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Source: *Ecological Monographs*, Vol. 61, No. 4 (Dec., 1991), pp. 437-464
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/2937050
Accessed: 23/04/2010 17:24

Ecological Monographs, 61(4), 1991, pp. 437–464

LOESS ECOSYSTEMS OF NORTHERN ALASKA: REGIONAL GRADIENT AND TOPOSEQUENCE AT PRUDHOE BAY

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Abstract. Loess-dominated ecosystems cover ≈14% (11 000 km^2) of the Arctic Coastal Plain and much of the northern portion of the Arctic Foothills. Knowledge of this poorly known ecosystem is important for sound land-use planning of the expanding developments in the region and for understanding the paleoecological dynamics of eolian systems that once dominated much of northern Alaska. A conceptual alkaline-tundra toposequence includes eight common vegetation types and associated soils that occur near the arctic coast. A model of the regional loess gradient describes soils and vegetation downwind of the Sagavanirktok River. The addition of calcareous loess affects numerous soil properties, including bulk density, pH, water retention properties, concentrations of soil nutrients, and seasonal thaw depths. Many plant taxa, particularly cryptogams, increase in abundance downwind of the river, apparently in response to higher amounts of nutrients and moisture associated with finer soil-particle sizes and greater organic content. For example, the highest extractable P values (8–12 $\mu g/g$) occur in areas with circumneutral pH and finer grained soils, and low P values (<2 $\mu g/g$) occur in acidic soils north of the loess region. Early, minerotrophic stages of tundra succession are maintained by loess blown from the Sagavanirktok, Canning, and other large braided-river floodplains. Areas downwind of these rivers provide analogues for vegetation that existed in unstable areas of the Alaskan Coastal Plain during and following full glacial conditions. Total aboveground phytomass in wet acidic sites at Prudhoe Bay (163 ± 21 g/m^2) is close to values from similar sites at Barrow and Devon Island. Only a small amount of data is available for alkaline areas, but there is indication of lower biomass near the major rivers, suggesting a response to lower nutrient regimes. Properties of loess tundra important for land-use planning include: (1) its high ice content, which contributes to its susceptibility to thermokarst; (2) high salinities, which hamper revegetation efforts; and (3) presence of certain plant species such as *Dryas intergrifolia*, which are particularly sensitive to disturbance. The loess gradient provides a natural analogue for road dust, an extensive disturbance associated with oil-field development.

Key words: arctic vegetation and soils; arctic wetlands; Beringia; calciphilous and basiphilous tundra plants; climate change; disturbance and recovery; fen; landscape ecology; loess; peatlands; periglacial features; permafrost; road dust; saline soils; toposequences.

INTRODUCTION

Importance of loess ecosystems in northern Alaska

Little is known about the ecological effects of modern arctic dust, although dust and its worldwide distribution by winds are recognized as important to the process of desertification and global biogeochemical cycles (Pewé 1981, Pye 1987, Schlesinger et al. 1990). Periods of intense global dust-blowing are correlated with cold, drier, and probably windier conditions during glacial intervals (Pye 1987), and are recorded in deep ice cores of Antarctica and Greenland (Hammer et al. 1985, Petit et al. 1990). During the glacial periods, vast loess deposits formed in Europe, North America, Beringia, China, Soviet Central Asia, Pakistan, Siberia, and the Ukraine. Although thick Quaternary loess deposits are common in Alaskan and Siberian arctic regions (Pewé 1975, Hopkins 1982, Tomirdiaro 1982, Carter 1988), modern arctic loess systems are restricted to relatively small areas near glacial outwash deposits and large braided rivers.

Ecological studies of modern loess ecosystems provide important information regarding the successional history of the Arctic relevant to the possible effects of climate change. Knowledge of these areas is also of practical importance because much of the oil development in northern Alaska is in loess ecosystems. Most

[1] Manuscript received 24 July 1989; revised 1 December 1990; accepted 13 December 1990.

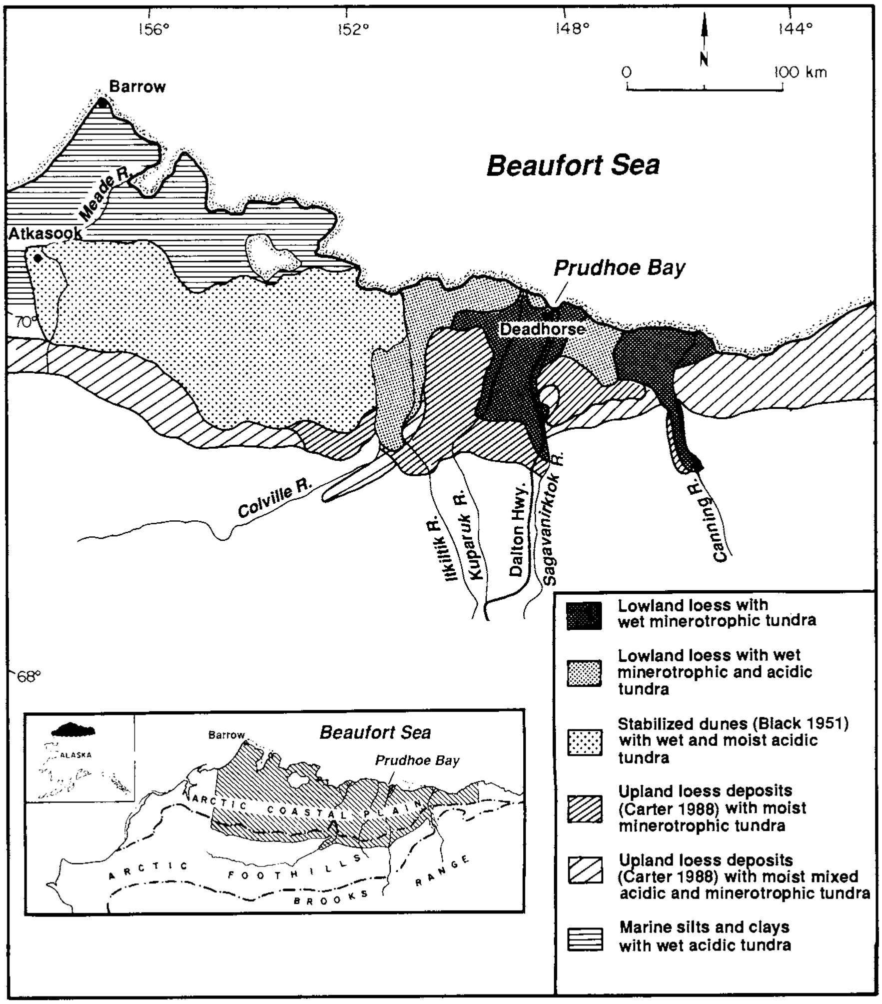


FIG. 1. Extent of minerotrophic and acidic tundras on the Alaskan North Slope based on Carter (1988) and AVHRR satellite-derived imagery. Upland loess occurs in the Arctic Foothills. Lowland loess occurs on the Arctic Coastal Plain.

tundra ecological information is from study sites uninfluenced by loess. For example, Barrow (Fig. 1), which was long the center of vegetation research in northern Alaska and the main United States study site for the International Biological Programme (IBP) Tundra Biome, is on acidic marine sediments (Britton 1967, 1973, Tieszen 1978, Brown et al. 1980). Similarly, none of the other IBP Tundra Biome sites is in an area with much modern influx of loess (Bliss et al. 1981). The Atkasook site for the RATE program (Research on Arctic Tundra Environments, Batzli 1980) is on stabilized eolian sands with low pH (4.3 to 5.5), and other major study sites in northern Alaska are also in areas without modern influx of loess (e.g., Cape Thompson [Wilimovsky and Wolfe 1966], Umiat [Bliss 1956, Cantlon 1961], Atkasook [Batzli 1980], Toolik Lake [Chapin and Shaver 1981, 1985, Shaver and Chapin 1986, Chapin et al. 1988], Imnavait Creek [Oechel 1989], Colville River [Bliss and Cantlon 1957], and Okpilak River [Brown 1962]).

The most extensive area of modern loess deposition in arctic Alaska occurs near the Sagavanirktok and Canning rivers. Here, calcareous loess (pH 6.0 to 8.4) downwind of the rivers favors development of minerotrophic plant communities. For example, *Dryas integrifolia, Eriophorum triste,* and *Tomenthypnum nitens* occur in moist sites, and *Carex aquatilis, Drepanocladus* spp., and *Scorpidium scorpioides* occur in most wet areas. In addition, the loess has important, and as yet poorly understood, effects on other ecosystem processes and components, such as production and mineralization rates, invertebrate populations, shorebirds, and mammals. Throughout this paper, areas with circumneutral to alkaline soils are referred to as minerotrophic tundra, in contrast to the acidic tundra regions which generally have soils with pH <6.0.

This paper summarizes recent studies of loess ecosystems in the Prudhoe Bay region and much other relevant information, focusing on soil and vegetation toposequences and ecological gradients downwind of

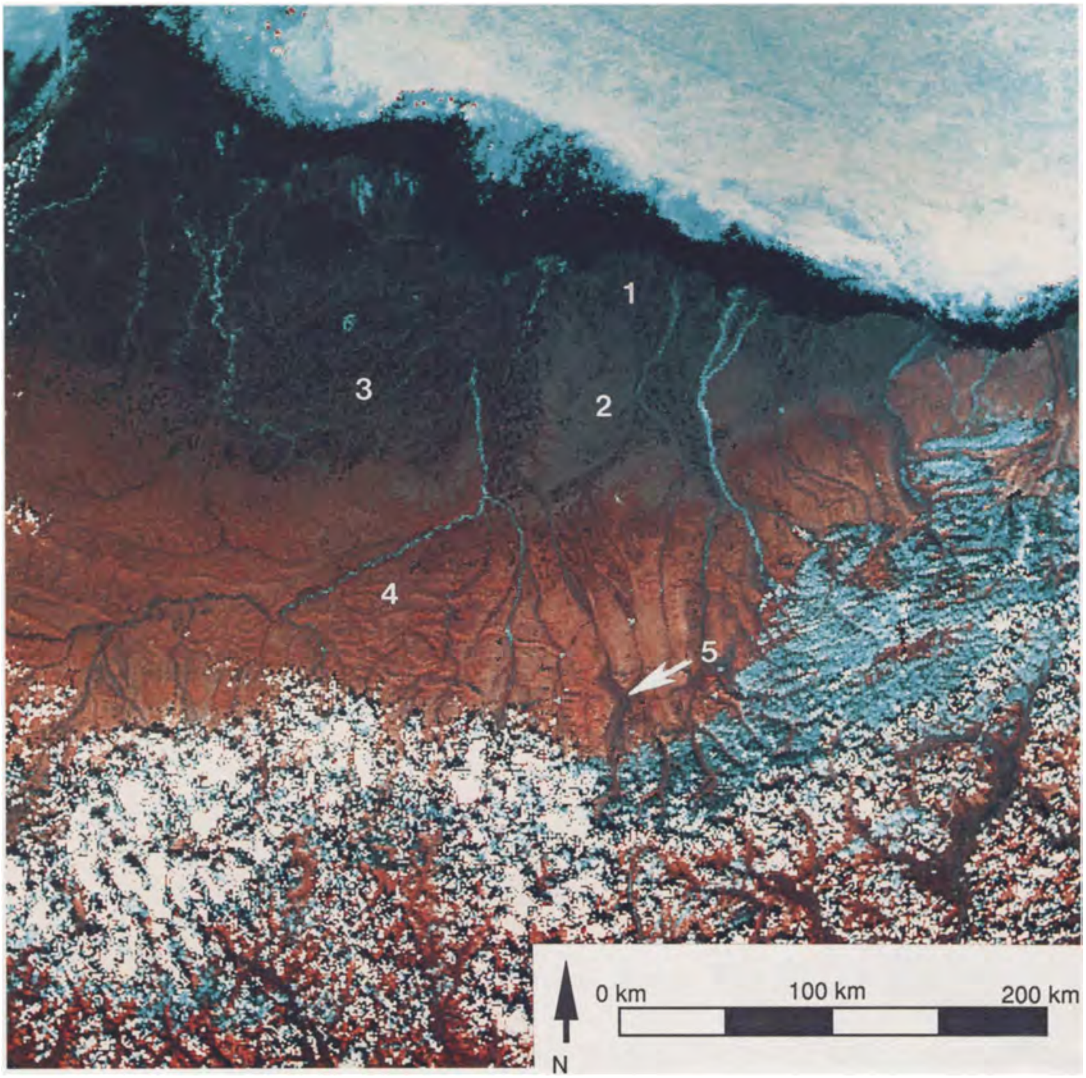


Plate 1. False color AVHRR image of northern Alaska showing (1) wet minerotrophic tundra associated with loess and riparian habitats on the coastal plain, (2) moist minerotrophic tundra associated with loess deposits in the northern foothills, (3) wet acidic tundra associated with a stabilized sand sea (Carter 1981), (4) moist acidic tundra on old glaciated surfaces in the Arctic Foothills, (5) minerotrophic tundra associated with Itkillik-age (late Pleistocene) glacial and glaciofluvial surfaces near Toolik Lake. (Image courtesy of William Acevedo, United States Geological Survey, and NASA.)

the major river systems. These areas provide an excellent example of the effects of substrate on tundra ecosystems. We also emphasize the role of loess as a chronic natural disturbance factor.

Extent of loess ecosystems in northern Alaska

The extent of minerotrophic ecosystems on the North Slope has been delineated on color satellite-derived images from the Advanced Very High Resolution Radiometer (AVHRR-2) aboard the NOAA-7 satellite (Plate 1). Minerotrophic tundra has a distinctly lighter spectral signature in the visible band (0.55–0.68 μm) compared to wet acidic tundra, and a darker spectral signature in the near-infrared (near-IR) band (0.72–1.1 μm) when compared to moist acidic tundra (Walker and Acevedo 1987). The causes of the spectral differences between the two tundra types have not been fully investigated, but the different vegetation canopies in acidic and minerotrophic regions is a likely contributing factor. Acidic areas have an abundance of deciduous shrubs, such as *Betula nana* and *Salix planifolia* ssp. *pulchra,* which have high reflectivity in the near infrared band. The red tones in Plate 1 are due primarily to the high near-IR reflectivity of deciduous shrub species in acidic tundra regions. Deciduous shrubs are relatively less abundant in the minerotrophic tundra areas. The minerotrophic areas also have generally more open plant canopies and relatively higher amounts of erect dead sedge material, which reduce their reflectance in the near-IR band.

Based on these spectral differences and information from extensive mapping surveys in 1982–1985 (Walker et al. 1982, Walker and Acevedo 1987), ≈14% (11 000 km^2) of the coastal plain is dominated by wet minerotrophic tundra similar to that at Prudhoe Bay. The principal minerotrophic region lies between the Canning and Itkillik rivers, and most of the modern loess comes from the Sagavanirktok and Canning rivers. West of the Colville River, the tundra is predominantly acidic in association with ancient dune deposits (Black 1951, Everett 1980*d*) and marine silts and clays (Tedrow 1977, Gersper et al. 1980, Komárková and Webber 1980) (Fig. 1).

