VEGETATION DISTURBANCE AND RECOVERY
AT THE OUMALIK OIL WELL,
ARCTIC COASTAL PLAIN,
ALASKA

by

James Jay Ebersole

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This Dissertation for the Doctor of Philosophy Degree by
James Jay Ebersole
has been approved for the
Department of
Environmental, Population, and Organismic Biology
by

Patrick J. Webber.
Patrick J. Webber

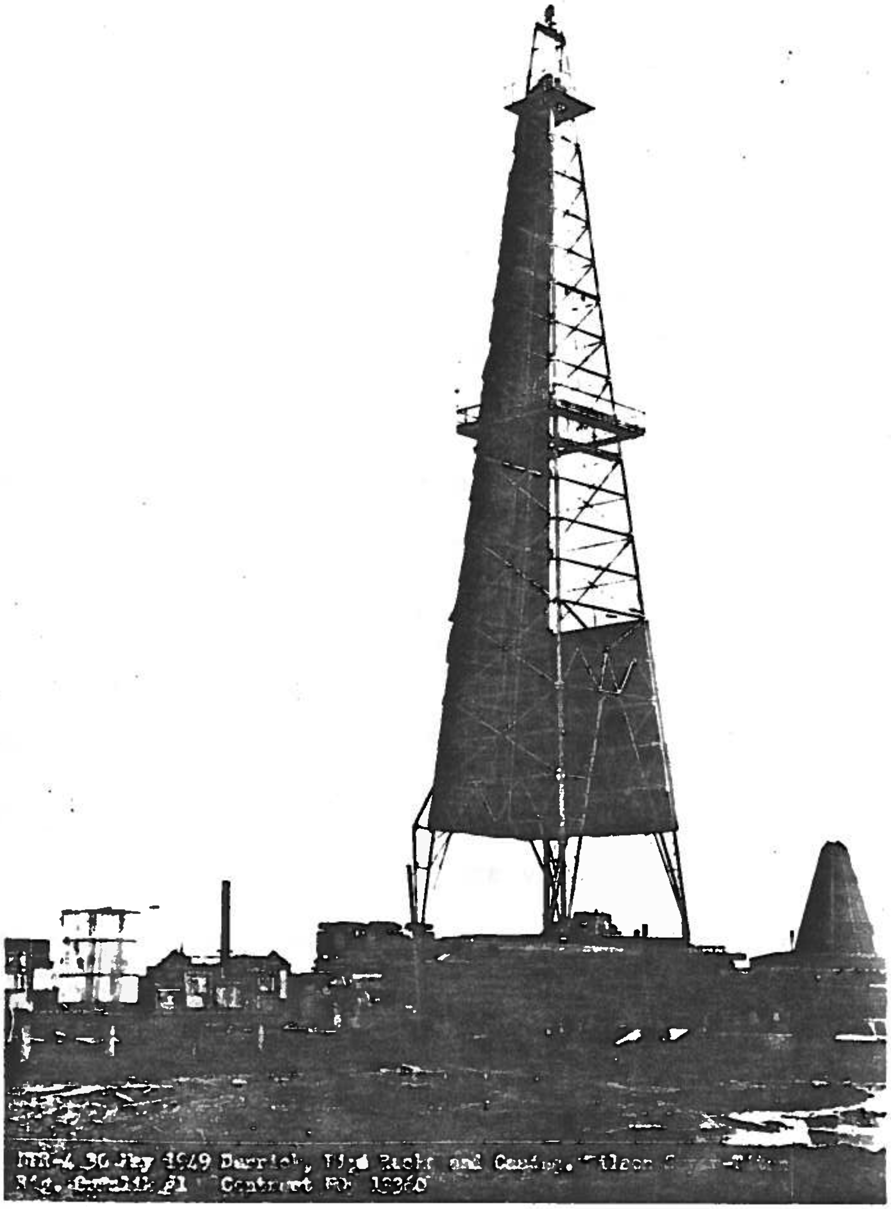
John T. Andrews

Michael C. Grant
Michael C. Grant

Vera Komárková

Sam Shushan
Sam Shushan

Date 5/1/85



Frontispiece. The drill rig at Oumalik shortly before drilling began. U.S. Geological Survey photo for contract NOy-13360, 30 May 1949.

Ebersole, James Jay (Ph.D., Biology)

Vegetation Disturbance and Recovery at the Oumalik Oil Well, Arctic Coastal Plain, Alaska

Thesis directed by Professor Patrick J. Webber

The 1949-1950 Oumalik Test Well allowed study of the previously little-known long-term recovery of northern Alaskan vegetation.

The surrounding undisturbed vegetation was described in order to place the disturbed vegetation into perspective. Classification defined 23 natural and 13 disturbed communities. Ordinations showed that moisture and a pH/organic matter gradient correlated most highly with the variation in vegetation.

Dominant taxa colonizing the disturbed areas are *Carex aquatilis* and *Eriophorum angustifolium* in wet sites and *Arctagrostis latifolia, Poa arctica* and erect *Salix* spp. on mesic sites. Grasses and willows grow more vigorously on mesic disturbed areas than in control areas. Measurements of willows showed that vegetative growth and reproductive effort are greater in disturbed areas, apparently due to warmer soils and greater decomposition rates.

The seedbanks of four undisturbed communities contained 4-10 taxa, which are all present in the mature vegetation. The tussock tundra results from Oumalik and from other studies show a decline in the number of taxa and total seeds with latitude.

Eriophorum vaginatum was not in the seedbank. Seeds of dominant colonizers of the disturbed areas, except for *Carex aquatilis,* were generally not in the seedbank. They probably colonize disturbed areas from seeds arriving after disturbance.

In small areas devoid of vegetation four years previously, vegetative colonization provided most of the cover. Seedlings of 35 taxa were present, and were most abundant on moisture-saturated soils. Cover was greater on the formerly bare areas surrounded by disturbed rather than undisturbed vegetation. Seedlings do not survive in the disturbed willow and grass communities, which apparently follow the inhibition model of succession.

Vegetation in wet sites is disturbed more easily (is less resistent to disturbance), but returns more quickly toward the original state (is more resilient) than mesic or dry vegetation. Because of its faster recovery of production and original floristic composition, it usually would be preferable to disturb wet sites rather than dry or mesic sites.

Extrapolation of Oumalik results is most reliable to northern Alaskan sites on fine-grained sediments in the Northern Foothills and on the Coastal Plain away from the coast.

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CHAPTER I

INTRODUCTION AND SITE DESCRIPTION

Introduction

Since the discovery of oil at Prudhoe Bay in 1968, development in northern Alaska has increased dramatically and will probably continue to expand in scope and area. With the development, has come concern about the impacts on the ecosystems in which the development occurs. Numerous projects have studied the short-term (several years) effects of these disturbances, but an understanding of the longer-term effects on the ecosystems was largely missing. This longer-term perspective is critical to help land managers to make sound decisions on the acceptability of certain impacts and to direct activities to sites that will be least damaged over the longer term.

This research began to fill the gap in knowledge of longer term recovery by studying the recovery of vegetation at the 1949-1950 Oumalik Test Well. The Oumalik Test Well and other similar sites disturbed during the U.S. Navy's petroleum exploration in northern Alaska offer excellent opportunities to observe and study the recovery of Low Arctic (sensu Polunin 1951) vegetation. The disturbances occurred at a known time and were uncomplicated by repeated disturbance or rehabilitation efforts until the cleanup of solid debris from 1976 to 1982 (Schindler and Smith 1983). The activities causing the disturbances and the initial effect on the vegetation and surface can usually be reconstructed from historical records (U.S. Navy 1950, Reed 1958) and evidence on the site. And undisturbed vegetation around the site is available for comparison to the disturbed vegetation. Knowing the original vegetation and having it available for comparison is a rare situation, and avoids the need to reconstruct the potential natural vegetation as in most temperate areas.

During a brief visit to Oumalik in 1978, the vegetation recovery patterns were observed to be much different than at the more coastal Fish Creek site, where a reconnaissance study was done by Lawson et al. (1978). Plants on the disturbed areas, especially the willows, grow more vigorously than the same taxa on undisturbed areas. Interest in explaining these responses, in doing a detailed study of the vegetation at one of these older sites, in evaluating the effects of the 1980 cleanup of solid debris, and in understanding the regional variation in recovery patterns of vegetation in northern Alaska led to this study.

The research began with a classification and ordination of the natural vegetation around the Oumalik well. This gives an understanding of the variation of the natural vegetation and of the environmental factors that correlate most highly with that variation, and provides a framework in which to interpret the disturbed vegetation. It also gives a detailed vegetation description of an area of northern Alaska that was previously not surveyed. A classification of the disturbed vegetation was done to provide communities for comparison to the natural vegetation, including natural disturbances, and an ordination of the disturbed vegetation showed the environmental factors that correlate most highly with the variation in the vegetation. Analysis of the recovery of vegetation was also organized by disturbance type in order to give land managers more long-term information on the response of vegetation to disturbance.

Several more specific studies were done to help answer some of the questions arising from the response of the vegetation to disturbance at Oumalik. A study to evaluate the size and composition of the seedbank of natural communities was done to address the question of whether the colonizers of the disturbed area originated from the seedbank, as at other Alaskan tundra sites, or from seeds dispersed to the area after disturbance. The growth responses of willows in relation to environmental factors were analyzed as a beginning toward understanding the reasons for the vigorous growth of willows, and by extrapolation, other taxa on the disturbed area. Colonization of small bare areas created by removing debris was studied to describe the taxa that colonize, the relative importance of colonization by seeds and vegetative means, and the rate at which colonization occurs. This is useful in evaluating the effects of the 1980 cleanup of solid debris at Oumalik, and also in helping to reconstruct the colonization of the bare areas created by the older Oumalik disturbance.

Several other sites in northern Alaska of similar age and disturbance history as Oumalik were visited briefly so that the regional variation in response to disturbance could be described. These observations also give an indication of the extent to which the detailed Oumalik results can be extrapolated to other northern Alaskan sites.

The observations at Oumalik and other sites prompted construction of models of the resistance (ability to withstand displacement from a given state) and resilience (ability to return to the original state after disturbance) of wet, mesic, and dry vegetation types. The models contrast the recovery patterns of wet and dry vegetation and illustrate the properties of these types that should be considered in making management decisions.

Location

Oumalik Test Well No. 1 is located about 160 km south of Barrow at 69°50'N, 155°59'W (Figure 1.1). It lies at the southern edge of the Teshekpuk section of the Arctic Coastal Plain physiographic province of Alaska (Wahrhaftig 1965). It lies in the Low Arctic zone of Polunin (1951), the Subarctic Tundra subregion of Aleksandrova (1980), and floristic zone 4 of Young (1971).

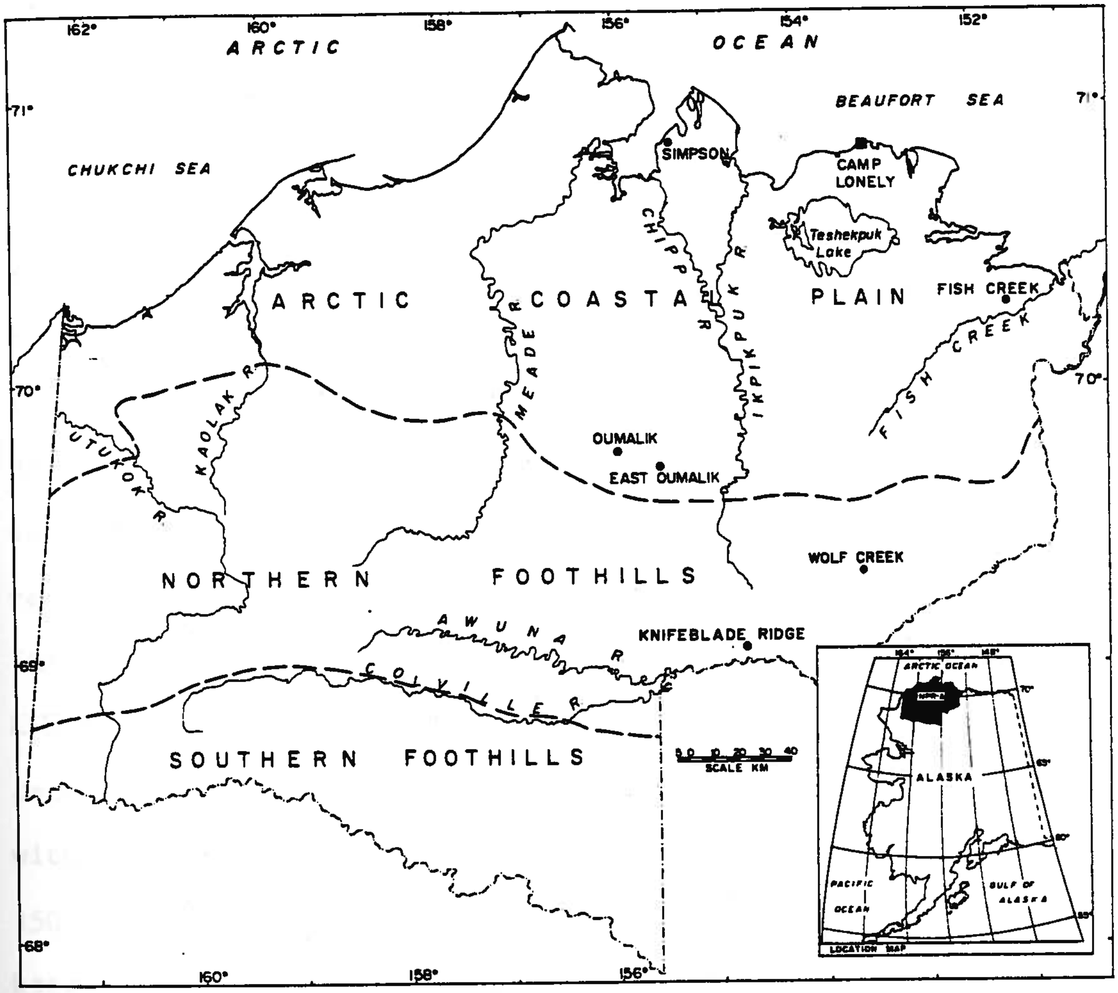

Figure 1.1. Location map of Oumalik in the National Petroleum Reserve-Alaska (NPR-A). Physiographic provinces are after Wahrhaftig (1965). Camp Lonely was the logistical base for the studies. The other sites were visited for brief periods and are discussed in Chapter VII.

Geology

The surficial deposits at Oumalik are part of the heterogeneous Gubik Formation (Black 1964) of latest Pliocene or Pleistocene age (Repenning 1983). At Oumalik the surficial deposits are a relatively uniform silt (Lawson 1983, Williams 1983) with a structure that is massive or faintly to strongly laminated with occasional strata of fine sandy silt (Lawson 1983). This silt is 5.5 m thick at the well head (U.S. Navy 1950), which is presumably a minimum given the low topographic position of the well. The thickness probably ranges up to about 20 m under the residual surfaces (see p. 17) unaffected by the thaw lake cycle. The age of the deposit is poorly defined. At East Oumalik, 20 km ESE of Oumalik, Lawson (1983) has radiocarbon dated organics at depths of 6 and 12 m in these silts at >37,000 B.P. Twelve samples within 2-3 m of the surface gave dates of 5980 ± 115 to 10,550 ± 150 B.P. This upland silt is generally considered eolian in origin because of its texture and position downwind from a large area of dunes (Williams 1983), which are described by Black (1951) and Carter (1981).

The bedrock below the upland silt does not significantly affect the vegetation in the Oumalik area since it is totally mantled by the silts and is deep enough to be permanently frozen. The nearest bedrock exposures are along the Ikpikpuk River, about 45 km east of Oumalik. Descriptions of the lithology and structure below the surficial deposits may be found in U.S. Navy (1950), Dutro (1981), Molenaar (1981), and Bird and Molenaar (1983).

