. ssp. *minor* (Willd.) Hult.

Specimens: 84-197
Vouchers: 95-13
KP, KD, TR

Ledum decumbens (Ait.) Small

(= *L. palustre* L. ssp. *decumbens* (Ait.) Hult.)
Specimens: 83-213, 83-204

Vouchers: 96-9, 96-10
KD

Ledum palustre L. ssp. *decumbens* (Ait.) Hult.
See *L. decumbens*

Lesquerella arctica (Wormsk.) S. Wats.
Specimens: 83-40, 84-10
Vouchers: 97-7, 97-14, 97-17, 97-20, 97-26, 97-32
PB, KD, TR

Leymus velutinus (Bowden) Löve & Löve
See *Elymus innovatus*

Lidia arctica (Stev.) Löve & Löve
See *Minuartia arctica*

Lloydia serotina (L.) Rchb.
Specimens: 83-80
Vouchers: 98-12, 98-13, 98-14, 98-15, 98-16, 98-17, 98-21, 98-22, 98-23, 98-24, 98-26, 98-27, 98-28, 98-29, 98-32, 98-33, 98-36, 98-37, 98-38, 98-39
All

Lupinus arcticus S. Wats.
Specimens: 83-144, 83-174, 84-102
Vouchers: 99-7, 99-28, 99-29
KP, KD, TR

Luzula arctica Blytt
Specimens: 83-82
Vouchers: 100-3, 100-6, 100-7, 100-8, 100-12, 100-13, 100-16, 100-23, 100-24, 100-25, 100-33, 100-34, 100-35, 100-38, 102-1, 102-8, 102-12, 102-15, 102-17, 102-18, 102-19, 102-20, 102-25, 102-29, 102-40
All

Luzula arcuata (Wahlenb.) Sw. ssp. *unalaschensis* (Buchenau) Hult.
Northernmost collection, also known from the Jago River (D. Murray, written comm.).
Vouchers: 102-9
KD

Luzula confusa Lindeb.
Specimens: 83-253, 84-94
Vouchers: 101-8, 101-9, 101-10, 101-11, 101-12, 101-18, 101-19, 101-20, 101-23, 101-24, 101-25, 101-33, 101-35
All

Specimens: 83-253, 84-94
Vouchers: 101-8, 101-9, 101-10, 101-11, 101-12, 101-18, 101-19, 101-20, 101-23, 101-24, 101-25, 101-33, 101-35
All

Luzula kjellmaniana Miyabe & Kuds
(= *L. tundricola* Gorodk.)
Specimens: 83-73, 83-180, 84-121, 86-20
Vouchers: 102-24, 102-34, 102-35, 102-38, 103-11, 103-35, 103-37
All

Luzula tundricola Gorodk.
See *L. kjellmaniana*

Lycopodium selago L. ssp. *appressum* (Desv.) Hult.
See *Huperzia selago* ssp. *appressa*

Melandrium affine J. Vahl
See *Gastrolychnis affinis*

Melandrium apetalum (L.) Fenzl ssp. *arcticum* (E. Fries) Hult.
See *Gastrolychnis apetalum*

Micranthus nelsoniana (D. Don) Small
See *Saxifraga nelsoniana*

Minuartia arctica (Stev.) Aschers. & Graebn.
(= *Lidia arctica* (Stev.) Löve & Löve)
Specimens: 83-50, 84-123
Vouchers: 107-8, 107-9, 107-11, 107-13, 107-14, 107-15, 107-16, 107-17, 107-18, 107-19, 107-22, 107-23, 107-24, 107-26, 107-27, 107-28, 107-29, 107-30, 107-31, 107-32, 107-34, 107-35, 107-36, 107-37, 107-38, 107-40, 108-40, 194-7b
All

Minuartia elegans Cham. & Schlect.
(= *Alsianthe rossii* (R. Br.) Löve and Löve; *Minuartia rossii* (R. Br.) Graebn.)
Specimens: 83-51
Vouchers: 109-13, 109-18, 109-35
PB, KP

Minuartia rossii (R. Br.) Graebn.
See *M. elegans*

Minuartia rubella (Wahlenb.) Graebn.
(= *Tryphane rubella* (Wahlenb.) Reichenbach.)
Specimens: 83-67, 83-92
Vouchers: 110-1, 110-2, 110-7, 110-11, 110-13, 110-14, 110-15, 110-16, 110-17, 110-20, 110-21, 110-22, 110-23, 110-24, 110-25, 110-28, 110-30, 110-33, 110-35, 110-36, 110-38
All

Muscaria sileneflora Sternb.
See *Saxifraga caespitosa*

Nardosmia frigida (L.) Hook.
See *Petasites frigidus*

Novosieversia glacialis (Adams) F. Bolle
(= *Geum glaciale* Adams)
Specimens: 83-184, 86-32
KD

Oligosporus groenlandicus (Hornem.) Löve & Löve
(= *Amargia arctica* Gorodk.)
Specimens: 83-184, 86-32
KD

Oligosporus groenlandicus (Hornem.) Löve & Löve
See *Artemisia borealis*

Orthilia secunda (L.) House ssp. *obtusata* (Turcz.) Böcher
(= *Pyrola secunda* L. ssp. *obtusata* (Turcz.) Hult.)
New regional record; fairly common on pingos but scattered elsewhere.
Specimens: 164-8, 164-9, 164-16, 164-18, 164-19, 164-28, 164-29, 164-30, 164-35, 164-37, 164-38
Vouchers: 84-125
All

Oxyria digyna (L.) Hill
Specimens: 83-86

Vouchers: 111-3, 111-9, 111-10, 111-11, 111-13, 111-21, 111-38
PB, KP, KD

Oxytropis arctica R. Br.

The name is used here in the broadest sense and includes two distinct morphological types that appear to be ecologically distinct as well. Only specimen nos. 84-88 and 112-13, from Pingos 7 and 13, represent *O. arctica* in the strict sense. These are gravelly alpine-like sites, and these plants have one to three large blue flowers and distinct "sausage-like processes" (Hultén 1968) on the stipules. Specimens from other sites have three to eight small flowers, indistinct or no processes on the stipules, and red peduncles. This second form is virtually indistinguishable from a white-flowered variety of *O. campestris* when in fruit. This type has an extremely caespitose growth form, while the specimens of *O. arctica* s.s. are more erect. More work is needed on this group before the proper names can be determined, and therefore while they have been placed together in the relevé data, careful work may reveal two or three distinct species in this complex.

Specimens: 83-42, 83-102, 84-12, 84-57, 84-35, 84-71, 84-83, 84-88, 84-90, 84-100, 84-187, 84-188

Vouchers: 112-7, 112-13, 112-32, 119-15

All

Oxytropis campestris (L.) DC. ssp. *gracilis* (Nels.) Hult.

Specimens: 84-193

Vouchers: 118-7, 118-14, 118-20, 118-22, 118-24, 118-25, 118-26, 118-27, 118-28, 118-29, 118-30, 118-31, 118-32, 118-33, 118-34, 118-37, 118-39

PB, KP, TR

Oxytropis campestris (L.) DC. ssp. *jordalii* (Pors.) Hult.

See *O. jordalii*

Oxytropis campestris (L.) DC. var. *varians* (Rydb.) Barneby

Vouchers: 113-7, 113-28, 113-29

TR

Oxytropis deflexa (Pall.) DC. var. *foliolosa* (Hook.) Barneby

Specimens: 83-44, 84-113

Vouchers: 115-23, 115-34, 115-38

PB, KP, KD

Oxytropis jordalii Porsild

(= *Oxytropis campestris* (L.) DC. ssp. *jordalii* (Pors.) Hult.)

Specimens: 83-148, 84-91, 84-124, 84-160

Vouchers: 114-7, 114-13, 114-15, 114-16, 114-17, 114-20, 114-22, 114-24, 114-25, 114-27, 114-29, 114-30, 114-31, 114-32, 114-37, 114-39, 121-17,

(≠ *Ὠξυτρόπις ἑμπεστρίς* (L.) DC. ssp. *jordalii* (Pors.) Hult.)

Specimens: 83-148, 84-91, 84-124, 84-160

Vouchers: 114-7, 114-13, 114-15, 114-16, 114-17, 114-20, 114-22, 114-24, 114-25, 114-27, 114-29, 114-30, 114-31, 114-32, 114-37, 114-39, 121-17, 121-39, 122-28

PB, KP, TR

Oxytropis maydelliana Trautv.

Specimens: 83-45, 84-48

Vouchers: 116-3, 116-8, 116-11, 116-14, 116-15, 116-18, 116-19, 116-23, 116-24, 116-25, 116-26, 116-29, 116-30, 116-34, 116-35, 116-37, 116-38

All

Oxytropis nigrescens (Pall.) Fisch. ssp. *bryophila* (Greene) Hult.

Specimens: 83-43

Vouchers: 117-2, 117-3, 117-7, 117-8, 117-11, 117-13, 117-14, 117-15, 117-16, 117-17, 117-18, 117-19, 117-22, 117-23, 117-26, 117-31, 117-33, 117-34, 117-35, 117-36, 117-38, 117-39

All

Oxytropis nigrescens (Pall.) Fisch. ssp. *pygmaea* Hult.

Specimens: 84-189

TR

Papaver hultenii Knaben var. *hultenii*

D. Murray (pers. comm.) considers *P. hultenii* as doubtfully distinct from *P. lapponicum*. On Kadleroshilik Pingo (no. 41), there was a pink-flowered type (see below) which was distinct from *P. lapponicum* in its capsule shape as well. Only one yellow-flowered specimen was considered to be closer to the *P. hultenii* type than to *P. lapponicum*.

Specimens: 84-18

PB

Papaver hultenii Knaben var. *salmonicolor* Hult.

See comments under *P. h. var. hultenii* above.

Specimens: 86-4

KD

Papaver lapponicum (Tolm.) Nordh. ssp. *occidentale* (Lundstr.) Knaben

Specimens: 84-34

Vouchers: 125-11, 125-13, 125-14, 125-16, 125-18, 125-19, 125-20, 125-21, 125-23, 125-24, 125-25, 125-33, 125-35, 125-36, 125-38, 125-40, 126-11, 126-17, 126-18, 126-21, 126-24

All

Papaver lapponicum (Tolm.) Nordh. ssp. *porsildii* Knaben

Specimens: 83-231

KD

Papaver macounii Greene var. *discolor* Hult.

Specimens: 83-69, 84-8, 84-173, 84-204

Vouchers: 124-9, 124-10, 124-11, 124-17, 124-20, 124-23, 124-25, 124-30, 124-31, 124-37, 124-38, 124-39, 124-40, 126-11, 127-1, 127-4, 127-11, 127-12, 127-14, 127-15, 127-16, 127-17, 127-18, 127-19, 127-20, 127-21, 127-22, 127-23, 127-24, 127-25, 127-26, 127-27, 127-28, 127-29, 127-30, 127-32, 127-33, 127-34, 127-35, 127-36, 127-37, 127-38, 127-39, 127-40

All

Parnassia kotzebuei Cham. & Schlecht.

Specimens: 83-224, 84-172

Vouchers: 128-37

All

Parnassia kotzebuei Cham. & Schlecht.

Specimens: 83-224, 84-172

Vouchers: 128-37

KD, TR

Parrya nudicaulis (L.) Regel

Specimens: 83-131, 84-9, 84-27

Vouchers: 129-1, 129-4, 129-6, 129-10, 129-14, 129-15, 129-16, 129-17, 129-18, 129-19, 129-20, 129-21, 129-22, 129-23, 129-24, 129-25, 129-27, 129-28, 129-29, 129-30, 129-31, 129-32, 129-34, 129-36, 129-37, 129-38, 129-40

All

Pedicularis capitata Adams

Specimens: 83-111, 84-29

Vouchers: 130-1, 130-5, 130-8, 130-9, 130-10, 130-11, 130-13, 130-14, 130-15, 130-16, 130-17, 130-19, 130-20, 130-21, 130-22, 130-23, 130-24, 130-25, 130-26, 130-27, 130-28, 130-29, 130-30, 130-31, 130-32, 130-33, 130-34, 130-35, 130-36, 130-37, 130-38, 130-39
All

Pedicularis kanei Durand ssp. *kanei*
See *P. lanata*

Pedicularis lanata Cham. & Schlecht.
(=*Pedicularis kanei* Durand)
Specimens: 83-182, 84-1, 84-28
Vouchers: 113-19b, 131-5, 131-8, 131-12, 131-13, 131-14, 131-15, 131-16, 131-17, 131-18, 131-19, 131-20, 131-21, 131-22, 131-23, 131-24, 131-25, 131-28, 131-30, 131-33, 131-34, 131-35, 131-36, 131-37, 131-38, 131-39, 131-40, 133-5
All

Pedicularis langsdoerffi Fisch. ssp. *arctica* (R. Br.) Pennell
Vouchers: 132-11
KP, KD

Pedicularis sudetica (Willd.) Hult.
Specimens: 83-75, 83-228
Vouchers: 133-5, 133-7, 133-12, 133-19, 133-21, 133-23, 133-25, 133-27, 133-32, 133-39
All

Pedicularis verticillata L.
TR

Pentaphylloides floribunda (Pursh) Löve & Löve
(=*Potentilla fruticosa* L.)
Specimens: 84-166
Vouchers: 155-29 TR

Petasites frigidus (L.) Franch.
(=*Nardosmia frigida* (L.) Hook.)
Specimens: 84-2
Vouchers: 135-1, 135-9, 135-11, 135-19, 135-21, 135-37, 135-39
All

Phippsia algida (Soland.) R. Br.
Specimens: 83-254, 83-270, 86-26, 86-37
KP, KD

Phlox sibirica L. ssp. *sibirica*
Specimens: 83-160, 84-181
Vouchers: 136-7
KD, TR

Poa alpigena (E. Fries) Lindm.
(=*P. rigens* Hartm.)
Specimens: 83-64, 83-77, 83-125, 84-74
Vouchers: 138-1, 138-3, 138-6, 138-8, 138-10, 138-12, 138-13, 138-15, 138-20, 138-21, 138-23, 138-24, 138-32, 138-33, 140-6, 140-13, 140-15
All

Poa arctica R. Br. ssp. *arctica*
Specimens: 83-74, 83-129
Vouchers: 138-11, 138-14, 138-16, 138-19, 138-22, 138-25a, 138-31, 139-20, 139-21, 139-22, 139-23, 141-1, 141-3, 141-7, 141-8, 141-12, 141-18, 141-19, 141-21, 141-25, 141-28, 141-29, 141-30, 141-33, 141-34, 141-35, 141-36, 141-37, 141-38, 141-40, 144-9
All

Poa glauca M. Vahl
Specimens: 83-32, 83-167a, 83-217, 84-195, 86-9, 86-23
Vouchers: 138-25b, 139-13, 139-14, 139-15, 140-33, 141-16, 141-17, 141-28b, 141-29b, 142-3, 143-3, 143-7, 143-8, 143-9, 143-10, 143-11, 143-17, 143-20, 143-25, 143-26, 143-29, 143-30, 143-32, 144-3, 144-36, 145-1, 145-3, 145-4, 147-20, 148-10, 149-20
All

Poa lanata Scribn. & Merr.
Specimens: 83-165
Vouchers: 141-9, 141-11, 144-7, 144-11, 144-18, 144-33
KP, KD, TR

Poa malacantha Kom.
Specimens: 83-78, 83-252
PB, KP

Poa pratensis L.
Vouchers: 146-6, 146-8
All

Poa rigens Hartm.
See *P. alpigena*

Polemonium acutiflorum Willd.
Specimens: 83-146, 83-179, 83-185, 83-210, 84-211
Vouchers: 151-10, 151-30, 151-33, 151-34, 141-37, 141-40
KP, KD, TR

Polemonium boreale Adams
Specimens: 83-59, 84-26
Vouchers: 152-8, 152-9, 152-13, 152-14, 152-15, 152-18, 152-20, 152-22
All

Polygonum bistorta L. ssp. *plumosum* (Small) Hult.
See *Bistorta plumosa*

Polygonum viviparum L.
See *Bistorta vivipara*

Potentilla biflora Willd.
Specimens: 86-1
KD

Potentilla fruticosa L.
See *Pentaphylloides floribunda*

Potentilla hookeriana Lehm. ssp. *chamissonis* (Hult.) Hult.
Specimens: 83-121, 83-151, 84-99
KD

- Potentilla hookeriana* Lehm. ssp. *hookeriana* var. *hookeriana*
Specimens: 83-29, 86-8, 84-23, 84-61, 84-87, 84-171, 84-182
Vouchers: 156-8, 156-9, 156-11, 156-15, 156-19, 156-20, 156-21, 156-28, 156-30, 162-9, 162-33
All
- Potentilla hyparctica* Malte
Vouchers: 157-12 157-18 157-24 157-25, 161-11
PB, KP, KD
- Potentilla nivea* L.
New coastal plain record.
Specimens: 83-201
KD
- Potentilla pulchella* R. Br.
As defined here, this species includes a morphological type that is densely caespitose, with very small leaves and mat-like growth habit, and at first glance it appears to be a distinct species (listed under specimens nos. as "small type"). Its ecology is very close to more typical forms of *P. pulchella*, as it is generally limited to coastal sites. It has not yet been determined if it should be given status as a new species, a new variety or subspecies of *P. pulchella*, or if it is simply an ecotype of *P. pulchella*.
- Specimens: 83-53, 83-61, 84-15, 84-97, 84-112, 84-219; small type: 83-107, 84-110, 84-134
Vouchers: 158-12, 158-16, 158-21, 158-22
PB, KP
- Potentilla uniflora* Ledeb.
There was considerable confusion surrounding this species in this study. The two most common *Potentillas* encountered were *P. hookeriana* and *P. uniflora*. *P. hookeriana* generally has two or more small flowers and a branched inflorescence, while *P. uniflora* has one or occasionally two larger flowers with an orange center. There was a distinct form present on the pingos that is most similar to *P. beringensis* Yurtsev, a Beringian species characterized by having marcescent chestnut stipules (as opposed to dark brown in typical *P. uniflora*) and a caespitose growth form. Typical *P. uniflora* was also found. The *P. beringensis* type may represent a hybrid or ecotype rather than a distinct species. This type was usually listed in field notes as *P. uniflora*, but was probably also called *P. hookeriana* on occasion. It is listed here under *P. uniflora* until there is sufficient evidence to separate it as a distinct species. This type was usually listed in field notes as *P. hookeriana*, but was probably also called *P. hookeriana* on occasion. It is listed here under *P. uniflora* until there is sufficient evidence to separate it as a distinct species.
Specimens: 83-62, 83-120, 83-230, 84-21, 84-33, 84-86, 86-7
Vouchers: 159-1, 159-3, 159-9, 159-11, 159-13, 159-14, 159-15, 159-17, 159-22, 159-36, 160-11
- Primula borealis* Duby
KP
- Puccinellia andersonii* Swallen
Specimens: 83-251
PB, KP
- Puccinellia angustata* (R. Br.) Rand & Redf.
Vouchers: 137-12
PB, KP