The effects of loess also extend into the northern front of the Arctic Foothills, where minerotrophic plant associations are common on upland surfaces up to ≈100 m above the floodplains of the major rivers. These areas have abundant *Dryas integrifolia, Drepanocladus* spp., *Tomenthypnum nitens,* and other minerotrophic taxa, and like minerotrophic areas on the coastal plain, are clearly discernible on color-infrared photographs and satellite imagery (Plate 1). Much of the lower elevations along the northern front of the foothills is blanketed by silt up to 30 m thick (Carter 1988). This silt was previously interpreted as having a fluvial or marine origin (O'Sullivan 1961), but has recently been recognized as loess that accumulated during middle and late Wisconsin time (Williams et al. 1978, Lawson 1983, 1986, Carter 1988). Radiocarbon and thermoluminescence dates from the base of loess deposits at three exposures described by Carter (1988) range between 28 600 and 35 300 yr BP, which is coincident with extensive dune and sand-wedge formation on the coastal plain (Carter 1981, 1983). The loess blanketed areas downwind of a large Pleistocene sand sea west of the Colville River (Black 1951, Carter 1981), and is particularly thick in the central and western portion of the northern foothills. Minerotrophic tundra occurs on much of this loess surface and similar areas near the Sagavanirktok and Canning rivers (Walker and Acevedo 1987). The Arctic National Wildlife Refuge in the northeast corner of Alaska has minerotrophic tundra on gently rolling surfaces primarily in association with outwash and old loess deposits (Carter et al. 1986), but modern loess does not appear to be a major factor in this region (Walker et al. 1982). Alkaline vegetation also occurs in association with the extensive limestone deposits of the Brooks Range. Minerotrophic tundra similar in many respects to that at Prudhoe Bay has also been described from the limestone-rich High Arctic IBP site on Devon Island (Muc 1977, Muc and Bliss 1977) and from Maria Pronchitsheva Bay, USSR (Matveyeva et al. 1975), but to our knowledge, descriptions of loess-influenced tundra and comparisons with acidic tundras have not been made. The following discussion focuses on the coastal plain, particularly the Prudhoe Bay region, from which we have the most ecological information.

Description of the Prudhoe Bay loess gradient

The Prudhoe Bay region is a good area to study the effects of loess because of its proximity to the Sagavanirktok River, a major loess source, and to nearby acidic tundra areas that are relatively uninfluenced by loess. Research in the Prudhoe Bay region was initiated in the early 1970s (Brown 1975, Walker et al. 1980, 1987*b*). The first botanists to visit the region were impressed by the differences in the floras of Prudhoe Bay and the other intensively studied areas on the northern coast of Alaska at Barrow and Cape Thompson. For example, Murray (1978) noted that, despite the broad similarities between the physiognomy of the terrain and the vegetation at all sites along the northern Alaskan coast, only 88 of the 172 vascular taxa then known at Prudhoe Bay were also found at Barrow. Most of the differences were attributed to the many calciphilous taxa at Prudhoe Bay and their scarcity at Barrow (Rastorfer et al. 1973, Neiland and Hok 1975, Webber and Walker 1975, Murray 1978, Steere 1978, Walker and Webber 1979).

The first mention of calcareous soils in the vicinity of the Sagavanirktok River was by Douglas and Tedrow (1960), who described soil profiles that were consistently alkaline in all horizons in the vicinity of Franklin Bluffs and the White Hills. Bilgin (1975) analyzed numerous soils in the Prudhoe Bay region and found strong correlations between soil characteristics within watersheds and nutrient concentrations in surface waters. He reported high pH values throughout the region and attributed these to calcareous loess. Everett and Parkinson (Everett 1975, Everett and Parkinson 1977, Parkinson 1978) described soil changes related to the loess gradient in the Prudhoe Bay region, showing an inverse linear relationship between $CaCO_3$ equivalence and the percentage of organic carbon. The high electrical conductivity of local surface water was also linked to the high-pH, calcium-rich soils (Bilgin 1975, Douglas and Bilgin 1975).

The large, braided gravel-bottomed rivers in the region are indirectly responsible for its soils and distinctive flora. The Sagavanirktok River, which discharges into Prudhoe Bay, has numerous tributaries that either originate in or pass through limestone deposits of the Lisburne Group in the Brooks Range (Keller et al. 1961). Calcareous silt of glacial origin is transported downstream along most of the major rivers in the central and eastern portion of the coastal plain. Most of the rivers in northeastern Alaska are heavily braided and provide wide source areas for the loess. The gravelly alluvium of the river floodplains contains large fractions of fine sand and silt. For example, the <2-mm fraction of a Sagavanirktok River alluvium profile at Prudhoe Bay contained 10–66% silt (Parkinson 1978). During high-water periods silt is deposited on all inundated surfaces. The finer particles (mainly <50 μm) are picked up and suspended by strong, predominantly

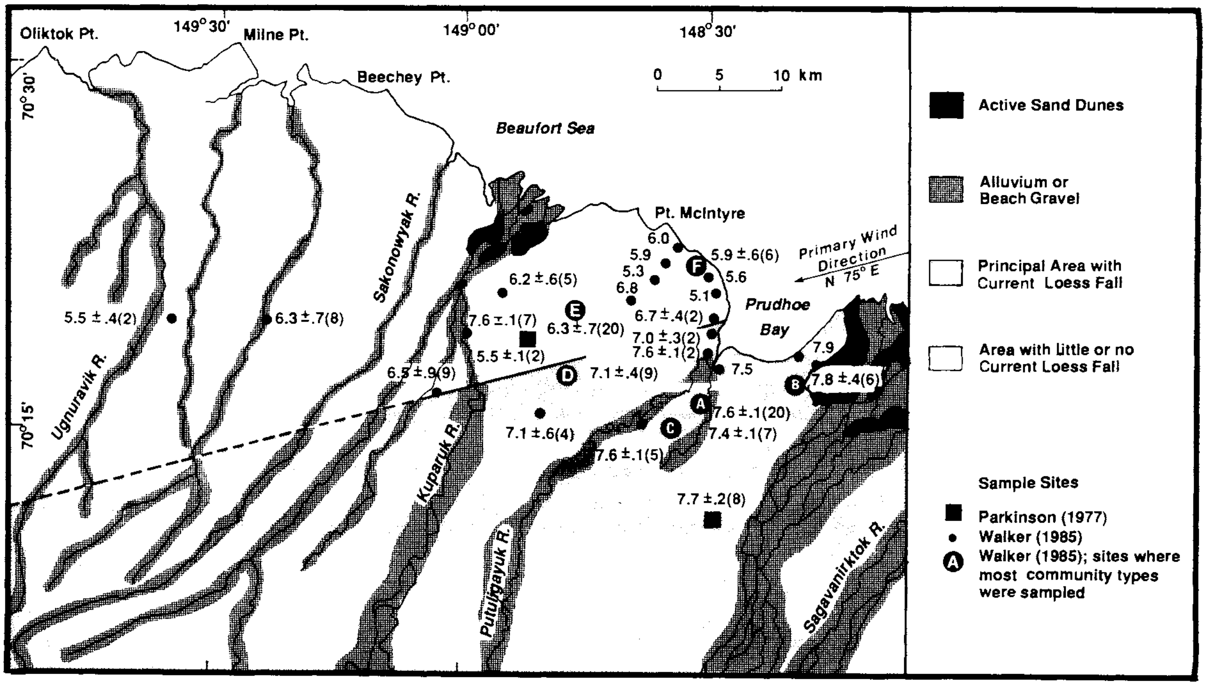


FIG. 2. Soil pH values at study sites in the Prudhoe Bay region (mean ± SE [number of samples]). Loess deposits are concentrated south of the line drawn S75° W from the delta of the Sagavanirktok River. Shaded areas south of this line and east of the Kuparuk have alkaline soils. West of the Kuparuk River wet areas tend to be acidic, but pH values are still considerably higher than north of the loess line. Wet areas north of the shaded area are consistently acidic throughout the region, with the exception of dunes, pingos, frost scars, beach sand, and river alluvium where the underlying alkaline mineral substrate is at the surface. Point (A) is the site of the photo in Fig. 4. Points A–F are the main study sites of Walker (1985) and provide the data for the Figs. 8, 9, 10, and 11. Data in Fig. 10 are from sites A–D (alkaline sites only). Soil pH values determined with a soil : water ratio of 1:2.5. (Modified from Walker 1985.)

east-northeasterly, winds. Mean annual wind velocity at Prudhoe Bay from June 1974 to June 1975 was 22 km/h (Gamara and Nunes 1976). A secondary wind direction from the west-southwest is primarily associated with storm events. The particles are transported considerable distance. Much of the silt-sized fraction (2 to 50 μm) is deposited as loess; whereas much of the clay-sized fraction (<2 μm) becomes part of the atmospheric dust load and may remain suspended for days or weeks and be transported globally (Pye 1987). The fine-sand-sized particles (0.05–2 mm) are moved much shorter distances and deposited as dunes, such as those in the deltas of the Sagavanirktok and Canning rivers (see below, Fig. 6). The amount of loess decreases downwind from the rivers, forming a loess gradient to the west-southwest of the rivers.

An area of acidic tundra north of the loess region at Prudhoe Bay (Fig. 2) provides an interesting contrast to the alkaline tundra because it has essentially the same climate and topography as the alkaline tundra region, but has a much reduced input of calcareous loess. This area is not downwind from the major loess source in the Sagavanirktok River delta, but instead is subject to winds directly from the Beaufort Sea.

Loess deposits in the Prudhoe Bay region between the Sagavanirktok and Kuparuk rivers are generally <2 m deep, thinning toward the west (Everett 1980*a*). They occur over gravels of late-Pleistocene-age glacial outwash and floodplain deposits that formed during high glacial discharge accompanying deglaciation in the central Brooks Range (Rawlinson 1983, *in press*). Hamilton (1986) dates deglaciation of the upper valleys in the Brooks Range at ≈11 800 yr BP. The loess is overlain by silt-rich peat. Minimum dates from the base of the peat deposits between the Sagavanirktok and Kuparuk rivers range from 1200 to 4700 yr BP (Everett 1980*b*, Walker et al. 1981), which implies that the modern peaty thaw-lake landscape of the Prudhoe Bay region is a relatively recent phenomenon associated with the eastward migration of the Sagavanirktok River channel during the Holocene. Peat has been forming for much longer periods in other areas of the coastal plain. Minimum basal peat dates of 6500 to 12 600 yr BP (Walker et al. 1981, Schell and Ziemann 1983) are associated with older surfaces both west of the Kuparuk River and east of the Sagavanirktok River. In these regions, the silt-rich peat overlies thin 1–3 m thick eolian sand deposits (Rawlinson, *in press*).

ALKALINE TUNDRA TOPOSEQUENCE

The following paragraphs describe a conceptual alkaline toposequence (Fig. 3) for Prudhoe Bay encom-

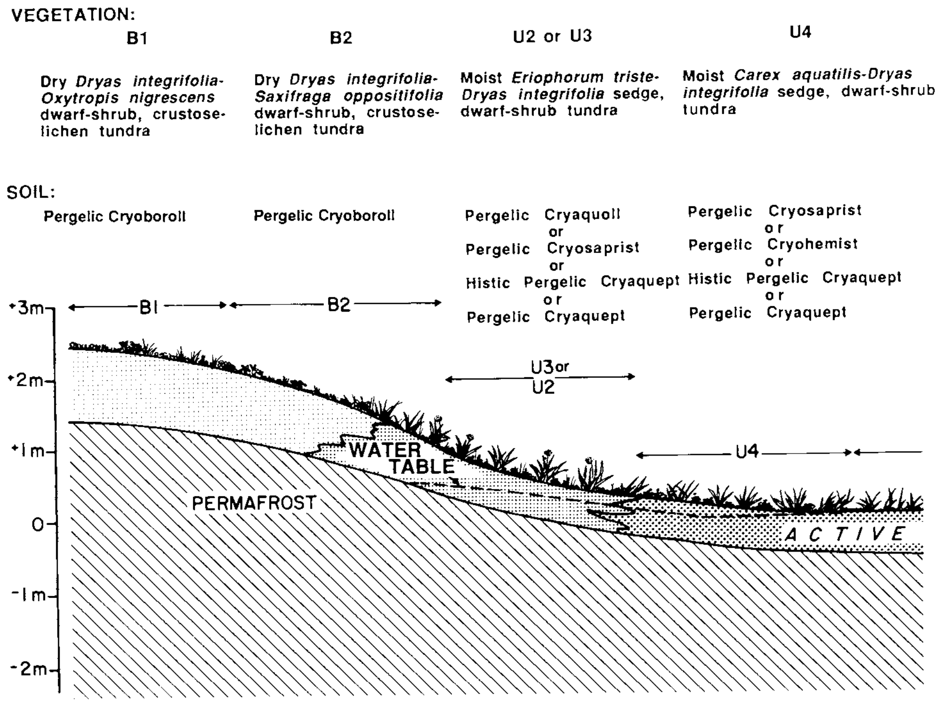


FIG. 3. Idealized Prudhoe Bay alkaline tundra toposequence. The shaded patterns in the active layer (zone of summer thaw) represent degree of organic matter decomposition with less decomposed darker soils in the wetter sites. (Modified from Walker 1985.)

passing eight common vegetation stand types. These are grouped according to moisture characteristics into dry, moist, wet, and aquatic tundra (see *Vegetation descriptions,* below). These units were used for vegetation mapping in the Prudhoe Bay region (Walker et al. 1980, 1986, 1987*b*). Data for the toposequence come from sites throughout the Prudhoe Bay region and thus do not represent a specific slope.

Methods

The vegetation and soils were sampled during 1974 and 1975. Sample sites were chosen subjectively (Mueller-Dombois and Ellenberg 1974) in homogeneous areas representative of mapped vegetation units (Walker et al. 1980). Ninety-one permanent plots were sampled, 30 of which occurred in the vegetation types along the conceptual toposequence described here. Of these 30, all except six were 10-m^2 plots (1 × 10 m). The other six were 1 m^2. Plant species nomenclature followed Hultén (1968) and Murray and Murray (1978) for vascular plants, Hale and Culberson (1975) for lichens, and Crum et al. (1973) for bryophytes. No attempt was made to determine optimum plot size, but for most vegetation types, the 1-m^2 plots undersample the total species diversity. (Compare the total species frequency in plots 1307, 1513, 1514, 1515, 1517, and 1518 with the 24 1 × 10 m plots in Table 1.) For future classification studies, larger homogeneous plots of at least 10 m^2 are recommended following the criteria of Westhoff and van der Maarel (1973). Percentage cover of species was visually estimated and later converted to Braun-Blanquet cover-abundance classes (Table 1). The descriptions below are based on a sorted table analysis (Table 1) that uses the Braun-Blanquet approach to identify groups of differentiating species for each unit (Braun-Blanquet 1932, Westhoff and van der Maarel 1973).

The units in Table 1 are arranged hierarchically; groups of species with broadest distribution from dry to wet areas are shown at the top of the table, with groups of species with progressively narrower distributions shown in blocks below. The stand types correspond approximately to associations or subassociations in the Braun-Blanquet system, but formal syntaxonomic designation should await more extensive phytosociological studies on the North Slope.

Soils were collected from 10-cm depth (root zone). Two 300-cm^3 cans of soil were removed from each plot for bulk density, and physical and chemical analyses. Soils were analyzed according to standard procedures described in Page et al. (1982) and Klute (1986). Specific methods are presented in the tables where the data appear. Depth of thaw was sampled 10 times at each plot using a ruled steel probe.