Permafrost

Oumalik lies in the continuous zone of permafrost. The depth to the base of the permafrost in this area is somewhat greater than 200 m (Péwé 1975), and the thickness of the active layer by the end of the growing season ranges from 30 to 50 cm in most areas to about 1 m in the rare, well-drained sites.

Permafrost on the Arctic Coastal Plain frequently has a great deal of ground ice. In the upland silts at Oumalik the amount of ice remains above 70% of the total volume to a depth of 12 m, and the top 2 m is greater than 85% ice (Figure 1.2). In the younger landforms the amount of ice declines more rapidly with depth, but is still > 70% in the top several meters. Ice lenses, which are horizontal layers of ice 1 mm to tens of m thick and several mm to hundreds of m in extent, are an important component of the ground ice at Oumalik. These segregations of ice were formed by water migrating to a freezing front as the sediments froze (Péwé 1975, Washburn 1980). Small to medium-sized ice lenses are common at Oumalik (Figure 1.3).

Ice wedges are another important component of the ground ice and are almost ubiquitous in the Oumalik area, whether they have surface expression or not. These are formed in contraction cracks caused by rapid winter cooling of the ground. The narrow

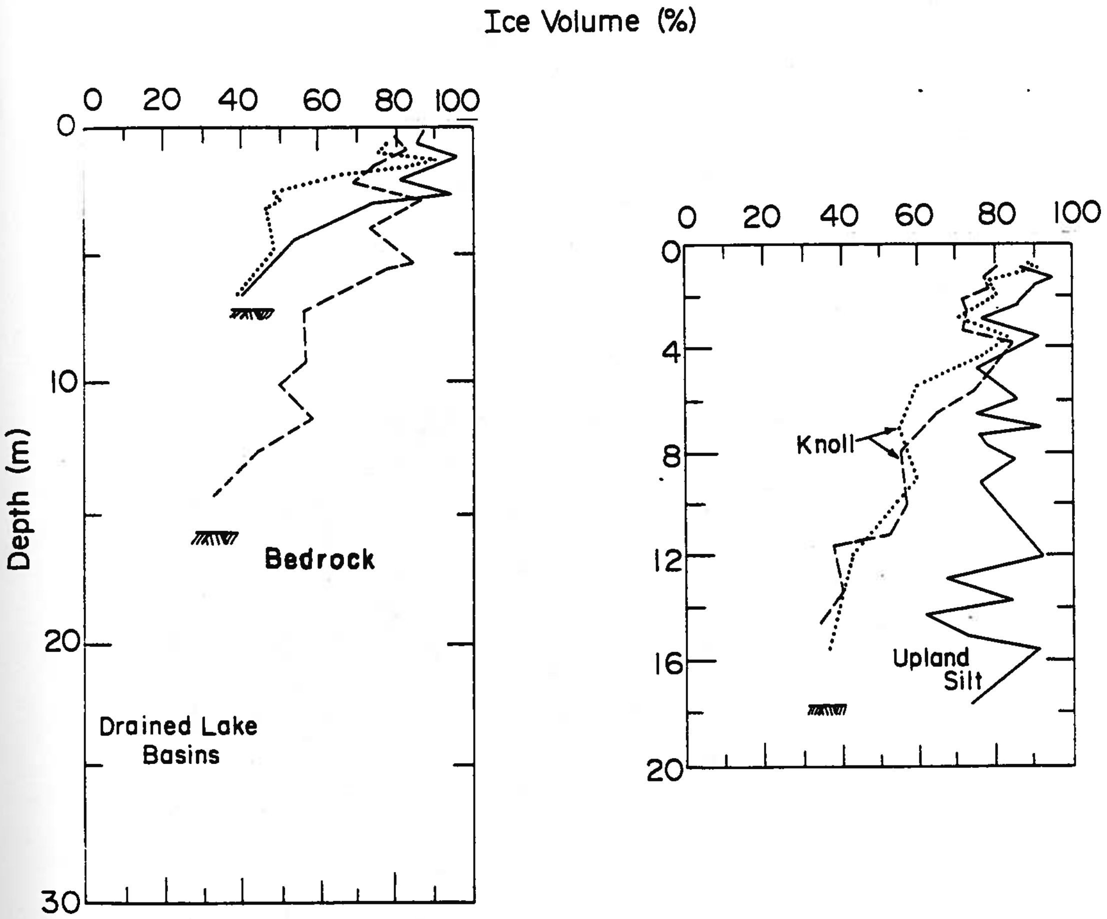

Figure 1.2. Ice content of Oumalik soils. From Lawson (1983).

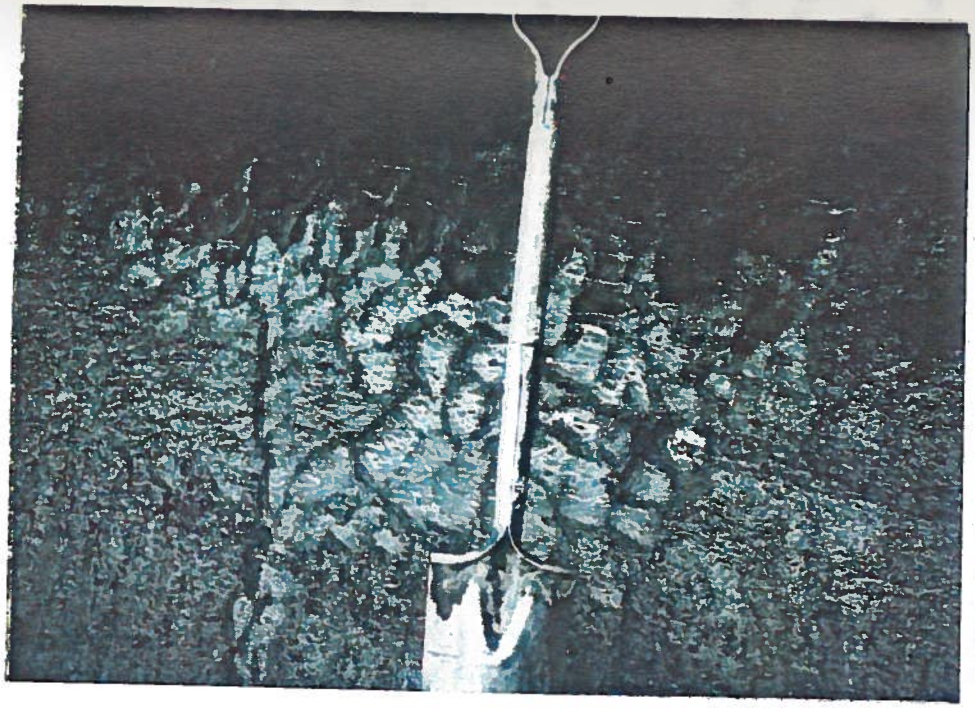

Figure 1.3. Ice lenses at Oumalik. These several cm long by half cm thick lenses are best seen in the darker organic horizon above, but are also present in the silts below. Photo 116-33, 2 August 1981. (All photos are by J.J. Ebersole unless otherwise noted.)

Figure 1.4. Ice wedge. This small wedge is about 80 cm wide. D.A. Walker photo.

cracks fill with winter hoarfrost or spring meltwater which refreezes. Over many years repeated cracking and infilling can produce wedges many meters in depth and several meters wide (Figure 1.4). The increase in volume of the ice wedge causes an upward heaving of the ground on both sides of the wedge, producing rims on either side of the wedge and a trough over the ice wedge. Since the contraction cracks form in polygonal patterns, the microrelief follows the same pattern to form the low-centered polygons typical of wet, flat permafrost environments (Figure 1.5). Low-centered polygons may be converted to high-centered polygons when drainage improves along down-cutting streams or drained lake basins. Tops of ice wedges melt, lowering the troughs and leaving the centers of the polygons elevated (Figure 1.6) (Lachenbruch 1962, Britton 1966, Péwé 1975, Peterson and Billings 1978, Everett 1980a, Washburn 1980).

Pingos of the hydrostatic type (closed system) are also an important geomorphic form and example of ground ice on the Arctic Coastal Plain. They usually form in drained lake basins due to the aggradation of permafrost in the thaw bulbs beneath deep (>2 m) lakes (Mackay 1979). Their drier environments in vast expanses of wet tundra are important habitats for some plants that are generally restricted to these habitats and as denning sites for animals.

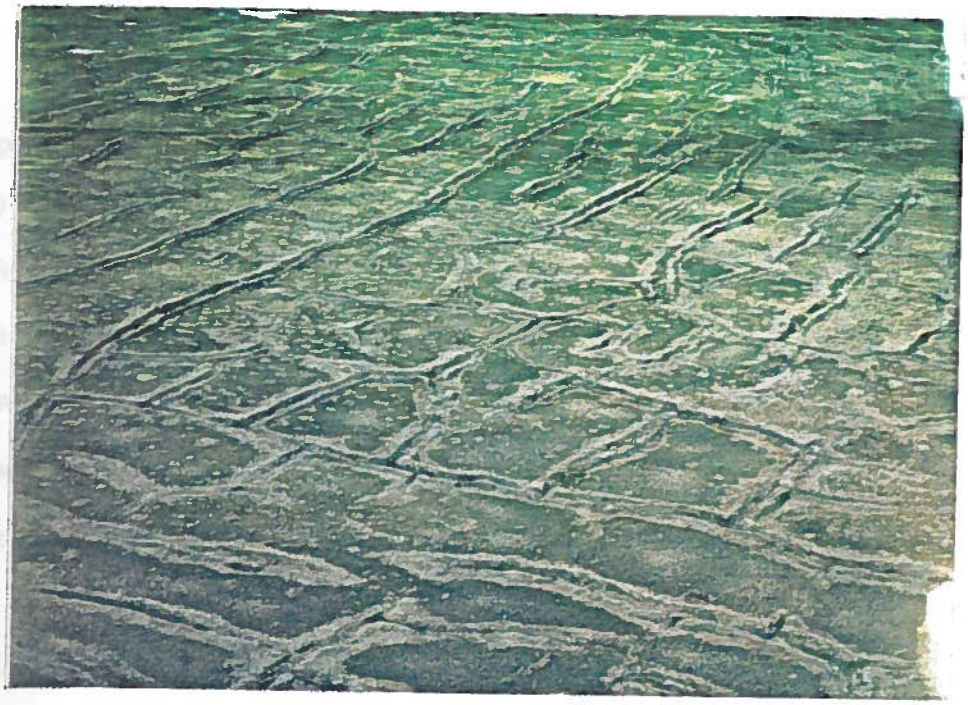

Figure 1.5. Low-centered polygons. D.A. Walker photo 81-108-32.

Figure 1.6. High-centered polygons. D.A. Walker photo 81-4-23.

Palsas (Washburn 1980, 1983) are common at Oumalik in large marshes that have little or no ice-wedge microrelief (Figure 1.7). They are peaty, flat-topped mounds 4 to 8 m in diameter and 30-40 cm above the surrounding marsh. The permafrost below the palsas is ice-rich with many thin ice lenses. The palsas support communities of *Betula nana* ssp. *exilis*, *Ledum palustre* ssp. *decumbens*, *Vaccinium vitis-idaea*, and *Salix planifolia* ssp. *pulchra*.

Frost scars (Everett 1981) (= nonsorted circles [Washburn 1980], frost boils, mudboils) are another important permafrost-related feature at Oumalik (Figure 1.8). These are roughly circular, slightly convex areas about 0.7 to 1 m in diameter where the mineral soil which underlies the organic soils horizons is locally present on the surface. Vegetation cover on the frost scars ranges from none to nearly complete. The mineral soil is apparently forced to the surface due to pressures generated during freezing of the active layer, but the process is not well understood (Washburn 1980). Long-term studies by Johnson and Neiland (1983) showed that little change in lateral extent of frost scars occurred in 20 years and that plant cover increased and decreased over time with little apparent pattern. At Oumalik frost scars are common in tussock tundra and occasional in other vegetation types.

Figure 1.7. Palsa. The dominant plants on palsas at Oumalik are *Betula nana, Ledum palustre* and *Salix planifolia.* Photo 38-25, 29 June 1979.

Figure 1.8. Frost scar. This unvegetated frost scar is about 70 cm in diameter. Photo 22-17, 3 August 1978.

Physical Effects of Disturbance in Permafrost Terrain

Damage to or removal of the surface layers in permafrost terrain can have drastic and long-term effects, especially in areas with large amounts of ground ice. Concern over damage to permafrost terrain and ecosystems caused by the rapidly increasing development in northern regions has led to numerous recent studies on the physical effects of damage (e.g. Brown et al. 1969, Bliss and Wein 1971, Heginbottom 1973, Lawson and Brown 1978, Brown and Grave 1979, Lawson 1982). Even relatively slight impact to the tundra surface can change its energy balance (Haag and Bliss 1974), increase the depth of thaw, and melt ice in the permafrost causing subsidence and possibly further erosion. The energy balance can be changed by darkening the surface, which decreases its albedo and allows greater heat flux into the soil. The darkening can occur by compressing the vegetation and upper soil horizons, making the area wetter and therefore darker, or by removing the light-colored vegetation which exposes darker peat or mineral soil. Compressing the peat also increases the heat flux into the soil by increasing the bulk density and therefore the thermal conductivity of the surface layers. However, the greatest increase in heat absorption is caused by removing the peat, which is a good insulator when wet due to its high specific heat and which has a low thermal conductivity relative to mineral soil (Nakano and Brown 1972). The increased heat flux thaws the soil deeper and melts the contained ice. The meltwater flows away, causing thermokarst and subsidence

(Brown et al. 1969, Bliss and Wein 1971, Heginbottom 1973, Lawson and Brown 1978, Brown and Grave 1979, Lawson 1982).

The thaw of ice-rich permafrost can also cause slumping of the sediments since it produces liquid water in excess of the pore space of the sediments. After the initial subsidence of an area, the thaw extends into the sediments on the sides of the depression. When thawed, these super-saturated sediments can fail, especially at the frozen/unfrozen interface, and flow downward to expose more ice-rich permafrost on the sides of the depression. If the failed sediments are removed by erosion, the process can occur repeatedly and greatly expand the original area of the disturbance. This has occurred extensively at East Oumalik, a well site of similar age and history as Oumalik, where expansion of thermokarst in areas of very high ice content (40-100%) enlarged the affected area into areas not originally disturbed (Lawson 1982). If the disturbance occurs on a slope, gullying can occur in vehicle trails, bulldozed trails, or polygon troughs (Hok 1969, Lawson and Brown 1978, Lawson 1982).

Stabilization of thermal erosion occurs as sediments in subsided areas thicken enough to provide sufficient insulation to prevent further melting of permafrost and as the slope angles of the sides of the depressions become low enough to stabilize. This may occur after only a year or two with only minor subsidence if the surface layers and vegetation are left relatively intact, or it may take longer than 30 years with the original surface and vegetation becoming totally destroyed and subsidence of up to 5 m occurring (Lawson and Brown 1978, Lawson 1982).

Geomorphology and Origin of the Present Topography

The thaw lake cycle is the dominant geomorphic process on the Arctic Coastal Plain. The cycle is hypothesized to initiate from ponds in the centers of low-centered polygons in which warm, wind-driven water erodes polygon rims to produce a small thaw pond which becomes larger and deeper through erosion (Britton 1967). Alternatively, Everett (1980a) hypothesizes that the cycle begins through climatic warming or disruption of the vegetation and organic cover. In either case, ice-rich sediments thaw to produce a small pond which enlarges to a thaw lake by melting of permafrost along its sides and bottom. The size and depth of the thaw lake are limited by regional topography and slope and amount of ground ice (Sellmann et al. 1975). The lakes eventually drain by stream capture or by breaching a low divide. Pingos may form in the drained lake basin (Mackay 1979). Ice wedges are reestablished or reaccentuated if they were not completely thawed, and the cycle may begin again (Britton 1967, Billings and Peterson 1980, Everett 1980a. Some of the thaw lakes at Oumalik are elliptical and oriented in a NNW-SSE direction. The generally accepted theory for this orientation is differential erosion at ends perpendicular to the prevailing ENE winds (Carson and Hussey 1962).