- Pulsatilla patens* (L.) Mill. subsp. *multifida* (Pritz.) Zamels
New coastal plain record.
Specimens: 86-15
KD
- Pyrola asarifolia* Michx. var. *purpurea* (Bunge) Fern.
New regional record; rare on the north slope.
Specimens: 83-173, 84-169
KD, TR
- Pyrola grandiflora* Radius
Specimens: 83-198, 84-126
Vouchers: 163-9, 163-10, 163-20, 163-25, 163-26, 163-28, 163-29, 163-30, 164-34
KP, KD, TR
- Pyrola secunda* L. ssp. *obtusata* (Turcz.) Hult.
See *Orthilia secunda* ssp. *obtusata*
- Ranunculus hyperboreus* Rottb. ssp. *hyperboreus*
Specimens: 86-3, 86-34
KP, KD
- Ranunculus nivalis* L.
Specimens: 83-110, 86-35
Vouchers: 165-11, 165-13
PB, KP, KD
- Ranunculus pedatifidus* Sm. ssp. *affinis* (R. Br.) Hult.
Specimens: 83-38, 83-219, 84-17, 84-103
Vouchers: 166-3, 166-12, 166-13, 166-14, 166-15, 166-16, 166-17, 166-18, 166-19, 166-20, 166-21, 166-22, 166-23, 166-24, 166-25, 166-33, 166-34, 166-36, 166-38, 166-40
All
- Ranunculus pygmaeus* Wahlenb. ssp. *pygmaeus*
New regional record.
Specimens: 83-269, 86-28, 86-36
KP, KD
- Rhododendron lapponicum* (L.) Wahlenb.
Specimens: 83-141
Vouchers: 167-26, 167-27, 167-28, 167-29, 167-30, 167-31, 167-37
TR
Specimens: 83-174
Vouchers: 167-26, 167-27, 167-28, 167-29, 167-30, 167-31, 167-37
TR
- Rubus chamaemorus* L.
Specimens: 84-130
KP
- Rumex arcticus* Trautv.
Specimens: 84-68
TR
- Sagina intermedia* Fenzl
Listed by Walker (1985) as infrequent on river gravels and pingos, but not recognized on pingos in this study.
- Salix arbusculoides* Anderss.
Specimens: 84-174

Vouchers: 168-10
KD,TR

Salix arctica Pall. *arctica*
Specimens: 84-6, 84-63
Vouchers: 169-21, 169-22, 169-24, 169-25, 169-26, 169-27, 169-40
All

Salix brachycarpa Nutt. ssp. *niphoclada* (Rydb.) Argus
(= *S. niphoclada* Rydb.)
Specimens: 83-226, 84-81, 84-151, 84-155
Vouchers: 170-8, 170-9, 170-10, 170-27, 170-28, 170-31, 170-32
PB,KD,TR

Salix fuscescens Anderss.
Vouchers: 172-34
KP

Salix glauca L.
Specimens: 83-156, 83-207, 84-62, 84-148, 84-149, 84-152, 84-157, 84-158, 84-159, 84-167, 84-184, 84-197a
Vouchers: 170-20, 170-29, 170-30, 170-37, 173-7, 173-10, 173-11, 173-21, 173-25, 173-26, 173-27, 173-28, 173-29, 173-30, 173-31, 173-32, 173-33, 173-34, 173-37, 173-39
All

Salix hastata L.
Specimens: 83-206
Vouchers: 171-10
KD

Salix lanata L. ssp. *richardsonii* (Hook.) A. Skortz.
Specimens: 84-150, 84-156
Vouchers: 174-15, 174-20, 174-28, 174-29, 174-30, 174-32, 174-37
KD,TR

Salix niphoclada Rydb.
See *S. brachycarpa* ssp. *niphoclada*

Salix ovalifolia Trautv. var. *ovalifolia*
Specimens: 83-256, 84-82
Vouchers: 175-11, 175-21, 175-36
KP,KD

Salix phlebophylla Anderss.
Specimens: 83-183
Vouchers: 176-8, 176-9, 176-11, 176-16, 176-22, 176-24
PB,KP,KD
Vouchers: 175-11, 175-21, 175-36
KP,KD

Salix phlebophylla Anderss.
Specimens: 83-183
Vouchers: 176-8, 176-9, 176-11, 176-16, 176-22, 176-24
PB,KP,KD

Salix planifolia Pursh ssp. *pulchra* (Cham.) Argus
(= *S. pulchra* Cham.)
Specimens: 83-205
Vouchers: 177-9, 177-10, 177-11, 177-21, 177-32, 177-37
KP,KD,TR

Salix polaris Wahlenb.
Uncertain determination; not previously reported from the north slope.
Specimens: 83-229
KP

Salix pulchra Cham.
See *S. planifolia* ssp. *pulchra*

Salix reticulata L. ssp. *reticulata*
Specimens: 83-37, 84-7
Vouchers: 11-23, 178-1, 178-7, 178-9, 178-10, 178-11, 178-13, 178-14, 178-15, 178-16, 178-17, 178-18, 178-19, 178-20, 178-21, 178-22, 178-23, 178-24, 178-25, 178-26, 178-27, 178-28, 178-29, 178-30, 178-31, 178-32, 178-33, 178-34, 178-35, 178-36, 178-37, 178-38, 178-39, 178-40
All

Salix rotundifolia Trautv. ssp. *rotundifolia*
Specimens: 83-36
Vouchers: 179-1, 179-4, 179-8, 179-9, 179-11, 179-12, 179-13, 179-14, 179-15, 179-16, 179-17, 179-18, 179-19, 179-20, 179-21, 179-22, 179-23, 179-24, 179-25, 179-31, 179-33, 179-34, 179-35, 179-36, 179-37, 179-38, 179-39, 179-40
All

Saussurea angustifolia (Willd.) DC.
Specimens: 83-142
Vouchers: 181-1, 181-8, 181-9, 181-10, 181-11, 181-14, 181-15, 181-16, 181-18, 181-19, 181-21, 181-23, 181-24, 181-26, 181-27, 181-28, 181-29, 181-30, 181-31, 181-32, 181-37, 181-38, 181-39, 181-40
All

Saxifraga bronchialis L. ssp. *funstonii* (Small) Hult.
(= *Ciliaria funstonii* (Small) Weber)
Specimens: 83-203, 86-12
Vouchers: 189-9
All

Saxifraga caespitosa L.
(= *Muscaria sileniflora* Sternb.)
Specimens: 83-106, 84-30, 84-199
Vouchers: 182-12, 182-16, 182-18, 182-19, 182-20, 182-24, 182-25, 182-33, 182-35, 182-38
PB,KD

Saxifraga cernua L.
Specimens: 83-176, 83-250, 84-132
Vouchers: 183-8, 183-12, 183-18, 183-24, 183-25, 183-40
All

Saxifraga davurica Willd. ssp. *grandipetala* (Engler & Irmsch.) Hult.
Specimens: 86-27
KD
Specimens: 83-176, 83-250, 84-132
Vouchers: 183-8, 183-12, 183-18, 183-24, 183-25, 183-40
All

Saxifraga davurica Willd. ssp. *grandipetala* (Engler & Irmsch.) Hult.
Specimens: 86-27
KD

Saxifraga hieracifolia Waldst. & Kit.
Specimens: 83-177
Vouchers: 184-8, 184-12, 184-19, 184-20, 184-21, 184-23, 184-25, 184-35
All

Saxifraga hirculus L.
(= *Hirculus prorepens* (Fisch. ex Sternberg) Weber)
Specimens: 83-133
Vouchers: 185-10, 185-16, 185-18, 185-19, 185-21, 185-33, 185-35
All

Saxifraga nelsoniana D. Don
(=*Micranthus nelsoniana* (D. Don) Small; *Saxifraga punctata* L. ssp. *nelsoniana* (D. Don) Hult.)
Specimens: 83-178
Vouchers: 187-8, 187-9, 187-10, 187-33
All

Saxifraga nivalis L.
New regional record; only a few localities on the north slope.
Specimens: 84-32
PB

Saxifraga oppositifolia L. ssp. *oppositifolia*
(=*Antiphylla oppositifolia* (L.) Fourr.)
Specimens: 84-85
Vouchers: 186-1, 186-7, 186-12, 186-13, 186-14, 186-15, 186-16, 186-17, 186-18, 186-19, 186-20, 186-21, 186-22, 186-23, 186-24, 186-25, 186-26, 186-27, 186-29, 186-30, 186-31, 186-32, 186-33, 186-34, 186-35, 186-36, 186-37, 186-38, 186-39, 186-40
All

Saxifraga punctata L. ssp. *nelsoniana* (D. Don) Hult.
See *S. nelsoniana*

Saxifraga reflexa Hook.
New coastal plain record; an alpine plant.
Specimens: 86-10
KD

Saxifraga rivularis L. var. *rivularis*
Specimens: 83-268, 86-29, 86-38
KP, KD, TR

Saxifraga tricuspidata Rottb.
(=*Ciliaria tricuspidata* (Retz.) Weber)
Specimens: 83-202, 84-117
Vouchers: 188-9, 188-11
PB, KD

Selaginella sibirica (Milde) Heiron.
Specimens: 83-234
Vouchers: 190-11
KD

Senecio atropurpureus (Ledeb.) Fedtsch. ssp. *frigidus* (Richards.) Hult.
(=*Tephroseris atropurpureus* (Ledeb.) Löve & Löve)
Specimens: 83-21
Vouchers: 190-11
KD

Senecio atropurpureus (Ledeb.) Fedtsch. ssp. *frigidus* (Richards.) Hult.
(=*Tephroseris atropurpureus* (Ledeb.) Löve & Löve)
Specimens: 83-71
Vouchers: 191-1, 191-8, 191-10, 191-12, 191-15, 191-16, 191-17, 191-18, 191-19, 191-20, 191-21, 191-22, 191-23, 191-24, 191-25, 191-26, 191-28, 191-29, 191-30, 191-32, 191-33, 191-34, 191-35, 191-36, 191-37, 191-38, 191-39, 191-40
All

Senecio congestus (R. Br.) DC.
KD

Senecio hyperborealis Greenm.
Specimens: 86-11
KD

Senecio lugens Richards.
Specimens: 83-47, 84-51, 86-18
PB, DK, TR

Senecio resedifolius Less.
Specimens: 83-115, 83-149, 84-141, 84-16
Vouchers: 192-3, 192-7, 192-11, 192-14, 192-15, 192-24, 192-26, 192-27, 192-28, 192-32, 192-39
All

Silene acaulis L.
Specimens: 83-85
Vouchers: 193-7, 193-8, 193-11, 193-12, 193-13, 193-14, 193-15, 193-16, 193-17, 193-18, 193-19, 193-20, 193-22, 193-23, 193-24, 193-26, 193-27, 193-28, 193-29, 193-30, 193-31, 193-32, 193-33, 193-34, 193-35, 193-37, 193-38, 193-39, 193-40
All

Silene involucrata (Cham. & Schlecht.) Bocq.
See *Gastrolychnis affinis*

Silene wahlbergella Chawd. ssp. *arctica* (Fr.) Hult.
See *Gastrolychnis apetala*

Solidago multiradiata Ait. var. *multiradiata*
Specimens: 84-164
TR

Stellaria laeta Richards.
Listed as frequent on pingos by D.A. Walker (1985), who did not list *Stellaria longipes* at all. This is undoubtedly the same species recognized as *S. longipes* in the present study.

Stellaria longipes Goldie
Specimens: 83-145, 83-216, 84-93
Vouchers: 194-7, 194-8, 194-9, 194-10, 194-11, 194-12, 194-13, 194-14, 194-15, 194-16, 194-17, 194-18, 194-19, 194-20, 194-21, 194-23, 194-24, 194-25, 194-29, 194-30, 194-31, 194-32, 194-33, 194-34, 194-35, 194-36, 194-37, 194-38, 194-39, 194-40
All

Stellaria umbellata Turcz.
Specimens: 86-25
Vouchers: 194-20, 194-21, 194-22, 194-23, 194-24, 194-25, 194-26, 194-27, 194-28, 194-29, 194-30, 194-31, 194-32, 194-33, 194-34, 194-35, 194-36, 194-37, 194-38, 194-39, 194-40
All

Stellaria umbellata Turcz.
Specimens: 86-25
KD

Taraxacum ceratophorum (Ledeb.) DC.
Specimens: 86-6
Vouchers: 195-3, 195-20, 195-39
PB, KP, KD

Taraxacum phymatocarpum J. Vahl
Specimens: 84-13
Vouchers: 195-17, 196-5, 196-12, 196-13, 196-14, 196-17, 196-22, 196-36
All

Tephrosia atropurpurea (Ledeb.) Löve & Löve
See *Senecio atropurpureus*

Thalictrum alpinum L.
Specimens: 84-183
Vouchers: 197-7, 197-26, 197-37
TR

Theroforon richardsonii Hook.
See *Boykinia richardsonii*

Tofieldia coccinea Richards.
New regional record; common in the foothills.
Specimens: 83-158
Vouchers: 198-7, 198-26, 198-28, 198-29, 198-31, 198-37
KD,TR

Tofieldia pusilla (Michx.) Pers.
Specimens: 83-159, 84-136
Vouchers: 199-7, 199-26, 199-30, 199-31, 199-32
KD,TR

Trisetum spicatum (L.) Richter
Specimens: 83-55, 83-65, 84-22
Vouchers: 200-3, 200-8, 200-11, 200-13, 200-14, 200-15, 200-17, 200-19,
200-20, 200-21, 200-22, 200-25, 200-33, 200-36, 200-37
All

Tryphane rubella (Wahlenb.) Reichenbach.
See *Minuartia rubella*

Vaccinium gaultherioides Bigelow
See *Vaccinium uliginosum* ssp. *microphyllum*

Vaccinium uliginosum L. ssp. *microphyllum* Lange
(=*Vaccinium gaultherioides* Bigelow)
Specimens: 83-140
Vouchers: 202-8, 202-9, 202-10, 202-11, 202-24, 202-26, 202-27, 202-28,
202-29, 202-30, 202-31, 202-32, 202-34, 202-37
All

Vaccinium vitis-idaea L. ssp. *minus* (Lodd.) Hult.
Specimens: 83-172, 84-128
Vouchers: 203-9
KD

Vouchers: 203-9
KD

Valeriana capitata Pall.
Specimens: 83-60, 83-223
PB,KD

Zygadenus elegans Pursh
New regional record, scattered localities on the northern coastal plain.
Specimens: 84-208
Vouchers: 204-37
TR

Lichens

Alectoria nigricans (Ach.) Nyl.
Vouchers: 300-1, 300-2, 300-3, 300-4, 300-5, 300-6, 300-7, 300-8, 300-9,
300-10, 300-11, 300-12, 300-13, 300-14, 300-15, 300-16, 300-17, 300-18,
300-19, 300-20, 300-21, 300-23, 300-24, 300-25, 300-26, 300-27, 300-28,
300-29, 300-30, 300-31, 300-32, 300-33, 300-34, 300-35, 300-36, 300-38,
300-40, 300-41, 303-7, 303-26, 303-32, 303-35, 303-38
All

Alectoria ochroleuca (Hoffm.) Mass.
Vouchers: 301-7, 301-8, 301-13, 301-16, 301-18, 301-19, 301-24, 301-26,
301-27, 301-30, 301-31, 301-32, 301-35, 301-41
All

Asahinea chrysanthia (Tuck.) W.L. & C.F. Culb.
Vouchers: 302-7, 302-13, 302-15, 302-16, 302-18, 302-23, 302-24, 302-26,
302-28, 302-38, 302-40, 302-41
All

Buellia punctata (Hoffm.) Mass.
Vouchers: 387-8, 387-12, 387-13, 387-16, 387-18, 387-19, 387-20, 387-21,
387-23, 387-24, 387-26, 387-29, 387-30, 387-31, 387-32, 387-34, 387-35,
387-38, 387-39, 387-40, 387-40
All

Caloplaca cinammonea (Th. Fr.) Oliv.
Vouchers: 304-18
PB

Caloplaca holocarpa (Hoffm.) Wade
Vouchers: 305-1, 305-2, 305-3, 305-4, 305-6, 305-10, 305-12, 305-13, 305-14,
305-15, 305-16, 305-18, 305-19, 305-20, 305-22, 305-23, 305-24, 305-25,
305-26, 305-29, 305-30, 305-31, 305-32, 305-33, 305-34, 305-35, 305-36,
305-38, 305-39, 305-40
All

Caloplaca stillicidiorum (Vahl) Lynge
Vouchers: 306-1, 306-4, 306-8, 306-10, 306-11, 306-12, 306-13, 306-15,
306-16, 306-17, 306-20, 306-23, 306-25, 306-26, 306-31, 306-33, 306-34,
306-37, 306-38, 306-39, 306-41
All

Caloplaca violacea Zahlbr.
306-37, 306-38, 306-39, 306-41
All

Caloplaca tirolensis Zahlbr.
Vouchers: 307-2, 307-11, 307-12, 307-14, 307-16, 307-18, 307-20, 307-22,
307-23, 307-25, 307-33, 307-36
PB,KP,TR

Caloplaca tornoënsis Magn.
Not previously recorded in this area; specimens were not expertly verified.
Vouchers: 388-1, 388-11, 388-35
PB,KP,TR

Cetraria andrejevii Oksn.
Not previously recorded in this area; specimens were not expertly verified.
Vouchers: 308-19, 308-40
KP

Cetraria cucullata (Bell.) Ach.

Vouchers: 309-1, 309-2, 309-3, 309-4, 309-5, 309-6, 309-7, 309-8, 309-9, 309-10, 309-11, 309-12, 309-13, 309-14, 309-15, 309-16, 309-17, 309-18, 309-19, 309-20, 309-21, 309-22, 309-23, 309-24, 309-25, 309-26, 309-27, 309-28, 309-29, 309-30, 309-31, 309-32, 309-33, 309-34, 309-35, 309-36, 309-37, 309-38, 309-39, 309-40, 309-41

All

Cetraria delisei (Bory ex Schaer.) Th. Fr.

Vouchers: 310-1, 310-2, 310-3, 310-5, 310-8, 310-12, 310-13, 310-16, 310-19, 310-23, 310-24, 310-32, 310-34, 310-36, 310-38, 310-39

All

Cetraria fastigiata (Del. ex Nyl. in Norrl.) Kärnef.

Not previously recorded in this area; specimens were not expertly verified.

Vouchers: 311-8, 311-20, 311-41

KP, KD

Cetraria islandica (L.) Ach. ssp. *crispiformis* (Rds.) Kärnef.

Not previously recorded in this area; specimens were not expertly verified.

Vouchers: 312-8, 312-25, 312-28, 312-30, 312-34, 312-35, 312-38, 312-40, 312-41

KP, KD, TR

Cetraria islandica (L.) Ach. ssp.

Vouchers: 313-1, 313-2, 313-3, 313-4, 313-5, 313-6, 313-7, 313-8, 313-9, 313-10, 313-11, 313-12, 313-13, 313-14, 313-15, 313-16, 313-17, 313-18, 313-19, 313-20, 313-21, 313-22, 313-23, 313-24, 313-25, 313-26, 313-27, 313-28, 313-29, 313-30, 313-31, 313-32, 313-33, 313-34, 313-35, 313-36, 313-37, 313-38, 313-39, 313-40, 313-41

All

Cetraria aevigata Rass.

Not previously recorded in this area; specimens were not expertly verified.

Vouchers: 314-2, 314-8, 314-9, 314-11, 314-12, 314-16, 314-18, 314-19, 314-21, 314-22, 314-24, 314-30, 314-34, 314-35, 314-37, 314-38, 314-40, 314-41

All

Cetraria nivalis (L.) Ach.

Vouchers: 315-1, 315-2, 315-3, 315-4, 315-5, 315-6, 315-7, 315-8, 315-9, 315-10, 315-11, 315-12, 315-13, 315-14, 315-15, 315-16, 315-17, 315-18, 315-19, 315-20, 315-21, 315-22, 315-23, 315-24, 315-25, 315-26, 315-27, 315-28, 315-29, 315-30, 315-31, 315-32, 315-33, 315-34, 315-35, 315-36, 315-37, 315-38, 315-39, 315-40, 315-41

All

Cetraria tilesii Ach.

Vouchers: 315-10, 315-11, 315-12, 315-13, 315-14, 315-15, 315-16, 315-17, 315-18, 315-19, 315-20, 315-21, 315-22, 315-23, 315-24, 315-25, 315-26, 315-27, 315-28, 315-29, 315-30, 315-31, 315-32, 315-33, 315-34, 315-35, 315-36, 315-37, 315-38, 315-39, 315-40, 315-41

All

Cetraria tilesii Ach.

Vouchers: 316-3, 316-4, 316-5, 316-7, 316-14, 316-15, 316-26, 316-27, 316-29, 316-30, 316-31, 316-32

PB, TR

Cladonia acuminata (Ach.) Norrl.