Vegetation descriptions

Toposequences associated with hillslopes, such as that portrayed in Fig. 3, are uncommon on the flat

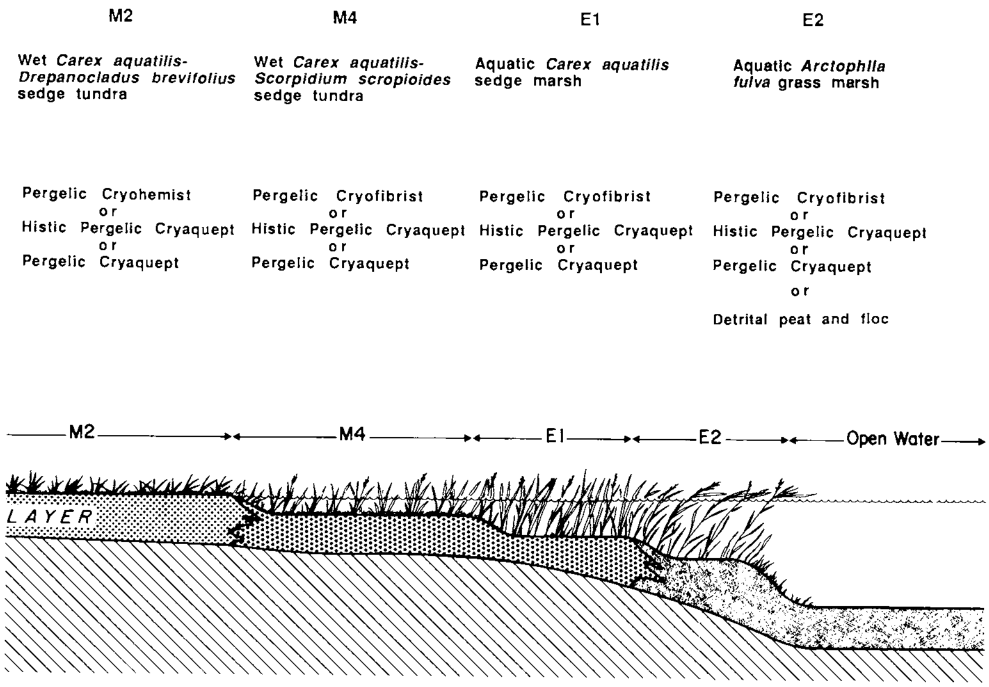


FIG. 3. Continued.

coastal plain except in association with pingos (large ice-cored mounds). Much more common are the patterns associated with ice-wedge polygons and small tundra streams (Figs. 4 and 5). Vegetation and soils are strongly controlled by microscale topographic variations produced under the periglacial climate. The vegetation and, to a substantial degree, the soils are highly predictable based on the microtopographic position. The same sequence of vegetation that occurs along hillslopes with several metres of relief can be found in association with ice-wedge polygons with only a few centimetres of relief. Patterned ground creates a mosaic of vegetation with only a few main plant community types repeating in small-scale patterns. For example, in networks of ice-wedge polygons, relatively elevated sites with moist or dry vegetation occur in association with polygon rims, peat hummocks, and high polygon centers; relatively low microsites, with wet or aquatic vegetation, are found in polygon basins, troughs, and interhummock areas. These patterns were recognized by Wiggins (1951) in the acidic tundra at Barrow and are portrayed here for the alkaline situation at Prudhoe Bay (Fig. 5). Complete phytosociological information for the plant-community types not mentioned here can be found in Walker (1985).

Dry tundra.—Dry sites occur on stabilized dunes, pingos, and some well-drained, stable, river-terrace elements. These sites commonly have mineral soils, the best developed of which are Pergelic Cryoborolls (Everett 1980*c*; soil nomenclature follows the United States Soil Taxonomy, Soil Survey Staff 1975). The soils thaw deeply (>1 m) during the summer and are rarely, if ever, saturated at 30 cm depth. Typically they have a mollic (dark-colored, organic-rich, base saturation >50%) surface horizon. Most soils have pedogenic carbonates in the A horizon. Pendant-shaped calcium carbonate accumulations (Forman and Miller 1984) are common on the underside of gravels and cobbles at the soil surface; these are attributed to eolian input from the Sagavanirktok River and to the dry climate (Everett and Parkinson 1977, Everett 1980*c*). Similar carbonate accumulations occur on the underside of the larger gravel fragments at greater depths. Thick silt coatings are common on the upper surfaces of the gravel and cobbles in the profiles and are caused by the seasonal downward transfer of the silt fraction by meltwater (Everett 1980*c*, Locke 1986).

The vegetation on the driest, snow-free sites, such as the gravelly north- and east-facing slopes of pingos and some river terraces, is usually *Dryas integrifolia–Oxytropis nigrescens* dwarf-shrub, crustose-lichen tundra (Walker 1985, Stand Type B1). This type is characterized by a discontinuous mat of prostrate shrubs and cushion plants (*Dryas integrifolia, Saxifraga oppositifolia, Oxytropis nigrescens*) with a few sedges (mainly *Carex rupestris*) and erect dicotyledons (e.g., *Draba alpina, Chrysanthemum integrifolium, Papaver lapponicum, Lesquerella arctica, Pedicularis lanata,* and *P. capitata*). Slightly moister sites with more evidence of cryoturbation, such as the centers of high-centered polygons, have *Dryas integrifolia–Saxifraga oppositifolia* dwarf-shrub, crustose-lichen tundra (Stand Type

TABLE 1. Sorted table of vegetation types occurring along the alkaline soil moisture gradient. Estimated cover follows the Braun-Blanquet cover-abundance scale: 5 = >75% cover, 4 = 50–75%, 3 = 25–50%, 2 = 5–25%, 1 = many with <5%, + = few, with small cover, r = single occurrence. Data are from homogenous areas of tundra varying from 1 to 10 m² (from Walker 1985). A single dot indicates that taxon was not observed in that plot.

Tundra type	Dry alkaline tundra								Moist alkaline tundra										Wet alkaline tundra									Aquatic tundra			
Stand type no.*	B1				B2				U3				U4						M2						M4			E1	E2		
Plot no.	1411	010B	1520	1001	1401	1505	010A	1513	1504	020B	1510	1515	030B	0303	030A	1512	1519	1514	1511	1516	1501	040A	040B	1503	050A	050B	1517	1518	060A	1307	FREQ
Site information																															
Plot size (m)	1×10	1×10	1×10	1×10	1×10	1×10	1×10	1×1	1×10	1×10	1×10	1×1	1×10	1×10	1×10	1×10	1×10	1×1	1×10	1×10	1×10	1×10	1×10	1×10	1×10	1×10	1×1	1×1	1×10	1×1	
Landform†	PGOS	PGOS	PGOS	PGOS	HCPL	HCPL	HCPL	HCPL	FLAT	FLAT	PLRM	PLRM	PLBS	PLRM	PLRM	PLBS	FLAT	DRLK	PLBS	PLBS	DRLK	DRLK	PLBS	LKMR	PLBS	PLBS	FLHM	POND	POND	POND	
pH‡	7.5	7.6	7.8	7.6	7.3	7.8	7.5	7.7	7.6	7.4	7.4	7.6	6.9	7.4	7.4	7.5	7.5	7.7	7.6	7.6	7.4	7.4	7.0	7.5	7.4	7.1	7.6	7.6	7.6	7.4	
Soil moisture (% dry mass, August 1977)	5	46	19	31	19	48	19	34	63	81	34	70	104	172	135	89	116	53	122	136	171	274	198	207	402	417	109	178	—	86	
Thaw depth (cm, 20 August 1977)	82	59	54	37	33	46	44	38	34	37	23	31	29	42	38	29	31	29	40	32	35	31	36	31	30	34	36	33	42	31	
Water depth (cm, August 1977)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	6	3	14	23	10	
Rock cover (%)	20	0	20	5	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Soil cover (%)	12	5	15	17	2	8	9	15	0	0	1	0	1	1	0	0	1	0	13	0	0	0	19	5	11	33	5	40	25	60	
Snow regime (scalar 1–5)§	1	1	1	4	2	2	2	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	
Moisture regime (scalar 1–5)‖	1	1	1	1	1	1	1	1	2	2	2	2	3	3	3	3	3	3	4	4	4	4	4	4	4	4	5	5	5	5	
Taxa occurring in dry to wet alkaline tundra																															
Distichium capillaceum¶	1	1	.	r	1	r	1	.	2	2	1	1	2	2	2	1	2	1	+	2	1	2	r	1	.	.	.	.	.	.	22
Dryas integrifolia ssp. *integrifolia*	3	4	3	3	3	4	3	5	4	2	3	4	2	.	2	2	.	3	r	r	.	r	.	r	.	.	.	.	.	.	20
Saxifraga oppositifolia	1	1	1	1	1	2	2	1	1	r	1	1	.	.	.	r	+	r	.	r	r	.	.	r	.	.	.	.	.	.	18
Salix reticulata ssp. *reticulata*	1	.	r	.	1	.	1	.	r	+	r	.	r	.	2	+	1	2	r	r	r	r	.	.	.	.	.	.	.	.	16
Polygonum viviparum	r	r	.	.	r	r	+	.	r	.	.	.	+	.	r	r	.	r	r	r	r	r	.	r	.	.	.	.	.	.	15
Encalypta alpina	r	.	.	.	+	r	1	.	r	1	r	.	r	1	.	+	.	.	r	r	r	r	.	.	.	.	.	.	.	.	14
Carex membranacea	.	r	.	.	+	.	r	.	1	2	2	2	r	.	.	2	2	.	1	r	.	.	.	1	.	.	.	.	.	.	13
Carex misandra	.	r	.	.	.	.	r	.	.	r	.	.	+	1	.	.	r	.	r	r	.	.	.	r	.	.	.	.	.	.	9
Taxa occurring in dry to moist alkaline tundra																															
Ditrichum flexicaule	r	1	r	1	+	1	2	1	3	3	2	2	1	1	1	2	3	2	.	r	.	.	.	r	.	.	.	.	.	.	20
Thamnolia vermicularis s.l.	1	1	1	1	1	1	1	1	2	2	1	2	r	.	.	r	1	1	.	.	.	.	.	r	.	.	.	.	.	.	17
Tomenthypnum nitens	.	1	.	1	1	r	1	.	2	3	3	3	2	2	3	1	2	1	.	.	r	1	.	.	.	.	.	.	.	.	17
Dactylina arctica	r	r	r	r	r	r	+	.	r	r	r	1	.	r	r	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	15
Cetraria islandica	r	+	r	+	1	+	1	.	+	1	1	1	r	1	.	r	.	.	.	.	.	.	.	r	.	.	.	.	.	.	15
Lecanora epibryon	1	2	2	1	1	2	2	2	r	r	r	r	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	14
Pedicularis kanei ssp. *kanei*	.	r	r	r	r	r	r	.	r	r	+	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11
Salix rotundifolia	r	.	r	.	2	r	r	r	r	.	.	r	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	9
Cratoneuron arcticum	.	r	.	.	r	r	.	.	r	r	r	.	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Peltigera canina s.l.	.	r	r	.	r	.	r	.	.	r	.	r	.	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Hypnum procerrimum	r	r	.	1	.	r	.	1	.	.	.	1	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Chrysanthemum integrifolium	.	r	.	.	.	r	+	.	r	r	r	r	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Senecio atropurpureus ssp. *frigidus*	.	.	.	.	r	.	r	.	+	+	r	r	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	7
Drepanocladus uncinatus	r	.	r	1	.	r	1	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	7
Plagiochila arctica	.	r	.	.	.	.	.	r	r	r	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Peltigera aphthosa	.	.	.	.	r	.	r	.	.	.	+	.	.	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Carex scirpoidea	.	1	.	.	.	r	.	.	r	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Didymodon asperifolius	.	.	.	.	.	r	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Cetraria cucullata	r	1	r	+	1	r	r	1	r	1	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
Papaver macounii	.	r	.	r	r	r	r	r	+	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9
Draba alpina	.	r	r	r	r	r	r	.	r	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9
Cetraria nivalis	+	+	r	1	+	r	r	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Minuartia arctica	.	r	.	r	.	1	1	r	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
Cetraria richardsonii	.	r	.	.	r	+	r	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
Pedicularis capitata	r	r	.	.	.	r	1	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
Cassiope tetragona ssp. *tetragona*	.	.	.	1	r	.	r	.	r	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Rhytidium rugosum	r	+	.	r	.	r	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5

TABLE 1. Continued.

Tundra type	Dry alkaline tundra								Moist alkaline tundra										Wet alkaline tundra									Aquatic tundra			
Stand type no.*	B1				B2				U3				U4						M2						M4			E1	E2		
Plot no.	1411	010B	1520	1001	1401	1505	010A	1513	1504	020B	1510	1515	030B	0303	030A	1512	1519	1514	1511	1516	1501	040A	040B	1503	050A	050B	1517	1518	060A	1307	FREQ
Cladonia pocillum	.	.	.	r	r	.	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Cardamine digitata	.	.	.	.	r	.	r	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Tetraplodon mnioides	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Bryum stenotrichum	.	.	.	.	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Parrya nudicaulis ssp. *nudicaulis*	.	.	.	.	.	r	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Taxa occurring in dry alkaline tundra																															
Thuidium abietinum	r	r	1	r	r	1	r	r	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
Lopadium fecundum	1	1	2	1	1	1	1	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Alectoria nigricans	r	r	.	r	+	r	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
Carex rupestris	1	1	.	2	+	2	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
Evernia perfragilis	r	1	r	.	r	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Hypogymnia subobscura	r	1	r	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Astragalus umbellatus	1	1	.	+	.	+	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Stereocaulon alpinum	r	r	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Lecidea vernalis	r	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Lloydia serotina	.	r	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Pertusaria coriacea	1	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Cornicularia divergens	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Saussurea angustifolia	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Ochrolechia frigida f. *thelephoroides*	r	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Stand type B1, *Dryas integrifolia–Oxytropis nigrescens*																															
Oxytropis nigriscens ssp. *bryophila*	1	1	2	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Xanthoria elegans	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Taxa occurring in moist to aquatic alkaline tundra																															
Carex aquatilis s.l.	.	.	.	.	.	.	.	.	.	.	r	.	2	2	3	1	.	.	2	2	2	3	2	2	3	2	4	2	1	.	16
Eriophorum angustifolium	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	.	2	2	1	1	2	1	2	+	1	1	.	.	13
Taxa occurring in moist to wet alkaline tundra																															
Salix arctica	.	.	.	.	r	.	r	.	1	1	1	1	1	.	2	1	r	r	+	r	r	r	r	+	.	.	.	.	.	.	17
Drepanocladus brevifolius	.	.	.	.	r	.	.	.	1	.	1	.	2	2	2	2	.	2	2	4	3	3	2	3	.	.	.	.	.	.	14
Campylium stellatum	.	.	.	.	.	.	r	.	1	r	+	.	2	2	2	1	1	.	r	r	r	1	.	1	.	.	.	.	.	.	14
Catoscopium nigritum	.	.	.	.	.	.	.	.	1	r	r	.	1	1	r	2	r	r	r	+	r	2	.	1	.	.	.	.	.	.	14
Equisetum variegatum	.	r	.	.	.	.	.	.	r	r	.	r	r	.	1	r	.	1	r	1	r	1	r	+	.	.	.	.	.	.	14
Orthothecium chryseum	.	.	.	.	.	.	.	.	r	+	1	.	+	2	1	2	2	.	.	r	r	2	.	1	.	.	.	.	.	.	12
Calliergon richardsonii	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	1	r	1	.	1	1	1	1	1	.	.	.	.	.	.	10
Meesia uliginosa	.	.	.	.	.	.	.	.	r	r	+	r	1	.	.	r	r	.	.	r	.	1	.	+	.	.	.	.	.	.	10
Aneura pinguis	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	r	1	.	r	+	.	.	.	r	.	.	.	.	.	.	7
Salix lanata ssp. *richardsonii*	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	r	r	.	.	r	.	r	.	r	.	.	.	.	.	.	7
Salix ovalifolia	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	1	.	r	r	r	.	r	.	.	.	.	.	.	6
Cinclidium arcticum	.	.	.	.	.	.	.	.	.	.	r	.	.	1	1	.	.	.	.	.	r	2	r	.	.	.	.	.	.	.	6
Carex marina	.	.	.	.	.	.	.	.	.	.	.	.	r	+	.	.	1	.	.	.	r	.	r	1	.	.	.	.	.	.	6
Saxifraga hirculus var. *propinqua*	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	.	.	.	r	.	.	r	r	.	.	.	.	.	.	5
Scorpidium turgescens	.	.	.	.	.	.	.	.	.	r	.	.	.	.	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	3
Taxa occurring in moist alkaline tundra																															
Eriophorum triste	.	r	.	.	.	r	r	.	2	1	2	2	2	2	1	2	2	3	.	.	.	.	.	.	.	.	.	.	.	.	13
Hypnum bambergeri	.	.	.	.	r	.	.	r	2	2	1	1	.	.	1	+	2	.	.	.	.	.	.	.	.	.	.	.	.	.	9
Carex bigelowii	.	.	.	.	.	.	.	.	2	2	1	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Arctagrostis latifolia s.l.	.	r	.	.	.	.	.	.	r	r	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Timmia austriaca	.	.	.	.	r	.	.	.	r	.	.	.	r	r	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	5
Tortella arctica	.	.	.	.	.	.	1	.	.	r	.	.	r	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Blepharostoma trichophyllum ssp. *brevirete*	.	.	.	.	.	r	.	.	r	.	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Aulacomnium turgidum	.	.	.	.	1	.	.	.	.	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3

TABLE 1. Continued.