The present landforms at Oumalik are a result primarily of the thaw lake cycle. Much of the terrain is coalesced drained lake basins (Figures 1.9, 1.10) that have flat bottoms and often low-centered polygons. Lacustrine deposits of silt or silty clay with occasional strata of fine sand and organics distributed throughout are 4-6 m thick in these lake basins (Lawson 1983).

In addition to the drained lake basins at Oumalik, there are residual surfaces of upland silt that have not been modified by the thaw lake cycle (Figures 1.9, 1.10). These all have approximately the same elevation, about 15 m above the drained lake bottoms. They are generally very gently rolling with broad interfluves between poorly defined drainages, but are flat if small areas have been isolated by the thaw lake cycle. There are several knolls at Oumalik that are lower than the residual upland surfaces (Figure 1.9). These are upland remnants modified by lake processes with lacustrine deposits mantling silts like those of the residual surfaces (Lawson 1983).

One pingo is in the immediate Oumalik area, about 2 km east of the well site. It is eroded on two sides by thaw lakes and the top of the ice core has melted somewhat (D.E. Lawson, personal communication).

Soils

Soils in northern Alaska are generally poorly developed. The cold temperature regime and waterlogged, often anaerobic,

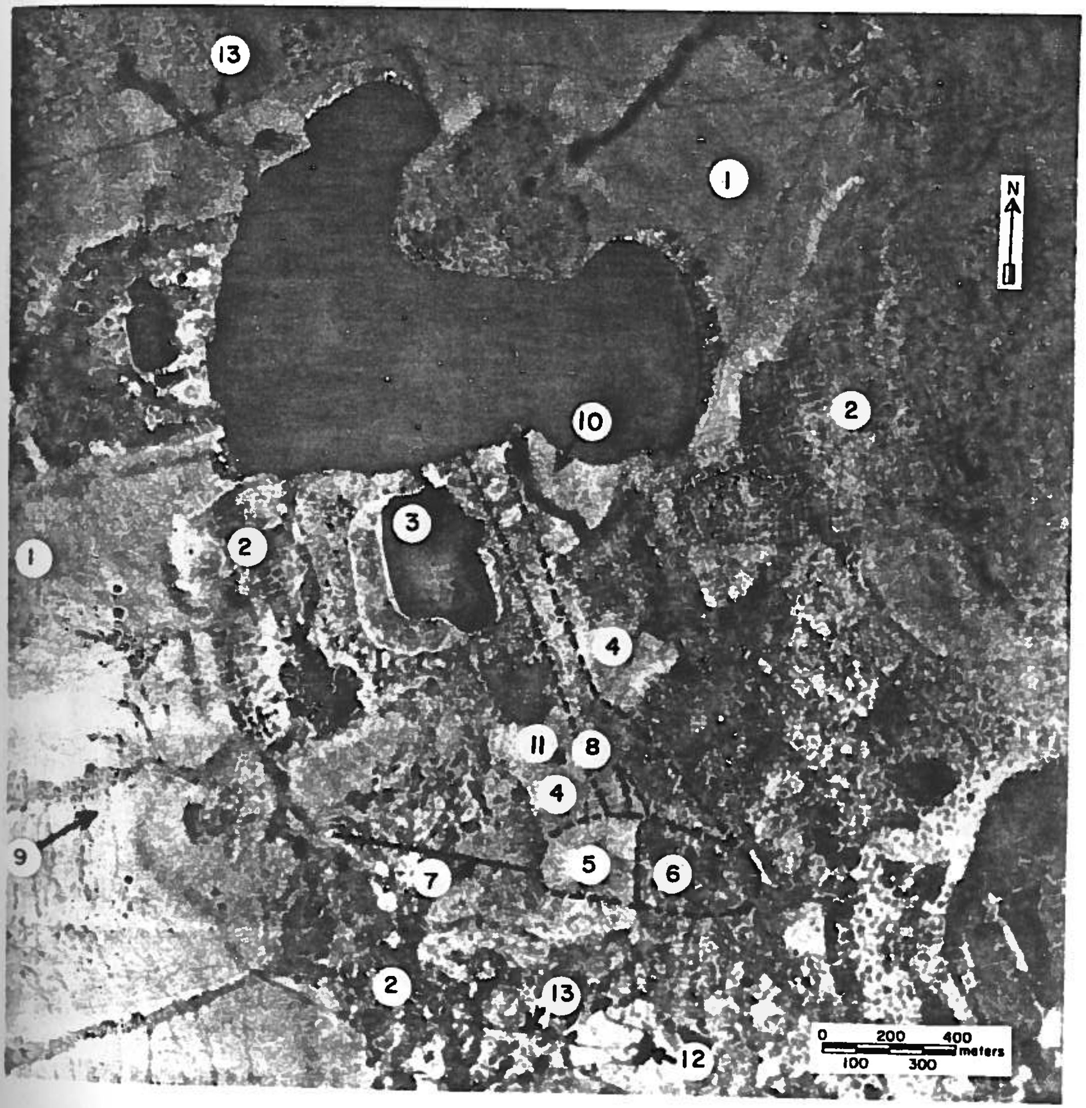

Figure 1.9. Predisturbance aerial photo of Oumalik showing major landforms and areas of disturbance. 1) residual upland surfaces 2) drained lake basins 3) lake that drained between 1949 and 1955 4) knoll 5) 1949-1950 camp 6) drill area 7) runway 8) area of multiple-pass vehicle trails, boundaries approximate 9) 1981 burial site 10) 1980 cleanup camp 11) crushing site 12) core test 13) single-pass vehicle trails. See text for further explanation. BAR photo 106-117, 4 September 1948.

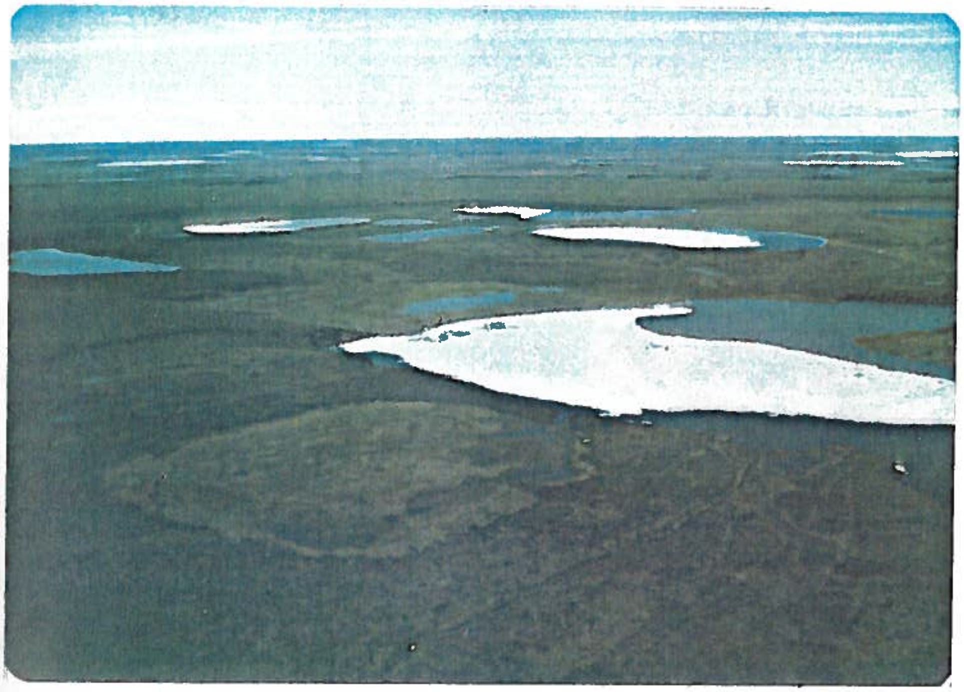

Figure 1.10. Drained lake basins and residual surfaces at Oumalik. Photo taken from over drill area (not visible, see Figure 1.9) looking northwest. P.J. Webber photo, late June 1979.

environment make chemical and biological changes slow, and consequently horizons develop slowly (Tedrow 1977, Everett et al. 1981). Oumalik soils follow this general trend and also show relatively little variation, being limited to the soil orders Histosols, Inceptisols, and possibly Mollisols. (Taxonomy and nomenclature follow Soil Survey Staff [1975]).

The dominant controlling factor of soil development and distribution in northern Alaska is moisture as influenced by topographic position and microrelief (Everett 1980c), and the relationship between landform/microrelief type and soils is very strong (Everett 1975, Walker et al. 1980, Walker 1981).

In marshes, such as the centers and troughs of low-centered polygons and featureless bottoms of drained lake basins, dead plant matter accumulates because decomposition is slow in the cold, low-oxygen environment. This creates a thick upper-horizon composed, by volume, almost entirely of organic matter in various states of decay. If this organic horizon is thick enough, the soil is classified as a Histosol; and if not, it is an Inceptisol. The most common soils in these wet areas are Pergelic Cryofibrists, Pergelic Cryohemists, Histic Pergelic Cryaquepts, and Pergelic Cryaquepts. If the Pergelic Cryofibrists or Pergelic Cryohemists are uplifted as low-centered polygon rims, the increased decomposition transforms them to Pergelic Cryaquepts (Everett 1979, 1980c).

On the poorly-drained, tussock-covered uplands at Oumalik, Pergelic Cryaquepts predominate. These soils have organic horizons overlying a strongly gleyed mineral horizon. The gray to bluish-gray colors of the B horizon are caused mainly by ferrous compounds formed in the anaerobic, reducing environment (Everett 1981, unpublished). Reddish-brown mottles within the gleyed B horizon show the presence of iron-manganese-humate coprecipitates and delimit the extent of oxidizing conditions late in the summer when the water table lowers (Everett 1980c). In these upland soils, cryoturbation (frost mixing) is also an important process. Organics are mixed downward and eruptions of mineral soil come to the surface as frost scars (Everett 1980b), making a mosaic of soil types. These frost scar soils are probably best considered Entisols, but there is no established taxon for them in that order (Everett 1981, unpublished), and they are currently classified as Pergelic Cryaquepts.

Some of the better drained sites at Oumalik, such as centers of high-centered polygons and drier rims of low-centered polygons, may have Mollisols, which are dark, moderately-drained, base-rich soils. These Pergelic Cryaquolls are created by the drainage of Histic Pergelic Cryaquepts, which increases the decomposition and oxidation in the soil. If the soil doesn't meet the $\geq$50% base saturation for a Mollisol, it is classified as a Humic Cryaquept (Everett 1981, unpublished). Base saturation was not measured in the Oumalik soils, but based on pH (usually <5.5) of the centers of high-centered polygons and based on the thinness of the organic horizon in more basic soils (e.g. *Dryas* tundra), Mollisols are probably rare at Oumalik.

Climate

Oumalik has a typical arctic climate with long, cold, dark winters and cool to warm summers. Spring and fall transitions between the two other seasons are brief. Since Oumalik lies about 135 km from the Arctic Ocean, summer temperatures are much warmer than coastal areas of arctic Alaska (Table 1.1, Figure 1.11). Summers are also clearer, evapotranspiration is higher, and there are fewer days with trace amounts of precipitation (Clebsch and Shanks 1968, Haugen and Brown 1980, Walker 1980). Summer weather is determined largely by the direction of the wind. Northeast winds bring fair weather with moderate to warm (10-26°C) daytime highs. In 1979, an unusually warm summer, wind direction often reversed in the afternoons when temperatures were high and brought thunderstorms from the southwest. Winds from the northwest bring cold temperatures (daytime highs of 1 to 5°C) and rain or snow. Humidity is high throughout the summer, and precipitation is light, in the range of 170 to 266 mm cited by Haugen (1982) for the Arctic Coastal Plain. Variation of summer temperature among years is high at Oumalik (Table 1.1). Myers and Pitelka (1979) noted the same high interyear variation at Barrow and explained it with variation in wind direction.

Table 1.1. Selected northern Alaska summer temperatures for the period for which data from Oumalik are available. See Figure 1.1 for location of the sites. Blanks indicate no data or data so fragmentary that it is not used.

		1979[1]					1980[2]					1941-1970[1]
		Oumalik	Sagwon	Franklin Bluffs	Umiat	Barrow	Oumalik	Sagwon	Franklin Bluffs	Umiat	Barrow	Barrow
June	average maximum	13.9	13.1	11.6	14.6	2.3	16.1	13.7		15.8	5.4	2.8
	average minimum	3.1	2.8	1.2	3.4	-2.2	6.3	5.0		7.0	0.2	-1.7
	average	8.5	7.9	6.4	9.0	0.0	11.2	9.4		11.4	2.8	0.6
	absolute maximum	25.0	22.8	22.8	24.4	9.4	21.5	21.0		23.9	10.0	5.6 (ave.)
	absolute minimum	-1.1	-2.8	-2.2	-2.8	-5.6	-0.5	-4.0		-3.9	-4.4	-4.4 (ave.)
July	average maximum	20.5	19.7	18.7	20.5	10.4	13.6		11.2	15.8	4.1	6.8
	average minimum	8.4	9.6	7.2	8.4	1.8	5.2		3.0	3.4	-0.0	0.6
	average	14.4	14.6	12.9	14.4	6.1	9.4		7.1	9.6	2.1	3.7
	absolute maximum	26.7	27.8	27.2	28.3	18.3	25.5		25.0	27.2	12.2	7.2 (ave.)
	absolute minimum	1.7	2.8	2.2	1.7	-2.8	-0.5		-3.0	-2.8	-2.2	0.0 (ave.)
August	average maximum	15.0	16.0	15.5	18.8	10.5	8.7			11.5	3.4	5.6
	average minimum	5.6	7.0	5.7	7.7	5.2	0.3			2.0	-1.4	0.6
	average	10.3	11.5	10.6	13.2	7.8	4.5			6.8	1.0	3.1
	absolute maximum	25.0	26.1	25.6	26.7	21.1	23.0			25.0	17.8	7.2 (ave.)
	absolute minimum	-1.7	-1.7	-1.1	1.1	1.1	-8.0			-4.4	-6.1	0.0 (ave.)

[1] Haugen (1982)
[2] Haugen (unpublished data)

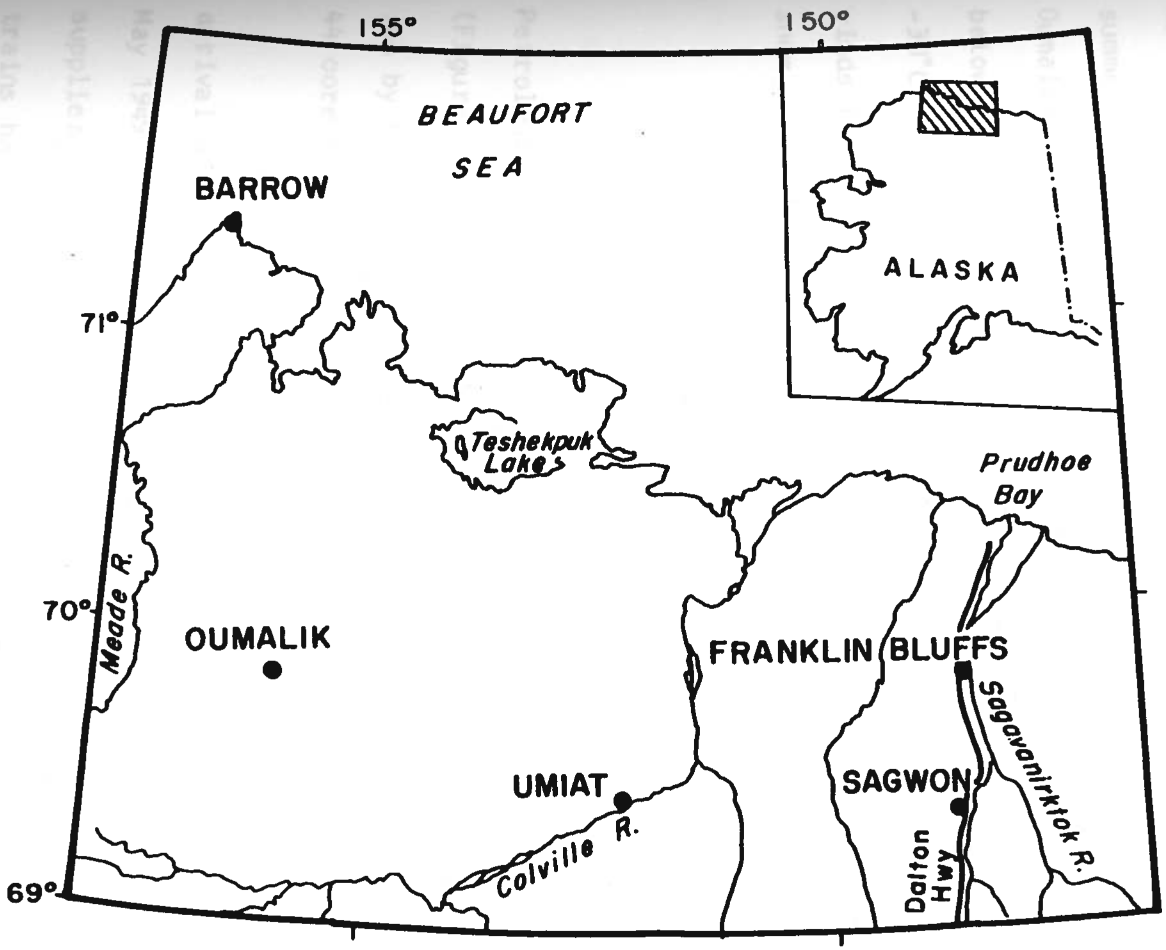

Figure 1.11. Map of climatic stations in Table 1.1.