Not previously recorded in this area; specimens were not expertly verified.

Vouchers: 317-9, 317-10

KD

Cladonia amaurocraea (Flörke) Schaer.

Vouchers: 318-8, 318-25, 328-9

KP, KD

Cladonia arbuscula (Wallr.) Rabenh.

Not previously recorded in this area; specimens were not expertly verified.

Vouchers: 319-19, 319-24

KP

Cladonia chlorophaea (Flörke) Spreng.

Not previously recorded in this area but collected from Pt. Barrow and common in the northern foothills; specimens were not expertly verified.

Vouchers: 320-8, 320-9, 320-10, 320-11, 320-18, 320-21, 320-24, 320-25, 320-26, 320-28, 320-29, 320-30, 320-31, 320-32, 320-33, 320-34, 320-35, 320-37, 320-41

All

Cladonia ecmocyna Leight.

Not previously recorded in this area but known from other coastal plain regions; specimens were not expertly verified.

Vouchers: 321-8, 321-9, 321-10, 321-11, 321-12, 321-13, 321-16, 321-18, 321-19, 321-20, 321-28, 321-29, 321-30, 321-33, 321-41

All

Cladonia fimbriata (L.) Fr.

Not previously recorded in this area but occurs in the northern foothills; specimens were not expertly verified.

Vouchers: 322-9, 322-10, 322-23, 322-25, 322-26, 322-27, 322-28, 322-32, 322-37, 322-39, 322-41

KP, KD, TR

Cladonia gracilis (L.) Willd.

Vouchers: 323-8, 323-9, 323-10, 323-11, 323-24, 323-29, 323-32, 323-34, 323-35, 323-37, 323-40, 323-41

KP, KD, TR

Cladonia phyllophora Hoffm.

Vouchers: 324-29

TR

Cladonia pocillum (Ach.) O. Rich.

Vouchers: 325-1, 325-2, 325-3, 325-4, 325-6, 325-7, 325-8, 325-9, 325-10, 325-11, 325-12, 325-13, 325-14, 325-15, 325-16, 325-17, 325-18, 325-19, 325-20, 325-21, 325-22, 325-23, 325-25, 325-26, 325-27, 325-28, 325-29, 325-31, 325-32, 325-33, 325-35, 325-36, 325-37, 325-38, 325-39, 325-41

All

Cladonia pocillum (Ach.) O. Rich.

Vouchers: 325-1, 325-2, 325-3, 325-4, 325-6, 325-7, 325-8, 325-9, 325-10, 325-11, 325-12, 325-13, 325-14, 325-15, 325-16, 325-17, 325-18, 325-19, 325-20, 325-21, 325-22, 325-23, 325-25, 325-26, 325-27, 325-28, 325-29, 325-31, 325-32, 325-33, 325-35, 325-36, 325-37, 325-38, 325-39, 325-41

All

Cladonia pyxidata (L.) Hoffm.

Vouchers: 326-2, 326-6, 326-7, 326-9, 326-10, 326-11, 326-12, 326-18, 326-19, 326-21, 326-23, 326-24, 326-25, 326-28, 326-31, 326-32, 326-34, 326-37, 326-39, 326-40, 326-41

All

Cladonia rangiferina (L.) Wigg.

Vouchers: 327-9

KD

Cladonia verticillata (Hoffm.) Schaer.

Not previously recorded in this area, has been found in the foothills region to the south; specimens were not expertly verified.

Vouchers: 329-10, 329-11

KD

Collema bachmanianum (Fink) Degel.

Vouchers: 330-1, 330-2, 300-3, 330-4, 330-5, 330-8, 330-10, 330-13, 330-14, 330-16, 330-17, 330-20, 330-21, 330-22, 330-23, 330-31, 330-33, 330-34, 330-35, 330-36, 330-38, 330-41

All

Collema undulata Laur. ex Flot.

Not previously recorded in this area; specimens were not expertly verified.

Vouchers: 331-9, 331-15, 331-20, 331-26, 331-40, 331-41

KP, KD, TR

Coriscium viride (Ach.) Vain.

Not previously recorded in this area but known from Pt. Barrow; specimens were not expertly

Vouchers: 333-3, 333-6, 333-7, 333-9, 333-11, 333-13, 333-14, 333-15, 333-26, 333-27, 333-41

All

Cornicularia divergens Ach.

Vouchers: 334-1, 334-2, 334-3, 334-6, 334-7, 334-8, 334-9, 334-11, 334-13, 334-38, 334-39, 334-40, 334-41

All

Dactylina arctica (Hook.) Nyl.

Vouchers: 335-1, 335-2, 335-5, 335-6, 335-8, 335-9, 335-10, 335-11, 335-12, 335-13, 335-14, 335-15, 335-16, 335-17, 335-18, 335-19, 335-20, 335-21, 335-22, 335-23, 335-24, 335-25, 335-26, 335-27, 335-28, 335-29, 335-30, 335-31, 335-32, 335-33, 335-34, 335-35, 335-36, 335-37, 335-38, 335-39, 335-40, 335-41

All

Dactylina beringica Bird & Thoms.

Not previously recorded in this area; specimens were not expertly verified.

Vouchers: 336-3, 336-4, 336-5, 336-7, 336-8, 336-13, 336-14, 336-15, 336-17, 336-19, 336-20, 336-21, 336-23, 336-24, 336-26, 336-27, 336-29, 336-30, 336-31, 336-32, 336-34, 336-36, 336-37, 336-38, 336-39, 336-40, 336-41

30, 336-31, 336-32, 336-34, 336-36, 336-37, 336-38, 336-39, 336-40, 336-41

All

Dactylina ramulosa (Hook.) Tuck.

Vouchers: 337-5, 337-8, 337-14, 337-15, 337-16, 337-19, 337-20, 337-23, 337-24, 337-30, 337-33, 337-34, 337-35, 337-38, 337-40, 337-41

All

Evernia perfragilis Llano

Vouchers: 339-1, 339-2, 339-3, 339-4, 339-5, 339-6, 339-7, 339-12, 339-13, 339-14, 339-15, 339-17, 339-19, 339-20, 339-33, 339-35, 339-36

All

Fistulariella almquistii (Vain.) Bowler & Rundel

(= *Ramalina almquistii* Vain.)

Vouchers: 340-1, 340-2, 340-3, 340-4, 340-5, 340-6, 340-7, 340-8, 340-9, 340-11, 340-13, 340-14, 340-15, 340-16, 340-17, 340-18, 340-19, 340-20, 340-21, 340-22, 340-23, 340-24, 340-25, 340-26, 340-27, 340-28, 340-29, 340-30, 340-31, 340-32, 340-33, 340-34, 340-35, 340-36, 340-37, 340-38, 340-39, 340-40, 340-41

All

Fistulariella roesleri (Hochst. ex Schaer.) Bowler & Rundel

Not previously recorded north of the Brooks Range. Det. by J.W. Thomson.

Vouchers: 377-10 377-30

KD, TR

Fulgensia bracteata (Hoffm.) Raes.

Vouchers: 341-2, 341-4, 341-6, 341-10, 341-12, 341-13, 341-14, 341-16, 341-17, 341-20, 341-22, 341-36, 341-38, 341-39

PB, KP, KD

Gyalecta foveolaris (Ach.) Schaer.

Vouchers: 404-4, 404-24

PB, KP

Hypogymnia physodes (L.) W. Wats.

Vouchers: 342-13, 342-25

KP

Hypogymnia subobscura (Vain.) Poelt

Vouchers: 343-1, 343-2, 343-3, 343-4, 343-5, 343-6, 343-7, 343-8, 343-9, 343-11, 343-12, 343-13, 343-14, 343-15, 343-16, 343-17, 343-18, 343-19, 343-20, 343-21, 343-22, 343-23, 343-24, 343-25, 343-26, 343-27, 343-28, 343-29, 343-30, 343-31, 343-32, 343-34, 343-35, 343-36, 343-37, 343-38, 343-39, 343-40, 343-41

All

Lecanora behringii Nyl.

Vouchers: 344-9, 344-10, 344-15, 344-17, 344-19, 344-25, 344-29, 344-32, 344-35, 344-37, 344-38, 344-40

All

Lecanora epibryon (Ach.) Ach.

Vouchers: 345-1, 345-2, 345-3, 345-4, 345-5, 345-6, 345-7, 345-8, 345-9, 345-10, 345-11, 345-12, 345-13, 345-14, 345-15, 345-16, 345-17, 345-18, 345-19, 345-20, 345-21, 345-22, 345-23, 345-24, 345-25, 345-26, 345-27, 345-28, 345-29, 345-30, 345-31, 345-32, 345-33, 345-34, 345-35, 345-36, 345-37, 345-38, 345-39, 345-40, 345-41

345-17, 345-20, 345-22, 345-23, 345-24, 345-25, 345-26, 345-27, 345-28, 345-29, 345-30, 345-31, 345-32, 345-33, 345-34, 345-35, 345-36, 345-37, 345-38, 345-39, 345-40, 345-41

All

Lecanora luteoventralis Brodo

Not previously recorded in this area, degree of range extension is uncertain.

Det. by J.W. Thomson.

Vouchers: 346-1, 346-3, 346-4, 346-6, 346-7, 346-8, 346-12, 346-13, 346-14, 346-15, 346-16, 346-18, 346-19, 346-20, 346-22, 346-23, 346-24, 346-25, 346-26, 346-27, 346-29, 346-30, 346-31, 346-32, 346-34, 346-35, 346-36, 346-37, 346-38, 346-39, 346-40

All

Lecanora verrucosa Ach.

Vouchers: 390-2, 390-3, 390-8, 390-12, 390-13, 390-18, 390-20, 390-21,

- 390-22, 390-33, 390-35, 390-36, 390-37, 390-39
PB, KP, KD
- Lecidea assimilata* Nyl.
Vouchers: 391-3, 391-5, 391-7, 391-12, 391-13, 391-14, 391-16, 391-17, 391-18, 391-20, 391-21, 391-22, 391-23, 391-24, 391-25, 391-27, 391-28, 391-29, 391-32, 391-33, 391-35, 391-36, 391-37, 391-38, 391-39, 391-41
All
- Lecidea ramulosa* Th. Fr.
Vouchers: 392-3, 392-5, 392-6, 392-13, 392-14, 392-16, 392-18, 392-23, 392-35, 392-40
PB, KP
- Lecidea uliginosa* (Schrad.) Ach.
Not previously recorded in this area but has been collected at Pt. Barrow; specimens were not expertly verified.
Vouchers: 393-13, 393-18
PB, KP, KD
- Lecidea vernalis* (L.) Ach.
Listed as occasional on dry tundra by Walker (1985) but not recorded in this study. Probably confused with *Lecanora luteovernalis* Brodo by both authors.
- Lepraria membranacea* (Dicks.) Vain.
Vouchers: 347-7, 347-13, 347-15, 347-25, 347-26, 347-30, 347-31
KP, TR
- Leptogium lichenoides* (L.) Zahlbr.
Not previously recorded in this area but collected in northern foothills; specimens were not expertly verified.
Vouchers: 348-20, 348-25, 348-27, 348-28, 348-36, 348-41
All
- Leptogium sinuatum* (Huds.) Mass.
Vouchers: 349-4, 349-13, 349-14, 349-17, 349-18, 349-19, 349-20, 349-21, 349-22, 349-24, 349-30, 349-31, 349-33, 349-34, 349-36, 349-37, 349-40, 349-41
All
- Lobaria linita* (Ach.) Rabenh.
Not previously recorded in this area but known from a number of other coastal plain locations. Specimens were not expertly verified.
Vouchers: 408-1, 408-25, 408-41
PB, KP, KD
- plain locations. Specimens were not expertly verified.
Vouchers: 408-1, 408-25, 408-41
PB, KP, KD
- Masonhalea richardsonii* (Hook.) Kärnef.
(= *Cetraria richardsonii* Hook.)
Vouchers: 350-1, 350-2, 350-3, 350-4, 350-6, 350-7, 350-8, 350-9, 350-11, 350-12, 350-13, 350-14, 350-15, 350-16, 350-18, 350-19, 350-20, 350-21, 350-22, 350-23, 350-24, 350-25, 350-26, 350-28, 350-29, 350-30, 350-31, 350-32, 350-33, 350-34, 350-35, 350-36, 350-37, 350-38, 350-39, 350-40, 350-41
All
- Nephroma arctica*
Vouchers: 351-9
KD

- Nephroma expallidum*
Vouchers: 352-8, 352-9, 352-11, 352-15, 352-25, 352-31, 352-35, 352-40, 352-41
All
- Ochrolechia frigida* (Sw.) Lynge
Vouchers: 353-1, 353-2, 353-3, 353-4, 353-6, 353-7, 353-8, 353-9, 356-10, 353-12, 353-13, 353-14, 353-15, 353-16, 353-18, 353-19, 353-20, 353-21, 353-23, 353-24, 353-25, 353-28, 353-29, 353-30, 353-31, 353-32, 353-33, 353-34, 353-35, 353-38, 353-39, 353-40, 353-41
All
- Ochrolechia upsaliensis* (L.) Mass.
Vouchers: 354-1, 354-2, 354-3, 354-7, 354-8, 354-10, 354-11, 354-13, 354-14, 354-15, 354-17, 354-18, 354-19, 354-20, 354-21, 354-23, 354-24, 354-26, 354-27, 354-28, 354-29, 354-30, 354-31, 354-32, 354-33, 354-34, 354-35, 354-36, 354-37, 354-38, 354-40, 354-41
All
- Pannaria pezizoides* (Web.) Trev.
Not previously recorded in this area but known from Pt. Barrow and other coastal plain locations. Specimens were not expertly verified.
Vouchers: 355-10, 355-11, 355-12, 355-18, 355-19, 355-35
PB, KP, KD
- Parmelia alpicola* Th. Fr.
Vouchers: 409-41
KD
- Parmelia omphalodes* (L.) Ach.
Vouchers: 356-1, 356-2, 356-7, 356-9, 356-11, 356-13, 356-18, 356-19, 356-23, 356-24, 356-25, 356-34, 356-35, 356-38, 356-40, 356-41
All
- Peltigera aphthosa* (L.) Willd.
Vouchers: 357-1, 357-3, 357-5, 357-7, 357-8, 357-9, 357-10, 357-11, 357-13, 357-14, 357-16, 357-18, 357-19, 357-20, 357-21, 357-22, 357-24, 357-25, 357-27, 357-28, 357-29, 357-30, 357-32, 357-34, 357-35, 357-38, 357-40, 357-41
All
- Peltigera canina* (L.) Willd.
Vouchers: 358-1, 358-2, 358-3, 358-4, 358-5, 358-6, 358-8, 358-9, 358-10, 358-11, 358-12, 358-13, 358-14, 358-15, 358-18, 358-19, 358-20, 358-21, 358-22, 358-24, 358-25, 358-26, 358-29, 358-30, 358-31, 358-32, 358-33, 358-34, 358-35, 358-36, 358-37, 358-38, 358-40, 358-41
All
- Peltigera canina* (L.) Willd. f. *sorediata* Schaer.
(= *Peltigera spuria* (Ach.) DC.)
Vouchers: 360-9, 360-10, 360-11, 360-14, 360-28, 360-40, 360-41
All
- Peltigera canina* var. *rufescens* (Weis.) Mudd
(= *Peltigera rufescens* (Weis.) Humb.)
Vouchers: 359-1, 359-3, 359-5, 359-7, 359-8, 359-9, 359-10, 359-11, 359-13, 359-16, 359-21, 359-23, 359-24, 359-26, 359-28, 359-29, 359-33, 359-

- 37, 359-39, 359-40
All
- Peltigera lepidophora* (Nyl.) Vain.
Not previously recorded in the Prudhoe Bay region but known from Franklin Bluffs in the Kadleroshilik area. Specimens were not expertly identified.
Vouchers: 362-5, 362-8, 362-9, 362-11, 362-12, 362-13, 362-18, 362-20, 362-21, 362-24
PB, KP, KD
- Peltigera malacea* (Ach.) Funck
Vouchers: 363-1, 363-2, 363-6, 363-8, 363-9, 363-10, 363-11, 363-13, 363-17, 363-21, 363-23, 363-25, 363-26, 363-28, 363-31, 363-36, 363-37, 363-41
PB
- Peltigera membranacea* (Ach.) Nyl.
Not previously recorded in this area; specimens were not expertly verified.
Vouchers: 364-2, 364-10, 364-14
PB, KD
- Peltigera polydactyla* (Neck.) Hoffm.
Vouchers: 365-8, 365-14
PB, KD
- Peltigera scabrosa* Th. Fr.
Not previously recorded in the Prudhoe Bay region but known from other coastal plain locations including Franklin Bluffs; specimens were not expertly verified.
Vouchers: 366-13, 366-28, 366-40
KP, TR
- Peltigera venosa* (L.) Baumg.
Vouchers: 367-8, 367-41
KD
- Pertusaria bryontha* (Ach.) Nyl.
Not previously recorded at Prudhoe Bay but known to occur at Franklin Bluffs; specimens were not expertly verified.
Vouchers: 405-8, 405-9, 405-40
KP, KD
- Pertusaria coriacea* (Th. Fr.) Th. Fr. var. *obducens* (Nyl.) Vain.
Not previously recorded in this area; specimens were not expertly verified.
Vouchers: 406-15
- Pertusaria coriacea* (Th. Fr.) Th. Fr. var. *obducens* (Nyl.) Vain.
Not previously recorded in this area; specimens were not expertly verified.
Vouchers: 406-15
TR
- Pertusaria dactylina* (Ach.) Nyl.
Vouchers: 369-8, 369-9, 369-21, 369-22, 369-24, 369-25, 369-26, 369-29, 369-35, 369-41
All
- Pertusaria glomerata* (Ach.) Schaer.
Not previously recorded on the North Slope, but Thomson (1979) stated that it was known from the Aleutian Islands and Northwest Territories and "...fully expected there [on the North Slope]..." Identification verified by J.W. Thomson.
Vouchers: 394-10
KD

- Pertusaria pangyra* (Ach.) Mass.
Vouchers: 353-11, 371-13, 371-15, 371-18, 371-24, 371-26, 371-30, 371-31, 371-32, 371-34, 371-41
All
- Pertusaria subobducens* Nyl.
Vouchers: 373-1, 373-2, 373-3, 373-4, 373-5, 373-6, 373-7, 373-8, 373-9, 373-10, 373-11, 373-13, 373-14, 373-15, 373-17, 373-18, 373-23, 373-24, 373-29, 373-30, 373-31, 373-24
All
- Phaeophyscia constipata* Norrl. & Nyl.
Not previously recorded north of the Brooks Range. This is only the third locality for this species in Alaska, which Thomson (1984) listed as very rare.
Det. by J.W. Thomson.
Vouchers: 395-11
KD
- Physcia aipolia* (Humb.) Fühnrohr
Vouchers: 396-10, 396-28, 396-30
KD, TR
- Physconia muscigena* (Ach.) Poelt
Vouchers: 375-1, 375-2, 375-3, 375-4, 375-5, 375-6, 375-7, 375-8, 375-9, 375-10, 375-10a, 375-11, 375-12, 375-13, 375-14, 375-15, 375-16, 375-17, 375-18, 375-20, 375-21, 375-22, 375-23, 375-24, 375-25, 375-26, 375-27, 375-28, 375-29, 375-30, 375-32, 375-33, 375-34, 375-35, 375-36, 375-37, 375-38, 375-39, 375-40
All
- Polyblastia sendtneri* Krempf.
Vouchers: 370-18, 370-23, 370-30
PB, KP
- Psoroma hypnorum* (Vahl) S. Gray
Vouchers: 376-9, 376-10, 376-11, 376-18, 376-22, 376-25
PB, KP, KD
- Rinodina mniaraea* (Ach.) Körb.
Vouchers: 407-29
TR
- Rinodina roscida* (Somm.) Arn.
Vouchers: 353-1b, 397-1, 397-4, 397-5, 397-6, 397-14, 397-17, 397-18, 397-21, 397-22, 397-27, 397-30, 397-32, 397-33, 397-34, 397-35, 397-36, 397-37, 397-38, 397-39, 397-40
PB, KP, TR
- Rinodina roscida* (Somm.) Arn.
Vouchers: 353-1b, 397-1, 397-4, 397-5, 397-6, 397-14, 397-17, 397-18, 397-21, 397-22, 397-27, 397-30, 397-32, 397-33, 397-34, 397-35, 397-36, 397-37, 397-38, 397-39, 397-40
PB, KP, TR
- Rinodina turfacea* (Wahlenb.) Körb.
Vouchers: 353-1c, 393-11, 398-2, 398-8, 398-9, 398-11, 398-13, 398-15, 398-16, 398-18, 398-19, 398-21, 398-23, 398-24, 398-25, 398-34, 398-35, 398-37, 398-38, 398-40, 398-41
All
- Solorina bispora* Nyl.
Not previously recorded at Prudhoe Bay but known from Franklin Bluffs; specimens were not expertly verified.