Tundra type	Dry alkaline tundra								Moist alkaline tundra										Wet alkaline tundra									Aquatic tundra			
Stand type no.*	B1				B2				U3				U4						M2						M4			E1	E2		
Plot no.	1411	010B	1520	1001	1401	1505	010A	1513	1504	020B	1510	1515	030B	0303	030A	1512	1519	1514	1511	1516	1501	040A	040B	1503	050A	050B	1517	1518	060A	1307	FREQ
Cirriphyllum cirrosum	.	.	.	.	.	.	.	.	+	r	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Drepanocladus revolvens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Taxa occurring in wet alkaline tundra																															
Nostoc commune	.	.	.	.	.	.	.	.	.	r	.	.	r	.	.	.	r	.	r	2	2	r	r	1	1	1	.	.	.	.	11
Scorpidium scorpioides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	3	1	2	3	4	.	.	.	6
Stand type M2, *Carex aquatilis–Drepanocladus brevifolius*																															
Cinclidium latifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	r	.	1	2	2	r	r	2	.	.	.	.	.	.	9
Eriophorum russeolum	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	r	.	r	r	1	.	.	+	.	1	.	.	7
Dupontia fisheri s.l.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	r	r	r	+	.	r	.	.	.	.	.	.	6
Carex atrofusca	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	r	1	.	r	r	1	.	.	.	.	.	.	6
Carex saxatilis ssp. *laxa*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	r	1	1	1	.	.	.	.	.	5
Meesia triquetra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	2	2	.	.	2	.	.	r	.	.	.	6
Juncus biglumis	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	r	r	.	r	.	r	.	.	.	.	.	.	5
Carex rotundata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	r	.	+	.	.	.	.	.	.	.	3
Carex rariflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	1	.	2
Stand type E2, *Arctophila fulva*																															
Arctophila fulva	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	2	2
Incompletely identified taxa																															
Bryum sp.	.	r	r	r	+	r	r	.	r	r	r	.	r	1	1	r	.	.	r	+	1	r	r	1	.	.	.	.	.	.	19
Calliergon sp.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	r	.	.	.	3
Caloplaca sp.	r	r	.	r	r	r	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
Encalypta sp.	.	.	.	r	.	.	+	.	.	.	.	.	.	.	.	r	1	r	.	.	.	.	r	.	.	.	.	.	.	.	6
Hypnum sp.	.	.	.	.	r	.	.	.	.	1	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Pertusaria sp.	.	.	r	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Solorina sp.	r	.	.	r	r	.	.	.	r	r	.	.	.	r	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Unknown crustose lichen	1	1	1	r	1	+	2	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9
Unknown dicot	.	.	.	.	r	r	.	.	r	r	.	.	r	.	.	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	7
Unknown fruticose lichen	.	r	.	r	r	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Unknown leafy liverworts	r	.	.	.	.	.	r	r	r	.	.	.	.	.	.	.	1	.	.	.	r	.	.	.	.	.	.	.	.	.	6
Unknown monocot	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Unknown moss	r	r	r	r	r	r	1	.	1	r	r	.	1	r	.	1	r	1	+	1	.	.	.	r	.	.	.	.	.	.	18
Total Species Frequency	38	48	30	34	62	45	52	19	51	53	41	24	35	31	30	38	38	22	28	31	30	28	21	34	5	5	5	3	3	1	0

Single occurrences (species name [plot no., cover-abundance value]):

Alopecurus alpinus (010A, r), *Artemisia arctica* ssp. *arctica* (1401, 1), *Bryum algovicum* (030A, r), *Braya purpurascens* (010B, r), *Calypogeia muelleriana* (030B, r), *Carex vaginata* (040B, r), *Cetraria tilesii* (1411, r), *Cinclidium* sp. (1514, r), *Cladonia* sp. (010B, r), *Dicranum* sp. (1505, 1), *Eriophorum vaginatum* (1504, r), *Fulgensia bracteata* (1520, r), *Harpanthus flotowianus* (030A, r), *Hypnum cupressiforme* (1520, 1), *Kobresia myosuroides* (1505, r), *Leptobryum pyriforme* (1401, r), *Leptogium sinnuatum* (020B, r), *Lesquerella arctica* (010A, r), *Luzula arctica* (1401, r), *Mnium blyttii* (0303, r), *Myurella julacea* (030A, r), *Papaver lapponicum* ssp. *occidentale* (1401, r), *Peltigera sorediata* (010A, 1), *Philonotis fontana* var. *pumila* (1401, r), *Poa arctica* (1401, 1), *Pohlia* sp. (1401, r), *Polytrichastrum alpinum* (1401, 1), *Radula prolifera* (1504, r), *Silene acaulis* (1401, r), *Melandrium apetalum* ssp. *arcticum* (1503, r), *Stellaria laeta* (010B, r), *Timmia megapolitana* var. *bavarica* (040A, r), *Voitia hyperborea* (0303, r)

* Code follows Walker (1985).
† Landforms: PGOS = side of pingo (large ice-cored mound), HCPL = top of high-centered polygon, FLAT = flat upland, PLRM = polygon rim, PLBS = polygon basin, DRLK = drained thaw lake; LKMR = lake or pond margin, FLHM = flat with aligned hummocks, POND = pond or lake.
‡ Soil : water ratio 1:2.5 by volume.
§ Snow regime: (1) Snow free most of winter, some snow may persist after storms but is blown free soon afterwards. (2) Snow free during spring melt. (3) Averge snow-cover. (4) Snow persists 1–2 weeks following main snowmelt. (5) Deep late melting snow.
‖ Site moisture regime: (1) xeric to subxeric; (2) subxeric to mesic; (3) mesic to subhygric; (4) subhygric to hygric; (5) hygric to aquatic.
¶ Taxonomic nomenclature according to Murray and Murray (1978) and Hultén (1968) for vascular plants, Hale and Culberson (1975) for lichens, Crum et al. (1973) for mosses, and Steere and Inoue (1978) for hepatics.

B2). These sites are richer in sedges (mainly *Eriophorum triste* and *Carex bigelowii*) and forbs adapted to soil movement by frost action, such as *Chrysanthemum integrifolium* and *Saxifraga oppositifolia*. A high percentage of the soil lacks vegetation or is covered with crustose lichens, including *Lecanora epibryon* and *Ochrolechia frigida*. Often there is a fine pattern of small, nonsorted, 20–50 cm diameter polygons that is apparently caused by a combination of frost activity and desiccation. The depressions between these small polygons are generally 5–15 cm deep and contain a rich assortment of mosses and lichens, including *Thamnolia subuliformis, Cetraria cucullata, C. islandica, Peltigera canina, Bryum* spp., *Encalypta alpina, E. procera,* and *Drepanocladus uncinatus*.

Moist tundra.—Typical moist tundra microsites are polygon rims, tops of poorly developed high-centered polygons, low hummocks and strangs in wet areas, and well-drained terrain along streams and the lower gentle slopes of pingos. Moist sites are normally drained of standing water soon after spring runoff. Soils in the moist tundra areas are commonly either Pergelic Cryaquolls in the better drained areas or Pergelic Cryosaprists in areas with thick well-decomposed organic layers. Pergelic Cryaquolls often show distinct red mottles of iron oxide above a certain level in the A horizon, which is interpreted as the mean lower level of seasonal oxidation (Everett 1980*c*).

Mesic upland sites generally have moist graminoid tundra with either *Eriophorum triste–Dryas integrifolia* sedge, dwarf-shrub tundra (Stand Type U3) or *Carex aquatilis–Dryas integrifolia* sedge, dwarf-shrub tundra (Stand Type U4). The primary floristic difference between these two types is the relative abundance of lichens; the latter (Stand Type U4) is wetter and has few or no fruticose lichens and often has the willow *Salix lanata* ssp. *richardsonii*. Both types are dominated by sedges (e.g., *Eriophorum triste, Carex aquatilis, C. bigelowii, C. membranacea,* and *C. misandra*), and dwarf shrubs (*Dryas integrifolia, Salix arctica,* and *S. reticulata*). The primary erect dicotyledons are *Chrysanthemum integrifolium, Senecio atropurpureus* ssp. *frigidus, Pedicularis lanata, P. capitata, Polygonum viviparum,* and *Papaver macounii*. Dominant mosses are *Tomenthypnum nitens, Aulacomnium turgidum, Calliergon richardsonii, Meesia uliginosa, Oncophorus wahlenbergii, Ditrichum flexicaule, Distichium capillaceum, Hypnum bambergeri, Orthothecium chryseum,* and *Drepanocladus brevifolius*). Common lichens in Type U3 include *Thamnolia subuliformis, Dactylina arctica, Cetraria islandica, C. cucullata, C. nivalis, Cladonia gracilis, Solorina bispora, Peltigera canina,* and *P. aphthosa*.

Wet tundra.—Wet sedge tundra is associated with poorly drained areas that usually have standing water, as least in early summer. Typical microsites include the basins and troughs of low-centered polygons, the margins of ponds, lakes and streams, and the intermittently wet areas of drained lake basins. Some sites drain during dry periods later in the summer, but the soils remain saturated at all times. Wet soils are commonly Pergelic Cryaquepts (if there is <20 cm of organic matter), Histic Pergelic Cryaquepts (20–39 cm organic matter), or Cryohemists (>40 cm organic matter in the upper 80 cm of the profile or >35% organic matter by mass). Soils in wet sites are consistently circumneutral to alkaline in most of the Prudhoe Bay region, with little change of the soil pH with depth in the soil horizons. Even in the wettest sites, soil pH values are above 7.0; the degree of alkalinity depends largely on the distance of the site from the source of loess in the Sagavanirktok River floodplain, as will be explained later. The organic matter of these soils is somewhat less decomposed than that of the Cryosaprists or Histic Pergelic Cryaquepts on more well-drained sites. There are recognizable plant parts, such as roots and leaves, in the peat (Everett 1980*c*). Areas with shallow organic layers have Pergelic Cryaquepts.

FIG. 4. Terrain of the Prudhoe Bay region in the vicinity of a small tributary of the Putuligayuk River. Oriented thaw lakes and ice-wedge polygons dominate the landscape. A typical sequence of vegetation associated with streambanks, such as that along the line A–A′, is portrayed in Fig. 5.

The most common plant community in wet sites is *Carex aquatilis–Drepanocladus brevifolius* sedge tundra (Stand Type M2). *Carex aquatilis* is the most common sedge, but others, such as *Eriophorum angustifolium, C. rotundata, C. atrofusca, C. saxatilis,* and *E. russeolum,* are also common. There are a few scattered dwarf shrubs (*Salix lanata, S. arctica*) and forbs (e.g., *Pedicularis sudetica* ssp. *albolabiata, Saxifraga hirculus, Silene wahlbergella,* and *Cardamine pratensis*). Common mosses include *Drepanocladus brevifolius, Calliergon richardsonii, Cinclidium latifolium, Distichium capillaceum, Campylium stellatum, Catoscopium nigritum, Meesia triquetra, M. uliginosa, Bryum* spp., and *Scorpidium scorpioides*. A somewhat wetter stand type, *Carex aquatilis–Scorpidium scorpioides* sedge tundra (Stand Type M4) has up to 10 cm of shallow standing water throughout the summer, and is considered a transitional type between the wet and

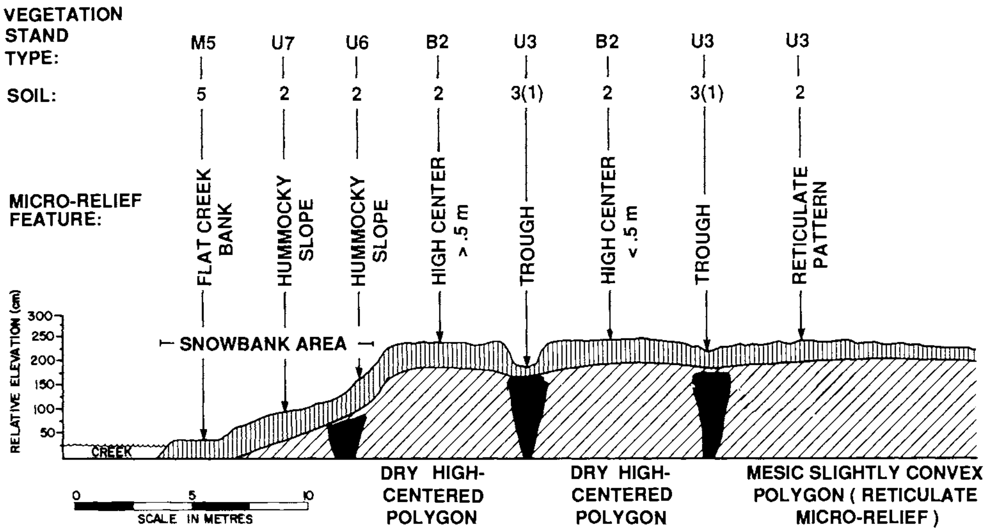


FIG. 5. Idealized cross section of Prudhoe Bay tundra showing various types of ice-wedge polygons adjacent to a small stream such as that in Fig. 4. Typical vegetation and relief are shown for each element of the polygons. In these situations, the small stream valleys fill with snow during the winter and snowbed vegetation occurs on the slope of the stream bluff. Near the top edge of the stream bluff, thermal erosion of the ice in the polygon troughs leads to relatively well-drained high-centered polygons. Areas farther from the bluff have somewhat subdued high-centered polygons with <0.5 m of relief. Still farther from the bluff (fourth polygon from the left) are low-centered polygons with slightly depressed basins. The polygon at the far right is very poorly drained with standing water in the polygon basin and troughs. Vegetation stand types from left to right: M5—wet *Carex aquatilis–Salix rotundifolia* sedge, dwarf-shrub tundra, U7—moist *Salix rotundifolia–Equisetum scirpoides* dwarf-shrub tundra, U6—dry *Cassiope tetragona–Dryas integrifolia* dwarf-shrub, fruticose-lichen tundra, B2—dry

aquatic tundra types. Here the sedges *Carex aquatilis, C. rotundata,* and *Eriophorum angustifolium* and the blue-green alga *Nostoc commune* are common. The moss *Scorpidium scorpioides* dominates the cryptogam layer of this type and is commonly covered with marl (calcium carbonate) deposits.

Aquatic vegetation.—Emergent communities are found in areas that are continuously covered with 10–100 cm of water throughout the summer. Typical microsites include protected embayments of lakes and ponds, small beaded ponds in tundra streams, and deep low-centered polygon basins. Accumulated organic matter shows virtually no signs of decomposition, and organic soils (Histosols) with >40 cm of organic matter are classed as Pergelic Cryofibrists.

Sites with up to ≈30 cm of water often have aquatic *Carex aquatilis* sedge marsh (Stand Type E1). *Eriophorum scheuchzeri, Caltha palustris,* and *Utricularia vulgaris* also occur. Type E1 areas normally occur in the shallow margins of lakes, and especially in partially drained lake basins with complex terrain of ponds and intermittent polygon rims, islands, and strangmoor.