Winter lasts about 7 mo at Oumalik. Some winter temperature data are available from Sagwon (Table 1.2). Based on distance from the coast, topographic position, and comparison of summer temperature data, Sagwon is the station most similar to Oumalik. The data show 6 mo of the year with average temperatures below -10°C and the same months with absolute minimums below -30°C. In addition to cold temperatures in the winter, strong winds frequently create severe wind chill factors, redistribute snow, and create a hard wind slab on the snow surface.

History of the Well Site

Oumalik Test Well No. 1 was drilled in 1949-1950 in Naval Petroleum Reserve No. 4 (now the National Petroleum Reserve-Alaska) (Figure 1.1). It was part of an exploration program in the Reserve run by the U.S. Navy from 1944 to 1953 that included 36 test wells, 44 core tests, seismic surveys, and geologic mapping (Reed 1958).

Construction at the Oumalik site began immediately after arrival of the first crew on 16 February 1949 and continued through May 1949. The initial crew and the bulk of the equipment and supplies (3829 metric tons) arrived at Oumalik by winter sledge trains hauled from the logistical center at Barrow by heavy tracked vehicles. Although these CAT trains traveled on river ice when possible and were generally used only when the ground was snow-covered and frozen, they caused a great deal of damage to the tundra along the still-visible "Oumalik Trail" from Barrow. Much

Table 1.2. Winter temperature data from Sagwon, Alaska. These data (Haugen 1982) can be used to approximate Oumalik winter temperatures. Comparison of Barrow temperatures for the same period to the Barrow 30-year mean showed this period to be warmer by about 2.5°C. For location of Sagwon see Figure 1.11.

	1977				1978				
	S	O	N	D	J	F	M	A	M
average maximum	6.0	-7.2	-20.1	-14.8	-15.3	-21.5	-21.2	-11.4	-5.8
average minimum	0.6	-11.1	-24.3	-21.0	-20.5	-26.7	-27.3	-20.4	-14.0
average	3.3	-9.1	-22.2	-17.9	-17.9	-24.1	-24.3	-15.9	-9.9
absolute maximum	17.2	6.1	0.0	-1.1	-2.8	-2.8	-6.7	2.8	10.0
absolute minimum	-6.7	-20.6	-34.4	-32.2	-35.0	-42.2	-41.1	-33.3	-23.3

of the damage occurred since "...much rough travel was eliminated, and much wear and tear saved, by a bulldozer attachment on the lead tractor" (Reed 1958, p. 35). Although most of the equipment and supplies were hauled during the winter, in the summer it was necessary to transport 288 metric tons to the site by LVT's (landing vehicle, tracked--an amphibious assault vehicle rated at 4 tons) (U.S. Navy 1950, Reed 1958) with severe damage to the tundra resulting.

For air transportation a 900 m runway (Figures 1.9, 1.12) was tamped down and backbladed in February 1949, and it was again stamped out the following fall as soon as there was sufficient snow. This served for large, multi-engine C-46 and C-47 aircraft which transported about 90 metric tons of equipment and supplies to Oumalik (Reed 1958). During the summer personnel and some supplies arrived via single-engine aircraft on floats which landed on a lake four miles to the northeast. Transportation from the lake to the drill site was by Weasel tracked vehicles (J.F. Schindler, written communication).

The camp (Figure 1.13) was built on a slight knoll (Figure 1.9) and consisted of five Quonsets, one Jamesway, and ten Wanigan buildings with all except the Wanigans on pilings. Thirty people occupied the camp during drilling with additional temporary personnel as needed. The camp was connected to the drill site, which lies in an area of low-centered polygons just to the east of

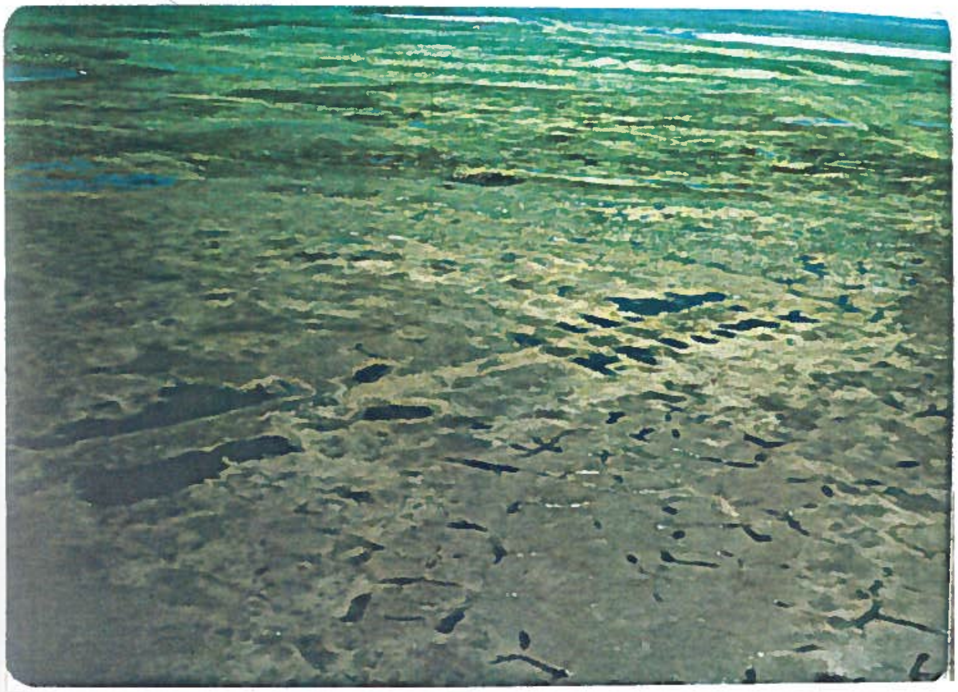

Figure 1.12. Runway at Oumalik. At some places along the length of the runway, soil was bulldozed from the areas that are now ponds to form the runway surface. Photo looking northeast. P.J. Webber photo, late June 1979.

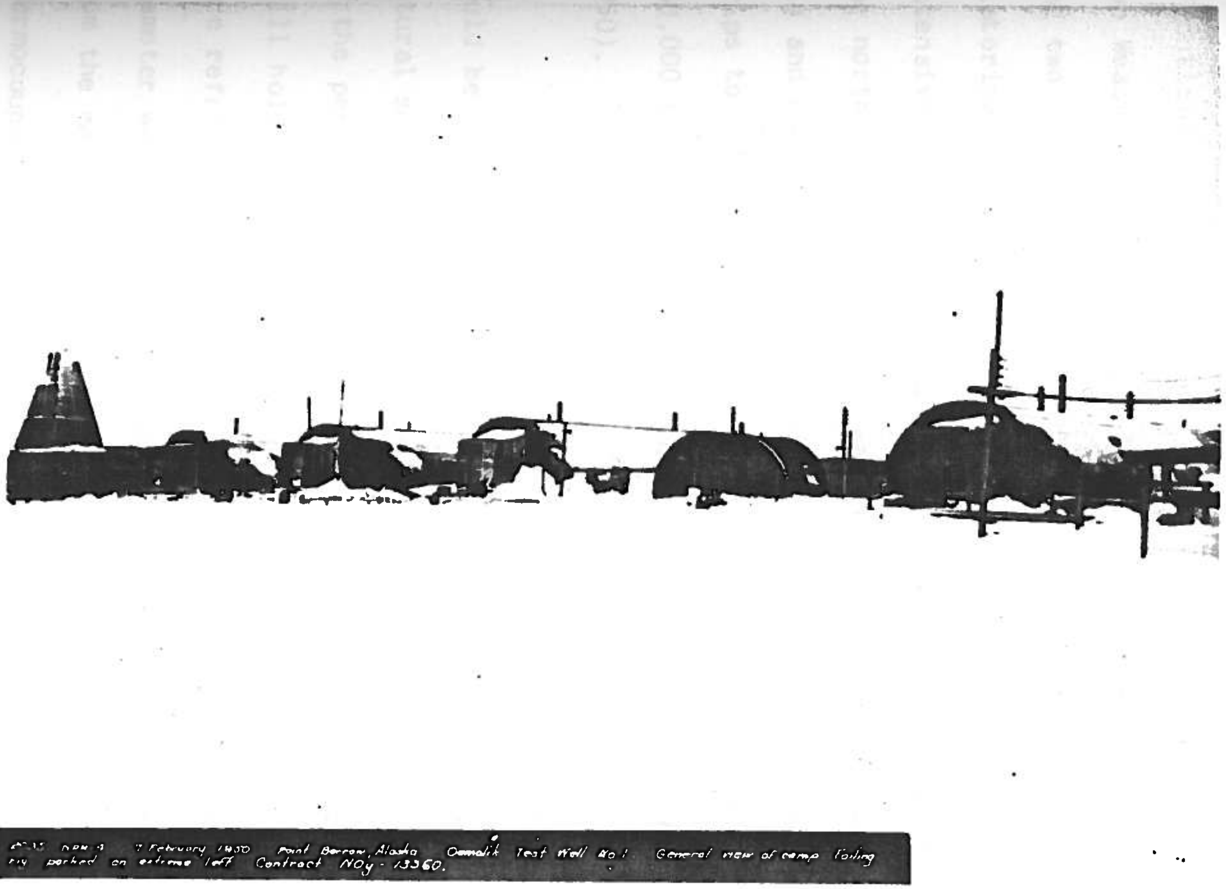

Figure 1.13. Historic photo of camp area. Quonset and Jamesway huts were living quarters. A coring rig is on the extreme left, U.S. Geological Survey photo 2035 for contract NOy-13360, 7 February 1950.

the camp knoll (Figure 1.9), by a wooden boardwalk about 250 m long. Several buildings and numerous storage platforms for pipe, casing, cement, and drill mud were located around the drill rig (Frontispiece, Figure 1.14). The vehicles at the site were two Weasels, one LVT, one D-8 and one D-6 Caterpillar with blades, and two cranes (U.S. Navy 1950). From current evidence and historical photographs, it can be seen that these vehicles drove extensively around the immediate area and to the lake about 1 km to the north. Much bulldozing was done immediately around the drill rig and a bladed track extends from the drill site to the lake. Trips to the lake apparently were for water since an average of 160,000 l wk^{-1}were used during the 45 weeks of drilling (U.S. Navy 1950).

Before construction there was apprehension that problems would be caused by the foundations of the well settling due to natural surface thawing during the summer as well as deeper thawing of the permafrost due to the circulation of warm fluids in the drill hole. To prevent such problems, foundation pilings and sills were refrigerated, and three refrigeration wells 10.2 cm in diameter were drilled to a depth of 73 m at a distance of 1.5 m from the main well. Subsurface temperatures were monitored with thermocouples, and diesel fuel as a refrigerant was circulated from 3 December 1949 to 29 April 1950. The foundation was adequate throughout the drilling operation (U.S. Navy 1950, Reed 1958).

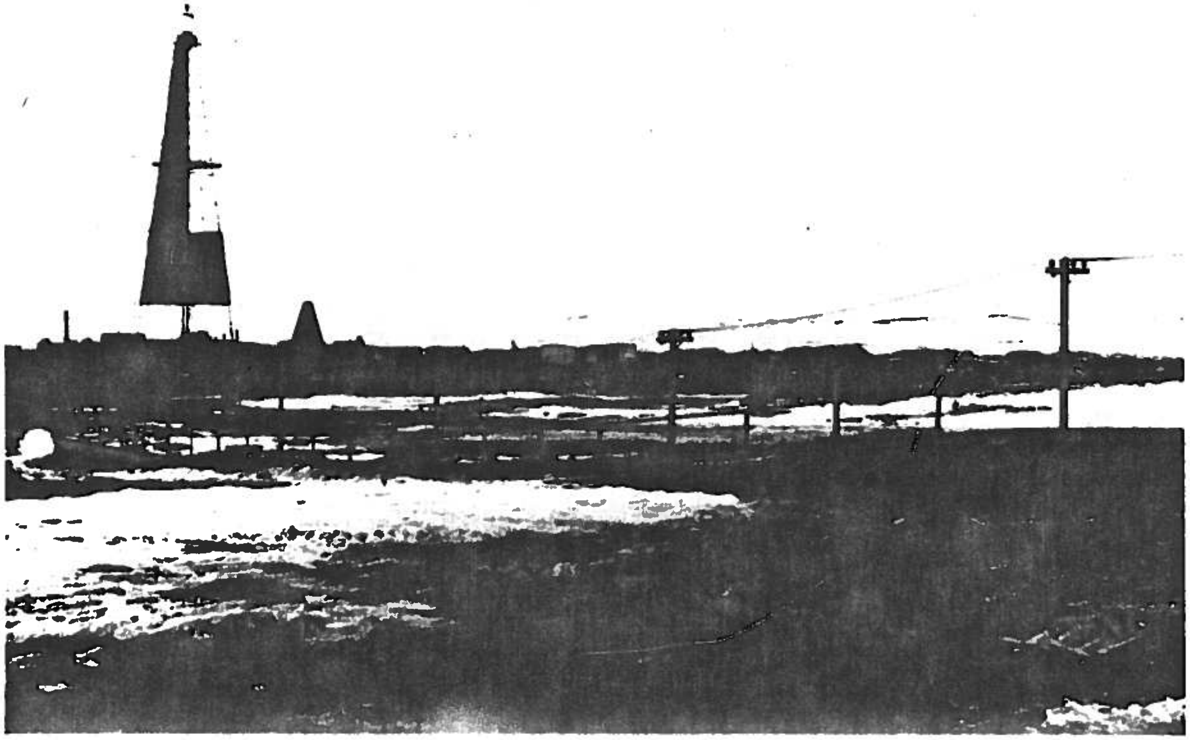

Figure 1.14. Historic photo of drill area from the camp area. Boardwalk connects the drill rig and the camp area. U.S. Geological Survey photo 1843 for contract NOy-13360, 30 May 1949.

The well was spudded on 12 June 1949. Drill cuttings and excess drilling mud were dumped directly onto the tundra surface immediately north of the well (personal observation). The final depth of 3620 m was reached on 23 April 1950, when operations were suspended. No economic shows of gas or oil were found.