Vouchers: 378-2, 378-3, 378-6, 378-7, 378-10, 378-11, 378-13, 378-15, 378-16, 378-25, 378-28, 378-31, 378-32, 378-34, 378-39, 378-41
All

Solorina octospora (Arn.) Arn.

Not previously recorded in this area; specimens were not expertly verified.

Vouchers: 379-11

KD

Solorina saccata (L.) Ach.

Vouchers: 380-1, 380-2, 380-3, 380-5, 380-8, 380-9, 380-13, 380-14, 380-15, 380-17, 380-19, 380-20, 380-21, 380-23, 380-24, 380-25, 380-26, 380-27, 380-28, 380-29, 380-30, 380-31, 380-32, 380-33, 380-34, 380-35, 380-36, 380-37, 380-38, 380-40, 380-41

All

Solorina spongiosa (Sm.) Anzi

Vouchers: 381-1, 381-2, 381-4, 381-5, 381-6, 381-7, 381-8, 381-9, 381-11, 381-12, 381-13, 381-14, 381-15, 381-17, 381-19, 381-21, 381-24, 381-27, 381-35, 381-38

All

Sphaerophorus globosus (Huds.) Vain.

Vouchers: 382-8, 382-9, 382-25, 382-41

KP, KD, TR

Stereocaulon alpinum Laur.

Vouchers: 383-1, 383-2, 383-3, 383-4, 383-5, 383-6, 383-7, 383-8, 383-9, 383-11, 383-12, 383-13, 383-14, 383-15, 383-16, 383-17, 383-18, 383-19, 383-20, 383-21, 383-22, 383-23, 383-24, 383-25, 383-26, 383-27, 383-29, 383-31, 383-32, 383-34, 383-35, 383-36, 383-37, 383-38, 383-40, 383-41

All

Stereocaulon paschale (L.) Hoffm.

Not previously recorded in this area but known from several other coastal plain localities; specimens were not expertly verified.

Vouchers: 384-22

PB

Stereocaulon rivulorum Magn.

Vouchers: 399-5

PB

Stereocaulon tomentosum E. Fries

Not previously recorded at Prudhoe Bay but known to occur at Franklin Bluffs;

KD

Stereocaulon tomentosum E. Fries

Not previously recorded at Prudhoe Bay but known to occur at Franklin Bluffs; specimens were not expertly verified.

Vouchers: 385-9, 385-10, 385-11, 385-20

KP, KD

Thamnia subuliformis (Ehrh.) W. Culb.

Not distinguished from *T. vermicularis* (Sw.) Ach. ex Schaer. in this study.

Vouchers: 412-1, 412-2, 412-3, 412-4, 412-5, 412-6, 412-7, 412-8, 412-9, 412-10, 412-11, 412-12, 412-13, 412-14, 412-15, 412-16, 412-17, 412-18, 412-19, 412-20, 412-21, 412-22, 412-23, 412-24, 412-25, 412-26, 412-27, 412-28, 412-29, 412-30, 412-31, 412-32, 412-33, 412-34, 412-35, 412-36, 412-37, 412-38, 412-39, 412-40, 412-41

All

Toninia caeruleonigricans (Lightf.) Th. Fr.

Not previously recorded in this area; specimens were not expertly verified.

Vouchers: 400-4, 400-6, 400-12, 400-14, 400-15, 400-20, 400-33, 400-35, 400-36, 400-39

All

Toninia lobulata (Somm.) Lynge

Vouchers: 401-3, 401-7, 401-13, 401-14, 401-15, 401-17, 401-21, 401-25, 401-26, 401-35, 401-36, 401-37, 401-38, 401-39

PB, KP, TR

Umbilicaria spp.

Vouchers: 411-41

KD

Xanthoparmelia separata (Th. Fr.) Hale

Vouchers: 410-41

KD

Xanthoria candelaria (L.) Arn.

Vouchers: 386-10

KD, TR

Bryophytes

Anastrophllum minutum (Schreb.) Schust.

Vouchers: 501-1, 501-2, 501-3, 501-4, 501-5, 501-8, 501-9, 501-10, 501-11, 501-14, 501-16, 501-17, 501-18, 501-19, 501-20, 501-21, 501-22, 501-23, 501-24, 501-25, 501-29, 501-32, 501-35, 501-38, 501-39, 501-40, 501-41

All

Aneura pinguis (L.) Dum.

Vouchers: 502-5, 502-16, 502-17

PB, KP

Aulacomnium acuminatum (Lindb. & Arnell) Kindb.

Vouchers: 503-1, 503-2, 503-8, 503-9, 503-10, 503-11, 503-18, 503-20, 503-21, 503-23, 503-25, 503-26, 503-28, 503-29, 503-30, 503-31, 503-32, 503-34, 503-37, 503-38, 503-39, 503-40

All

Aulacomnium palustre (Hedw.) Schwaegr.

Vouchers: 504-1, 504-10, 504-14, 504-15, 504-19, 504-41

All

Aulacomnium palustre (Hedw.) Schwaegr.

Vouchers: 504-1, 504-10, 504-14, 504-15, 504-19, 504-41

All

Aulacomnium turgidum (Wahlenb.) Schwaegr.

Vouchers: 505-2, 505-8, 505-9, 505-10, 505-11, 505-18, 505-24, 505-25, 505-28, 505-32, 505-33, 505-35, 505-40, 505-41

All

Blepharostoma trichophyllum (L.) Dum.

Vouchers: 506-10, 506-12, 506-13, 506-15, 506-16, 506-17, 506-19, 506-23, 506-25, 506-26, 506-27, 506-30, 506-32, 506-33, 506-37, 506-38, 506-40, 506-41

All

Brachytheciaceae

Vouchers: 510-1, 510-2, 510-3, 510-4, 510-5, 510-6, 510-7, 510-8, 510-9, 510-10, 510-11, 510-12, 510-13, 510-15, 510-17, 510-18, 510-19, 510-21, 510-22, 510-23, 510-24, 510-25, 510-26, 510-27, 510-29, 510-30, 510-31, 510-32, 510-33, 510-34, 510-35, 510-37, 510-39, 510-40

All

Bryaceae

Vouchers: 507-1, 507-2, 507-3, 507-4, 507-5, 507-6, 507-7, 507-8, 507-9, 507-10, 507-11, 507-12, 507-13, 507-14, 507-15, 507-16, 507-17, 507-18, 507-19, 507-20, 507-21, 507-22, 507-23, 507-24, 507-25, 507-26, 507-27, 507-28, 507-29, 507-30, 507-31, 507-32, 507-33, 507-34, 507-35, 507-36, 507-37, 507-38, 507-39, 507-40, 507-41

All

Bryum wrightii Sull. and Lesq.

Specimens: 83-128

PB

Calliergon richardsonii (Mitt.) Kinkdb. ex Warnst.

Vouchers: 508-23, 508-29, 508-31, 508-41

KP, KD, TR

Campylium stellatum (Hedw.) C. Jens.

Vouchers: 509-1, 509-5, 509-10, 509-14, 509-19, 509-24, 509-25, 509-28, 509-29, 509-30, 509-31, 509-32, 509-33, 509-34, 509-35, 509-37, 509-39, 509-40, 509-41

All

Cirriphyllum cirrosum (Schwaegr. ex Schultes) Grout

Usually recorded as Brachytheciaceae.

Vouchers: 510-41

KD

Cratoneuron arcticum Steere

Listed by Walker as frequent in dry tundra but not recorded in this study.

Dicranaceae

Vouchers: 511-3, 511-11, 511-14-2, 511-14-3, 511-14-6, 511-19, 511-21, 511-23, 511-24, 511-26, 511-30, 511-31, 511-35, 511-37

All

Dicranella crispa (Hedw.) Schimp.

Vouchers: 512-1, 512-2, 512-4

PB

Dicranella crispa (Hedw.) Schimp.

Vouchers: 512-1, 512-2, 512-4

PB

Dicranum angustum Lindb.

Vouchers: 513-1, 513-2, 513-9, 513-10, 513-11, 513-12, 513-13, 513-15, 513-16, 513-18, 513-19, 513-20, 513-23, 513-24, 513-25, 513-28, 513-32, 513-33, 513-34, 513-35, 513-38, 513-41

All

Dicranum elongatum Schleich. ex Schwaegr.

Vouchers: 514-1, 514-2, 514-3, 514-6, 514-7, 514-8, 514-9, 514-10, 514-11, 514-12, 514-13, 514-14, 514-15, 514-16, 514-17, 514-18, 514-19, 514-20, 514-21, 514-22, 514-23, 514-24, 514-25, 514-27, 514-28, 514-29, 514-30, 514-31, 514-32, 514-33, 514-34, 514-35, 514-36, 514-37, 514-38, 514-39,

514-40, 514-41

All

Distichium capillaceum (Hedw.) B.S.G.

Vouchers: 516-1, 516-2, 516-3, 516-4, 516-5, 516-6, 516-7, 516-8, 516-9, 516-10, 516-11, 516-12, 516-13, 516-14, 516-15, 516-16, 516-17, 516-18, 516-19, 516-20, 516-21, 516-22, 516-23, 516-24, 516-25, 516-26, 516-28, 516-29, 516-30, 516-31, 516-32, 516-33, 516-34, 516-35, 516-36, 516-37, 516-38, 516-39, 516-40, 516-41

All

Distichium inclinatum (Hedw.) B.S.G.

Vouchers: 517-1, 517-2, 517-3, 517-5, 517-6, 517-7, 517-8, 517-10, 517-11, 517-12, 517-13, 517-14, 517-15, 517-16, 517-22, 517-23, 517-25, 517-26, 517-27, 517-28, 517-30, 517-31, 517-32, 517-33, 517-34, 517-35, 517-36, 517-38, 517-41

All

Ditrichum flexicaule (Schwaegr.) Hampe

Vouchers: 518-1, 518-2, 518-3, 518-4, 518-5, 518-6, 518-7, 518-8, 518-9, 518-10, 518-11, 518-12, 518-13, 518-14, 518-15, 518-16, 518-17, 518-18, 518-19, 518-20, 518-21, 518-22, 518-23, 518-24, 518-25, 518-26, 518-27, 518-28, 518-29, 518-30, 518-31, 518-32, 518-33, 518-34, 518-35, 518-36, 518-37, 518-38, 518-39, 518-40, 518-41

All

Drepanocladus revolvens (Sw.) Warnst.

Vouchers: 519-13, 519-19, 519-41

KP, KD

Drepanocladus uncinatus (Hedw.) Warnst.

Vouchers: 520-1, 520-2, 520-3, 520-4, 520-5, 520-6, 520-7, 520-8, 520-9, 520-10, 520-11, 520-12, 520-13, 520-14, 520-15, 520-16, 520-17, 520-18, 520-20, 520-21, 520-22, 520-23, 520-24, 520-25, 520-28, 520-29, 520-30, 520-31, 520-32, 520-33, 520-34, 520-35, 520-36, 520-37, 520-38, 520-39, 520-40, 520-41

All

Encalypta alpina Sm.

Vouchers: 521-2, 521-6, 521-10, 521-11, 521-12, 521-17, 521-18, 521-19, 521-25, 521-27, 521-31, 521-32, 521-33, 521-36, 521-39, 521-41

All

Encalypta mutica Hag.

Vouchers: 522-3, 522-4, 522-13, 522-22, 522-23, 522-24, 522-34, 521-25, 521-27, 521-31, 521-32, 521-33, 521-36, 521-39, 521-41

All

Encalypta mutica Hag.

Vouchers: 522-3, 522-4, 522-13, 522-22, 522-23, 522-24, 522-34

PB, KP

Encalypta procera Bruch

Listed by Walker (1985) as frequent in dry tundra but not recorded in this study.

Encalypta rhabdocarpa Schwaegr.

Vouchers: 523-1, 523-2, 523-3, 523-4, 523-5, 523-6, 523-7, 523-8, 523-9, 523-10, 523-11, 523-12, 523-13, 523-14, 523-15, 523-16, 523-17, 523-18, 523-19, 523-20, 523-23, 523-24, 523-26, 523-27, 523-28, 523-29, 523-30, 523-31, 523-32, 523-33, 523-34, 523-35, 523-36, 523-37, 523-38, 523-39, 523-41

All

Eurynchium pulchellum (Hedw.) Jenn.

Vouchers: 524-1, 524-2, 524-3, 524-4, 524-5, 524-6, 524-7, 524-8, 524-9, 524-10, 524-11, 524-12, 524-13, 524-14, 524-15, 524-16, 524-17, 524-18, 524-19, 524-20, 524-21, 524-22, 524-23, 524-24, 524-25, 524-26, 524-27, 524-28, 524-29, 524-30, 524-31, 524-32, 524-33, 524-35, 524-36, 524-37, 524-39, 524-40, 524-41

All

Funaria arctica (Berggr.) Kindb.

Listed by Walker (1985) as occasional in several habitats commonly present on pingos, but not recorded in this study.

Hylocomium splendens (Hedw.) B.S.G. var. *obtusifolium* (Geh.) Par.

Vouchers: 525-1, 525-2, 525-3, 525-8, 525-10, 525-13, 525-16, 525-18, 525-19, 525-20, 525-22, 525-23, 525-24, 525-25, 525-26, 525-28, 525-29, 525-30, 525-31, 525-32, 525-33, 525-34, 525-35, 525-37, 525-38, 525-40, 525-41

All

Hypnum bambergeri Schimp.

Vouchers: 526-7

TR

Hypnum cupressiforme Hedw.

Vouchers: 527-3, 527-4, 527-5, 527-6, 527-7, 527-13, 527-14, 527-15, 527-17, 527-18, 527-19, 527-22, 527-23, 527-24, 527-25, 527-26, 527-28, 527-30, 527-31, 527-32, 527-34, 527-36, 527-37, 527-38, 527-40

PB, KP, TR

Hypnum procerrimum Mol.

Vouchers: 528-1, 528-2, 528-4, 528-5, 528-6, 528-8, 528-10, 528-11, 528-12, 528-14, 528-15, 528-17, 528-19, 528-20, 528-22, 528-23, 528-25, 528-27, 528-28, 528-30, 528-31, 528-32, 528-33, 528-34, 528-36, 528-37, 528-38, 528-39, 528-40, 528-41

All

Hypnum revolutum (Mitt.) Lindb.

Vouchers: 529-2, 529-3, 529-7, 529-12, 529-16, 529-18, 529-22, 529-29

PB, KP, TR

Leptobryum pyriforme (Hedw.) Wils.

Listed by Walker (1985) as common in several habitats that are often present on pingos, but not recorded in this study.

Marchantia alpestris Nees

Listed by Walker (1985) as common in several habitats that are often present on pingos, but not recorded in this study.

Marchantia alpestris Nees

Vouchers: 530-13, 530-26, 531-37

KP, TR

Marchantia polymorpha L.

Vouchers: 531-13

KP

Mnium blytii B.S.G.

Vouchers: 533-9, 533-10, 533-11, 533-13, 533-14, 533-15, 533-17, 533-18, 533-21, 533-24, 533-25, 533-27, 533-29, 533-30, 533-33, 533-34, 533-35, 533-37, 533-40, 533-41

All

Mnium thomsonii Schimp.

Vouchers: 534-9, 534-11, 534-15, 534-16, 534-19, 534-23, 534-25, 534-26, 534-30, 534-32, 534-37, 534-41

KP, KD, TR

Plagiochila arctica Bryhn & Kaal.

Vouchers: 535-3, 535-5, 535-8, 535-10, 535-11, 535-12, 535-13, 535-14, 535-15, 535-16, 535-17, 535-18, 535-19, 535-20, 535-21, 535-22, 535-23, 535-24, 535-25, 535-26, 535-27, 535-29, 535-30, 535-31, 535-32, 535-33, 535-34, 535-35, 535-36, 535-37, 535-38, 535-40, 535-41

All

Polytrichastrum alpinum (Hedw.) G.L. Smith

Vouchers: 536-1, 536-2, 536-3, 536-5, 536-6, 536-8, 536-9, 536-10, 536-11, 536-12, 536-13, 536-14, 536-16, 536-18, 536-19, 536-20, 536-23, 536-24, 536-25, 536-31, 536-32, 536-33, 536-34, 536-35, 536-38, 536-39, 536-40, 536-41

All

Polytrichum commune Hedw. var. *nigrescens* Warnst.

Vouchers: 537-23, 537-34, 537-38, 537-40

KP

Polytrichum juniperinum Hedw.

Vouchers: 538-9, 538-10, 538-11, 538-15, 538-18, 538-24, 538-30, 538-35, 538-41

All

Polytrichum piliferum Hedw.

Vouchers: 554-41

KD

Ptilidium ciliare (Web.) Hampe

Vouchers: 539-2, 539-8, 539-9, 539-11, 539-16, 539-18, 539-19, 539-20, 539-23, 539-24, 539-25, 539-30, 539-33, 539-34, 539-35, 539-38, 539-40, 539-41

All

Racomitrium lanuginosum (Hedw.) Brid.

Vouchers: 540-8, 540-18, 540-19, 540-23, 540-24, 540-34, 540-35, 540-41

PB, KP, KD

Rhizomnium andrewsianum Steere

Vouchers: 555-41

KD

Rhizomnium andrewsianum Steere

Vouchers: 555-41

KD

Rhytidium rugosum (Hedw.) Kindb.

Vouchers: 541-1, 541-2, 541-3, 541-4, 541-5, 541-6, 541-7, 541-8, 541-9, 541-10, 541-11, 541-12, 541-13, 541-14, 541-15, 541-16, 541-17, 541-18, 541-19, 541-20, 541-21, 541-22, 541-23, 541-24, 541-25, 541-26, 541-27, 541-28, 541-29, 541-30, 541-31, 541-32, 541-33, 541-34, 541-35, 541-36, 541-37, 541-38, 541-39, 541-40, 541-41

All

Sphagnum warnstorffii Russ.

Specimens: 83-208

KD

Splachnum vasculosum Hedw.

Vouchers: 543-22, 543-26, 543-28
PB,TR

Tetraplodon miniodes (Hedw.) B.S.G.

Vouchers: 544-3, 544-4, 544-5, 544-8, 544-9, 544-11, 544-12, 544-16, 544-21, 544-22, 544-25, 544-26, 544-28, 544-30, 544-32, 544-34
All

Thuidium abietinum (Hedw.) B.S.G.

Vouchers: 546-1, 546-2, 546-3, 546-4, 546-5, 546-6, 546-7, 546-9, 546-11, 546-12, 546-13, 546-14, 546-15, 546-17, 546-18, 546-19, 546-20, 546-21, 546-22, 546-23, 546-24, 546-25, 546-26, 546-27, 546-28, 546-29, 546-30, 546-31, 546-32, 546-33, 546-34, 546-35, 546-36, 546-37, 546-38, 546-39, 546-40, 546-41
All

Timmia austriaca Hedw.