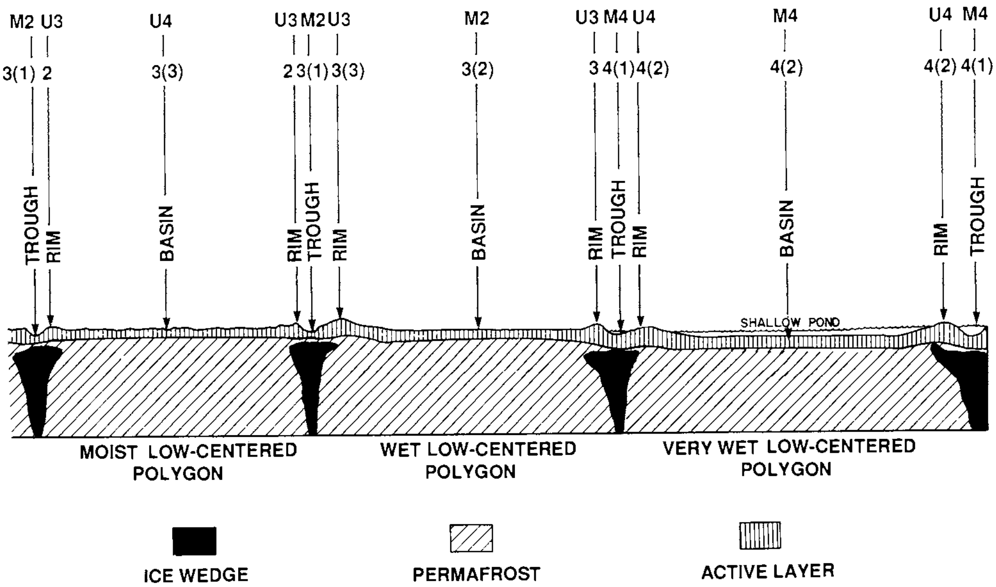
A distinctive band of vegetation, composed almost exclusively of the grass *Arctophila fulva* (Stand Type E2), occurs in water up to 1 m deep, but at the coast it occurs mainly in much shallower water (<15 cm). This type is especially common in partially drained lake basins with protected embayments. In some inland areas, especially in ponds of beaded streams, the emergent vegetation may include other taxa, such as *Caltha palustris, Hippuris vulgaris, Utricularia vulgaris,* and occasionally *Sparganium hyperboreum* and *Calliergon giganteum.* Most shallow ponds in the alkaline areas of the region have thick coatings of marl on the peat and aquatic mosses.

Regional Loess Gradient Downwind of the Sagavanirktok River

A conceptual model (Fig. 6) describes the effects of loess on the soils and vegetation in the Prudhoe Bay region. The following sections describe the details of a 20-km loess gradient downwind of the Sagavanirktok River.

Soils

The presence of permafrost and the generally wet conditions favor peat formation and give the wet alkaline tundra soils at Prudhoe Bay most of the same characteristics of gleyed soils in other Low-Arctic tundra regions (Ivanova and Rozov 1962, Tedrow 1977, Everett et al. 1981, Everett and Brown 1982). Three main gradients associated with loess contribute to the regional soil patterns: (1) a gradient of mineral material added to the peaty soils downwind of the Sagavanirktok River; (2) a gradient of soil particle sizes associated with distance from the loess source, and (3) a pH gradient associated with the carbonate-rich eolian material (Fig. 6). When compared with acidic regions of the coastal plain, representative moist and wet alkaline soils from ice-wedge polygons at Prudhoe Bay have



Dryas integrifolia–*Saxifraga oppositifolia* dwarf-shrub, crustose-lichen tundra, U3—moist *Eriophorum angustifolium–Dryas integrifolia–Cetraria cucullata* sedge, dwarf-shrub tundra, M2—wet *Carex aquatilis–Drepanocladus brevifolius* sedge tundra, M4—wet *Carex aquatilis–Scorpidium scorpioides* sedge tundra; soils: 5 Pergelic Cryorthent, 2 Pergelic Cryaquoll, 3(1) Histic Pergelic Cryaquept, 3(3) Pergelic Cryosaprist, 4(1) Histic Pergelic Cryaquept, 4(2) Pergelic Cryofibrist. (Modified from Walker 1985.)

relatively high silt content and high pH in all soil horizons (Tedrow 1977, Komárková and Webber 1978, Everett 1980*d*, Gersper et al. 1980, Webber et al. 1980). Organic content at Prudhoe Bay is generally lower than in most other coastal areas, although the sandy soils of the dune region west of the Colville River have comparable percentages of organic matter by mass.

Organic content.—The relatively low percentages of organic matter result in lower percentages of soil water (as determined by mass) than in acidic soils (Fig. 7). Parkinson (1978) noted that although wet soils near the Sagavanirktok River are visually similar to Histosols elsewhere on the coastal plain, they are sufficiently low in organic carbon (<12% by mass) that they should technically be classified as Inceptisols according to United States soil taxonomy criteria. The high mineral content affects numerous physical characteristics of the soil, including the percentage content of organic material, soil bulk density, and water retention properties. The percentage of organic matter is higher in acidic tundra areas and in microsites with high soil moisture due to anaerobic conditions and slow decomposition rates (Fig. 8a). Dry acidic soils at Prudhoe Bay average 50.2 ± 20.3% organic matter ($\bar{X}$ ± SE) and wet acidic soils average 55.5 ± 4%, whereas alkaline dry soils average 14.7 ± 4.5%, and alkaline wet soils average 33 ± 5.3% (Walker 1985). A sample from a low-centered polygon 0.3 km downwind of the Sagavanirktok River had only 18% organic matter, whereas a comparable wet site 20 km downwind had 43% (Fig. 9a). This contrasts with wet soils outside the loess area, which have up to 70% organic matter. Water retention of the soils consequently increases downwind. For example, the field capacity (determined at 100 kPa [≅1 atmosphere]) of dry alkaline soils is 0.34 ± 0.1 kg/kg, whereas that of dry acidic soils is 0.92 ± 0.28 kg/kg. The field capacity at the wet site closest to the river is 0.53 kg/kg, and 1.03 kg/kg at 20 km downwind from the river (Walker 1985).

Bulk density of alkaline tundra is on average greater than acidic soils in all moisture regimes due to the increased volume of eolian mineral material (Fig. 8b). For example, a wet low-centered-polygon site immediately west of the Sagavanirktok dunes had a bulk density of 0.89 g/cm^3 in the Oe (hemic organic) horizon (10 cm depth). At 9 km from the river, bulk densities of Oe horizons at the same depth range between 0.31 and 0.51 g/cm^3, and in wet acidic sites north of the loess area, bulk densities range between 0.12 and 0.31 g/cm^3 (Walker 1985).

The soil organic matter and bulk density strongly affect the soil insulating properties and the depth of summer thaw. Thaw in alkaline soils is generally deeper than in acidic soils (Fig. 8c). Dry alkaline mineral soils have the greatest depth of thaw (47 ± 5.5 cm). (The deepest recorded summer thaw at Prudhoe Bay is 213 cm on a gravelly south-facing pingo slope [M. D. Walker, *personal observations*, 1990].) Dry peaty acidic sites, however, have relatively shallow thaw; the two dry acidic plots of the study had thaw of 24 ± 1 cm. The dry, low-bulk-density peat acts as a good insulator, whereas the gravelly mineral soils have higher

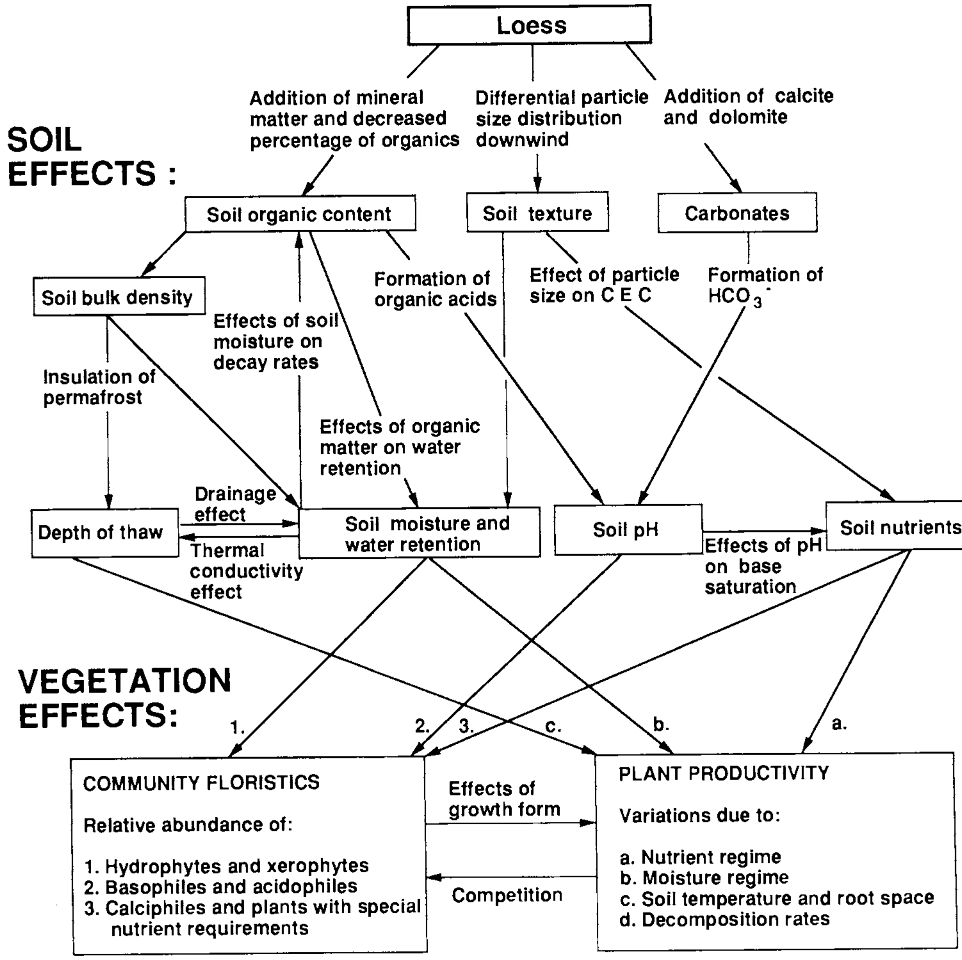


FIG. 6. Conceptual model of known loess effects downwind of major braided rivers in northern Alaska. Loess continually adds carbonate-rich silt and fine sand to peat, affecting soil bulk density, which in turn affects the depth of thaw, soil moisture, and water retention properties. Addition of carbonates and fine sand affects soil pH and nutrient capacity through changes to the cation exchange capacity (CEC) and base saturation of the soil. These properties in turn affect tundra floristics and productivity. (Modified from Walker 1985.)

heat flux and deeper thaw. In wet alkaline sites near the dunes, thaw can exceed 50 cm, whereas in wet acidic regions thaw does not exceed 30 cm in similar microsites. In the wet plots of the Prudhoe Bay vegetation study (Walker 1985) bulk density accounted for 72% of the variance in thaw depth (Fig. 10). The following parameters were correlated with thaw depth at the .001 significance level (ranked by the magnitude of the correlation coefficients) in the 93 plots in all moisture regimes of the study: (1) soil organic matter, (2) slope, (3) percentage cover of bare soil, (4) percentage of soil moisture, (5) percentage cover of bryophytes, (6) mean July air temperature, and (7) percentage cover of prostrate dead vegetation. Variables correlated at the .05 significance level were: (1) percentage clay, (2) percentage of erect dead vegetation, and (3) percentage sand.

Soil texture.—The texture of the alkaline soils is more silty than that of the acidic soils (Fig. 8d, e, and f). Mineral subhorizons of most of the alkaline soils are either silt loams or loams, whereas those of the acidic soils range from clay loams to sandy clay loams (Parkinson 1978, Walker 1985). The coarser particle sizes near the Sagavanirktok River are due mostly to windblown materials. The percentage of fine sand drops from >30% near the dunes to <10% 20 km downwind from the river (Fig. 9b). The higher percentage of sand in the <2-mm fraction increases permeability, drainage, and thaw depths near the river.

Carbonates.—The high pH of the soils in the loess areas (Figs. 2 and 11a) is directly related to the percentage of carbonates in the soils. In roughly equivalent wet alkaline tundra sites, the pH drops from 7.6 near the sand dunes to 7.0 at 20 km downwind, and the corresponding carbonate equivalences drop from 24 to 6% (Walker 1985). Soil pH values as high as 8.4 occur in the dry sands at the Sagavanirktok River dunes, and as high as 7.6 in nearby wet peaty sites. In areas with current deposition of carbonate-rich loess, the soils are alkaline in all microsites. North of the loess region, soils are consistently acidic except where the alkaline parent material is at the tundra surface, such as in riparian areas, frost scars, and coastal beaches. The lowest measured pH within the Prudhoe Bay region is 4.5 near West Dock, which is well outside the area of major loess influx; however, the pHs north of the loess line (Fig. 2) are generally higher than recorded in other acidic tundra at Barrow (pH = 5.1 to 5.8, Gersper et al. 1980) and Meade River (pH = 4.3 to 5.5, Everett 1980*d*), and suggest that there is a small amount of eolian input throughout the region including the area north of the "loess line." High soil salinities caused by calcium carbonates have been noted as a problem limiting revegetation efforts in the Kuparuk Oil Field just west of Prudhoe Bay (Jorgenson 1988*a, b*).

Soil nutrients.—NO_3, P, K, Ca, and Mg in wet sites are positively correlated with distance from the Sagavanirktok River (Walker 1985; Fig. 9d for NO_3, P, and K). The greater organic matter and clay concentrations in the western part of the region cause higher cation exchange capacities (CECs) and higher exchangeable nutrient values. Most of the variation in CEC at Prudhoe Bay is due to the percentage of organic matter (Bilgin 1975). The dependence of CEC on organic matter is more pronounced than in other tundra regions because of the relatively low clay content of the Prudhoe Bay soils (Bilgin 1975).

Exchangeable nitrates and potassium are highest in well-drained sites with pH in the range of 6.2 to 7.0, an optimal range for microbial nitrogen mineralization. Although both nutrients increase toward the west, there is not a clear difference in nitrate or potassium values in the acidic and alkaline areas (Walker 1985; Figs. 9d and 11b, d).

Extractable phosphorus (Fig. 11c), however, shows a strong regional distribution pattern with increased values toward the west but not towards the north, where soils are excessively acidic. At low pH (less than ≈6), phosphorus forms insoluble compounds due to increased activity of iron, aluminum, and manganese; at pHs above ≈7, phosphates react with calcium and calcium carbonates to form complex insoluble calcium phosphates (Bohn et al. 1985). These patterns are important because phosphorus has been shown to be the main limiting nutrient in Prudhoe Bay tundra (McKendrick and Mitchell 1978, Jorgenson 1988*a*). Phosphorus was the main added nutrient (of N, P, K, and Mg) to significantly affect 14-yr recovery of oil-damaged wet tundra at Prudhoe Bay. Phosphorus fertilization (145 kg/ha) increased mean vegetation cover from 66 to 113% on abandoned mesic-to-dry silt-loam road surfaces (McKendrick 1987). The trends noted along the loess gradient suggest that phosphorus increases downwind within the area of the study where pHs are consistently above 7.0, due primarily to higher exchange capacities of the finer, more organic-rich soils,

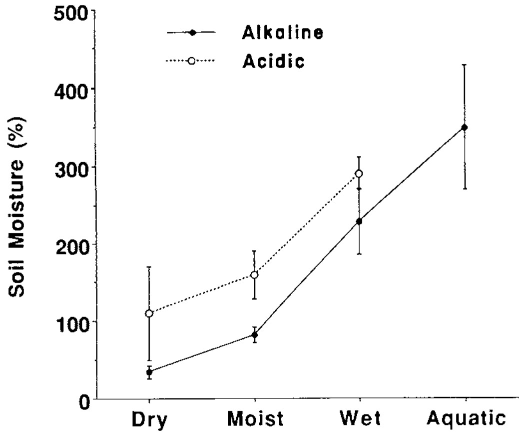


FIG. 7. Soil moisture measured at end-of-growing-season (20 August 1977) vs. subjective site moisture regime classes for acidic and alkaline tundra. Dry sites are well drained all summer; moist sites are generally drained of standing water by early summer; wet sites have saturated soils all summer, and aquatic sites are submerged all summer. Percent soil moisture determined according to the gravimetric method (Gardner 1986). (Modified from Walker 1985.)

but in the northern part of the region where the deposition of loess cannot keep pace with the acidifying effects of peat accumulation, the available phosphorus is quite low. Areas with high CEC and circumneutral soil pH have the highest phosphorus values and possibly the highest productivity (see paragraphs below).