The site was abandoned, and buildings and drilling equipment were moved to the East Oumalik site (U.S. Navy 1950, Reed 1958). An immense amount of material was left on the site including roughly 5000 empty 55-gal fuel drums. The barrels were left both scattered (Figure 1.15) and in large piles (Figure 1.16). Other debris left on the site included pilings, lumber and crates (Figures 1.17 and 1.18), pieces of canvas, and many small, miscellaneous items.

The site remained undisturbed until the cleanup of solid debris in June and July 1980 (Schindler 1983, Schindler and Smith 1983). A tent camp for a crew of about 18 people was established on the south shore of the lake 1 km to the north of the drill site. All cleanup was by hand and helicopter to minimize further surface damage. Pilings were cut at ground level, and combustibles were burned in two of the large bare areas exposed by removing large piles of barrels and lumber (Figure 1.19). Barrels were crushed and stockpiled with other noncombustibles on previously undisturbed, tussock-covered uplands 2 km to the west (Figure 1.19). They were buried in March 1981 using bulldozers, and the

Figure 1.15. Scattered barrels left on the site after abandonment. Shallow thermokarsts are in the foreground, and a pile of barrels is in the back right. Photo 51-35, 7 August 1979.

Figure 1.16. Massive pile of barrels. Willows are growing among the jumbled barrels in the foreground and on the left. After the barrels were removed, the bare area was used as a burn site during the 1980 cleanup (Figure 1.19). Photo 38-7, 30 June 1979.

Figure 1.17. Piles of lumber left on the site after abandonment. This was used as a burn site during the 1980 cleanup. Photo 49-22, 11 August 1979.

Figure 1.18. Some of the scattered pieces of wood left on the site. Photo 47-7, 22 July 1979.

Figure 1.19. Burning debris during the 1980 cleanup. This is on the site of the barrel pile in Figure 1.16. Photo 69-17, 7 July 1980.

Figure 1.20. Burial site for non-combustibles removed during the 1980 cleanup. The photo was taken in the third summer after burial. Note the patchy revegetation and the areas of subsidence. Photo 156-27, 11 July 1983.

area was reseeded (Schindler 1983, Schindler and Smith 1983, Tetra Tech 1983) (Figure 1.20).

Additional damage caused by the cleanup was limited to moderate trampling around the tent camp and severe trampling with loss of vegetation at the site where the barrels were crushed. Small amounts of diesel fuel and other hydrocarbons still in the barrels were spilled when they were crushed. The burial pit was dug in a landform with very high ice content (Lawson 1983). Some subsidence below the surrounding terrain had occurred in spots by July 1983. More subsidence of the surface and possibly some subsidence of the areas adjacent to the pit may occur before the site equilibrates.

Animals

This section outlines the known information on the animals found at Oumalik that have significant effects on vegetation similar to that of Oumalik. A list of mammals for the region may be found in Bee and Hall (1956), and information on bird distributions and habits is in Gabrielson and Lincoln (1959) and Pitelka (1974).

Caribou

Oumalik is in the summer range of the Western Arctic caribou *(Rangifer tarandus grantii)* herd (NPRA Task Force 1978a). This herd experienced a drastic population decline due to uncertain reasons in the mid-1970's when it went from about 242,000 animals in 1970 to about 75,000 in 1977 (Davis 1978). Since then, the general feeling is that numbers have increased to some extent although good census data are lacking. The usual winter range of the herd is the Noatak drainage south of the Brooks Range, although in some winters many may stay north of the Brooks Range but north of Oumalik (NPRA Task Force 1978a). In spring, the caribou migrate in large groups across the Brooks Range to the calving ground along the upper Utukok River. After calving, they break into smaller herds for most of the summer before reassembling for the fall migration south. All major migration routes miss Oumalik (NPRA Task Force 1978a). The number of caribou and signs of grazing or browsing during the times I spent at Oumalik were low.

The caribou have definite diet preferences for certain plants. At Atkasook, about 90 km northwest of Oumalik, tethered reindeer avoided very wet areas with emergent vegetation and low-centered polygons with semi-emergent graminoids, and spent more time feeding on lichen ridges, stream and lake banks, and high-centered polygons. *Eriophorum vaginatum* is generally avoided except for flower buds in early spring, which are eaten extensively, or new, green growth of overgrazed tussocks or tussocks along banks or thermokarsts that are unusually green. Evergreen shrubs are rarely eaten. Single graminoids such as *Carex* spp. and *Eriophorum* spp. are eaten, but less than their proportion in the vegetation. *Salix* spp. and *Betula nana* leaves are eaten heavily. On a lake margin *Salix* leaves comprised about 75% of the vegetation taken. Lichens and forbs, especially *Pedicularis* spp., are also important parts of the diet (White and Trudell 1980).

Rodents

Arctic ground squirrels *(Spermophilus parryi)* are not abundant at Oumalik, presumably because of the lack of well-drained burrow sites. They are locally present on the relatively dry and deep-thawing lake bluffs that are eroding and high points of knolls left by the thaw lake cycle.

At Atkasook in July and August forb shoots, seeds, and horsetails made up about 85% of the ground squirrel's diet. In May and June, monocot shoots, mosses, deciduous shrubs, and dried roots were also significant parts of the diet. Most foraging was within 30 m of burrows (Batzli and Sobaski 1980) so impact on the vegetation is local although it may be substantial immediately around burrows (McKendrick et al. 1980).

The two most abundant microtines at Oumalik are *Lemmus sibiricus* (brown lemming) and *Dicrostonyx torquatus* (collared lemming). Most of the following information is from research done by Batzli and Jung (1980) at Atkasook. *Lemmus* is found mainly in wetter habitats, such as polygon troughs and wet meadows, while *Dicrostonyx* prefers drier habitats such as tussock tundra although it also occurs in wetter habitats associated with *Salix* *planifolia.* The summer food of *Lemmus* is primarily monocotyledons, especially *Carex aquatilis* and *Eriophorum* spp. *Dicrostonyx* eats mainly dicotyledons, especially *Salix* spp. and *Vaccinium vitis-idaea.* Other evergreen shrubs are strongly avoided by both species.

Although there is considerable variation among years in population numbers of both microtines at Atkasook, there is no evidence of the extreme cyclic fluctuations found at Barrow. Total microtine density at Atkasook is 1 to 5 animals ha^{-1} compared to Barrow's <1 to >100 ha^{-1}. Densities at Oumalik appear to be similar to those at Atkasook. This smaller number of microtines makes their impact on the vegetation less than at Barrow. Short-term (1-yr) grazing trials with microtines at Atkasook showed no detectable differences from controls (McKendrick et al. 1980). However, girdling of willows by *Dicrostonyx* may be important (Batzli and Jung 1980).

Rodents at Atkasook appear to be important to vegetation because they redistribute nutrients. Nutrients, especially phosphorus and nitrogen, are higher near ground squirrel and lemming burrows where most of the feces and urine are deposited. The productivity and nutrient content of grasses is increased around ground squirrel burrows. Experimental addition of nitrogen and phosphorus increase production of graminoids which supports the hypothesis that the grasses are responding to the increased nutrients (McKendrick et al. 1978, 1980).

Birds

Willow ptarmigan *(Lagopus lagopus)* are the only bird species with a noticeable effect on the Oumalik vegetation. They are occasional to moderately abundant at Oumalik. The variability may be due to cyclic population fluctuations, but the existence of these cycles is not firmly established. Many of the North Slope ptarmigan migrate south of the Brooks Range for the winter, but I have seen scat on the snow surface at Oumalik in April. The birds are most common in mesic areas with a high cover of *Salix* spp. During the winter, they eat bud and twig tips of *Salix* spp.; during the summer, berries and willow leaves; and during the fall, berries and willow buds and twigs (NPRA Task Force 1978b).

Other birds, e.g. geese and swans, can significantly affect vegetation on other parts of the North Slope, but they are not present or are rare at Oumalik (NPRA Task Force 1978c).

Vegetation Overview

The warmer summer temperatures at Oumalik compared to the coast result in a greater number of plant species, greater tussock development, more shrubs, and an increased importance of mosses relative to coastal areas (Cantlon 1961, Clebsch and Shanks 1968, Walker 1981). Vegetation in the Oumalik areas has components from both the Coastal Plain and Foothills provinces. On residual surfaces that are unaffected by the thaw lake cycle, tussock communities typical of the Foothills province cover most of the surface (Figure 1.11). The tussock sedge *Eriophorum vaginatum* dominates these communities. The dwarf shrubs *Betula nana* ssp. *exilis* and *Salix planifolia* ssp. *pulchra* are common, as are the prostrate shrubs *Vaccinium vitis-idaea* and *Ledum palustre* ssp. *decumbens*. Broad, poorly-defined drainage channels on these uplands are dominated by *B. nana* ssp. *exilis*, *S. planifolia* ssp. *pulchra*, and *Carex aquatilis*. At Oumalik, microrelief created by ice wedge formation or degradation is usually not present on these uplands, and the variation in vegetation caused by this microrelief is not present. A vegetation description of the Umiat area that includes these communities can be found in Churchill (1955).

On surfaces that have been reworked by thaw lakes, vegetation typical of the Coastal Plain is present. The flat terrain and presence of permafrost create slow drainage which leads to a wet to moist sedge-dominated vegetation. The vegetation in these low-lying areas is strongly affected by the succession (Britton 1967, Webber 1978, Billings and Peterson 1980) associated with the thaw lake cycle (Hopkins 1949, Everett 1980a). After a lake is drained, mosses are the first invaders, followed by *Saxifraga cernua*, *Eriophorum scheuchzeri*, and *Arctophila fulva*. *Eriophorum angustifolium* and *Carex aquatilis* enter later, and eventually *C. aquatilis* dominates, with lesser amounts of *Salix* spp., *Eriophorum* spp., and herbaceous dicots present.

On a finer scale, the vegetation of the drained lake basins is controlled by the microrelief associated with ice wedges (Wiggins 1951, Cantlon 1961, Britton 1967, Webber 1978, Walker et al. 1980, Walker 1981). Differences in microrelief height of a few tens of centimeters can create differences in communities through the direct and indirect effects of soil moisture. Rims of low-centered polygons may support a community of *Carex aquatilis, C. vaginata, Dryas integrifolia.* and *Salix planifolia* ssp. *pulchra* while the centers are dominated by *Carex aquatilis, C. chordorrhiza,* and *Eriophorum angustifolium* ssp. *subarcticum.* Troughs of high-centered polygons are dominated by *C. aquatilis* and *E. angustifolium* ssp. *subarcticum,* while the centers are a *Betula nana* ssp. *exilis-Ledum palustre* ssp. *decumbens-Vaccinium vitis-idaea* -lichen heath.

Other vegetation studies of Coastal Plain vegetation in northern Alaska include Webber (1978) at Barrow, Komarkova and Webber (1980) at Atkasook, Komarkova and Webber (1978) at Fish Creek, Walker (1981) at Prudhoe Bay, and Walker et al. (1982) in the Arctic National Wildlife Refuge in northeastern Alaska.

CHAPTER II

NATURAL VEGETATION

Introduction

Natural vegetation, as used here, means vegetation not anthropogenically disturbed. Natural vegetation includes vegetation affected by "natural" disturbances such as animal activity, frost action, thermal and mechanical erosion, and draining of thaw lakes.

Methods

Vegetation Sampling

The vegetation within about 3 km of the test well was sampled using the relevé method (Westoff and Maarel 1978, Mueller-Dombois and Ellenberg 1974). Sample sites were chosen subjectively to represent the full range of vegetation in the area with replication. Stratified, subjective sampling is used more often by plant ecologists than regular or random sampling (Gauch 1982), and has the advantages over regular or random sampling of being more rapid, better able to represent the full range of communities, and of not sampling floristically or environmentally nonhomogeneous areas. The disadvantages are that the observer's preconceptions and biases may cause errors and that statistical procedures are limited to descriptive purposes rather than hypothesis testing since the assumption of random sampling is violated (Gauch 1982).

Sample sites were chosen for uniformity in floristic composition and environmental conditions. A conscious effort was made to sample those homogeneous areas intermediate in floristic composition between other community types. The plot shape and size were varied to sample homogeneous areas. The size was about 25 m^2 if possible and was normally greater than the 10 m^2 minimum given by Westhoff and Maarel (1978) for this type of vegetation. In some cases, e.g. moss hummocks and thrust features, the size was necessarily smaller. Each plot was marked with a stake, and its location marked on aerial photographs.

For each relevé, plants that could be identified in the field were listed along with their percent cover. Plants whose identities were uncertain (mostly mosses and lichens) were collected for identification in the laboratory and/or for verification by experts. See Appendix A for a list of plants collected in the Oumalik area and for notes on voucher specimens.

At each sample site numerous environmental factors were measured or estimated (Table 2.1). A simple soil description was done, and soil was collected at a depth of 10 cm for physical and chemical analysis (Table 2.2). Ten cm was chosen as the depth to sample because most roots occur in the uppermost 10 cm (Dennis and

Table 2.1 Site description data collected at each relevé site

	units
microrelief type	-----
microrelief height	cm
slope aspect	degrees from true north
slope inclination	degrees
depth of thaw	cm
water cover	%
bare soil cover	%
depth of water	cm
site moisture	ordinal scale*
soil moisture	ordinal scale
summer air temperature	ordinal scale
duration of snow cover	ordinal scale
wind	ordinal scale
surface age	ordinal scale
surface stability	ordinal scale
cryoturbation	ordinal scale
intensity of disturbance	ordinal scale
caribou sign	ordinal scale
microtine sign	ordinal scale
ground squirrel sign	ordinal scale
ptarmigan sign	ordinal scale
other bird sign	ordinal scale
insect sign	ordinal scale
other animal sign	ordinal scale
total animal score	sum of animal scores

*Ordinal scales are in Appendix C. They are from Walker et al. (1979), who modified them from Komárková (1979).

Table 2.2. Physical and chemical soil characteristics determined for selected relevé sites.

parameter*	units
pH	--
$N\text{-}NH_4$	ppm
$N\text{-}NO_3$	ppm
N-total	ppm
P	ppm
K	ppm
Ca	ppm
Mg	ppm
cation exchange capacity	meq/100 g
percent sand	Wentworth scale
percent silt	Wentworth scale
percent clay	Wentworth scale
organic matter	%
hygroscopic moisture	%
water absorption	%
field capacity	%
wilting point	%
available water	%
carbonates	%

*Chemical analysis was done at the University of Alaska Agricultural Experiment Station, Palmer. The methods used were:

pH	McLean (1975)
$N\text{-}NO_3$	Technicon (1973a), Keeney and Nelson (1982)
$N\text{-}NH_4$	Technicon (1973b)
N-Total	sum of $N\text{-}NO_3$ and $N\text{-}NH_4$
P	Technicon (1973c), Olsen and Sommers (1982)
K, Ca, Mg	Carson (1975), Knudsen et al. (1982)
CEC	Chapman (1965)

Physical analysis was done at the INSTAAR Sedimentology Laboratory. The methods were:

particle size	pipette method of Robinson (1922)
organic matter	Walkley and Black (1934)
hygroscopic moisture	weight loss of soil from air dry to oven dry (105°C), relative to oven dry weight
water absorption	weight of water absorbed upward into soil, relative to oven dry weight
field capacity	weight of water retained by soil in pressure membrane apparatus with pressure differential of 1/3 bar, relative to oven dry weight
wilting point	pressure membrane apparatus, 15 bars
available water	difference between field capacity and wilting point
carbonates	Dreimanis (1962), but no separation of particles by size

Johnson 1970, Shaver and Cutler 1979), and because it allows direct comparison with numerous other samples from northern Alaska by other members of INSTAAR's Plant Ecology Laboratory. Soil analysis methods are referenced in Table 2.2. The environmental factors are listed for each sample and graphed by community in Appendix C.

Data Analysis

Both classification and ordination techniques were used to analyze the vegetation data. In the past these two methods were seen as mutually exclusive, and plant ecologists expended a great deal of effort debating whether classification or ordination was the preferred technique. The method chosen depended on one's view of the "true" nature of vegetation. If the researcher's conceptual model was that vegetation is composed of discrete community units, he or she chose classification to analyze and present the results of the research. If the model was that vegetation varied continuously, then ordination was used.