Vouchers: 547-1, 547-2, 547-3, 547-5, 547-6, 547-7, 547-8, 547-9, 547-10, 547-11, 547-12, 547-15, 547-16, 547-17, 547-18, 547-19, 547-20, 547-21, 547-22, 547-23, 547-24, 547-25, 547-26, 547-28, 547-31, 547-32, 547-33, 547-34, 547-35, 547-36, 547-37, 547-40, 547-41
All

Timmia megapolitana Hedw.

Vouchers: 548-11
KD

Timmia norvegica Zett.

Listed by Walker (1985) from snowbank of Pingo 6, but not recorded in this study.

Tomenthypnum nitens (Hedw.) Loeske

Vouchers: 549-1, 549-2, 549-3, 549-4, 549-5, 549-6, 549-7, 549-8, 549-9, 549-10, 549-11, 549-13, 549-14, 549-15, 549-16, 549-17, 549-18, 549-19, 549-20, 549-21, 549-22, 549-23, 549-24, 549-25, 549-26, 549-27, 549-28, 549-29, 549-30, 549-31, 549-32, 549-33, 549-34, 549-35, 549-36, 549-37, 549-38, 549-39, 549-40, 549-41
All

Tortella arctica (Arn.) Crundw. and Nyh.

Listed by Walker (1985) as frequent on dry tundra, but not recorded in this study. Probably confused with *T. fragilis* in one or both studies.

Tortella fragilis (Drumm.) Limpr.

Vouchers: 515-1, 515-3, 515-18, 515-22, 515-25, 515-27, 515-28, 515-29, 515-30, 515-31, 515-32, 515-34, 515-37, 515-38, 515-40, 515-41

Listed by Walker (1985) as frequent on dry tundra, but not recorded in this study. Probably confused with *T. fragilis* in one or both studies.

Tortella fragilis (Drumm.) Limpr.

Vouchers: 515-1, 515-3, 515-18, 515-22, 515-25, 515-27, 515-28, 515-29, 515-30, 515-31, 515-32, 515-34, 515-37, 515-38, 515-40, 515-41
All

Tortula mucronifolia Schwaegr.

Vouchers: 550-7, 550-15, 550-22, 550-28
PB,TR

Tortula ruralis (Hedw.) Gaertn., Meyer & Scherb.

Vouchers: 551-1, 551-2, 551-3, 551-4, 551-5, 551-6, 551-7, 551-8, 551-9, 551-10, 551-11, 551-12, 551-13, 551-14, 551-15, 551-16, 551-17, 551-18, 551-19, 551-20, 551-21, 551-22, 551-23, 551-24, 551-25, 551-26, 551-27, 551-28, 551-29, 551-30, 551-31, 551-32, 551-33, 551-34, 551-35, 551-36, 551-37, 551-38, 551-39, 551-40, 551-41
All

APPENDIX B

CLASSIFICATION SUMMARY TABLES

The classification summary tables are in the back pocket of this volume. They are divided up by group, with Group *Dryas integrifolia* - *Lecanora epibryon* in Appendix B1, Group *Dryas integrifolia* - *Tortula ruralis* in Appendix B2, and Group *Dryas integrifolia* - *Tomenthypnum nitens* in Appendix B3. The two-part plot numbers consist of the pingo number and the microsite number, with a dash in between. See Chapter III or Appendix C3 for an explanation of the microsite numbers. Boxes are drawn around the differentiating and associated species for each group, stand type, and facies.

APPENDIX C

DATA

C1	Morphological data for the 41 pingos.....	255
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Table C1. Morphological data for the fox for the forty-one pingos.

Pingo	Study Area ¹	Type ²	Morpho-logical Class	Height (m)	Diameter (m)	Area (ha)	Landscape Type ³	Regional Terrain Type ⁴	pH	S.D. pH	Distance to coast ⁵	Distance to nearest pingo	Distance to nearest river	Excavation Disturb. ⁶	Vehicle Disturb.	Debris Disturb.
1	1	1	2	7.5	8	7.5	84	1	6.5	.36	8.4	.1	7.4	0	2.0	1.0
2	1	1	2	5.5	7	5.5	74	1	7.0	.27	8.3	.1	7.7	3.0	0	1.5
3	1	1	2	13.5	14	13.5	146	1	6.9	.21	12.1	.3	2.7	0	2.0	2.0
4	1	1	2	6.0	5	6.0	53	1	7.1	.21	6.7	1.1	1.3	0	0	3.0
5	1	1	1	7.0	6	7.0	65	1	7.2	.18	3.8	3.2	2.2	0	2.0	4.0
6	1	2	3	12.0	18	12.0	182	1	7.3	.15	10.9	.8	3.9	0	3.5	2.0
7	4	1	3	28.0	20	28.0	200	2	7.2	.45	64.5	1.1	.9	0	0	2.0
8	3	1	2	15.0	16	15.0	168	1	6.6	.61	21.7	.7	10.0	0	0	1.0
9	3	1	3	28.0	16	28.0	162	2	5.0	.54	46.0	.2	6.1	0	0	0
10	3	1	1	30.0	21	30.0	213	2	5.5	.40	42.3	.2	3.0	0	0	0
11	3	1	2	11.5	5	11.5	95	2	4.7	.58	29.1	.5	3.6	0	0	1.0
12	2	1	1	8.0	17	8.0	175	2	7.2	.81	.8	7.8	1.2	2.0	1.0	2.0
13	2	2	3	16.5	31	16.5	315	2	6.6	.31	11.7	2.3	1.0	0	1.0	2.0
14	1	1	1	6.0	5	6.0	58	1	7.1	.09	14.8	.9	.5	0	3.5	2.0
15	4	1	2	17.0	16	17.0	169	1	7.1	.18	36.2	.8	3.2	0	3.0	2.0
16	2	2	4	7.5	21	7.5	210	2	6.0	.54	19.8	.1	1.0	0	2.0	3.0
17	1	1	1	4.5	8	4.5	84	1	7.1	.12	13.5	.9	.5	0	2.0	1.0
18	2	2	4	6.0	16	6.0	162	2	5.8	.46	8.5	3.9	1.5	0	4.0	2.0
19	2	1	3	6.0	12	6.0	122	2	6.4	.59	19.2	.9	.1	0	0	0
20	2	1	2	6.5	10	6.5	106	2	6.9	.23	18.0	.7	.5	0	0	1.0
21	2	1	1	4.5	6	4.5	66	2	6.9	.17	20.5	.4	.2	0	0	0
22	1	1	1	3.8	10	3.8	108	3	7.2	.23	12.2	3.8	1.8	0	2.0	.5
23	2	1	4	4.5	12	4.5	120	2	6.8	.23	15.5	.4	1.0	0	4.0	0
24	2	2	3	13.5	18	13.5	185	2	6.1	.49	19.5	.4	1.2	0	0	1.5
25	2	1	1	4.0	5	4.0	98	2	6.5	.44	1.8	2.7	1.5	0	1.0	0
26	4	1	4	10.0	11	10.0	115	2	6.9	.23	64.8	.3	.3	1.0	1.0	0
27	4	2	2	12.0	17	12.0	172	2	7.0	.21	64.8	.3	.5	0	0	0
28	4	1	3	7.8	6	7.8	69	2	6.7	.41	63.8	1.1	2.2	0	0	0

Table C1. (concluded).

29	4	1	2	7.5	8:7.5	83	.7	1	2	6.7	.43	64.3	.6	1.3	0	0	0
30	4	1	1	5.5	5:5.5	59	.4	1	2	6.7	.32	63.3	1.1	1.9	0	0	0
31	4	1	2	9.0	6:9.0	66	.5	1	2	6.9	.35	66.0	.4	.3	0	0	0
32	4	1	3	5.5	6:5.5	60	.4	1	2	7.0	.23	63.1	1.1	.5	0	0	0
33	2	1	1	6.5	9:6.5	96	.7	1	2	6.6	.64	1.9	2.7	.2	0	4.0	4.0
34	2	2	4	5.5	16:5.5	163	1.2	2	2	6.7	.31	15.0	.2	1.0	0	2.5	1.5
35	2	2	4	11.0	19:11.0	199	2.7	2	2	6.5	.55	15.8	.4	.8	0	2.0	0
36	1	1	1	5.5	5:5.5	54	.3	1	1	7.2	.19	7.5	.7	2.4	0	1.0	1.0
37	4	1	2	14.0	19:14.0	197	3.2	1	1	6.6	.57	67.0	1.0	4.5	0	1.0	1.0
38	2	2	1	8.0	13:8.0	136	1.3	2	2	6.6	.28	16.8	.2	.1	0	2.5	1.0
39	2	2	1	4.5	9:4.5	91	.5	1	2	7.1	.34	17.5	.2	1.2	0	2.0	1.0
40	2	1	4	5.0	33:5.0	334	2.3	2	2	6.4	.20	15.8	.4	.2	0	1.0	1.0
41	3	1	3	51.0	61:51.0	618	35.6	2	2	5.8	.92	20.0	5.4	.8	0	2.5	1.5

1₁ - Prudhoe Bay; 2 - Kuparuk; 3 - Kadleroshilladleroshilik; 4 - Toolik River2₁ - Steep-sided; 2 - Broad-based.3₁See Chapter III for codes.4₁See Chapter III for codes.5₁All distances are in ha.6₁See Chapter III for disturbance scales.

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Table C2. Number of species in each major taxonomic category and each floristic category for the forty-one pingos.

Pingo	Species	Environmental Regions										Northern Limit Zones										Geographic Range			
		WNA-Vascular					Arctic- Alpine					Arctic- Arctic					Circum- polar					NA- NA-			
		Species	Restricted	Species	Species	Species	Species	Species	Species	Species	Species	Species	Species	Species	Species	Species	Species	Species	Species	Species	Species	NA- NA-	NA- NA-	NA- NA-	NA- NA-
1	60	33	25	0	0	0	21	34	4	1	13	31	16	0	36	1	0	1	1	5	1	5	6	3	2
2	46	36	27	1	1	1	16	27	2	1	13	23	10	0	26	1	0	1	1	1	1	5	7	2	2
3	67	34	29	3	3	3	17	47	3	0	15	33	18	1	38	3	0	1	5	0	4	9	4	3	3
4	63	28	19	2	2	2	17	42	4	0	10	34	18	1	33	1	1	1	3	1	5	13	3	2	2
5	48	32	23	0	0	0	14	33	0	1	9	27	12	0	25	2	0	1	1	3	1	4	7	3	2
6	58	30	21	0	0	0	20	32	4	2	12	29	16	1	34	1	0	1	0	2	2	5	9	3	1
7	93	36	22	15	15	15	32	53	8	0	10	31	39	13	37	3	2	1	12	4	8	14	6	6	6
8	72	46	25	3	3	3	21	45	6	0	13	32	22	5	40	1	0	1	7	2	7	7	5	2	2
9	81	47	29	6	6	6	24	48	9	0	11	32	33	5	44	2	1	0	8	3	6	8	5	4	4
10	72	38	30	3	3	3	20	44	8	0	12	28	29	3	41	2	1	0	8	0	5	6	5	4	4
11	94	47	33	6	6	6	28	55	9	2	13	41	35	4	47	1	1	1	10	5	9	12	5	3	3
12	60	31	23	0	0	0	20	32	3	5	21	35	5	0	38	0	0	2	4	1	5	5	2	3	3
13	64	48	31	3	3	3	23	39	1	1	14	37	12	1	37	0	0	1	2	1	5	8	6	4	5
14	59	37	22	1	1	1	21	34	3	1	11	29	19	0	28	0	0	1	2	5	2	5	12	3	3
15	79	43	26	2	2	2	23	49	6	1	11	32	35	1	34	2	1	1	9	3	7	13	4	5	5
16	61	34	25	2	2	2	18	38	4	1	16	29	15	1	38	0	0	1	3	1	5	8	4	1	1
17	53	33	23	1	1	1	18	31	2	2	12	28	13	0	26	1	0	2	4	1	4	10	3	3	3
18	56	45	30	1	1	1	17	35	3	1	17	26	12	1	33	0	0	1	3	2	4	7	4	2	2
19	55	41	31	1	1	1	14	34	6	1	12	24	18	1	32	0	0	1	5	1	4	7	4	1	1
20	70	38	21	1	1	1	22	42	4	2	15	33	22	0	42	1	0	1	3	1	4	13	5	1	1
21	63	37	19	0	0	0	19	37	5	2	15	33	14	1	36	1	0	1	4	1	4	10	3	3	3
22	55	28	26	1	1	1	15	35	3	2	12	29	14	0	31	0	0	1	3	1	5	8	3	3	3
23	55	39	31	1	1	1	18	31	5	1	12	26	16	1	29	2	0	1	3	1	4	8	4	2	2
24	70	43	29	3	3	3	22	43	5	0	20	28	19	3	41	0	0	1	5	1	4	11	4	3	3
25	68	40	32	1	1	1	21	43	3	1	18	30	20	0	42	0	0	1	4	1	4	10	3	3	3
26	80	36	23	10	10	10	20	49	10	1	10	28	38	4	37	3	1	1	9	2	4	14	4	5	4
27	59	26	19	4	4	4	22	34	3	0	8	24	23	4	24	1	2	1	7	3	3	9	5	4	4
28	71	34	25	6	6	6	24	40	7	0	8	25	32	6	31	3	0	1	10	3	4	11	4	4	4

Table C2. (concluded).

29	65	33	21	6	23	6	23	35	7	0	10	22	28	5	28	4	1	1	7	2	4	10	4	4
30	62	35	29	3	18	3	18	38	6	0	9	20	30	3	28	2	1	1	6	2	2	12	4	4
31	54	33	27	4	18	4	18	32	4	0	7	22	23	2	21	4	1	1	6	1	4	9	4	3
32	62	34	30	3	21	3	21	37	4	0	9	21	30	2	28	1	1	1	8	2	3	12	3	3
33	70	30	27	1	20	1	20	41	3	6	18	35	16	1	46	0	0	2	5	1	5	5	1	5
34	61	38	29	2	19	2	19	35	6	1	15	26	19	1	34	1	0	1	4	2	4	9	4	2
35	49	44	28	1	17	1	17	28	4	0	15	21	12	1	29	0	0	1	4	0	4	7	4	0
36	45	33	19	0	16	0	16	28	1	0	11	23	10	1	24	0	0	0	3	1	4	8	3	2
37	81	32	27	6	24	6	24	48	7	2	13	30	33	5	37	2	2	1	9	2	5	12	6	5
38	61	38	25	1	18	1	18	35	6	2	15	25	19	2	36	1	0	1	5	2	4	7	4	1
39	53	31	20	1	16	1	16	31	4	2	11	24	17	1	28	1	0	2	4	1	4	6	3	4
40	49	42	28	0	16	0	16	28	5	0	13	23	13	0	30	0	0	1	3	0	3	7	5	0
41	133	66	38	15	41	15	41	77	14	1	20	57	46	10	65	4	1	1	15	7	12	13	8	7

Table C3. Environmental data for the 293 data for the 293 detailed sample plots.

Plot	Pingo pH ¹⁴	site ¹	Slope (deg) ²	Slope (deg) ³	Position	Slope (deg) ³	Position ⁴	Equivalent (deg) ⁵	Exposure ⁶	Thaw (cm) ⁷	Moisture ⁸	Duration ⁹	Stability ¹⁰	Cryour- relief (%) ¹¹	Micro- relief (cm) ¹²	Type ¹³	
1	1	1	12	49	2.0	49	2.0	75.0	4.0	200	3.0	1.0	2.0	0	3	2	6.5
2	1	2	0	0	1.0	0	1.0	70.0	3.0	53	4.0	2.5	2.0	0	6	1	6.3
3	1	3	17	250	2.0	250	2.0	59.8	1.5	37	4.0	6.0	2.5	5.0	30	3	7.1
4	1	4	13	229	3.5	229	3.5	59.9	1.0	30	4.0	5.0	2.0	0	25	3	6.0
5	1	5	2	240	5.0	240	5.0	68.9	1.0	23	5.0	6.0	1.0	0	10	5	6.8
6	1	6	12	168	2.0	168	2.0	58.2	1.5	200	3.5	4.0	3.0	0	2	2	6.3
7	1	7	13	2	3.0	2	3.0	83.0	3.8	71	2.0	2.5	3.0	60.0	10	2	6.4
8	2	1	2	46	2.0	46	2.0	71.3	4.0	200	2.0	1.0	2.0	2.0	2	6	6.9
9	2	2	0	0	1.0	0	1.0	70.0	3.5	200	3.0	2.0	2.0	2.0	6	3	6.9
10	2	3	17	224	2.0	224	2.0	55.8	1.5	54	4.0	4.5	3.0	5.0	25	3	6.9
11	2	4	10	202	3.0	202	3.0	60.5	1.0	38	4.0	6.0	3.0	5.0	30	3	6.6
12	2	5	7	254	4.0	254	4.0	67.1	1.5	49	4.5	5.0	1.5	0	6	5	7.0
13	2	6	23	206	2.0	206	2.0	48.1	3.0	200	2.8	4.0	4.0	2.0	12	7	6.9
14	2	7	6	344	2.5	344	2.5	75.7	3.8	200	2.0	2.5	3.0	40.0	3	7	7.5
15	3	1	22	42	2.0	42	2.0	75.1	4.0	200	2.0	1.0	3.0	0	2	2	6.6
16	3	2	0	0	1.0	0	1.0	70.0	2.0	100	3.5	4.0	2.0	0	0	1	7.1
17	3	3	20	210	2.0	210	2.0	51.4	1.0	100	4.0	5.5	3.0	5.0	22	2	7.1
18	3	4	14	222	4.0	222	4.0	58.2	1.0	80	4.0	6.0	3.0	0	15	10	6.9
19	3	5	16	268	5.0	268	5.0	64.2	1.0	45	4.0	5.0	3.0	0	3	10	7.2
20	3	6	23	179	2.0	179	2.0	47.0	2.5	120	3.0	4.0	3.0	0	0	2	6.9
21	3	7	34	346	3.0	346	3.0	74.7	3.0	200	2.5	2.0	3.0	10.0	3	6	6.8
22	4	1	9	70	2.0	70	2.0	71.2	4.0	200	2.0	1.0	2.5	40.0	12	2	6.9
23	4	2	0	0	1.0	0	1.0	70.0	2.0	200	4.0	2.5	3.0	0	10	2	7.4
24	4	3	10	244	2.5	244	2.5	64.1	1.5	200	4.0	5.0	3.0	2.0	15	2	7.0

Table C3. (continued).