Calcium (Fig. 11e), an easily leached cation, has relatively low exchangeable concentrations in the sandy soils near the Sagavanirktok, Putuligayuk, and Kuparuk rivers (500–3500 μg/g). Total calcium is abundant near the rivers, but it is bound as unweathered $CaCO_3$. Parkinson (1978) found calcium carbonate equivalences of 15–28% in the <0.2 mm fraction of Sagavanirktok River alluvium. Most of the calcium is bound in the form of calcite and dolomite (10–22% calcite and 4.5–6% dolomite in Sagavanirktok River alluvium [Parkinson 1978]). Downwind from the Sagavanirktok River, the exchangeable calcium concentrations increase in response to the higher exchange capacities associated with finer textured and more organic-rich soils (up to ≈9000 μg/g). North of the loess region the acidic soils show a more typical positive correlation between soil pH and calcium concentration; some of the lowest exchangeable calcium concentrations occur in the acidic soils near the coast.

Exchangeable magnesium shows a strong negative correlation with soil pH (Fig. 11f). Magnesium is highly soluble in the more acidic soils and is released by weathering from the dolomite-rich parent materials. The highest amounts of exchangeable magnesium are found near the coast. This contrasts with the pattern found with calcium, which has relatively low concentrations in these areas. This is thought to be due partly to the greater solubility of calcium, which would cause it to be more easily leached from these soils, and partly

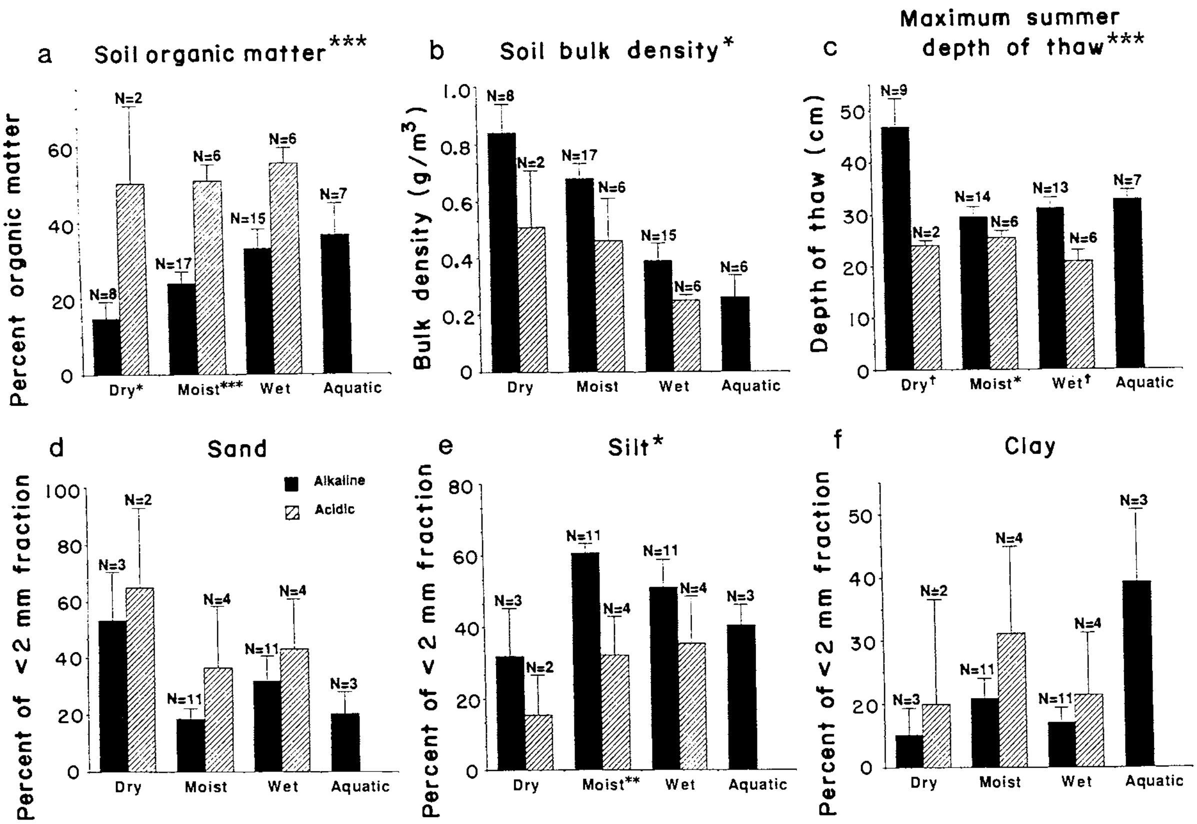


FIG. 8. Physical properties of soils along the moisture gradient for acidic and alkaline tundra: (a) soil organic matter, (b) bulk density, (c) maximum depth of summer thaw, (d) sand, (e) silt, and (f) clay. Data represent mean values at 10-cm depth at 67 plots in acidic (pH < 7) and alkaline (pH > 7) sites representative of the moisture gradient. Soil organic matter was determined by loss on ignition at 400°C for 5 h. Bulk density was determined by the core method (Blake and Hartge 1986). Maximum thaw is the mean of 10 measurements on 15 August 1977. Soil texture was determined according to the pipette method (Gee and Bauder 1986). Sites where the vegetation was predominantly controlled by edaphic factors other than soil moisture and pH, such as snowbeds, frost scars, riparian areas, estuaries, beaches and animal dens, were not included in this analysis in order to isolate the effects of soil pH as much as possible. Student's *t* tests: †$P \leq .1$, *$P \leq .05$, **$P \leq .01$, ***$P \leq .001$. (Data from Walker 1985.)

to the coastal influence with the saline soils contributing higher amounts of magnesium.

Flora

Vascular plants.—Arctic fens (minerotrophic wetlands) have been described from other arctic areas (e.g., Sjörs 1963), but those maintained by influx of eolian loess have not been described. As in other fens, the flora of the Prudhoe Bay wetlands is characterized by a predominance of sedges, calcicoles, and minerotrophic mire species. Within the Prudhoe Bay region, numerous calciphilous taxa, such as *Salix lanata* ssp. *richardsonii, Dryas integrifolia, Saxifraga oppositifolia, Chrysanthemum integrifolium, Equisetum variegatum,* and *Minuartia arctica,* are more common in the loess areas, but there do not appear to be any taxa limited solely to the highest pH areas within the Prudhoe Bay region because of relatively high pHs throughout the region (Walker 1985). On the other hand, there are several taxa limited to the acidic sites, including *Salix planifolia* ssp. *pulchra, Saxifraga foliolosa, Luzula arctica, Polygonum bistorta, Vaccinium vitis-idaea, V. uliginosum,* and *Carex rariflora.* Others not limited to, but much more common in, acidic areas include *Carex misandra, Eriophorum scheuchzeri, E. vaginatum, Ranunculus pallasii,* and *Saxifraga cernua.* Calciphiles common on drier sites in the loess region include *Androsace chamaejasme, Dryas integrifolia, Saxifraga oppositifolia, Chrysanthemum integrifolium, Braya purpurascens, Draba subcapitata, Carex scirpoidea, Lesquerella arctica, Polemonium boreale, Oxytropis nigrescens,* and *Salix lanata* ssp. *richardsonii.*

There is also a strong north–south floristic gradient associated with the cold coastal influence. North of about the 7°C mean July temperature isotherm (Littoral tundra zone of Cantlon [1961], Floristic Zone 2 of Young [1971], and Areas A and B of Walker [1985]), the tundra is noticeably depauperate compared to warmer areas to the south. This temperature gradient is not described in detail here because of the focus on

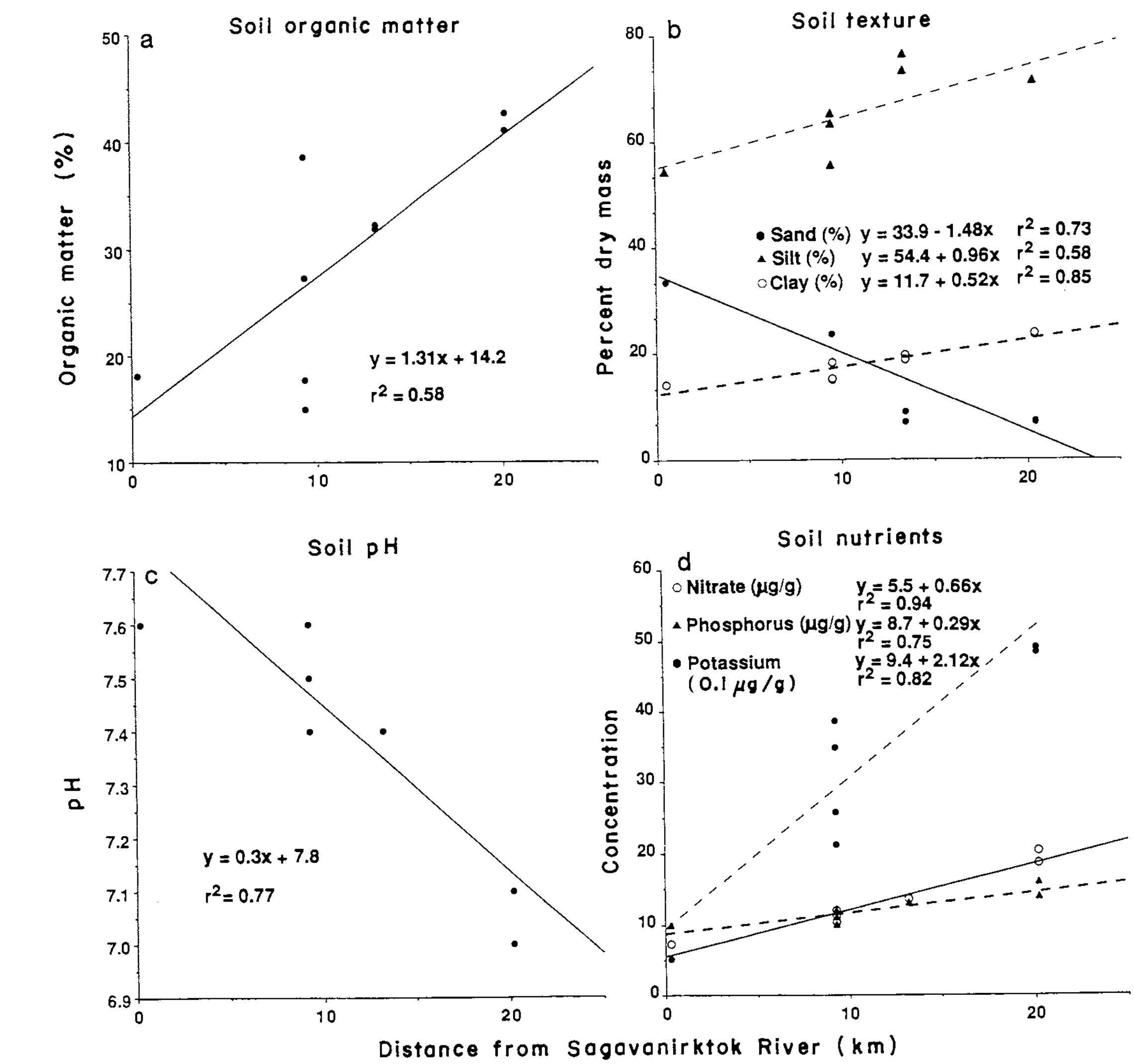


FIG. 9. Soil properties along the loess gradient downwind of the Sagavanirktok River: (a) soil organic matter, (b) particle size, (c) pH, and (d) soil nutrients. Plots north of the loess area were excluded from this analysis (see Fig. 2). These data are from nine topographically similar wet alkaline microsites in low-centered-polygon basins and drained thaw-lake basins. The variability at 9.3 km is probably due to different site histories related to meanders of the Little Putuligayuk River. See Fig. 11 for soil methods. (Modified from Walker 1985.)

the influence of loess; however, several common minerotrophic plant taxa are rare or absent in the Prudhoe Bay region but common farther south. Examples include *Rhododendron lapponicum, Arctous rubra, Tofieldia pusilla, Bupleurum triradiatum, Hedysarum alpinum* ssp. *americanum, H. mackenzii, Lupinus arcticus, Salix glauca,* and *Senecio hyperborealis.* Most of these taxa are Low-Arctic species (Typical tundra of Cantlon [1961] and Zone 3 or 4 of Young [1971]) and are limited to more inland areas by cold temperatures near the Beaufort Sea coast. The vegetation types described above are thus specifically representative of the coastal alkaline tundra region within 20 km of the Beaufort Sea. More diverse vegetation types occur farther inland but are broadly similar in physiognomy and floristic composition to the types described above for Prudhoe Bay.

Bryophytes.—Minerotrophic mosses are abundant throughout the region. Common species are *Drepanocladus brevifolius, Scorpidium scorpioides, Tomenthypnum nitens, Hypnum procerrimum, Ditrichum flexicaule, Distichium capillaceum,* and *Orthothecium chryseum.* Steere (1978) commented on the abundance of calciphilous mosses and the scarcity of acidophiles such as *Sphagnum, Dicranum,* and members of the Polytrichaceae. So far, *Sphagnum* has been found only in the northern parts of the region (Spatt 1983) and in the Kuparuk Oil Field. *Dicranum* and *Polytrichum* are found in abundance only in the acidic area, as are numerous other bryophytes, including *Ptilidium cil-*

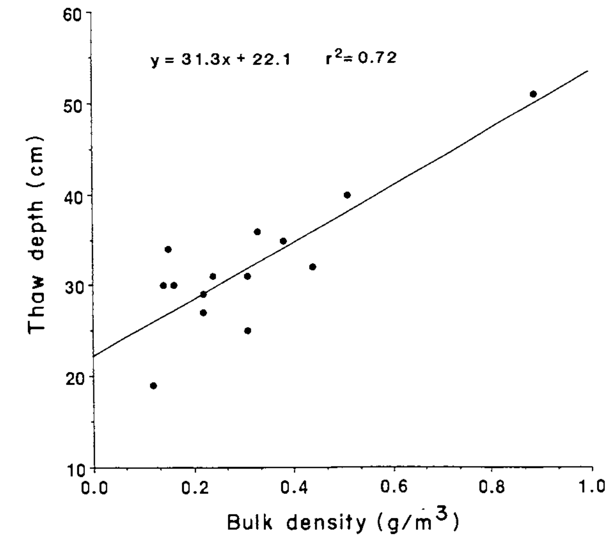


FIG. 10. Maximum depth of summer thaw vs. bulk density at the 15 wet tundra sites. Alkaline and acidic plots were included in this analysis. (Modified from Walker 1985.)

iare, Hylocomium splendens, Distichium inclinatum, Oncophorus wahlenbergii, Mnium blyttii, Scapania simmonsii, Lophozia spp., and numerous other liverworts. *Ditrichum flexicaule, Hypnum bambergeri, Catoscopium nigritum,* and *Drepanocladus uncinatus* are more common in the loess area (Walker 1985).

Rastorfer et al. (1973) noted the exceptionally rich bryoflora in the northwestern portion of the Prudhoe Bay Oil Field (near point E in Fig. 2), particularly for members of the liverwort family Lophoziaceae. The higher percentages of clay toward the west may be an important factor for the liverworts. The higher water retention properties of more clay-rich and organic-rich soils in the western part of the oil field are surely an important factor for mesic cryptogams that rely on moisture at the tundra surface during the dry summers at Prudhoe Bay (≈70 mm of summer rainfall, Walker et al. 1980). Walker (1985) noted 26 cryptogams with positive correlations between percentage plant cover and soil clay content.