At this time that strong dichotomy between the two methods no longer exists. The choice of analysis and presentation is made on the basis of research purpose (Webber 1978, Gauch 1982) rather than on one's concept of the "true" nature of vegetation. If the goal is to investigate and communicate the relation of vegetation and/or species to environmental gradients, then ordination is used. If discrete units are needed for mapping, management, experimentation, or ease in communication, then classification is used. Using classification does not imply rejection of the idea that communities vary continuously (Whittaker 1975); and conversely, using ordination does not deny that it is useful to think of vegetation occurring in more or less discrete units. The two methods are seen today as complementary and are often used together (Webber 1978, Westhoff and Maarel 1978, Komárková 1979, 1980, Gauch 1982).

Of the 269 relevés done at Oumalik, 87 were selected for the ordination analysis, and 53 of these were of natural vegetation. This large reduction in sample size was necessary because financial constraints limited the number of soil analyses that could be done, the time necessary to identify bryophytes and lichens is immense, and some of my first relevés were of poor quality due to my initial inexperience. An additional 61 relevés with only vascular plant data were used to help define communities.

Data transformation. For all numerical analyses, percent cover of each species was transformed using a slight modification of the ordinal transformation of Westhoff and Maarel (1978: 309) (Table 2.3). The slight modification was necessary since the original data were taken in percent cover rather than using Braun-Blanquet cover-abundance values. The transformation was done for several reasons. For the mosses that I identified in the lab, reconstructing what the percent cover had been in the sample was not always possible, but I could quite reasonably assign a class of

Table 2.3. Ordinal transformation of cover values. This transformation is a slight modification from Westhoff and Maarel (1978: 309).

Percent Cover	Transformation
<1	1
1	2
2-3	3
4-5	4
6-12	5
13-24	6
25-49	7
50-74	8
75-100	9

the transformation to each of the species. Also, it seemed to me that this transformation, which gives proportionally greater weight to rarer species compared to abundant species than percent cover does but not so much as the octave scale (Gauch 1977, 1982) or presence/absence, is closest to how I mentally weight abundances when looking at vegetation. Maarel (1979) has recommended this type of intermediate transformation for similar reasons. Gauch (1982) justified using transformations for several reasons. First, since species abundances of replicate samples typically have a scatter of ± 15 to 100% of the mean, estimating abundance with an accuracy greater than the noise in the data may not be ecologically meaningful. Second, results of ordinations are affected little even by severe rounding of input data, and finally, the Braun-Blanquet tablework is based primarily on presence/absence rather than abundance values.

Classification. The Oumalik vegetation was classified to provide an inventory of Arctic Coastal Plain vegetation from an area previously undescribed, to permit comparison with other northern Alaskan sites, and to provide a basis on which to describe the response of vegetation to disturbance. The Braun-Blanquet table method (Mueller-Dombois and Ellenberg 1974, Westhoff and Maarel 1978) was used to determine the communities. The Braun-Blanquet method is the most common classification method in Europe, but is less frequently used in English-speaking countries.

It uses the entire floristic composition of samples to classify them. The assumptions of the method are that the full species composition of communities expresses the relationships to each other and to the environment better than other community characteristics and that certain species (character or diagnostic species) are more sensitive expressions of these relationships than others (Whittaker 1975).

The advantages of the method are that it allows human input that cannot yet be quantified into the classification process, that results from many studies can be incorporated into a single system, that it uses information on all the species to make classification decisions, and that species and samples are simultaneously arranged. The disadvantages are that it requires workers trained in the method, it is subjective and results will vary some with the ecologist using the method, and it is difficult to apply to new areas (Westhoff and Maarel 1978, Gauch 1982).

Other community characteristics that can be used as a basis for classification are dominance and physiognomy. Physiognomy is appropriate for classifying the vegetation of large areas such as continents or the world into broad types such as biomes. The dominance approach is useful for smaller areas and finer resolution, but when dominant species are geographically and/or ecologically wide-ranging (for example *Carex aquatilis* and *Salix planifolia* ssp. *pulchra* in this study) the community types that result include a great deal of variation (Whittaker 1975). Neither of these approaches is satisfactory for the fine resolution in the small area that this study needed.

More objective, numerical techniques have been developed for classifying vegetation. One of these, a dendrogram produced by an agglomerative, average-linkage algorithm based on percent similarity using species abundances (INSTAAR Plant Ecology Lab program ASPEN) was tried, but it failed to produce the desired resolution. Some identifiable clusters were produced, but they were broader than desired for this study. Also, series occurred in which samples were joined one at a time at progressively lower levels of similarity to a group (chaining), an undesirable outcome in classification. Other numerical techniques exist (perhaps most notably TWINSPAN, two-way indicator species analysis [Hill 1979a, Gauch and Whittaker 1981), but they were not easily available. In any case, the classification generated using the Braun-Blanquet method was entirely satisfactory.

In the Braun-Blanquet tablework groups of character species (or in some cases, taxa at other levels) are sought which define communities. Character species normally occur in the given community and are absent, less frequent, or occur with less abundance in other communities (Westhoff and Maarel 1978). The matrix of species by relevés is rearranged to obtain blocks of character species occurrences along the main diagonal. Species that are somewhat more wide-ranging, e.g. occurring in two or three communities, are also useful in this process. Rare and wide-ranging species are kept as separate groups since they are not useful in defining communities even though some of the wide-ranging species may be dominants. Some of the wide-ranging species may be character species of Braun-Blanquet syntaxa at levels above the association. The communities are taken from the final table. See Westhoff and Maarel (1978) for a more complete description of the method.

In this description of the Oumalik vegetation the communities obtained from the table work are not named as formal Braun-Blanquet associations and are not proposed as associations in the formal Braun-Blanquet syntaxonomy. The area sampled was too limited, the sample size is too small, and I am too inexperienced with the method for this to be done, especially in an area where so little vegetation work has been done with the Braun-Blanquet method.

Ordination. Indirect ordination was also used to analyze the vegetation data. The purpose was to investigate the relation of environmental factors to the vegetation and to infer the controlling factors (Bray and Curtis 1957, Austin 1976a, Whittaker 1978, Greig-Smith 1980, Gauch 1982). The ordinations are useful both for helping the ecologist understand vegetation-environment relationships and for communicating that information to others. Indirect ordination was chosen instead of direct ordination because of the research question. Direct ordination is useful when the relationships of samples and species to known environmental gradients are sought. Its weakness is that the important environmental gradients must already be known or guessed at (Hill 1974, Gauch 1982). When the ecologist wishes to investigate the controlling factors of the vegetation, as in this study, indirect ordination is the best technique.

Indirect ordination attempts to reduce the many-dimensional vegetation data into a few dimensions so that it can be better comprehended within the limitations of the human mind, better communicated within the limitations of pen and paper, and more easily related to environmental factors. The way in which this is done can be conceptualized as starting with an n-dimensional species space where each axis represents a species in the data set. Each sample has a score on an axis corresponding to the abundance of that species in the sample, and its location in the species-space is determined by the abundances in it of all the species. Even though this space has many dimensions, the axes are not orthogonal since the occurrence of a species is frequently positively or negatively correlated with the occurrence of others. This means that much of the variation of the data set lies along only several vectors through the space. It is this property that allows the reduction of a many-dimensional data set into just a few dimensions with a minimal loss of information. The axes of this few-dimensional space are now complex floristic gradients, and the samples are plotted within this space.

In addition to summarizing the data set in this way, the second goal of indirect ordination is to relate environmental gradients to the floristic space that is created. Environmental factors include the obvious abiotic factors such as moisture and snow, and also historical (disturbance) factors (Bray and Curtis 1957, Gauch 1982) and biotic factors, such as herbivore and pathogen effects (Austin 1976a). The purpose of relating these factors to the space is to conceptually change the floristic space into an ecological space in which each sample is positioned according to its environmental characteristics. The results are used to infer and generate hypotheses on what the controlling environmental factors of the vegetation are.

This approach to the study of vegetation is very useful and is a well-established technique in plant ecology. However, it suffers from the same faults as all inferential ecology. Relationships of environmental factors with species or community variables are nonlinear and complex. Factors interact, forming complex environmental gradients (Billings 1952, Whittaker 1967, Webber 1971, 1978), and not all the important factors might have been measured. In addition, it is a correlative approach and determines only association of environmental change and vegetation change. Cause and effect relationships cannot be determined. Another weakness of indirect ordination is that it cannot reveal anything about the importance of plant-plant interactions, most notably competition. The sample positions and the species ecological ranges all reflect the workings of these interactions, but there is no way of assessing their importance.

However, if these short-comings are recognized, the approach is extremely useful. It reduces the vast amount of information in the relevé by species matrix to a more comprehendible form which provides a basic description of the vegetation and its variation and relates the change in vegetation to change in environmental factors. This is useful in and of itself and also for generating hypotheses for later experimental work investigating the controls on the ecological distributions of species and the environmental controls of community composition (Whittaker 1967, Austin 1976a).

Detrended correspondence analysis (DCA) as described by Hill and Gauch (1980) and as programmed by Hill (1979b) in the program DECORANA was chosen as the indirect ordination technique. The computational details of DCA are in Appendix D, and the method is discussed from an intuitive approach here. DCA is an improved version of reciprocal averaging (RA) (= correspondence analysis), and is an eigenvector technique closely related to principal components analysis and canonical correlation (Hill 1974). Conceptually, both RA and DCA can be thought of as extensions of the weighted-averages ordination of Whittaker (1956) and Curtis (1959). In the weighted-averages technique each species is subjectively assigned a score according to its position on one environmental gradient, e.g., a score of one for species with modes at the dry end of the moisture gradient and ten for species at the wet extreme. Scores for samples are the averages of the species scores that occur in them, with each species score weighted by the value of that species in the sample. The sample scores are used to arrange the samples along the given environmental gradient, in this case moisture. Additional axes can be created by assigning species scores on other gradients. The main disadvantages of this method are the subjectivity in assigning scores to species and the necessity of knowing or guessing the important environmental gradients before doing the analysis.

RA improved on the weighted averages technique through an iterative procedure which begins with arbitrary species scores and uses weighted averages to calculate sample scores. The sample scores are then used to calculate new species scores. The procedure is repeated until scores for both samples and species stabilize to the unique solution, producing simultaneous sample and species ordinations. Additional axes can be calculated by correcting for previous axes, and repeating the iterative procedure. This has advantages over weighted averages in objectivity and simultaneous species and sample ordinations, but as in all indirect ordinations produces axes that may be difficult to interpret environmentally.

Other commonly used ordinations are principal components analysis (PCA) and polar ordination (PO). Theoretically, RA and its modification DCA should be superior to PCA because they avoid the incorrect assumption of PCA that species have linear responses to environmental gradients (Beals 1973). They are expected to be better than PO because they avoid basing ordinations on similarity measures of samples to only a few reference samples. Sample similarity measures have the undesirable property of approaching a limit as ecological distance between samples increases, which causes the overall patterns in ordinations to be distorted even though local patterns are correct (Gauch 1973). They are also expected to be better than PO because their axes are constrained to be orthogonal.

The theoretical advantages of RA over PCA and PO have been substantiated by tests with both simulated and field data. RA consistently reproduces the structure of simulated data better than the other methods, and in particular avoids involuting the ends of longer vegetational gradients as PCA does (Austin 1976b, Gauch et al. 1977). (For an exception, in which RA involuted a coenocline, see Austin [1976b]). With field data, RA simply produces more interpretable ordinations than PCA or PO (Hill 1973, Austin 1976b, Robertson 1978, Moral 1980, Gauch 1982). However RA still retains the undesirable arch effect of PCA (Gauch et al. 1977).

There are also nonmetric methods of ordination which maintain only the order relationships of samples in the output and do not seek to maintain a linear relationship between the input sample dissimilarity matrix and the output distances (Prentice 1977). They, therefore, may have the milder assumption of monotonicity (Prentice 1977) about the shape of the species-abundance curve rather than the linear assumption of PCA. Multidimensional scaling is the best known and most effective of this group of techniques. It can often produce ordinations about as satisfactory as RA, but also has some serious drawbacks. It is an iterative process, and the final outcome is not necessarily unique or even satisfactory, depending on the initial configuration (Gauch et al. 1981, Gauch 1982). Results vary with the number of dimensions calculated and best results depend on choosing the proper number; this can be difficult to determine with field data (Moral 1980). All nonmetric methods are very demanding of computer time, and their application to large data sets may be impossible (Hill and Gauch 1980, Gauch et al. 1981, Gauch 1982).

DCA is an improved modification of RA, and has been directly tested against other techniques and shown to be superior (Hill and Gauch 1980, Moral 1980, Gauch et al. 1981, Gauch 1982). At this time it is the best single choice for indirect ordinations (Hill and Gauch 1980, Gauch et al. 1981, Gauch 1982). DCA corrects the arch problem of RA by detrending axes subsequent to the first with respect to previous axes so that they have no systematic relation with previous axes. By contrast, in RA subsequent axes are constrained to only be orthogonal to previous axes, allowing the common quadratic relationships (arch) to occur. The second major fault of RA is that the ends of the gradient are compressed relative to the middle. This means that the same ecological distance is represented by different distances in various parts the ordination diagrams, an undesirable property. DCA corrects this problem by equalizing as much as possible the mean within-sample dispersion of the species scores at all points along the gradient. This average within-sample variance is set to 1, which means that the "average" species-abundance curve has a standard deviation of 1. The ordination axes are scaled in these standard deviation units (sd). In these units, an average species appears, rises to its mode, and disappears in about 4 sd, and samples that are 1 sd apart are about 50% similar. Thus, 1 sd is approximately equal to a half-change of Gauch (1973).

Even though DCA is apparently the best available ordination technique, it has several weak points. Like all other ordinations, it does not cope with extreme outliers well, and these are best eliminated before analysis. The widths of large gaps in the data can be poorly estimated although short gaps are handled well. Species ordinations are not as good as sample ordinations, and species modes which lie outside of the sampled region may be estimated poorly (Hill and Gauch 1980).

The natural vegetation data set was ordinated in two ways in an attempt to understand the effect of natural disturbances on the vegetation. Samples of natural disturbances were first eliminated, and the undisturbed samples were ordinated alone; and then the entire data set was ordinated. To make this separation, natural disturbances were considered to be areas where the vegetation has not more or less equilibriated to the site. These areas include areas of continual disturbance such as ground squirrel mounds, intermittent disturbance such as frost boils, and recent one-time disturbances such as slumping lake bluffs or recently drained lake basins. Older drained lake basins were classified as undisturbed since the vegetation has had substantial time to equilibriate to the site.

In order to prevent rare species from having too much influence on the ordination outcome (Hill and Gauch 1980), species that occurred only once were eliminated. In addition, the downweighting option of DECORANA was used. This reduces the abundance values of species whose frequencies are less than 20% of the frequency of the commonest species. The result of these changes is that unusual samples containing rare species are not so different from other samples as they would be without reducing the influence of rare species (Hill and Gauch 1980).

The sample ordinations were used as the basis for interpreting the results. Species ordinations were not used and are not presented because they were less satisfactory and less useful, probably because strong crossed gradients exist (the pH gradient is important only in mesic sites). When this is the case, the species ordinations are unreliable (Hill and Gauch 1980). Even in the best of circumstances, the species ordinations are limited because they show only the mode of the species and give no indication of ecological amplitude.