25	4	4	14	257	3,557	3.0	63.3	1.0	85	4.5	6.0	3.5	5.0	27	3	6.9
26	4	5	2	244	4,644	4.0	69.1	2.0	53	5.5	5.0	2.0	0	10	10	7.1
27	4	6	18	164	2,664	2.5	52.4	3.0	200	2.5	2.5	2.0	0	3	2	7.4
28	4	7	20	346	3,446	3.0	85.2	3.5	200	3.0	2.0	3.0	10.0	2	2	7.1
29	5	1	14	42	2,142	2.0	76.7	4.0	200	2.5	1.0	2.5	10.0	3	2	7.1
30	5	2	0	0	1,100	1.0	70.0	2.0	100	5.0	4.0	2.0	0	6	1	6.9
31	5	3	7	277	2,677	2.0	69.7	1.5	47	5.0	5.0	3.0	5.0	14	3	7.3
32	5	4	16	52	3,552	3.0	74.0	2.0	80	4.0	6.0	3.0	5.0	20	3	7.4
33	5	5	2	82	5,182	5.0	70.2	2.0	52	5.0	5.0	2.0	0	4	5	7.2
34	5	6	14	145	3,145	3.0	57.6	2.5	200	99.0	99.0	3.5	0	3	2	7.2
35	5	7	99	399	3,699	3.0	99.0	3.0	58	2.0	2.0	4.0	5.0	5	2	7.4
36	6	1	2	66	2,166	2.0	70.7	4.0	200	3.0	1.5	1.5	5.0	3	3	7.2
37	6	2	0	0	1,100	1.0	70.0	3.0	76	3.0	2.0	4.0	0	15	1	7.4
38	6	3	7	279	3,679	3.0	69.9	1.5	55	4.0	5.0	3.0	3.0	99	7	7.2
39	6	4	15	284	4,684	4.0	68.3	1.5	100	4.0	6.0	3.0	2.0	30	3	7.1
40	6	5	2	284	5,684	5.0	70.4	1.0	46	5.0	5.0	3.0	0	17	5	7.5
41	6	6	7	187	3,187	3.0	63.0	3.0	200	2.5	2.5	3.0	0	5	1	7.4
42	6	7	5	2	2,102	2.0	75.0	3.0	200	2.5	2.0	3.0	10.0	3	3	7.2
43	7	1	10	35	2,135	2.0	76.0	4.0	200	3.0	1.0	3.0	20.0	2	2	7.2
44	7	2	0	0	1,100	1.0	69.0	2.5	200	3.0	4.0	5.0	0	10	1	6.2
45	7	3	12	255	2,555	2.5	63.4	2.0	58	4.0	5.0	3.0	2.0	30	3	7.3
46	7	4	10	244	4,644	4.0	63.1	1.5	61	5.0	6.5	3.5	0	17	5	6.8
47	7	4	17	144	3,144	3.0	53.9	2.0	73	5.0	6.0	2.0	2.0	30	5	7.5
48	7	6	6	201	3,601	3.0	63.3	3.0	200	3.0	3.5	3.0	0	7	3	7.3
49	7	7	9	339	2,339	2.5	77.0	3.0	200	3.0	2.0	3.0	10.0	8	2	7.0
50	8	1	7	126	2,126	2.0	64.3	3.5	73	3.0	1.5	2.0	5.0	8	3	7.3
51	8	2	0	0	1,100	1.0	69.0	3.0	55	4.0	4.0	4.5	0	12	1	6.8
52	8	3	5	301	2,301	2.5	71.1	2.0	77	4.0	5.0	3.0	1.0	12	5	6.1
53	8	4	10	295	3,695	3.0	71.0	1.5	35	4.0	6.0	3.0	0	20	5	5.9
54	8	5	4	303	5,803	5.0	70.9	2.0	39	5.0	7.0	2.0	0	16	5	5.9
55	8	6	10	171	2,171	2.5	59.1	2.0	60	4.0	3.0	3.0	0	8	3	6.9
56	8	7	9	13	2,113	2.0	77.6	3.0	65	3.0	2.0	3.5	5.0	6	7	7.2
57	9	1	30	68	2,168	2.0	61.1	4.0	200	2.5	1.0	3.0	150.0	3	8	4.7

Table C3. (continued).

58	9	2	0	0	1,100	1.0	69.0	3.0	200	3.0	2.0	2.0	0	2	8	4.4
59	9	3	8	279	3,379	3.5	68.8	1.3	52	5.0	7.0	2.0	0	20	10	4.3
60	9	4	19	91	3,911	3.0	61.7	2.0	200	4.0	5.0	4.0	0	15	11	4.2
61	9	5	26	279	3,679	3.0	68.6	2.0	42	5.0	6.0	3.0	0	40	11	4.2
62	9	6	26	184	2,184	2.5	43.0	2.5	200	4.0	4.0	5.0	0	2	8	5.5
63	9	7	20	21	2,121	2.5	82.6	4.0	200	2.0	1.0	99.0	10.0	3	7	5.4
64	10	1	28	91	2,191	3.0	55.2	3.0	42	4.0	4.0	4.0	0	30	13	6.0
65	10	2	0	0	1,100	1.0	69.0	3.0	43	3.0	2.0	99.0	150.0	10	13	5.9
66	10	3	10	351	3,851	3.0	78.8	2.0	21	4.0	5.0	3.0	0	19	13	5.7
67	10	4	16	294	3,694	3.0	69.7	1.5	38	4.0	6.0	3.0	0	28	13	5.3
68	10	4	15	279	4,679	4.0	66.4	2.0	32	4.5	6.0	3.0	0	30	10	5.5
69	10	5	4	271	5,671	5.0	68.7	2.0	38	5.0	6.0	2.0	0	16	13	5.1
70	10	6	25	175	2,175	2.5	44.0	1.5	39	4.0	5.0	4.0	0	99	13	5.4
71	11	1	15	110	2,110	2.0	60.5	4.0	74	2.0	1.0	2.0	150.0	2	8	5.5
72	11	2	0	0	1,100	1.0	69.0	3.5	68	3.0	4.0	5.0	0	10	9	5.6
73	11	3	8	142	2,142	2.0	62.3	2.5	35	5.0	6.0	2.0	0	18	8	4.7
74	11	4	35	332	3,832	3.0	71.1	2.0	33	4.0	7.5	4.0	0	8	8	4.3
75	11	5	16	263	4,663	4.0	62.3	2.0	41	5.0	6.0	3.0	0	12	8	4.3
76	11	6	25	198	2,198	2.5	44.6	2.5	200	2.0	3.0	3.0	0	3	2	6.1
77	11	7	25	340	2,340	2.5	81.3	4.0	56	2.0	1.0	3.0	0	3	2	6.2
78	12	1	6	20	2,120	2.0	75.5	4.0	29	2.0	1.0	2.0	0	3	13	7.7
79	12	2	0	0	1,100	1.0	70.0	4.0	31	3.0	1.5	2.0	0	8	3	6.3
80	12	4	10	45	3,145	3.0	75.3	3.0	28	4.0	6.0	2.0	10.0	15	13	9.0
81	12	5	5	60	5,160	5.0	72.0	2.0	34	3.5	5.0	1.0	0	4	13	6.4
82	12	6	5	165	3,165	3.0	65.1	3.0	29	3.0	2.0	2.0	20.0	4	13	7.9
83	12	7	9	338	2,338	2.5	77.9	3.5	26	3.0	2.0	1.5	20.0	5	13	7.9
84	13	1	10	51	2,151	2.0	74.3	4.0	200	2.0	1.0	2.0	0	2	2	6.6
85	13	2	0	0	1,100	1.0	70.0	4.0	100	3.0	4.0	4.0	0	8	3	6.2
86	13	3	16	88	2,188	2.5	65.0	2.0	100	4.0	5.0	3.0	10.0	6	3	6.5
87	13	4	25	96	3,196	3.0	54.4	1.5	100	4.0	7.5	3.0	0	22	3	6.6
88	13	6	6	320	3,120	3.0	75.5	4.0	200	3.0	2.0	2.0	0	2	2	7.0
89	13	7	7	350	3,350	3.0	76.8	4.0	200	2.5	1.0	2.0	0	4	2	6.9
90	13	8	0	99	5,199	5.0	70.0	1.0	40	4.0	8.0	4.0	0	5	12	9.0

Table C3. (continued).

92	14	1	14	80	2	80	2.0	67.8	4.0	95	3.0	1.0	1.0	5.0	5	2	7.1
93	14	2	0	0	1	0	1.0	70.0	3.0	80	4.0	4.0	4.0	0	0	2	7.1
94	14	3	12	210	2	210	2.5	59.0	1.5	200	4.0	4.0	4.0	0	10	6	7.3
95	14	4	13	240	3	240	3.0	61.3	1.0	50	4.0	6.0	3.0	0	15	2	7.1
96	14	5	5	220	4	220	4.0	66.0	1.5	38	5.0	7.0	1.0	0	15	5	7.0
97	14	6	17	180	3	180	3.0	53.0	2.5	60	3.0	1.0	2.0	0	4	2	7.2
98	14	7	29	20	2	20	2.5	77.9	4.0	110	2.0	1.0	2.0	13.0	12	6	7.1
99	15	1	15	40	3	40	3.0	77.3	4.0	64	3.0	1.0	2.5	5.0	10	6	7.2
100	15	2	0	0	1	0	1.0	70.0	3.0	63	3.0	2.0	4.0	0	5	2	7.0
101	15	3	17	210	2	210	2.0	54.3	1.0	65	3.5	5.0	3.0	0	15	2	6.8
102	15	4	16	260	3	260	3.0	62.5	1.5	60	3.5	6.0	3.0	0	18	6	6.9
103	15	5	3	270	5	270	5.0	69.8	2.0	26	5.0	7.0	1.0	0	10	5	7.0
104	15	6	28	160	2	160	2.5	42.8	2.0	100	2.5	2.0	3.0	0	5	6	7.3
105	15	7	17	0	2	0	2.0	87.0	4.0	64	3.0	1.0	2.5	5.0	15	2	7.2
106	15	6	28	160	2	160	2.0	42.8	2.0	100	2.5	2.0	3.0	0	5	99	9.0
107	16	1	4	85	2	85	2.0	70.0	4.0	80	3.0	1.0	1.0	0	5	8	5.4
108	16	2	0	0	1	0	1.0	70.0	4.0	50	3.0	2.0	4.0	0	99	8	5.2
109	16	3	3	240	2	240	2.0	68.4	2.0	200	4.0	4.0	2.5	15.0	15	3	6.5
110	16	4	12	265	0	265	0	65.9	1.0	36	4.5	6.0	1.5	0	25	3	6.6
111	16	5	3	240	5	240	5.0	68.4	1.0	28	5.0	6.0	1.0	0	10	11	6.4
112	16	6	6	180	3	180	3.0	64.0	2.0	82	3.5	4.0	2.0	20.0	8	3	6.4
113	16	7	5	355	2	355	2.0	75.0	2.0	73	3.5	4.0	3.0	150.0	10	7	5.7
114	17	1	5	75	3	75	3.0	70.7	4.0	74	3.0	1.0	2.0	0	6	2	7.1
115	17	2	0	0	1	0	1.0	70.0	4.0	200	3.5	1.5	4.0	0	5	3	7.2
116	17	3	15	285	3	285	3.0	68.5	1.0	24	4.0	6.5	1.5	5.0	20	3	7.1
117	17	4	7	290	4	290	4.0	71.3	1.0	38	4.5	6.5	1.5	0	10	3	7.0
118	17	5	3	270	5	270	5.0	69.8	1.0	36	5.0	6.5	1.0	0	6	3	6.9
119	17	6	8	185	2	185	2.0	62.0	2.0	32	3.0	3.5	2.0	3.0	5	3	7.3
120	17	7	10	355	3	355	3.0	79.9	4.0	68	3.0	2.0	2.0	0	6	2	7.1
121	18	1	5	115	2	115	2.0	67.4	4.0	60	2.5	1.0	1.5	0	4	7	5.3
122	18	2	0	0	1	0	1.0	70.0	4.0	18	4.0	1.0	1.0	0	10	3	5.9
123	18	3	7	150	3	150	3.0	63.7	1.5	70	4.0	5.0	1.5	5.0	12	7	5.9
124	18	4	4	110	3	110	3.0	68.3	1.0	38	5.0	6.0	1.0	0	13	8	6.2

Table C3. (continued).

125	18	5	2	120	5.0	120	5.0	68.9	1.0	18	5.5	6.0	1.0	0	12	8	5.7
126	18	6	7	140	2.5	140	2.5	64.3	2.0	60	4.5	5.0	2.5	15.0	10	3	6.4
127	18	7	3	325	2.0	325	2.0	72.4	3.0	47	3.5	2.0	3.0	50.0	11	3	6.2
128	19	1	6	25	2.0	25	2.0	75.2	4.0	37	3.0	1.0	2.0	10.0	6	7	6.8
129	19	2	0	0	1.0	0	1.0	70.0	4.0	22	3.0	1.0	2.0	0	5	3	5.6
130	19	3	4	235	2.5	235	2.5	67.5	2.0	40	4.5	4.5	3.0	15.0	14	6	6.8
131	19	4	13	50	3.5	50	3.5	74.8	1.0	32	4.5	6.0	1.0	0	16	3	5.7
132	19	5	3	45	5.0	45	5.0	72.0	1.0	36	5.0	6.0	1.0	0	8	5	5.8
133	19	6	5	155	3.0	155	3.0	65.4	2.0	36	4.5	4.0	2.0	20.0	10	3	7.0
134	19	7	4	5	2.0	5	2.0	74.0	4.0	200	3.0	1.0	4.0	8.0	5	2	6.9
135	20	1	7	30	2.0	30	2.0	75.6	4.0	47	3.0	1.0	2.0	0	4	3	6.9
136	20	2	0	0	1.0	0	1.0	70.0	4.0	19	4.0	1.0	2.0	0	5	3	6.7
137	20	3	15	195	2.0	195	2.0	55.3	1.5	35	4.0	5.0	1.0	5.0	17	3	6.7
138	20	4	15	200	3.5	200	3.5	55.5	1.5	56	4.0	5.5	1.0	0	22	5	7.1
139	20	5	2	200	5.0	200	5.0	68.1	1.0	28	5.0	6.0	1.0	0	10	11	6.5
140	20	6	5	180	2.0	180	2.0	65.0	2.0	52	4.0	3.0	3.0	10.0	6	3	7.1
141	20	7	5	360	2.0	360	2.0	75.0	4.0	44	3.0	1.0	3.0	10.0	7	3	7.2
142	21	1	5	90	2.0	90	2.0	69.4	4.0	45	3.0	1.0	4.0	0	15	3	6.9
143	21	2	0	0	1.0	0	1.0	70.0	4.0	31	3.0	1.0	4.0	0	12	3	6.6
144	21	3	7	275	3.0	275	3.0	69.4	1.5	30	4.0	3.0	1.0	0	15	3	6.8
145	21	4	20	70	3.0	70	3.0	67.4	1.5	34	4.0	6.0	3.0	0	99	2	7.1
146	21	5	2	75	5.0	75	5.0	70.4	1.5	12	5.5	6.0	1.0	0	5	11	6.9
147	21	6	6	165	2.5	165	2.5	64.2	2.0	60	4.0	4.0	4.0	0	20	1	7.1
148	21	7	14	360	3.0	360	3.0	84.0	3.0	24	4.0	4.0	1.0	0	12	3	7.1
149	22	1	3	110	2.0	110	2.0	68.8	4.0	30	3.0	1.0	1.0	0	10	3	7.3
150	22	2	0	0	1.0	0	1.0	70.0	4.0	25	3.0	1.0	1.0	0	20	3	7.2
151	22	3	4	200	2.0	200	2.0	66.2	1.5	33	4.5	5.0	1.0	5.0	15	3	6.6
152	22	4	3	245	4.0	245	4.0	68.6	1.0	32	5.0	6.0	1.0	0	15	3	7.2
153	22	5	2	260	5.0	260	5.0	69.6	1.0	32	5.0	6.5	1.0	0	8	5	7.3
154	22	6	5	195	2.5	195	2.5	65.1	2.0	32	4.0	4.0	2.0	5.0	6	7	7.2
155	22	7	5	340	3.0	340	3.0	74.6	3.0	23	3.5	2.0	3.0	15.0	6	3	7.3
156	23	1	2	20	2.0	20	2.0	71.9	4.0	50	3.0	1.0	2.0	10.0	6	2	6.7
157	23	2	0	0	1.0	0	1.0	70.0	4.0	40	3.0	1.0	1.0	0	10	6	6.9

Table C3. (continued).

158	23	3	4	230	2.0	230	2.0	67.2	2.0	32	4.0	3.0	2.0	20.0	10	3	6.9
159	23	4	15	230	3.0	230	3.0	58.3	1.0	60	4.0	6.0	3.0	0	20	3	6.3
160	23	5	6	210	5.0	210	5.0	64.6	1.0	50	5.0	6.5	2.0	0	8	4	6.8
161	23	6	5	175	3.0	175	3.0	65.0	2.5	54	4.0	3.0	2.0	0	10	3	6.8
162	23	7	3	360	2.0	360	2.0	73.0	4.0	60	3.0	1.0	1.0	0	8	2	7.0
163	24	1	4	125	2.0	125	2.0	67.5	4.0	60	3.0	1.0	1.0	0	3	7	6.4
164	24	2	0	0	1.0	0	1.0	70.0	4.0	65	3.0	1.0	1.0	0	4	8	5.2
165	24	3	6	230	2.0	230	2.0	65.7	1.5	40	4.0	4.5	2.0	5.0	99	3	6.6
166	24	4	5	220	3.0	220	3.0	66.0	1.0	45	4.0	6.0	1.0	0	10	8	5.6
167	24	5	1	195	5.0	195	5.0	69.0	1.0	35	5.0	7.0	1.0	0	12	7	6.6
168	24	6	5	200	2.0	200	2.0	65.2	2.0	65	3.0	2.5	1.0	0	2	3	6.1
169	24	7	3	10	2.0	10	2.0	72.9	4.0	200	3.0	1.0	2.0	15.0	8	3	6.2
170	25	1	3	10	2.0	10	2.0	72.9	4.0	50	3.0	1.0	2.0	10.0	10	3	7.0
171	25	2	0	0	1.0	0	1.0	70.0	4.0	42	3.0	1.0	4.0	0	30	1	6.9
172	25	3	1	230	3.0	230	3.0	69.3	1.0	22	4.0	5.0	1.0	0	12	3	6.5
173	25	4	6	45	3.5	45	3.5	73.7	1.0	32	4.0	6.0	1.0	0	15	10	5.9
174	25	5	2	210	5.0	210	5.0	68.2	1.0	28	5.0	5.5	1.0	0	10	11	5.8
175	25	6	3	170	2.5	170	2.5	67.0	2.0	40	4.0	4.0	1.0	0	10	3	6.5
176	25	7	4	350	2.0	350	2.0	73.9	4.0	42	3.0	1.0	1.0	0	8	3	6.8
177	26	1	10	75	2.0	75	2.0	69.3	4.0	62	3.0	1.0	1.0	0	6	2	9.0
178	26	2	0	0	1.0	0	1.0	69.0	4.0	56	3.0	1.0	2.0	0	15	7	7.0
179	26	3	10	260	3.0	260	3.0	65.3	1.5	60	4.0	5.0	1.0	0	12	2	7.1
180	26	4	15	260	3.0	260	3.0	62.3	1.0	60	4.0	6.0	1.0	0	20	6	6.6
181	26	5	3	260	5.0	260	5.0	68.3	1.0	34	6.0	5.0	1.0	0	15	11	6.6
182	26	6	5	200	2.0	200	2.0	64.2	2.0	60	3.0	4.0	2.0	5.0	10	2	7.0
183	26	7	8	340	3.0	340	3.0	76.3	4.0	200	3.0	1.0	1.0	5.0	10	2	7.2
184	27	2	0	0	1.0	0	1.0	69.0	4.0	45	3.0	1.0	1.0	0	15	7	7.0
185	27	4	10	230	3.0	230	3.0	61.6	1.0	45	4.0	6.0	3.0	0	12	11	7.2
186	27	5	8	250	5.0	250	5.0	65.2	1.0	48	5.5	6.0	3.0	0	6	12	6.6
187	27	6	14	170	3.0	170	3.0	55.1	1.5	46	4.0	5.0	3.0	0	13	3	7.1
188	27	7	10	20	2.0	20	2.0	77.9	3.0	200	4.0	2.0	3.0	5.0	10	3	7.1
189	28	1	5	35	2.0	35	2.0	72.9	4.0	35	3.0	1.0	2.0	0	10	11	7.0
190	28	2	0	0	1.0	0	1.0	69.0	4.0	33	3.0	1.0	1.0	0	20	12	6.0

Table C3. (continued).