One consequence of the assemblage of minerotrophic mosses is a regionally thin moss carpet. Cryptogam accumulations are generally only 3–7 cm thick, and the

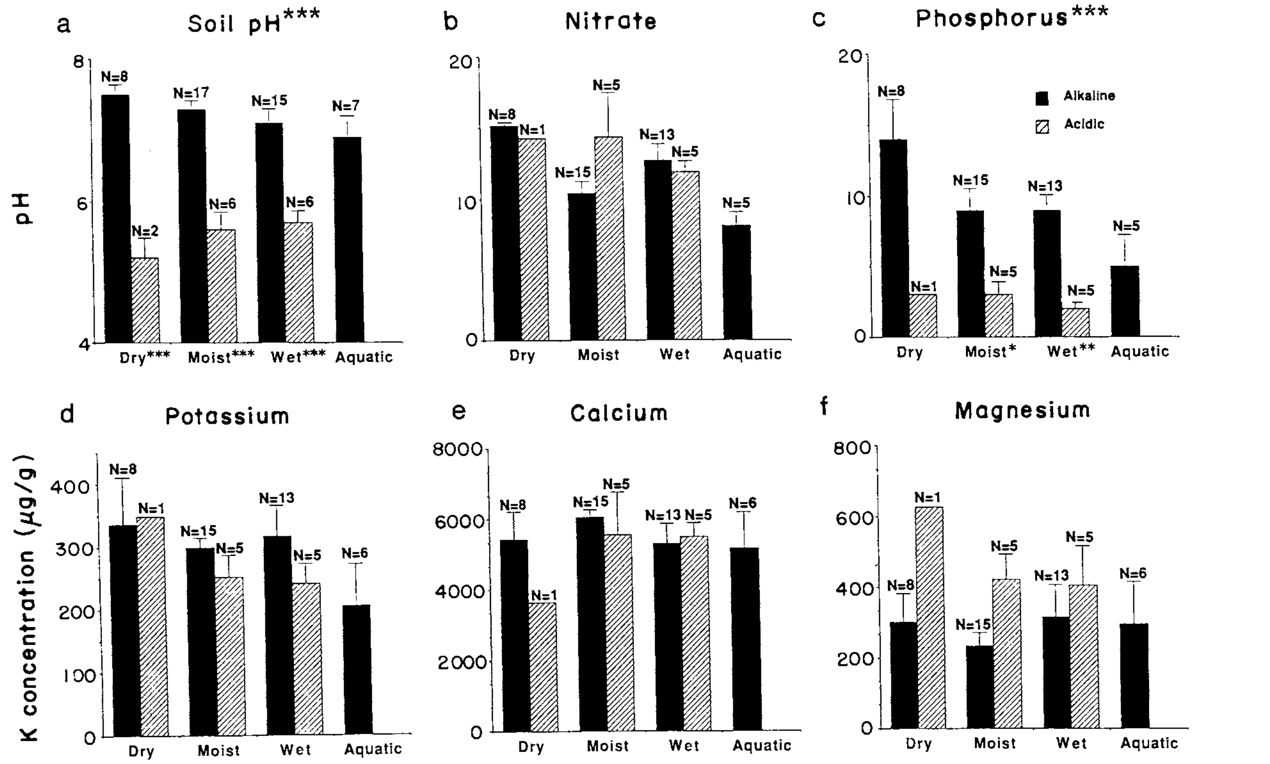


FIG. 11. Chemical properties of soils along the moisture gradient in acidic and alkaline tundra: (a) pH, (b) exchangeable nitrates, (c) available phosphorus, (d) exchangeable potassium, (e) exchangeable calcium, and (f) exchangeable magnesium. Data are from the same sites as in Fig. 10. Soil pH was measured using a soil : water ratio of 1:2.5 by volume. Exchangeable NO_3^- was extracted with 2 mol/L KCl and analyzed using the colorimetric method (Keeney and Nelson 1982). Available P was analyzed using an extracting solution of 0.5 mol/L $NaHCO_3$ (pH 8.5) for neutral to alkaline soils and 0.025 mol/L HCl in 0.03 mol/L NH_4F (pH 2.6 ± 0.05) (Olsen and Sommers 1982). K, Ca, and Mg were extracted using 1 mol/L NH_4OAc (Lanyon and Heald 1982). Student's *t* tests: †$P \leq .1$, *$P \leq .05$, **$P \leq .01$, ***$P \leq .001$. (Data from Walker 1985.)

deepest living moss carpets are ≈10 cm thick. This contrasts with *Sphagnum*-dominated areas in the foothills where the living moss carpets sometimes exceed 20 cm.

Lichens.—Many lichens also exhibit a negative response to higher loess concentrations. The Cladoniaceae, in particular, are more abundant in the acidic region; *Cladonia gracilis, C. lepidota, C. phyllophora,* and *C. squamosa* are all more abundant in areas far downwind from the Sagavanirktok River. Other lichens that are more common in the acidic areas are *Alectoria nigricans, Cornicularia divergens, Dactylina ramulosa, Psoroma hypnorum, Lecidea ramulosa, Ochrolechia frigida* f. *thelephoroides,* and *Stereocaulon alpinum.*

Vegetation downwind of the Sagavanirktok sand dunes: relevance to climate change.—The desert-like character of the sand dunes in the delta of the Sagavanirktok River is a striking contrast to the surrounding wet tundra (Fig. 12). Similar dune fields occur in the deltas of most of the larger rivers of the North Slope and are remnants of formerly more extensive dunes that were present during long intervals of the Pleistocene glaciations (Black 1951, Carter 1981). The vegetation within and adjacent to the dune fields provides insights regarding successional processes that occurred as the present-day thaw-lake landscape developed during the Holocene. Peterson and Billings (1978) describe a vegetation sequence downwind of noncalcareous dunes of the Meade River where autogenic succession on dry sites proceeds towards a lichen–health community dominated by *Diapensia lapponica, Vaccinium vitis-idaea, Ledum decumbens* ssp. *palustre,* and *Alectoria nigricans.* The following description portrays the sequence downwind of calcareous dunes (Table 2).

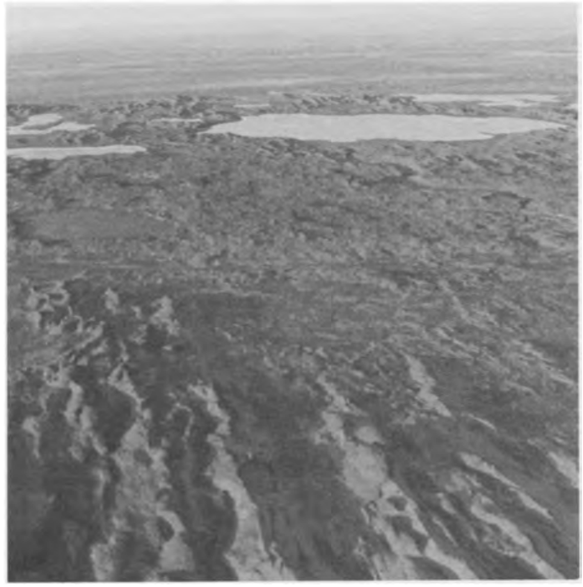


FIG. 12. Longitudinal sand dunes near the mouth of the Sagavanirktok River. This view is toward the east with longitudinal dunes oriented in the prevailing ENE winds (toward the camera). Note the lakes perched within the dune region due to permafrost which prevents their drainage. The small lake in the right background is about 200 m long.

The succession of vegetation types within and downwind of the dunes follows the progression outlined in Table 2. The most active dunes are barren or sparsely vegetated with *Elymus arenarius.* Slightly more stable dunes include *Dupontia fisheri, Polemonium boreale, Androsace chamaejasme, Draba lactea, D. cinerea, Artemisia glomerata, A. borealis,* and *Festuca rubra.* Sandy interdune areas often lack vegetation or contain scattered individuals of *Salix ovalifolia.* Semistable areas are likely to have all of the above plus *Dryas integrifolia, Parrya nudicaulis, Armeria maritima, Kobresia myosuroides, Oxytropis nigrescens, Distichium capillaceum,* and *Ditrichum flexicaule.*

Some areas within the dunes contain extensive stands of *Artemisia borealis* mixed with numerous grasses, primarily *Deschampsia caespitosa, Poa* spp., and *Trisetum spicatum* (Fig. 13). This may be an analogue of so-called "steppe-tundra" vegetation that occurred in unstable areas of coastal Beringia during the coldest portions of the last glaciation and the warming period during the early Holocene (e.g., Guthrie 1968, Hopkins et al. 1982, Ritchie 1984). Pollen diagrams from sites throughout northern Beringia indicate that during the glacial periods of the Pleistocene the vegetation had large components of Poaceae and *Artemisia,* whereas dominants of the modern coastal plain vegetation, such as sedges, *Sphagnum,* willow, and birch, were relatively insignificant (Livingstone 1955, Nelson 1982, Anderson 1985, Anderson and Brubaker 1986). This has led some investigators (e.g., Giterman and Golubeva 1967, Yurtsev 1972, 1982) to speculate that the vegetation had strong floristic affinities with the steppes of central Asia, and Young (1982) has described the vegetation of the extensive, more or less stabilized, eolian deposits as a "loess steppe." In the far northern parts of the coastal plain the vegetation was undoubtedly sparse because of the cold dry climate.

Ice-wedge polygons just west of the Sagavanirktok dunes receive substantive dune-derived eolian material. Mosses are much less abundant on these polygon rims than those elsewhere in the Prudhoe Bay region, probably due to the generally drier soil surface conditions associated with sandy substrates. The wet basins of the polygons, in contrast, have lush moss and sedge carpets composed of *Drepanocladus brevifolius, Calliergon richardsonii, Cinclidium latifolium, Meesia triquetra, Carex aquatilis, Dupontia fisheri,* and *Pedicularis sudetica* ssp. *albolabiata* (Stand Type M3, Walker 1985). This association consistently occurs in wet sandy polygonal areas along the Sagavanirktok and Kuparuk rivers. The difference in the moss cover on the basins and the rims causes large differences in the depth of maximum summer thaw within the confines of single ice-wedge polygons. For example, depth of summer

TABLE 2. Vegetation sequence downwind of the Sagavanirktok River dunes. Stand type codes follow Walker (1985).

	Common plant species		
Topographic situation	Dry sites	Moist sites	Wet sites (without standing water)
Active dunes	*Elymus arenarius, Polemonium boreale* (B9)		Barren
Partially stabilized dunes	*Salix ovalifolia, Dryas integrifolia, Artemisia borealis, Parrya nudicaulis, Oxytropis nigrescens, Androsace chamaejasme, Kobresia myosuroides, Chrysanthemum integrifolium, Polygonum viviparum, Pedicularis langsdorffii* (B5)		*Carex aquatilis, Dupontia fisheri, Salix ovalifolia, Deschampsia caespitosa* (M11)
Ice-wedge polygons with sandy substrates (pH >8) within 1 km downwind of the dunes		*Carex aquatilis, Dryas integrifolia, Polygonum viviparum, Distichium capillaceum, Salix ovalifolia, Equisetum variegatum* (U14)	*Carex aquatilis, Drepanocladus brevifolius, Meesia triquetra, Cinclidium latifolium, Pedicularis sudetica, Calliergon richardsonii, Distichium capillaceum, Dupontia fisheri* (M3)
Ice-wedge polygons with silty substrates (pH 7.0–7.5) within 20 km downwind of the dunes	*Dryas integrifolia, Saxifraga oppositifolia, Salix reticulata, Distichium capillaceum, Ditrichum flexicaule, Lecanora epibryon, Thamnolia subuliformis* (B1, B2)	*Eriophorum triste, Carex membranacea, C. bigelowii, Dryas integrifolia, Salix reticulata, S. arctica, S. lanata, Polygonum viviparum, Tomenthypnum nitens, Ditrichum flexicaule, Thamnolia subuliformis, Cetraria* spp., *Dactylina arctica* (U3, U4)	*Carex aquatilis, Eriophorum angustifolium, Pedicularis sudetica, Drepanocladus brevifolius, Catascopium nigritum, Saxifraga hirculus, Silene wahlbergella, Nostoc commune* (M2)
Ice-wedge polygons (pH 7.0–6.0) greater than 20 km downwind of the dunes		*Eriophorum vaginatum, Cassiope tetragona, Polygonum bistorta, Salix planifolia* ssp. *pulchra, Tomenthypnum nitens, Carex bigelowii, Eriophorum triste, Ptilidium ciliare, Carex misandra, Dryas integrifolia, Salix reticulata, Distichium capillaceum, Ditrichum flexicaule, Orthothecium chryseum, Cladonia gracilis, Thamnolia subuliformis, Oncophorus wahlenbergii, Aulocomnium turgidum, A. palustre* (U1)	*Carex aquatilis, C. rariflora, C. rotundata, C. misandra, Saxifraga foliolosa, Drepanocladus brevifolius, Eriophorum angustifolium, Saxifraga hirculus, Nostoc commune* (M1)

thaw on the polygon rims often exceeds 80 cm because of the lack of an insulating moss cover and the sandy soil, whereas the thaw in the basins is generally <45 cm. Similar dramatic changes in the active layer likely accompanied the paludification (process of mire formation over previously dry land) of the Prudhoe Bay region during the Holocene. Important vascular taxa on the polygon rims include *Carex aquatilis, Dryas integrifolia, Salix ovalifolia* and *Polygonum viviparum* (Stand Type U14, Walker 1985).

Further downwind, the vegetation is that of the typical Prudhoe Bay toposequences described above. West of the Kuparuk River there is a gradual transition toward more acidophilous tussock tundra vegetation with increasing amounts of *Eriophorum vaginatum*, ericaceous shrubs (e.g., *Vaccinium* spp., *Arctous rubra, Ledum palustre* ssp. *decumbens*), *Betula nana, Salix planifolia* ssp. *pulchra, Sphagnum* spp., *Aulacomnium palustre, Polytrichum* spp., and *Cladonia* spp.

The modern ecosystems occurring downwind from dunes in the Sagavanirktok River delta provide insights regarding the vegetation succession that likely occurred during the Holocene. The successional sequence (Table 2) is probably a remnant of more extensive unstable areas that were prevalent during the Holocene as the tundra became progressively wetter and the Sagavanirktok River migrated eastward from its ancient floodplain that once followed the modern Putuligayuk River (see Fig. 2) (Rawlinson 1983).

Tundra not influenced by loess normally becomes acidic due to the accumulation of humic acids associated with peat development. *Sphagnum* and other bryophytes are key plants in the process of low-arctic and bog landscape evolution, particularly in inland areas of the North Slope, because of their pronounced influence on soil pH, water availability, carbon storage, and active layer thickness. The alkalinity and high calcium levels of soils in local areas on the coastal plain and northern foothills are maintained today by a combination of loess from the major rivers and cryoturbation (process of stirring, heaving and thrusting due to frost action) that continually brings unleached loess to the surface. Loess, thus, acts to maintain the vegetation in a relatively early successional state.

Questions regarding the influence of climate change on arctic peatlands are important because of possible feedback mechanisms related to greenhouse gases generated during the decomposition of peat or to the sequestering of carbon with increased peat accumulation. If the past provides relevant clues, former warm intervals were accompanied by peat accumulation on the North Slope, and cold glacial periods have generally been dry with extensive eolian activity (Hopkins 1982); however, to predict future trends detailed studies of the long-term trends of peat accumulation in the Arctic are needed in conjunction with the observations of experimentally altered climate regimes. Detailed studies of peat profiles downwind of the Sagavanirktok River may also provide clues for the future by elucidating the geomorphic and paleobotanical changes that occurred as the region warmed at the end of the last glacial and peat began to accumulate. However, future landscapes are likely to be strongly affected by successional momentum already established in the boggy landscapes. The consequences of a climatic warming are likely to be very different in an already paludified landscape than they were on the raw surfaces that dominated the region at the end of the last glacial.