To interpret the ordination space environmentally, values for a particular site factor were plotted into the space at the locus of the sample where it was measured or estimated. The resulting diagrams were examined for trends. Many of the site factors listed in Tables 2.1 and 2.2 were examined, but only those that showed trends are presented. Isolines were drawn by eye where possible and only these lines are shown rather than including the individual values so that the results are clearer and less cluttered. As many lines as possible were drawn, but in some cases only a single line could be drawn separating values above and below a given value. A regression approach was used in drawing the isolines; that is, when values could not be divided perfectly, the line was subjectively drawn to minimize deviations of values not classified correctly. This approach to showing the relation of environmental factors though the space was used by May (1973), Webber (1978), and Komárková (1979, 1980). Some measure of the strength of the trends of the environmental factors and amount of variation explained by the isolines was desired. I used the subjective scale given in Table 2.4 to do this. The scale is based

Table 2.4. Strength of trends of environmental factors through the ordination space.

very strong (VS)	Clear, continual trends through the space; several isolines can be drawn that misclassify relatively few points
strong (S)	Trends visible through at least most of the space; several isolines can be drawn, but they misclassify a moderate number of points
moderate (M)	Trends visible through just a part of the space, or much scatter of values and only 1(-2) isolines can be drawn

on how continuous the trends are through the ordination space and how much scatter there is among the values.

Other approaches to environmental interpretation have been used. Pearson correlation coefficients between sample scores on the axes and environmental factors have been used (Bray and Curtis 1957, Webber 1971), but these have the limitations of assuming that environmental gradients have linear relationships to the axes and that both variables are normally distributed and that variances are homoscedastic. Using the nonparametric Spearman correlation coefficient avoids making these assumptions, but still assumes that the relationships are simple, that is, low values for an environmental factor are at one end of an axis increasing to high values at the other end. (See the patterns of NH_4, NO_3, and total N in Figure 2.26 for examples of this assumption not being justified.) When correlation coefficients are used, there is a tendency for the reader to assume that the environmental gradients are parallel to the axes, even though this is not an assumption of the method. Dargie (1984) used a technique which rotated axes to find the maximum correlation to correct this problem, but the assumption of simple relationships that correlation makes is still a problem. Despite these limitations, correlation coefficients are useful in interpreting the ordinations environmentally, and are presented as an adjunct to the graphs of trends in environmental factors through the ordination space. Another approach, perhaps the commonest, has been just a subjective evaluation of the principal environmental gradients with no supporting data presented (e.g. Robertson 1978, Hill and Gauch 1980, Moral 1980, Peet 1980).

It should be noted that no approach to interpreting environmental factors into the ordination-space can show factors that are uniform across the space as important. A factor, for example, cool summer air temperature, may be controlling to the entire vegetation, but will not appear as important in the ordination. Only factors that vary within the sample universe can potentially be interpreted in relation to the variation of the vegetation.

The relationships of communities to each other and to environmental factors was shown by drawing lines around all samples belonging to a particular community. This allows easier interpretation than the sample ordinations alone because the amount of detail is reduced to a more comprehendible level.

The distributions of selected taxa were examined by plotting species values into the sample ordinations in the same way as environmental factors. Thirty taxa were selected to represent the range of variation in distributions. In most cases the taxa are species or subspecies; but the erect *Salix* spp. were grouped together and *Arctagrostis* spp. and *Poa* spp. were grouped together because both groups are disturbance indicators. Several of the most common taxa, which are wide-ranging, were chosen because their ecologies are well known to other workers. Taxa that are indicative of specific ecological conditions, e.g. standing water, acid sites, frost boils, or disturbed areas, were also chosen. I also plotted growth forms into the ordination space in the same way as species.

Isolines were drawn for the taxa and growth forms in the same way as for environmental factors. As many lines were drawn as the scatter in values allowed. Again, the lines were drawn in a generalized way rather than necessarily to include every point of that value or higher. However, the lines drawn for the taxa rarely need to be generalized since the patterns are continuous as expected, since the ordination space was constructed from these abundance values. For every taxon, a line was drawn around all occurrences to show the ecological limits of that taxon. This line is labeled "1" since that is the lowest species value in my data set.

Classification Results

The Braun-Blanquet tables for the natural vegetation are presented in Appendices B1 and B2 (in pocket). Appendix B1 is for the data set of 87 plots with vascular plants and cryptogams, and Appendix B2 is of the 61 plots with vascular plants only. Species that occur only once are listed at the bottom of the table by community.

The community descriptions follow below. The communities are named with dominant taxa or with constantly occurring subordinate taxa if the dominant taxa do not uniquely identify them. The descriptions include a listing of the dominant and subordinate taxa and the type of habitat in which the communities occur.

1) *Arctophila fulva-Hippuris vulgaris*

The grass *Arctophila fulva* dominates this community (Figure 2.1), and small amounts of *Hippuris vulgaris* and sometimes *Caltha palustris* ssp. *arctica* are present. *H. vulgaris* is unique to this community and characterizes it. Other taxa are found only infrequently. This community grows along lake and pond margins where the water is approximately 30 to 100 cm deep.

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2) *Arctophila fulva - Eriophorum scheuchzeri*

A. fulva, E. scheuchzeri var. *scheuchzeri, E. angustifolium* ssp. *subarcticum,* and the mosses *Rhizomnium andrewsianum* and *Calliergon giganteum* dominate this successional community (Figure 2.2). Other species that occur with a high constancy are *Epilobium palustre, Chrysosplenium tetrandrum, Saxifraga cernua,* and *Carex aquatilis.* Species that may occur are *Rumex arcticus* and *Caltha palustris* ssp. *arctica.* This graminoid-dominated community occurs at Oumalik in a lake basin that drained between 1949 and 1955 (based on aerial photographs taken in those years). The soil is saturated and may have shallow standing water. *A. fulva* seems to be a remnant from an earlier successional community when the water was deeper.

Figure 2.1. Community 1; *Arctophila fulva-Hippuris vulgaris.* D.A. Walker photo.

Figure 2.2 Community 2; *Arctophila fulva-Eriophorum scheuchzeri.* Photo 69-24, 7 July 1980.

Appendix B1: 172
Appendix B2: 173, 238

3) *Carex aquatilis-Eriophorum angustifolium*

This floristically-poor community (Figure 2.3) is dominated by *C. aquatilis* and *E. angustifolium* ssp. *subarcticum*, and has only small amounts of a few other taxa. It seems to be an early successional community in wet areas, such as natural thermokarsts, that have standing water. Relevé 239 is included here as an older, drier, and better-developed variant of the modal type. This variant occurs in only one drained lake basin that apparently was wetter at one time, and the vegetation is changing toward a drier type with *Arctagrostis latifolia* var. *arundinacea* and *Equisetum arvense*.

Appendix B1: 185, 239 (atypical)
Appendix B2: 178

4) *Eriophorum russeolum-Hierochloë pauciflora*

E. russeolum var. *albidum*, *H. pauciflora*, *E. angustifolium* ssp. *subarcticum*, and *Carex aquatilis* dominate this community (Figure 2.4), which occurs in standing water in low-centered polygon centers and in marshes without microrelief. Important mosses are *Drepanocladus revolvens*, *Cinclidium latifolium*, and *Scorpidium scorpioides*. Vascular subdominants are *Pedicularis sudetica* ssp. *albolabiata* and *Juncus triglumis* ssp. *albescens*. This community occurs infrequently at Oumalik.

Appendix B1: 251

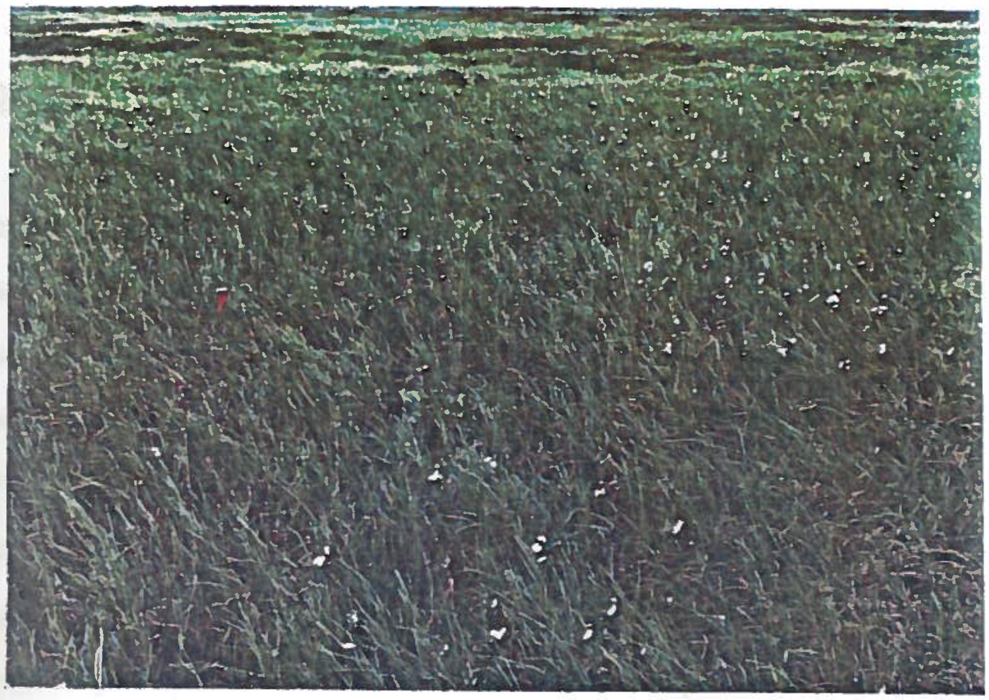


Figure 2.3. Community 3; *Carex aquatilis-Eriophorum angustifolium*. Photo 76-4, 14 July 1980.

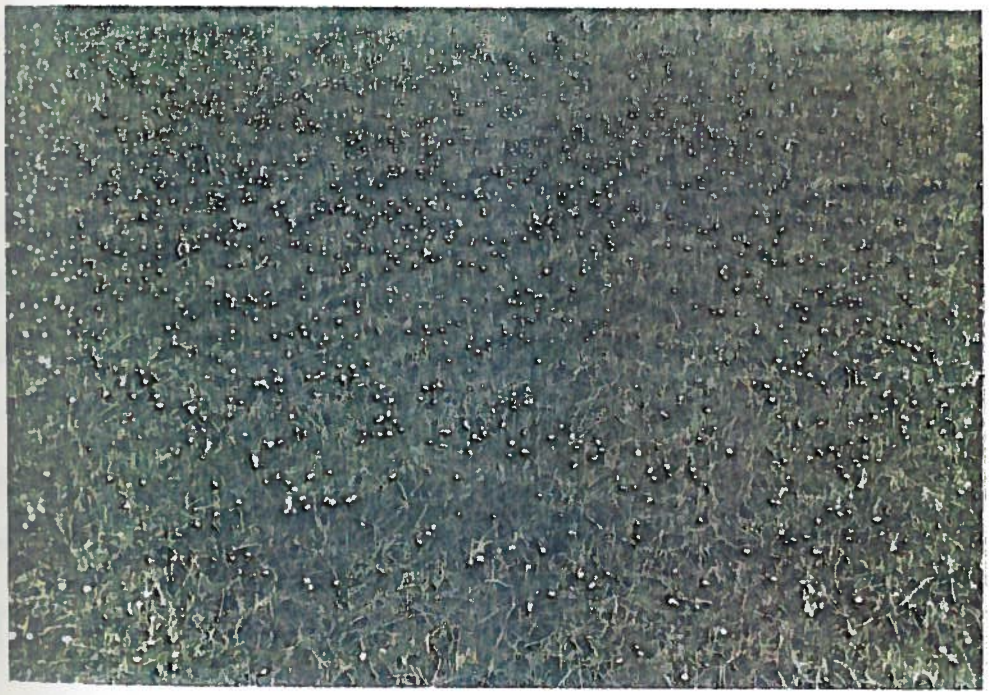


Figure 2.4. Community 4; *Eriophorum russeoleum-Hierochloë pauciflora*. Photo 107-30, 3 July 1981.

5) *Carex chordorrhiza-C. rotundata*

In addition to the species in the name, *C. aquatilis*, *Eriophorum angustifolium* ssp. *subarcticum*, *E. russeolum* var. *albidum*, *C. saxatilis* ssp. *laxa*, and *Scorpidium scorpioides* dominate this marsh community (Figure 2.5). *Pedicularis sudetica* ssp. *albolabiata* occurs frequently but with low abundance. This community is found in the centers of low-centered polygons and in marshes without microrelief where there is standing water at least in the first part of the growing season. Even if standing water is not present later in the growing season, the soil remains saturated. This is the best-developed sedge marsh community at Oumalik and has the highest floristic diversity of the marshes.

The marsh communities, to a greater extent than the other Oumalik communities, intergrade to some extent. The *C. chordorrhiza-C. rotundata* community intergrades with the *Eriophorum russeolum-Hierochloë pauciflora* marsh, which usually lacks many of the *Carex* spp. that this community has; and also with the *Carex chordorrhiza-Salix planifolia* marsh, which often lacks some of the *Carex* spp. of this community but has a well-developed shrub layer.

Appendix B1: 176, 169, 257, 206
Appendix B2: 203, 171, 209

Figure 2.5. Community 5; *Carex chordorrhiza-C. rotundata*. Photo 69-20, 7 July 1980.

Figure 2.6. Community 6; *Carex chordorrhiza-Salix planifolia*. Photo 74-3, 11 July 1980.

6) *Carex chordorrhiza-Salix planifolia*

This is quite similar to, and intergrades with, the *Carex chordorrhiza-Carex rotundata* marsh, but has a shrub layer of *Salix planifolia* ssp. *pulchra* (Figure 2.6). It also occurs in similar habitats.

Appendix B1: 181, 250
Appendix B2: 182

7) *Salix planifolia-Carex aquatilis*

Dominants in this community (Figure 2.7) are *S. planifolia* ssp. *pulchra, C. aquatilis, Betula nana* ssp. *exilis, Hylocomium splendens, Sphagnum* spp., and *Aulacomnium turgidum.* Somewhat less important taxa are *Eriophorum angustifolium* ssp. *subarcticum, Tomenthypnum nitens, Dryas integrifolia* ssp. *integrifolia* (except in the wetter examples of this community type), and *Campylium stellatum.* This is most frequently found on low-centered polygon rims and in drainages coming off of the uplands.

Appendix B1: 268, 44, 183, 170, 258, 175, 167
Appendix B2: 240, 204

8) *Salix lanata-S. planifolia*

The willow species *S. lanata* ssp. *richardsonii* and *S. planifolia* ssp. *pulchra* dominate the shrub layer, *Carex aquatilis* and *Eriophorum angustifolium* ssp. *subarcticum* dominate the herb layer, and *Hylocomium splendens* and *Tomenthypnum nitens* dominate the moss layer in this community (Figure 2.9). Important subordinate taxa are *Betula nana* ssp. *exilis, Dryas*

Figure 2.7. Community 7; *Salix planifolia-Carex aquatilis*. Photo 69-27, 8 July 1980.

Figure 2.8. Community 8; *Salix lanata-S. planifolia*. Photo 79-19, 24 July 1980.

integrifolia ssp. *integrifolia*, *Pyrola grandiflora*, *Poa arctica* ssp. *arctica*, and *Dicranum spadiceum*. Stands of this vegetation type are found in drained lake basins where there is not standing water but the soil is near saturation throughout the growing season. Releve 180 has a younger successional character to it than more typical samples for this type, with greater amounts of *Arctagrostis latifolia* var. *arundinacea*, *Equisetum arvense*, *Stellaria edwardsii*, *Ceratodon purpureus*, and *Bryum* spp.

Appendix B1: 82, 218, 180
Appendix B2: 177, 220

9) *Salix lanata-Equisetum arvense*

This type is rare at Oumalik and is found growing only in small creeks (Figure 2.9). *S. lanata* ssp. *richardsonii* grows densely with an understory of *Equisetum arvense*, *Carex aquatilis*, *Eriophorum angustifolium* ssp. *subarcticum*, *Calliergon giganteum*, and *Brachythecium* spp. *Valeriana capitata* and *Petasites frigidus* also have substantial cover.

Appendix B1: 24

10) *Eriophorum vaginatum-Salix planifolia*

This is the well-known tussock tundra (Figure 2.10) that dominates the landscape in the foothills of the North Slope and is also common on the Arctic Coastal Plain. At Oumalik it occurs primarily on the uplands that are unaffected by the thaw lake cycle, and also on slightly raised banks of drained lake basins, on slopes of some knolls, and as "islands" within a marsh-palsa-

Figure 2.9. Community 9; *Salix lanata-Equisetum arvense.* Photo 34-4, 20 June 1979.