191	28	3	10	265	2.5	265	2.5	66.1	1.5	31	4.0	4.5	3.0	0	20	3	7.0
192	28	4	9	255	3.0	255	3.0	65.2	1.0	36	4.5	6.0	3.0	0	25	12	6.4
193	28	5	3	275	5.0	275	5.0	69.1	2.0	36	5.0	7.0	2.0	0	17	12	6.4
194	28	6	20	140	2.0	140	2.0	51.6	2.0	48	3.0	4.0	3.0	0	15	3	7.1
195	28	7	3	300	1.5	300	1.5	70.3	4.0	34	3.0	1.0	3.0	0	8	11	7.1
196	29	2	0	0	1.0	0	1.0	69.0	4.0	48	3.0	1.0	2.0	0	20	3	6.9
197	29	3	10	100	2.0	100	2.0	65.3	1.5	34	4.0	4.5	1.0	0	20	11	6.9
198	29	4	17	60	3.0	60	3.0	70.9	1.0	38	5.0	6.0	1.0	0	25	12	5.7
199	29	5	2	250	5.0	250	5.0	68.2	1.0	48	5.0	6.5	1.0	0	7	12	6.8
200	29	6	13	170	2.0	170	2.0	56.1	2.0	40	4.0	3.0	3.0	0	14	3	6.8
201	29	7	10	325	2.0	325	2.0	76.0	4.0	40	3.0	1.0	2.0	0	15	3	6.8
202	30	1	6	25	2.0	25	2.0	74.2	4.0	36	3.0	1.0	2.0	5.0	15	11	7.0
203	30	2	0	0	1.0	0	1.0	69.0	4.0	37	3.0	1.0	3.0	0	15	3	7.0
204	30	3	5	35	2.5	35	2.5	72.9	2.0	29	4.0	4.5	2.0	5.0	15	7	7.0
205	30	4	7	80	3.0	80	3.0	69.1	1.0	37	4.0	6.0	2.0	0	15	7	6.4
206	30	5	2	235	4.0	235	4.0	67.8	1.0	40	5.0	6.5	1.0	0	7	11	6.2
207	30	6	4	160	3.0	160	3.0	65.2	2.0	46	4.0	4.0	2.0	0	15	3	6.6
208	30	7	4	310	3.0	310	3.0	71.3	3.0	38	3.0	2.0	2.0	5.0	10	3	7.0
209	31	1	9	65	2.0	65	2.0	71.0	4.0	53	3.0	1.0	3.0	10.0	15	7	6.9
210	31	2	0	0	1.0	0	1.0	69.0	4.0	36	3.0	1.0	4.0	0	15	3	7.1
211	31	3	12	290	3.0	290	3.0	69.8	2.0	65	3.5	4.5	3.0	5.0	12	3	7.1
212	31	4	15	270	3.0	270	3.0	64.4	1.0	42	4.0	6.0	2.0	0	20	12	7.0
213	31	5	2	245	4.0	245	4.0	68.1	1.0	44	5.5	6.5	2.0	0	10	12	6.1
214	31	6	13	160	3.0	160	3.0	56.5	2.0	37	3.5	4.0	2.0	0	13	3	7.2
215	31	7	13	5	3.0	5	3.0	81.9	3.0	60	3.5	2.0	2.0	10.0	9	2	7.1
216	32	2	0	0	1.0	0	1.0	69.0	4.0	39	3.0	1.0	4.0	0	15	3	6.7
217	32	3	15	350	2.0	350	2.0	83.3	2.0	33	3.0	2.0	2.0	0	20	11	7.0
218	32	4	12	350	3.0	350	3.0	80.6	2.0	33	4.0	2.0	2.0	0	20	12	7.1
219	32	5	2	245	5.0	245	5.0	68.1	1.5	44	5.0	4.5	1.5	0	5	11	6.6
220	32	6	4	160	2.0	160	2.0	65.2	2.0	47	3.0	4.0	2.0	5.0	8	2	7.2
221	32	7	10	305	3.0	305	3.0	72.8	3.0	39	3.0	2.0	2.0	10.0	13	6	7.2
222	32	9	3	120	3.0	120	3.0	67.4	1.5	39	4.0	4.5	2.0	10.0	10	12	7.1
223	33	2	0	0	1.0	0	1.0	70.0	4.0	85	3.0	1.0	3.0	0	8	1	7.3

Table C3. (continued).

224	33	3	20	330	2,330	2.5	79.8	2.0	46	4.0	3.0	1.0	5.0	8	7	7.0
225	33	4	14	75	3, 75	3.0	68.9	2.0	32	4.0	5.5	1.0	0	15	8	5.3
226	33	5	8	230	4,230	4.0	64.2	1.0	54	5.0	7.0	1.0	0	10	5	6.8
227	33	6	8	145	2,145	2.0	63.1	2.0	58	3.0	3.0	1.0	0	8	3	7.2
228	33	7	4	340	3,340	3.5	73.7	3.0	100	4.0	3.0	3.0	1.0	7	5	7.1
229	34	1	2	95	2, 95	2.0	69.7	4.0	41	3.0	1.0	1.0	5.0	7	1	6.8
230	34	2	0	0	1, 0	1.0	70.0	4.0	60	3.0	1.0	4.0	0	10	3	6.8
231	34	3	2	200	2,200	2.0	68.1	2.0	38	4.0	4.0	1.0	5.0	9	3	6.9
232	34	4	4	210	3,210	3.5	66.5	2.0	52	4.0	5.5	1.0	0	10	3	6.7
233	34	5	2	125	5,125	5.0	68.8	1.5	40	5.5	7.0	1.0	0	7	10	6.0
234	34	6	3	180	2,180	2.5	67.0	1.5	70	4.0	4.0	2.0	15.0	12	3	6.9
235	34	7	3	330	2,330	2.0	72.5	2.0	65	3.0	2.0	1.0	0	6	1	6.7
236	35	1	1	120	2,120	2.0	69.5	4.0	75	3.0	1.0	1.0	10.0	8	7	5.5
237	35	2	0	0	1, 0	1.0	70.0	4.0	76	3.0	1.0	2.0	0	9	1	6.5
238	35	3	3	300	2,300	2.5	71.3	2.0	56	3.5	4.0	1.0	5.0	10	3	6.5
239	35	4	4	255	3,255	3.0	68.6	2.0	38	4.0	6.0	1.0	0	10	3	6.0
240	35	5	0	0	1, 0	1.0	70.0	1.5	30	4.0	6.0	1.0	0	15	5	5.8
241	35	6	6	190	2,190	2.0	64.1	2.0	62	3.5	3.0	2.0	10.0	5	2	7.0
242	35	7	4	360	2,660	2.0	74.0	4.0	200	3.0	1.0	3.0	20.0	4	6	7.0
243	36	1	5	80	2,180	2.0	70.3	4.0	43	3.0	1.0	2.0	10.0	6	7	7.1
244	36	2	0	0	1, 0	1.0	70.0	4.0	31	3.0	1.0	4.0	0	6	3	7.5
245	36	3	12	80	2,180	2.0	68.7	2.0	32	4.0	5.0	2.0	5.0	15	3	7.1
246	36	4	3	260	3,260	3.0	69.3	2.0	30	4.5	5.0	1.0	0	12	5	7.0
247	36	5	7	70	4,170	4.0	71.3	1.5	47	5.0	7.0	1.0	0	8	10	7.1
248	36	6	8	210	2,210	2.0	62.8	2.0	35	3.0	3.0	1.0	3.0	8	3	7.4
249	36	7	5	10	2, 10	2.5	74.9	4.0	56	3.5	1.0	4.0	25.0	5	2	7.1
250	37	2	0	0	1, 0	1.0	69.0	4.0	36	3.0	1.0	4.0	0	14	8	5.5
251	37	3	9	280	2,280	2.0	68.7	2.0	41	4.0	4.0	1.0	0	9	5	6.9
252	37	4	6	290	3,290	3.0	70.3	1.0	39	4.0	6.0	1.0	0	15	5	6.4
253	37	5	10	275	4,275	4.0	67.6	1.0	38	5.0	7.5	2.0	0	5	5	7.1
254	37	6	12	300	2,600	2.0	71.9	2.0	39	3.0	4.0	1.0	0	10	3	6.7
255	37	7	11	335	2,535	2.5	78.1	4.0	34	3.0	1.0	2.0	8.0	6	3	7.2
256	37	4	20	360	3,560	3.5	89.0	1.5	33	5.0	7.0	3.0	0	10	12	9.0

Table C3. (continued).

257	38	1	8	100	2,000	2.0	67.3	4.0	60	3.0	1.0	3.0	30.0	6	3	6.6
258	38	2	0	0	1, 0	1.0	70.0	4.0	60	3.0	1.0	4.0	0	4	1	6.2
259	38	3	3	245	2,045	2.0	68.6	3.0	50	3.0	2.0	1.0	5.0	9	3	6.9
260	38	4	25	60	3,060	3.0	67.5	1.5	72	4.0	6.0	1.0	0	10	3	6.1
261	38	5	6	95	4,595	4.5	68.7	1.0	60	6.0	7.0	1.0	0	9	3	6.6
262	38	6	2	160	2,60	2.0	68.1	3.0	73	3.0	2.0	2.0	10.0	10	1	6.8
263	38	7	3	350	2,050	2.0	72.9	4.0	60	3.0	1.0	2.0	15.0	8	2	6.9
264	39	1	5	45	2,645	2.0	73.2	4.0	33	3.0	1.0	3.0	20.0	10	13	7.2
265	39	2	0	0	1, 0	1.0	70.0	4.0	35	3.0	1.0	4.0	0	18	13	7.1
266	39	3	13	220	3,020	3.0	58.9	1.5	38	4.0	6.0	1.0	0	18	13	6.8
267	39	5	2	220	5,020	5.0	68.4	1.0	28	5.0	6.5	1.0	0	5	13	7.7
268	39	6	10	160	2,60	2.0	60.4	1.5	29	3.5	4.0	1.0	10.0	8	13	6.9
269	39	7	18	350	3,050	3.0	86.2	4.0	30	3.0	1.0	1.0	10.0	6	13	7.3
270	40	1	1	85	2,685	2.0	70.1	4.0	33	4.0	1.0	1.0	3.0	6	11	6.3
271	40	2	0	0	1, 0	1.0	70.0	4.0	31	4.0	1.0	4.0	0	13	11	6.3
272	40	3	2	230	2,230	2.0	68.7	2.0	47	4.0	3.0	1.0	3.0	8	3	6.3
273	40	4	7	240	3,040	3.0	65.8	1.5	60	5.0	5.0	1.0	0	9	5	6.4
274	40	5	2	245	5,045	5.0	69.1	1.0	36	6.0	6.0	1.0	0	5	5	6.6
275	40	6	3	160	2,160	2.5	67.2	1.5	52	4.0	4.0	1.0	4.0	9	5	6.8
276	40	7	3	355	2,655	2.0	73.0	3.0	42	4.0	2.0	1.0	2.0	99	5	6.1
277	41	1	14	75	2, 75	2.5	68.9	4.0	200	3.0	1.0	2.0	1.0	4	99	5.2
278	41	2	0	0	1, 0	1.0	70.0	2.0	200	4.0	3.0	5.0	0	4	20	7.0
279	41	3	15	247	3,047	3.0	60.8	2.0	200	4.0	5.0	3.0	10.0	30	99	7.1
280	41	4	32	254	3,254	3.5	48.3	1.5	200	4.5	6.0	3.0	0	30	99	6.5
281	41	5	15	244	4,044	4.0	60.3	1.0	200	5.0	7.0	4.0	0	15	99	6.0
282	41	6	38	180	3,080	3.0	32.0	3.5	200	2.0	1.5	2.5	0	6	99	6.4
283	41	7	10	360	3,360	3.5	80.0	4.0	200	2.5	1.0	2.0	2.0	4	99	5.3
284	41	8	27	250	4,250	4.0	51.6	1.0	200	5.0	7.0	3.0	0	12	99	6.1
285	41	9	0	250	5,250	5.0	70.0	1.0	200	8.0	8.0	1.0	0	10	99	5.3
286	41	8	3	252	5,052	5.0	68.9	1.0	200	7.0	8.0	1.0	0	10	99	5.9
287	41	8	15	250	5,050	5.0	61.3	1.5	200	5.0	6.0	3.0	0	12	99	5.0
288	41	7	10	357	4,357	4.0	80.0	2.5	200	3.0	3.0	2.0	5.0	4	99	5.2
289	41	4	8	340	2,340	2.0	77.2	3.0	200	4.0	4.0	1.0	0	35	99	3.8

Table C3. (concluded).

290	41	6	15	167	2.0	167	2.0	55.2	3.0	200	3.5	3.0	2.0	0	4	99	6.9
291	41	6	26	183	3.0	183	3.0	44.0	3.0	200	3.5	4.0	3.0	0	6	99	5.4
292	41	4	27	197	3.5	197	3.5	43.5	1.5	200	5.0	6.0	3.0	0	45	99	4.8
293	9	6	99	18	3.5	18	3.5	999.0	99.0	200	99.0	99.0	99.0	150.0	99	99	9.0

11 - ENE side; 2 - summit; 3 - WSW side; 4 - midWSW side; 4 - middle snowbank; 5 - bottom snowbank; 6 - S slope; 7 - N slope; 8 - very late-lying or permanent snowbank; 9 - other.

299 = missing.

3399 = missing.

41 - summit; 2 - shoulder; 3 - backslope; 4 - footsackslope; 4 - footslope; 5 - toeslope.

5999 = missing.

6See Chapter III for scalar values; 99 = missing. ∞; 99 = missing.

7200 = missing; values of 100 cm indicate at least m indicate at least 100 cm, but may be greater.

8See Chapter III for scalar values; 99 = missing. ∞; 99 = missing.

9See Chapter III for scalar values; 99 = missing. ∞; 99 = missing.

10See Chapter III for scalar values; 99 = missing. ∞; 99 = missing.

11150 = missing.

1299 = missing.

131 - Pacific Pergelic Cryoboroli; 2 - Calcic Pergelic Cryoboroli; 3 - Calcic Pergelic Cryoboroli; 4 - Cumulic Pergelic Cryoboroli; 5 - Pergelic Cryaquoli; 6 - Calcic Pergelic Cryochrept; 7 - Pergelic Cryochrept; 8 - Pe Cryochrept; 8 - Pergelic Cryumbrept; 9 - Pacific Pergelic Cryumbrept; 10 - Pergelic Cryaquept; 11 - Histic Pergelic Cryaquept; 12 - Pergelic Cryosaprist; 13 - Pergelic Cryorthentfergelic Cryorthent; 99 = missing.

149 = missing.

Table C4. Number of species in each taxonomic category and in each floristic category within each of the 293 detailed sample plots.

Plot	Vascular	Bryo- Rest- ict	Diver- sity Index ¹	Diver- sity Index ¹	Arctic	Arctic Alpine	Arctic- Boreal	Arctic- Coas- tal	1	2	3	4	Circum- polar	NA WNA	NA- Asia	NA- Asia- Eur	NA- Asia- Eur
1	16	6	0	1.12	3	1.12	3	13	0	7	6	3	0	0	0	2	0
2	24	8	6	.98	6	.98	6	16	1	1	14	5	0	0	2	2	0
3	13	19	14	0	.74	7	7	6	0	3	8	2	0	0	3	2	0
4	16	13	10	0	.98	10	5	1	0	4	8	4	0	0	0	3	0
5	24	10	8	0	1.06	10	11	3	0	6	10	8	0	0	1	3	1
6	20	14	7	0	.97	6	13	1	0	2	12	6	0	0	2	4	2
7	13	19	4	0	1.00	5	8	0	0	6	4	3	0	0	1	1	0
8	14	17	2	1	1.40	4	9	0	1	7	7	0	0	0	1	2	0
9	16	17	9	1	.83	5	10	0	1	6	9	1	0	0	1	1	0
10	12	14	15	0	.69	1	11	0	0	4	6	2	0	0	1	2	1
11	15	17	15	0	.90	7	8	0	0	3	8	4	0	0	0	3	4
12	19	15	12	0	1.12	9	9	1	0	5	9	5	0	0	0	4	2
13	15	16	9	1	.84	4	11	0	0	6	6	3	0	0	0	2	0
14	8	14	8	0	.71	1	7	0	0	3	4	1	0	0	1	1	0
15	7	11	7	0	.85	3	4	0	0	3	4	0	0	0	0	1	0
16	24	7	16	0	.88	6	18	0	0	3	15	6	0	0	0	2	1
17	18	12	13	0	.73	7	11	0	0	2	10	6	0	0	0	4	2
18	13	18	13	0	.92	6	7	0	0	4	5	4	0	0	0	2	1
19	17	4	12	0	.46	5	9	3	0	7	6	4	0	0	0	1	0
20	21	15	10	2	1.39	4	17	0	0	4	5	4	0	0	0	3	0
21	22	13	0	1.22	3	1.22	3	7	0	1	13	6	1	0	0	2	2
22	9	10	8	0	.91	2	7	0	0	2	5	2	0	0	0	2	0
23	16	9	13	0	1.02	2	13	1	0	3	8	4	1	0	0	1	0
24	17	11	8	0	.83	5	11	1	0	2	9	6	0	0	0	2	0
25	23	11	11	1	1.13	8	14	1	0	5	11	7	0	0	0	3	2
26	26	7	14	0	1.18	6	17	3	0	5	11	10	0	0	1	4	3
27	12	15	6	1	1.30	2	10	0	0	2	7	3	0	0	1	1	0
28	10	17	8	0	.96	0	10	0	0	3	5	2	0	0	0	2	0
29	11	12	10	0	.80	2	8	0	1	4	5	2	0	0	0	1	1
30	17	9	7	0	1.14	4	13	0	0	5	10	2	0	0	1	2	2

Table C4. (continued).

[illegible]

Table C4. (continued).

[illegible]

Table C4. (continued).

[illegible]

Table C4. (continued).