Phytomass and higher trophic levels

Detailed aboveground phytomass data for the Prudhoe Bay region are from a relatively acidic area along the West Road, where the soil pH varies from 4.5 to 7.1 (mean pH 5.5) (Table 3; Klinger et al. 1983*a*). Total phytomass values range from 163 ± 21 g/m^2 in wet sites to 691 ± 96 g/m^2 in dry sites. When compared to Barrow, Prudhoe Bay has much larger standing crops in dry and moist sites (Table 4). This is due primarily to the dominance of the prostrate evergreen shrub *Dryas integrifolia*, which is a rare plant at Barrow. No attempt has been made to determine annual production for *Dryas*; thus it is difficult to calculate annual production for dry and moist sites at Prudhoe Bay. The wet site data, however, are closely comparable to data from Point Barrow (Webber 1978) and Devon Island (Muc 1977). Total aboveground phytomass in wet sites at Barrow averages 174 g/m^2 and is 168 g/m^2 at Devon Island, compared to 163 g/m^2 at Prudhoe Bay. Because there are few woody plants in wet sites, annual aboveground vascular plant production in wet sites can be estimated by adding the phytomass for graminoids and forbs, plants that die back annually and can be easily sorted into live and dead fractions. On this basis, the average aboveground vascular plant production in wet sites is 41 g·m^{-2}·yr^{-1} at the Prudhoe Bay site, compared to 47 g·m^{-2}·yr^{-1} at Barrow, and 45 g·m^{-2}·yr^{-1} at Devon Island.

FIG. 13. Partially stabilized dune area dominated by *Artemisia borealis, Deschampsia caespitosa, Poa* sp., *Trisetum spicatum* and *Salix ovalifolia.* This vegetation is a possible analogue of vegetation that occurred in unstable areas that covered much of the coastal plain during the late Pleistocene.

Only a small amount of phytomass data is available from the wet alkaline areas at Prudhoe Bay (White et al. 1975). Because of the different methods used to collect the data, it is difficult to make a full comparison with the acidic tundra data. Mean total phytomass, including standing dead but excluding cryptogams, in the alkaline *Eriophorum* areas was 98.8 ± 14.3 g/m^2 (n = 12) and 70.7 ± 10.4 g/m^2 (n = 9) in the alkaline *Carex aquatilis* areas, compared to 128.5 ± 20.1 g/m^2 in the Prudhoe Bay wet acidic areas (see Table 3, calculated on the basis of total phytomass in wet plots minus bryophytes, lichens, and algae, with no distinction between *Eriophorum*- and *Carex*-dominated tundra). This supports a general impression that vegetation productivity is lower in the more alkaline sandy areas near the Sagavanirktok River, particularly in wet low-centered polygon sites dominated by *Carex aquatilis*. However, this may also be due to the relative predominance of low-centered polygons in the eastern portion of the region, whereas drained lake basins without low-centered polygons dominate the northwestern portion of the region. Webber (1978) and Klinger et al. (1983*a*) noted that productivity in low-centered polygon basins is less than in drained lakes because of restricted flux of nutrients through the polygon basins.

TABLE 3. Average phytomass (g/m²) and leaf area index (LAI) values of growth forms in an acidic area at Prudhoe Bay (from Klinger et al. 1983*a*). LAI is based on the inclined point frame method (Warren Wilson 1959) using 100 points per 1 × 1 m plot. Phytomass is based on clip harvest of 0.2 × 1 m plots within the LAI plots. Data are means ± 1 SE.

Growth form	Dry plots (N = 23)	Moist plots (N = 23)	Wet plots (N = 23)	All plots (N = 69)
Bryophytes				
Phytomass	80.95 ± 17.15	105.06 ± 22.21	29.85 ± 6.24	71.95 ± 9.44
LAI	0.49 ± 0.06	0.90 ± 0.07	0.60 ± 0.06	0.66 ± 0.04
LAI : phytomass ratio	0.006	0.009	0.020	0.009
Lichens				
Phytomass	108.71 ± 23.02	54.56 ± 11.54	1.09 ± 0.23	54.79 ± 8.46
LAI	0.74 ± 0.05	0.45 ± 0.04	0.01	0.40 ± 0.02
LAI : phytomass ratio	0.007	0.008	0.009	0.007
Shrubs				
Phytomass	72.35 ± 15.35	56.05 ± 11.87	0.40 ± 0.01	42.81 ± 6.37
LAI	0.35 ± 0.03	0.36 ± 0.03	0.00	0.24 ± 0.01
LAI : phytomass ratio	0.005	0.006	···	0.006
Graminoids				
Phytomass	2.80 ± 0.58	33.49 ± 7.07	39.08 ± 8.23	25.12 ± 3.57
LAI	0.06 ± 0.02	0.31 ± 0.04	0.48 ± 0.05	0.28 ± 0.02
LAI : phytomass ratio	0.021	0.009	0.012	0.011
Forbs				
Phytomass	0.37 ± 0.07	2.63 ± 0.56	1.93 ± 0.41	1.64 ± 0.23
LAI	0.06 ± 0.02	0.02 ± 0.01	0.01	0.03 ± 0.01
LAI : phytomass ratio	0.162	0.008	0.005	0.018
Algae				
Phytomass	0.03 ± 0.01	0.55 ± 0.12	3.14 ± 0.66	1.24 ± 0.22
LAI	0.00	0.01	0.07 ± 0.01	0.03 ± 0.01
LAI : phytomass ratio	···	0.018	0.022	0.024
Total live				
Phytomass	265.21 ± 32.56	252.34 ± 28.59	75.13 ± 10.36	170.89 ± 14.63
LAI	1.70 ± 0.09	2.05 ± 0.10	1.17 ± 0.08	1.64 ± 0.05
LAI : phytomass ratio	0.006	0.008	0.016	0.008
Total dead				
Phytomass	425.62 ± 90.49	297.95 ± 63.13	87.47 ± 18.30	270.36 ± 36.73
LAI	1.18 ± 0.08	1.82 ± 0.12	1.62 ± 0.09	1.54 ± 0.06
LAI : phytomass ratio	0.003	0.006	0.018	0.006
Total phytomass	690.83 ± 96.17	550.29 ± 69.31	162.60 ± 21.03	467.91 ± 39.54
Total LAI	2.88 ± 0.12	3.87 ± 0.16	2.79 ± 0.12	3.18 ± 0.08
LAI : phytomass ratio	0.004	0.007	0.017	0.007

This effect has been labeled the "polygon basin syndrome" (MacLean 1975). The nutrient-poor sandy soils near the river may enhance this effect, causing even lower production, but this needs to be examined more closely with detailed fully comparable biomass studies in both acidic and alkaline areas. Such a study may reveal differences in production that correspond to the spectral differences between acidic and alkaline areas observed on false-color satellite images of the North Slope (Plate 1).

Very little is known regarding differences in higher trophic levels occurring in minerotrophic and acidic tundras, although there is sufficient cause for a close examination of this question. Early studies in the Prudhoe Bay region noted major differences between Prudhoe Bay and Barrow with regard to insects (MacLean 1975), bird populations (Norton et al. 1975), and mammals (Feist 1975, White et al. 1975).

DISTURBANCE AND RECOVERY IN LOESS-DOMINATED ECOSYSTEMS

Calcareous loess has numerous important physical and chemical characteristics that influence disturbance and recovery in arctic tundra regions. Investigations at 30-yr-old drill sites in northern Alaska (Lawson et al. 1978, Lawson 1983, 1986, Ebersole 1985) showed that drill sites on upland loess deposits are highly unstable following disturbance and that terrain morphology is subsequently modified by complex interactions of slumping, sediment flow, and thermal and mechanical erosion. Silt-rich areas of the foothills along the trans-Alaska pipeline are similarly modified by disturbance (Brown and Berg 1980). Areas with coarser sediments are much less modified by thermokarst (irregular terrain caused by the melting of massive ground ice) because of generally smaller amounts of ground ice and greater resistance to mechanical failure (Lawson 1986).

TABLE 4. Mean phytomass values (g/m²) from three arctic locations.

	Dry plots		Moist plots		Wet plots		
Growth form	Prudhoe Bay acidic tundra*	Pt. Barrow†	Prudhoe Bay acidic tundra	Pt. Barrow	Prudhoe Bay acidic tundra	Pt. Barrow	Devon Island‡
Forbs	0.4	5.2	2.6	0.9	1.9	1.8	1.4
Shrubs	72.3	31.0	56.1	31.1	0.0	0.0	0.0
Graminoids	2.8	4.1	33.5	31.1	39.1	44.8	44.0
Total live above moss layer	75.5	40.3	92.2	63.1	41.0	46.6	45.4
Total dead above moss layer	425.6	159.5	297.9	152.5	87.5	90.2	123.0
Total phytomass above moss layer	501.1	199.8	390.1	215.6	128.5	136.8	168.4
Lichens	108.7	37.3	54.6	55.1	1.1	0.2	Not determined
Bryophytes	80.9	7.5	105.1	244.0	29.9	36.7	Not determined
Total phytomass	690.7	244.6	549.8	514.7	159.5	173.7	···

* From Klinger et al. (1983*a*).
† From Webber (1978).
‡ From Muc (1977), excludes lichens and bryophytes.

Silty deposits can develop large volumes of segregated ice, largely due to the platey structure common to these wind-blown deposits. Interstitial water moves by capillary action along moisture tension gradients to freeze into lens-shaped bodies of segregated ice ranging in thickness from a few millimetres to several metres (Everett 1980*c*). Segregations of nearly pure ice in 1 m thick loess at Prudhoe Bay can account for between 10 and 70% of a given volume. Massive ice wedges cutting the loess and extending into underlying alluvial and marine deposits may be as much as 5 m thick (Everett 1980*a*). In areas of deep loess, such as the northern foothills, ice wedges can form much larger fractions of the total stratigraphy. In the foothills loess deposits, ground ice does not decrease with depth as it usually does, because the ice formed as the loess accumulated during the Pleistocene (Carter 1988). The greater ice volumes combined with the small grain sizes make thick loess deposits particularly susceptible to massive thermokarst. Loess deposits at Prudhoe Bay are less susceptible to massive thermokarst because, although they are highly ice-rich, they are generally thin and overlay stable alluvial gravels (Everett 1980*c*).

Also important are the different sensitivies of the dominant acidic and alkaline tundra species. For example, *Dryas integrifolia,* a prostrate evergreen shrub and an important component of most mesic and xeric communities in alkaline regions, is easily killed by relatively small levels of impact from a wide variety of disturbances, including oil spills (Walker et al. 1978), salt-water spills (Simmons et al. 1983), and flooding (Klinger et al. 1983*b*). On the other hand, *Sphagnum,* a common component of mesic to wet acidic tundra, is highly sensitive to many of the same disturbances plus several others, including increased calcium levels (Clymo 1973), road dust (Spatt and Miller 1981), and physical disturbance and compression due to off-road vehicles (Walker et al. 1987*b*, Felix and Raynolds 1989*a, b*). Numerous other plants also show distinctive responses to particular types of disturbance. For example, Jorgenson (1988*a, b*) noted several species that are relatively intolerant of calcium carbonate salts that have formed on revegetated sites in the Kuparuk Oil Field.

The loess gradient has special significance with regard to prediction of the effects of road dust, which is considered one of the broadest scale disturbances associated with oil-field development on the North Slope and a disturbance with clear differences in response between acidic and alkaline tundras (Walker and Everett 1987). Observations along the Dalton Highway indicate a gradient of response similar in many ways to the gradient found downwind of Sagavanirktok sand dunes (Walker and Everett 1987). The response of alkaline tundra areas to dust is much less noticeable than in acidic areas, indicating that in these regions natural processes have selected sets of species better adapted to all except the worst dust loads.

Although areas with high amounts of naturally occurring dust are good analogues for anthropogenically generated dust, there are differences in the two phenomena that require further study. For example, dust control measures cause differences in dust chemistry. Dust abatement at Prudhoe Bay has utilized waste oil, reserve pit fluids from the drill sites, and calcium chloride, all of which cause chemical effects in wetlands and roadside vegetation (Techman Engineering 1982). The chemical composition of road dust can also vary considerably depending on the source area for the road gravel. Most road-surface materials south of the coastal plain are composed of crushed bedrock, largely quartzose sandstone and conglomerate, but on the coastal plain, surface materials are largely the same source materials as the loess (Walker and Everett 1987).

A second difference is that within a narrow, ≈10 m wide roadside zone, the size fractions of road dust are much coarser than natural loess. Vehicles, particularly large trucks, lift soil particles ranging from clay to sand and even gravel into the wind (Walker and Everett 1987).

Third, roadside dust loads exceed the natural background dust levels by many times (except perhaps for natural areas in the dunes where dust loads have not been measured). Within 10 m of the Dalton Highway, dust loads sometimes exceed 700 g/m² during the summer months (Walker and Everett 1987). When this level of dust builds up over many years, as has happened along the Prudhoe Bay Spine Road, most of the vegetation is smothered and eliminated. At 1000 m from the road, deposition is much less; only ≈1–8 g/m² of dust were collected at 1000 m during the summer months of 1977 and 1978 along very heavily traveled roads (Walker and Everett 1987), but this is probably still higher than the natural background levels of dust in the region.

The dust-load data are useful for determining the amount of dust required to maintain the alkaline nature of the tundra. Since the construction of the Dalton Highway, which parallels the Sagavanirktok River, it has been difficult to determine the natural background levels of dust because of the great amount of dust from the road. Based on the available information, we must currently assume that very low levels of loess deposition, less than those measured at 1000 m from the Dalton Highway, are sufficient to maintain the alkaline nature of the tundra, although it is also possible that the natural alkalinity is maintained by unusual duststorm events.

Conclusions

1) Alkaline tundra is common in many areas of northern Alaska in association with areas of calcareous loess, limestone deposits, and late-Pleistocene-age glacial till. Modern loess affects soil pH, the organic layer, water availability, nutrient availability, and vegetation patterns over vast areas of the North Slope.

2) Loess acts to maintain the vegetation in an early successional state. Tundra not influenced by loess normally becomes acidic due to the accumulation of *Sphagnum* and humic acids associated with peat development. The alkalinity of soils in local areas on the coastal plain and northern foothills is being maintained today by a combination of loess and cryoturbation.

3) The fundamental geobotanical interrelationships in alkaline tundra areas have been described here, but the full implications for other processes and components of the ecosystem, such as production, mineralization, biogeochemical cycles, and higher trophic levels, still need to be studied.

4) The modern ecosystems occurring downwind from dunes in the Sagavanirktok River delta provide insights regarding the vegetation succession that likely occurred during the Holocene and are relevant to current hypotheses regarding future ecosystem response to climate change.

5) The sensitivity of alkaline loess areas to anthropogenic disturbances is different from that of acidic regions due to greater amounts of ground ice, saline soils, and the different responses of the dominant plant taxa to disturbance. The loess gradient is a useful analogue to study the response of tundra vegetation to road dust.

Acknowledgments

This work was funded by grants from the U.S. Army Cold Regions Research and Engineering Laboratory (CRREL) who obtained monies from the oil industry and U.S. Federal Highway Administration, the National Science Foundation (DPP-8520754), and the Department of Energy, Office of Health and Environmental Research/Ecological Research Division (DOE Grant DE-FG02-84ER60242 as part of the research in Response, Resistance, Resilience to, and Recovery from Disturbance [R4D] in Arctic Ecosystems program). The early vegetation mapping at Prudhoe Bay was performed as part of the U.S. Tundra Biome portion of the International Biological Programme (IBP). The logistical support and cooperation of the North Slope Borough, ARCO Alaska Inc., and SOHIO Petroleum Co. are much appreciated. The phytomass data are from the Prudhoe Bay Waterflood Environmental Monitoring Program funded by the oil industry through Woodward Clyde Consultants.

Drs. Jerry Brown and Patrick Webber played large roles throughout this research program, and we are especially grateful for their support. Special thanks to numerous other individuals who helped us with the research including field assistance, taxonomic and soils expertise, and reviews of this paper: William Acevedo, John Andrews, Peter Birkeland, Ken Bowman, Max Britton, John Cantlon, David Cate, David Cooper, Vicki Dow, Jim Ebersole, Joanne Flock, Rolf Kihl, Lee Klinger, Vera Komárková, Nancy Lederer, Iggy Litaor, Vera Markgraf, Jay McKendrick, Don Mills, Barbara Murray, David Murray, Kate Palmer, Bob Parkinson, Kathleen Salzberg, Sam Shushan, Peter Spatt, William Steere, John Tedrow, John Thomson, Tom van Dreser, Marilyn Walker, Thomas Webb, William Weber, Eleanor Werbe, Jane Westlye, and Mandy Wilson.

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