142	18	17	8	0	1.14	2	1	2	15	0	1	5	10	3	0	12	0	0	0	0	0	0	2	0	1	1	0	
143	26	13	7	0	1.13	6	5	6	9	0	1	6	17	3	0	15	1	0	0	0	0	0	4	0	3	3	1	0
144	15	17	12	0	1.06	6	5	6	9	0	0	2	8	5	0	4	0	0	0	0	0	0	0	1	3	5	0	0
145	21	18	11	0	1.13	6	5	6	12	2	1	5	12	4	0	10	0	0	0	0	0	0	2	0	3	4	1	0
146	15	6	10	0	1.08	5	3	5	7	3	0	4	8	3	0	8	0	0	0	0	0	0	1	1	2	2	0	0
147	30	9	4	0	1.19	8	5	8	19	1	2	6	18	6	0	19	1	0	0	0	0	0	4	0	1	4	0	0
148	16	15	8	0	1.05	4	5	4	12	0	0	5	8	3	0	7	0	0	0	0	0	0	0	0	2	3	2	2
149	18	9	4	1	.91	5	1	5	11	0	2	5	9	4	0	8	0	0	0	0	0	0	0	0	1	4	1	1
150	23	10	10	0	1.06	6	5	6	15	0	2	6	15	2	0	13	0	0	0	0	0	0	2	0	1	4	1	2
151	19	11	10	0	1.08	5	3	5	14	0	0	7	7	5	0	12	0	0	0	0	0	0	0	1	2	1	3	0
152	22	14	19	0	1.25	10	5	10	11	1	0	5	11	6	0	11	0	0	0	0	0	0	0	0	4	4	3	2
153	23	3	9	0	1.01	9	1	9	11	3	0	5	11	7	0	14	0	0	0	0	0	0	0	0	3	4	4	0
154	18	8	10	1	.90	6	5	6	11	1	0	5	6	7	0	7	0	0	0	0	0	0	0	1	2	4	2	1
155	18	14	9	0	1.08	6	3	6	12	0	0	6	6	6	0	8	0	0	0	0	0	0	0	0	1	3	3	0
156	13	18	6	0	.95	4	5	4	9	0	0	4	7	2	0	4	0	0	0	0	0	0	0	0	1	0	0	0
157	26	18	10	0	1.15	7	5	7	18	1	0	4	7	2	0	4	0	0	0	0	0	0	0	0	3	2	3	0
158	16	21	10	0	1.25	4	5	4	12	0	0	4	8	4	0	6	0	0	0	0	0	0	0	0	1	0	1	4
159	19	17	14	0	1.15	5	5	5	13	1	0	3	10	6	0	7	0	0	0	0	0	0	0	0	1	2	3	4
160	21	13	15	0	1.12	8	2	8	11	2	0	0	3	6	1	4	0	0	0	0	0	0	0	0	1	2	3	3
161	19	9	5	0	.95	3	5	3	8	0	0	4	6	1	0	5	0	0	0	0	0	0	0	0	0	1	1	0
162	11	19	5	0	1.02	3	2	3	7	0	0	4	3	3	0	3	0	0	0	0	0	0	0	0	0	1	1	2
163	10	18	5	1	1.05	5	5	5	16	0	0	10	8	2	1	14	0	0	0	0	0	0	0	0	0	1	3	4
164	21	11	4	1	1.06	6	0	6	7	0	0	4	6	3	0	6	0	0	0	0	0	0	0	0	0	1	1	0
165	13	22	15	1	.90	13	6	6	17	0	0	4	6	2	0	6	0	0	0	0	0	0	0	0	0	1	1	0
166	27	23	13	0	1.28	12	8	12	15	0	0	7	14	6	0	12	0	0	0	0	0	0	0	0	0	3	2	2
167	17	10	12	0	.95	9	5	9	6	2	0	2	8	7	0	6	0	0	0	0	0	0	0	0	0	3	5	4
168	12	13	3	1	.96	4	6	4	8	0	0	5	3	4	0	6	0	0	0	0	0	0	0	0	0	3	5	0
169	10	20	3	1	.95	3	5	3	7	0	0	4	4	2	0	4	0	0	0	0	0	0	0	0	0	0	2	0
170	14	18	11	1	1.07	4	7	4	10	0	0	4	7	3	0	4	0	0	0	0	0	0	0	0	0	0	3	2
171	35	10	11	1	1.17	11	7	11	22	1	1	9	14	12	0	23	0	0	0	0	0	0	0	0	1	3	2	0
172	25	11	14	0	1.24	11	4	11	14	0	0	8	11	6	0	14	0	0	0	0	0	0	0	0	0	1	1	1
173	16	21	17	0	1.36	8	6	8	7	1	0	6	8	2	0	9	0	0	0	0	0	0	0	0	0	3	5	2
174	20	10	15	0	1.04	10	4	10	9	1	0	7	11	2	0	12	0	0	0	0	0	0	0	0	0	3	3	1
175	19	25	14	1	1.26	8	6	8	11	0	0	5	8	6	0	8	0	0	0	0	0	0	0	0	0	3	5	0
176	13	15	6	1	1.18	5	8	5	8	0	0	4	6	3	0	6	0	0	0	0	0	0	0	0	0	3	1	1
177	12	23	9	1	1.28	7	8	1	11	2	0	0	4	5	0	5	0	0	0	0	0	0	0	0	0	2	3	0
178	24	11	9	1	1.08	7	8	7	14	2	0	1	2	9	13	0	0	0	0	0	0	0	0	0	0	1	4	0
179	21	23	12	1	1.11	3	1	3	17	0	1	2	10	9	0	13	0	0	0	0	0	0	0	0	0	0	4	2
180	22	1	1	0	1.11	3	1	3	17	0	1	2	10	9	0	8	0	0	0	0	0	0	0	0	0	0	4	2

Table C4. (continued).

15	12	2	1.26	5	26	5	19	3	0	0	3	9	15	0	14	0	0	0	0	1	3	0	1	1	6	2	0
180	27	0	.89	4	39	4	14	3	0	0	3	9	6	1	12	0	0	0	0	1	3	0	1	1	3	0	0
21	5	6	.81	4	4	4	18	0	0	0	3	12	6	0	7	1	1	1	1	1	2	0	1	3	1	2	2
182	22	7	1.26	4	23	4	19	0	0	0	3	14	6	0	9	0	0	0	0	1	2	0	1	6	1	0	2
183	23	10	3	1.23	5	9	5	10	0	0	3	4	7	1	6	0	0	0	0	1	2	0	1	8	0	2	2
14	11	2	.99	5	10	0	0	0	0	0	3	4	7	1	8	0	0	0	0	0	3	1	1	9	3	1	0
185	23	4	7	2	1.00	9	14	0	0	0	3	7	12	1	8	0	0	0	0	0	3	1	1	9	3	1	0
186	20	1	3	0	.96	6	12	2	0	0	3	6	11	0	8	0	0	0	0	1	2	2	1	6	1	0	0
187	15	12	2	2	.79	3	12	0	0	0	2	6	6	1	6	0	0	0	0	1	2	0	1	4	1	0	0
188	21	17	9	3	1.06	7	14	0	0	0	5	10	5	1	8	1	0	0	0	1	2	0	1	4	2	2	2
189	19	15	2	1.10	7	0	7	12	0	0	2	10	6	1	7	0	0	0	0	0	3	0	2	5	1	1	1
190	29	12	11	1.15	8	5	18	3	0	0	4	12	11	2	16	2	0	0	0	0	5	0	1	4	3	0	0
191	19	11	10	2	.84	9	10	0	0	0	3	7	9	0	6	1	0	0	0	1	1	1	1	4	3	0	0
192	20	11	11	2	1.10	7	7	11	2	0	2	6	11	1	10	1	0	0	0	1	1	1	1	4	3	0	0
193	20	8	1	1.15	7	5	7	10	3	0	2	7	10	1	11	1	0	0	0	0	2	2	1	5	0	0	0
194	23	13	6	1.05	8	15	14	1	0	0	4	7	12	0	11	0	0	0	0	0	4	1	0	6	0	0	0
195	13	15	7	.94	4	14	4	9	0	0	1	8	4	0	4	0	0	0	0	0	0	0	1	3	0	0	0
196	16	4	10	0	1.04	6	10	0	0	0	4	5	7	0	10	1	0	0	0	0	0	2	1	0	1	0	0
197	19	16	11	2	1.00	8	10	1	0	0	3	8	7	1	10	1	0	0	0	0	1	0	0	6	1	0	0
198	25	12	9	1	1.13	10	12	3	0	0	3	9	12	1	12	1	0	0	0	0	2	0	1	0	3	0	0
199	29	2	12	1	1.00	11	17	1	0	0	3	10	14	2	11	1	0	0	0	0	3	0	1	8	2	3	3
200	19	13	12	2	.83	5	14	0	0	0	4	5	9	1	7	1	1	0	0	0	0	0	0	6	2	1	1
201	24	19	12	2	1.11	7	17	0	0	0	4	11	9	0	9	0	0	0	0	1	1	0	2	7	3	1	1
202	21	19	14	2	1.18	6	15	0	0	0	5	4	11	1	9	0	0	0	0	1	0	1	0	6	3	1	1
203	26	7	8	1	1.05	7	16	3	0	0	5	9	11	1	14	2	0	0	0	0	5	0	0	3	1	1	1
204	20	16	14	1	1.21	8	12	0	0	0	4	8	8	0	9	0	0	0	0	1	0	0	2	5	3	0	0
205	22	14	13	0	1.25	8	14	0	0	0	3	9	10	0	10	0	0	0	0	2	0	0	2	6	2	0	0
206	25	3	7	1	.89	10	14	1	0	0	4	9	12	0	10	0	0	0	0	1	2	0	1	8	2	0	0
207	18	13	11	1	1.18	7	11	0	0	0	4	7	7	0	7	0	0	0	0	1	2	0	1	5	2	0	0
208	16	17	8	1	1.18	6	10	0	0	0	4	7	11	0	11	0	0	0	0	1	2	0	1	3	3	0	0
209	22	20	11	1	1.06	5	17	0	0	0	4	7	11	0	11	0	0	0	0	1	2	0	1	4	2	1	1
210	12	6	7	0	.72	5	5	7	0	0	1	6	5	0	6	1	0	0	0	2	1	0	1	1	1	1	1
211	18	15	10	0	1.08	5	13	0	0	0	2	9	7	0	7	0	0	0	0	0	0	2	1	4	1	1	1
212	22	10	10	0	1.08	7	15	0	0	0	3	9	10	0	9	0	0	0	0	0	0	2	0	7	2	0	0
213	23	9	11	0	1.27	9	12	2	0	0	2	11	10	0	11	0	0	0	0	0	3	1	1	3	3	0	0
214	14	15	12	3	.80	3	11	0	0	0	2	7	4	1	5	1	1	0	0	0	0	0	1	4	1	1	1
215	19	17	1	1	1.07	7	12	0	0	0	4	6	9	0	9	0	0	0	0	1	0	0	1	4	1	1	1
216	19	4	11	0	.84	6	13	0	0	0	3	7	9	0	10	0	0	0	0	0	4	0	1	5	3	0	0

Table C4. (continued).

[illegible]

Table C4. (concluded).

[illegible]

Table C4. (concluded).

[illegible]

¹ Shannon-Weiner diversity index, see Chapter III > Chapter III for details.

Table C5. Human and animal disturbance values for each of the 293 detailed sample plots.¹

Plot	Human	Caribou	Fox	Squirrel	Bear	Lemming	Bird
1	2.0	0	0	3.0	0	0	0
2	1.5	1.0	1.0	4.0	0	0	0
3	0	1.0	1.0	2.0	0	0	0
4	0	1.0	2.0	0	0	1.0	2.0
5	0	1.0	1.0	2.5	0	1.0	0
6	0	1.0	5.0	2.0	5.0	0	0
7	1.0	1.0	1.0	1.0	0	0	1.0
8	1.5	0	1.0	0	0	0	0
9	0	1.0	0	4.0	0	0	0
10	0	0	0	1.5	0	0	0
11	0	1.0	0	1.0	0	0	0
12	0	1.0	0	0	0	0	1.0
13	0	1.0	0	3.5	0	0	1.0
14	0	1.0	0	1.0	0	0	0
15	0	0	0	0	0	0	0
16	3.0	1.0	4.0	4.0	0	1.0	0
17	0	1.0	1.0	0	0	1.0	1.0
18	0	1.0	1.0	0	0	1.0	1.0
19	0	1.0	0	0	0	1.0	1.0
20	0	2.0	0	1.0	0	0	1.0
21	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0
23	4.5	0	3.0	3.0	0	0	1.0
24	0	1.0	1.0	1.0	5.0	0	1.0
25	0	1.0	1.0	0	0	3.0	1.0
26	1.0	1.0	1.0	0	0	2.0	1.0
27	1.0	1.0	0	1.0	4.0	1.0	1.0
28	0	0	0	0	0	0	0
29	1.0	1.0	1.0	0	0	0	0
30	2.0	1.0	1.0	3.0	0	0	1.0
31	1.0	1.0	1.0	1.0	0	0	1.0
32	1.0	3.0	1.0	1.0	0	1.0	1.0
33	1.0	2.0	1.0	0	0	3.0	1.0
34	1.0	1.0	2.0	1.0	0	0	1.0
35	1.0	1.0	0	0	0	0	0
36	2.0	2.0	0	0	0	0	0
37	1.0	1.0	3.0	5.0	0	0	1.0
38	1.0	2.0	0	0	0	2.0	1.0
39	1.0	2.0	1.0	0	0	3.0	1.0
40	1.0	2.0	1.0	0	0	3.0	1.0
41	4.0	1.0	1.0	1.0	0	0	1.0
42	2.0	0	0	0	0	0	0
43	0	1.0	0	0	0	0	0
44	4.0	1.0	1.0	3.0	5.0	0	1.0
45	1.0	1.0	1.0	1.0	0	0	1.0
46	0	3.0	2.0	0	5.0	3.0	1.0

Table C5. (continued).

47	0	2.0	1.0	0	1.0	3.0	1.0
48	0	2.0	1.0	4.0	5.0	0	1.0
49	0	1.0	1.0	0	0	0	1.0
50	0	1.0	1.0	0	0	0	1.0
51	0	2.0	1.0	1.0	0	0	1.0
52	0	2.0	1.0	1.0	0	0	0
53	0	1.0	0	0	0	3.0	2.0
54	0	1.0	1.0	0	0	1.0	2.0
55	0	2.0	1.0	1.0	0	0	1.0
56	0	2.0	0	0	0	0	1.0
57	0	0	0	0	0	0	1.0
58	0	0	1.0	2.0	0	0	2.0
59	0	2.0	0	6.0	0	3.0	2.0
60	0	2.0	0	0	0	0	0
61	0	3.0	2.0	0	3.0	2.0	2.0
62	0	2.0	2.0	3.0	0	0	1.0
63	0	0	0	0	0	0	0
64	0	0	0	0	1.0	0	1.0
65	2.0	0	0	0	0	0	2.0
66	0	1.0	0	0	0	0	1.0
67	0	1.0	1.0	0	0	4.0	2.0
68	0	2.0	0	0	0	3.0	1.0
69	0	2.0	0	0	0	1.0	0
70	0	0	0	0	0	1.0	0
71	0	1.0	0	0	0	0	2.0
72	0	0	0	3.0	0	0	2.0
73	0	2.0	0	1.0	0	0	1.0
74	0	2.0	0	0	0	3.0	1.0
75	0	2.0	0	0	5.0	3.0	2.0
76	0	1.0	0	1.0	0	0	1.0
77	0	1.0	0	0	0	0	0
78	0	1.0	2.0	0	0	0	0
79	3.0	1.0	2.0	3.0	0	0	2.0
80	0	2.0	0	0	0	0	0
81	0	1.0	0	0	0	2.0	1.0
82	0	2.0	2.0	0	0	0	1.0
83	3.0	3.0	1.0	0	0	0	1.0
84	0	1.0	1.0	0	0	0	0
85	2.0	1.0	1.0	4.0	0	0	2.0
86	0	2.0	1.0	0	0	0	1.0
87	1.0	1.0	2.0	0	0	3.0	1.0
88	0	1.0	0	0	0	3.0	1.0
89	0	1.0	0	1.0	0	0	0
90	0	1.0	0	0	0	0	0
91	0	1.0	0	0	0	0	3.0
92	0	0	0	0	0	0	0
93	5.0	1.0	1.0	1.0	0	0	1.0
94	0	1.0	1.0	0	0	0	0
95	1.0	1.0	1.0	0	0	1.0	0
96	1.0	0	0	0	0	1.0	0
97	4.0	0	0	1.0	0	0	1.0
98	0	1.0	0	0	0	0	0

Table C5. (continued).

99	0	1.0	0	0	0	0	1.0
100	0	1.0	1.0	0	0	0	1.0
101	0	1.0	1.0	0	0	0	1.0
102	0	0	0	3.0	0	3.0	0
103	0	0	0	0	0	1.0	1.0
104	1.0	0	0	1.0	0	0	1.0
105	0	1.0	0	2.0	0	0	1.0
106	0	1.0	0	2.0	0	0	1.0
107	0	0	0	0	0	0	0
108	2.0	1.0	1.0	4.0	0	0	1.0
109	0	1.0	0	0	0	2.0	0
110	0	1.0	1.0	0	0	2.0	0
111	0	0	0	0	0	0	0
112	0	1.0	0	0	0	0	0
113	0	1.0	0	0	0	0	1.0
114	0	1.0	0	0	0	0	0
115	2.0	1.0	1.0	4.0	0	2.0	0
116	0	0	0	0	0	1.0	0
117	0	1.0	1.0	0	0	1.0	1.0
118	0	0	0	0	0	0	0
119	0	0	1.0	0	0	0	1.0
120	0	1.0	1.0	1.0	0	0	0
121	2.0	1.0	0	0	0	0	0
122	4.0	1.0	0	0	0	0	0
123	0	1.0	0	0	0	0	0
124	1.0	0	0	0	0	0	1.0
125	1.0	1.0	0	0	0	1.0	0
126	2.0	1.0	0	0	0	0	0
127	2.0	1.0	0	0	0	1.0	0
128	0	1.0	0	0	0	0	1.0
129	1.0	2.0	3.0	0	0	0	0
130	0	1.0	2.0	0	0	1.0	0
131	0	2.0	1.0	0	0	1.0	0
132	0	1.0	1.0	0	0	0	0
133	0	1.0	1.0	0	0	0	0
134	0	2.0	3.0	0	0	0	0
135	0	1.0	0	0	0	0	1.0
136	4.0	1.0	1.0	0	0	0	1.0
137	0	1.0	1.0	0	0	1.0	1.0
135	0	1.0	0	0	0	0	1.0
136	4.0	1.0	1.0	0	0	0	1.0
137	0	1.0	1.0	0	0	1.0	1.0
138	0	0	0	0	0	2.0	1.0
139	0	2.0	1.0	0	0	0	0
140	0	1.0	0	0	0	0	0
141	0	1.0	0	0	0	0	1.0
142	0	1.0	2.0	0	0	0	1.0
143	4.0	1.0	4.0	0	0	0	1.0
144	0	1.0	1.0	0	0	0	0
145	0	0	3.0	0	0	3.0	0
146	0	1.0	2.0	0	0	1.0	0
147	0	1.0	5.0	0	0	0	0
148	0	1.0	1.0	0	0	0	0
149	0	0	1.0	1.0	0	0	0
150	0	1.0	2.0	2.0	0	0	1.0

Table C5. (continued).

151	0	1.0	0	0	0	2.0	0
152	0	1.0	0	0	0	0	0
153	0	1.0	0	0	0	1.0	0
154	0	1.0	0	0	0	0	0
155	0	1.0	0	0	0	0	0
156	0	1.0	0	0	0	0	0
157	4.0	1.0	2.0	3.0	0	0	1.0
158	4.0	1.0	0	0	0	0	0
159	0	1.0	0	0	0	2.0	0
160	0	2.0	0	0	0	1.0	0
161	3.0	1.0	0	0	0	0	1.0
162	4.0	2.0	0	0	0	0	1.0
163	0	1.0	0	0	0	0	0
164	2.0	1.0	1.0	0	0	0	0
165	0	1.0	2.0	0	0	1.0	1.0
166	0	1.0	1.0	0	0	2.0	1.0
167	0	1.0	0	0	0	0	2.0
168	0	0	0	0	0	0	0
169	0	1.0	0	0	0	1.0	0
170	0	1.0	1.0	0	0	0	0
171	0	1.0	5.0	0	0	0	2.0
172	0	2.0	1.0	0	0	3.0	0
173	0	2.0	2.0	0	0	0	0
174	0	2.0	0	0	0	1.0	0
175	3.0	1.5	0	0	0	1.0	0
176	4.0	1.0	0	0	0	0	0
177	0	1.0	3.0	0	0	0	1.0
178	0	0	0	3.0	0	0	1.0
179	0	1.0	3.0	1.0	0	0	1.0
180	0	0	3.0	0	0	3.0	1.0
181	0	0	0	0	0	0	1.0
182	0	1.0	0	0	0	3.0	1.0
183	0	2.0	0	0	0	0	1.0
184	0	1.0	0	3.0	0	3.0	1.0
185	0	0	0	0	0	3.0	0
186	0	0	0	0	0	3.0	0
187	0	1.0	0	0	2.0	3.0	0
188	0	1.0	0	0	0	0	0
189	0	1.0	0	0	0	0	1.0
187	0	1.0	0	0	2.0	3.0	0
188	0	1.0	0	0	0	0	0
189	0	1.0	0	0	0	0	1.0
190	0	1.0	0	3.0	0	0	2.0
191	0	1.0	0	0	0	3.0	1.0
192	0	1.0	0	0	0	3.0	0
193	0	0	0	0	0	3.0	0
194	0	1.0	0	3.0	0	0	1.0
195	0	1.0	0	3.0	0	3.0	1.0
196	0	1.0	0	3.0	3.0	0	1.0
197	0	1.0	0	0	0	3.0	1.0
198	0	1.0	0	0	0	3.0	1.0
199	0	0	0	0	0	0	0
200	0	0	0	0	0	3.0	1.0
201	0	1.0	0	3.0	0	0	1.0
202	0	1.0	0	0	0	0	1.0