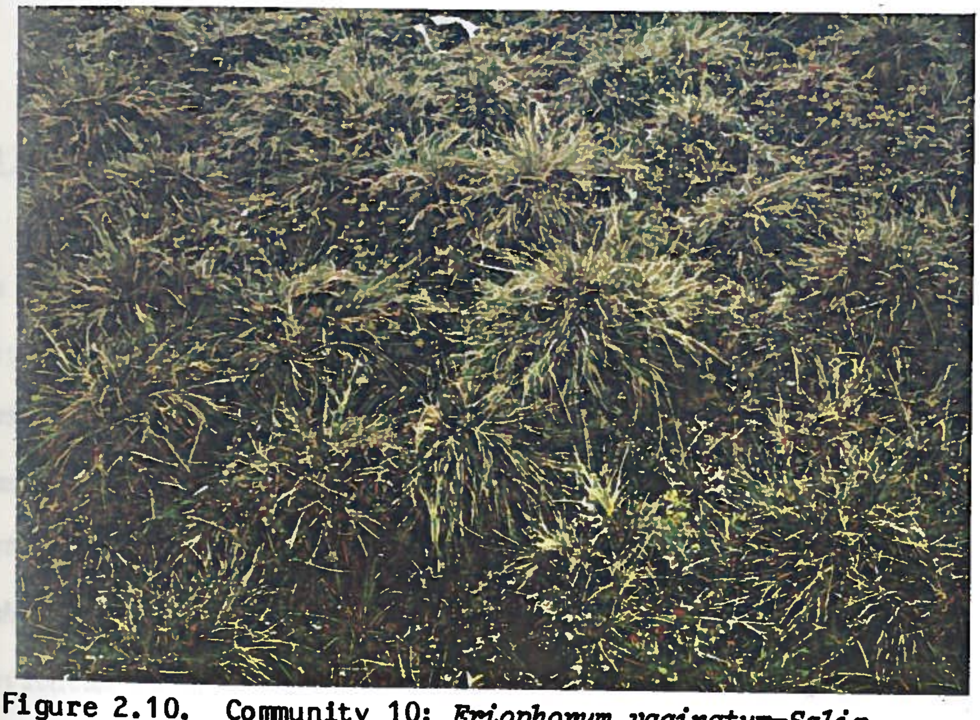


Figure 2.10. Community 10; *Eriophorum vaginatum-Salix planifolia.* Photo 79-35, 26 July 1980.

tussock tundra complex. The shrub layer is dominated by *S. planifolia* ssp. *pulchra* and *Betula nana* ssp. *exilis*. In addition to *E. vaginatum* the herb layer is dominated by *Ledum palustre* ssp. *decumbens* and *Vaccinium vitis-idaea*. spp. *minus*. Important bryophytes are *Hylocomium splendens*, *Anastrophyllum minutum*, and *Dicranum elongatum*. Other species that have lower covers, but usually occur in this community are *Arctagrostis latifolia* s.l., *Poa arctica* ssp. *arctica*, *Saxifraga nelsoniana*, *Bistorta plumosa*, *Carex bigelowii*, *Cetraria cucullata*, *Ptilidium ciliare*, and *Thamnolia vermicularis*. Species that occur with a lower constancy, but are important in some stands are *Nephroma arcticum*, *Peltigera aphthosa*, and *Rubus chamaemorus*.

Appendix B1: 76, 155, 229
Appendix B2: 210, 164, 205, 158, 160, 161,

11) *Salix rotundifolia*

S. rotundifolia ssp. *rotundifolia* is generally restricted to this snowbed community (Figure 2.11), and occurs in it with a high abundance. *Dryas integrifolia* ssp. *integrifolia*, *S. reticulata* ssp. *reticulata*, *Petasites frigidus*, *Arctagrostis latifolia* var. *arundinacea*, *Carex bigelowii*, *Cassiope tetragona* ssp. *tetragona*, *Equisetum arvense*, *Oncophorus wahlenbergii*, *Tomenthypnum nitens*, *Hylocomium splendens*, and *Ptilidium ciliare* are more wide-ranging, but usually are present in the community. Snowbed communities are rare in the Oumalik area because long-lasting snowbanks are infrequent. In most of the

Figure 2.11. Community 11; *Salix rotundifolia*. Photo 112-28, 19 July 1981.

Figure 2.12. Community 12; *Dryas integrifolia-Eriophorum vaginatum*. Photo 70-9, 2 July 1980.

places where they do occur, other factors, especially the instability and newness of the surface of eroding lake bluffs, predominate and prevent snowbed communities from developing. The community is found at Oumalik on the lower slopes of creek banks, and in a few cases, on slopes between the uplands and drained lake basins.

Appendix B1: 223, 264
Appendix B2: 224

12) *Dryas integrifolia-Eriophorum vaginatum*

Superficially, this community (Figure 2.12) appears to be *Eriophorum vaginatum-Salix planifolia* tussock tundra (community 10) because of the visual dominance of the tussock. However, floristically it is much closer to the *Dryas integrifolia-Salix glauca* community described next, but with *E. vaginatum* as an added dominant and *Rhacomitrium lanuginosum* as an additional subordinate species. It is a community intermediate between the two mentioned above, but is distinct and moderately extensive.

Appendix B1: 168, 269, 159
Appendix B2: 162, 165

13) *Dryas integrifolia-Salix glauca*

Salix glauca is usually the only dwarf shrub in this species-rich community (Figure 2.13). *D. integrifolia* ssp. *integrifolia* and *Salix reticulata* ssp. *reticulata* dominate the herb layer along with lesser amounts of *Saussurea angustifolia, Poa*

Figure 2.13. Community 13; *Dryas integrifolia-Salix glauca.* Photo 41-23, 12 July 1979.

Figure 2.14. Community 14; *Ledum palustre-Cassiope tetragona.* Photo 107-33, 3 July 1981.

arctica ssp. *arctica, Carex bigelowii, Arctous rubra,* and *Arctagrostis latifolia* s.l. Species that are sometimes present are *Cassiope tetragona* ssp. *tetragona* and *Eriophorum triste* . The most important mosses are *Aulacomnium turgidum, Hylocomium splendens,* and *Dicranum elongatum.* This community is associated with moist solifluction slopes and reticulate-patterned ground found on knolls left by the thaw lake cycle and on slopes of residual surfaces.

Several relevés are different than the main type. Relevé 234 is located on a now-stabilized lake bluff. It lacks some of the subordinate species of this community and has greater amounts of species associated with disturbance, such as *Arctagrostis latifolia* var. *arundinacea* and *Poa arctica* ssp. *arctica.* The dominant species are present, however, and this successional community is classified with the modal type here. Relevé 242 was done on the warm, fairly dry, south-facing slope of the eroding pingo 2 km east of the well site. The species of the modal type are present, but others that are infrequent to very rare in the Oumalik area occur as well. The occasional species *Festuca baffinensis, Astragalus alpinus* ssp. *alpinus, Poa glauca, Anemone parviflora,* and *Arnica frigida* are present, and the rare species *Kobresia myosuroides, Calamagrostis stricta,* and *Gentianella propinqua* ssp. *arctophila* also occur. Because the community that this relevé represents is extremely localized at Oumalik, I have included it in the more widespread *Dryas* type.

Appendix B1: 87, 73, 84, 242 (pingo)
Appendix B2: 234 (successional)

14) *Ledum palustre-Cassiope tetragona*

This prostrate shrub community occurs on mounds that are occasionally present at the intersection of troughs of low-centered polygons (Figure 2.14). The use of these high areas as perches by jaegers, owls, and other birds probably strongly influences the vegetation. The prostrate shrubs *Ledum palustre* ssp. *decumbens*, *Cassiope tetragona* ssp. *tetragona*, *Vaccinium vitis-idaea* ssp. *minus*, and *Betula nana* ssp. *exilis* and the graminoids *Carex bigelowii*, *Arctagrostis latifolia* s.l., *Poa arctica* ssp. *arctica*, and *Luzula confusa* are the conspicuous vascular taxa. The most important mosses are *Ceratodon purpureus*, *Pohlia cruda*, *Tomenthypnum nitens*, *Hylocomium splendens*, and *Polytrichum strictum*. Crustose lichens, which form a conspicuous part of the community, are *Lecanora epibryon* and *Ochrolechia frigida*.

Appendix B1: 136
Appendix B2: 252, 261, 262

15) *Eriophorum angustifolium-Ochrolechia upsaliensis*

This type occurs on frost boils in wet areas where the surface of the frost boil is continually moist and the subsurface is wet (Figure 2.15). *E. angustifolium* ssp. *subarcticum* and *O. upsaliensis* dominate; other taxa that occur are *Dryas integrifolia* ssp. *integrifolia*, *Carex capillaris*, *Equisetum*

Figure 2.15. Community 15; *Eriophorum angustifolium-Ochrolechia upsaliensis*. Photo 109-11, 11 July 1981.

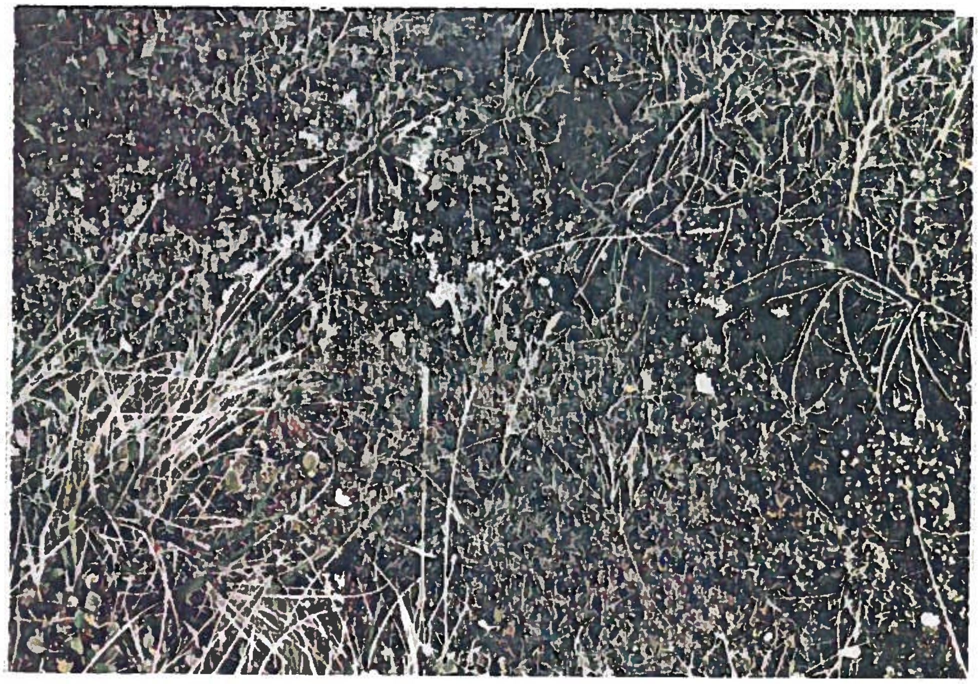


Figure 2.16. Community 16; *Dryas integrifolia-Ochrolechia upsaliensis*. Photo 102-28, 29 June 1980.

scirpoides, *E. variegatum*, *Saxifraga oppositifolia* ssp. *oppositifolia*, *Ditrichum flexicaule*, *Ceratodon purpureus*, and *Tomenthypnum nitens*. The total cover on these frost boils is 30-75% with much of the cover of those in the upper end of the range from crustose lichens.

Appendix B1: 246
Appendix B2: 247, 253

16) *Dryas integrifolia-Ochrolechia upsaliensis*

This frost-boil community (Figure 2.16) occurs in more mesic sites than the previous community. It is most commonly found within *Eriophorum vaginatum-Salix planifolia* tussock tundra or the *Dryas integrifolia-Salix glauca* community. The frost boils are in various stages of revegetation, and total cover ranges from 20 to 90%, often with crustose lichens being a large part of this. *D. integrifolia* ssp. *integrifolia* and *Carex bigelowii* are the dominant vascular plants, and *O. upsaliensis* and *Lecanora epibryon* are the crustose lichens that occur. Other species that occur in some examples of this community are *Saxifraga oppositifolia* ssp. *oppositifolia*, *Silene acaulis* ssp. *arctica*, *Bistorta vivipara*, *Festuca brachyphylla*, *Eriophorum vaginatum*, and *Juncus biglumis*.

Appendix B1: 244, 243
Appendix B2: 248, 249, 245, 254

17) *Dryas integrifolia-Carex* spp.

A high species diversity characterizes this vegetation type (Figure 2.17), which at Oumalik occurs on moist, flat surfaces without microrelief on drained lake basin banks. In addition to the dominant *D. integrifolia* ssp. *integrifolia, Salix reticulata* ssp. *reticulata* occurs frequently, and a number of *Carex* spp. are prominent-- *C. bigelowii, C. scirpoidea, C. vaginata,* and to a lesser extent *C. misandra.* The common, abundant bryophytes are *Ptilidium ciliare, Tomenthypnum nitens, Anastrophyllum minutum,* and *Dicranum elongatum.* This community is infrequent at Oumalik.

Appendix B1: 179, 236, 263

18) *Betula nana-Ledum palustre*

Dwarf and prostrate shrubs dominate this community (Figure 39). *B. nana* ssp. *exilis* and *L. palustre* ssp. *decumbens* are the most abundant, while *Salix planifolia* ssp. *pulchra* and *Vaccinium vitis-idaea* spp. *minus* are less plentiful but usually present. Small amounts of the lichens *Cetraria cucullata* and *Dactylina arctica* occur consistently. The mosses that are usually present and are prominent are *Aulacomnium turgidum, Hylocomium splendens, Ptilidium ciliare, Anastrophyllum minutum,* and *Dicranum elongatum.* The community is common and occurs on moist palsas and high-centered polygon centers. Releve 163 has a different physiognomic appearance because of the small amount of *B. nana* and

Figure 2.17. Community 17; *Dryas integrifolia-Carex* spp. Photo 82-1, 31 July 1980.

Figure 2.18. Community 18; *Betula nana-Ledum palustre*. Photo 70-4, 1 July 1980.

the large amount of *Rubus chamaemorus*, but is kept within this community.

Appendix B1: 156, 163, 184, 207, 157, 154
Appendix B2: 166, 208, 217

19) *Hierochloë alpina-Arctagrostis latifolia*

This relatively dry type is restricted to the immediate vicinity of ground squirrel mounds (Figure 2.19). *H. alpina*, *A. latifolia* var. *latifolia*, and *Poa arctica* ssp. *arctica* are the dominants. Subordinate taxa are *Salix planifolia* ssp. *pulchra*, *Vaccinium vitis-idaea*, ssp. *minus*, *Dicranum elongatum*, *Ochrolechia frigida*, and *Tomenthypnum nitens*. *Tetraplodon mnioides*, which is considered an indicator of fecal material or dead animal remains, occurs in moderate amounts.

Appendix B1: 259
Appendix B2: 222

20) *Salix glauca-Poa arctica*

The shrub layer of this community (Figure 2.20) is dominated by *Salix glauca* and the herb layer by *Poa arctica* ssp. *arctica* and *Arctagrostis latifolia* var. *latifolia*. Smaller amounts of *Carex bigelowii*, *Dryas integrifolia* ssp. *integrifolia*, *Polemonium acutifolium*, and *Ceratodon purpureus* are present. Relevé 256 also has a large amount of *Salix arbusculoides*. The community occurs on two distinct mesic sites--stabilized lake bluffs and mounds at the intersection of low-centered polygon rims.

Figure 2.19. Community 19; *Hierochloë alpina-Arctagrostis latifolia*. Photo 79-21, 24 July 1980.

Figure 2.20. Community 20; *Salix glauca-Poa arctica*. Photo 41-10, 10 July 1979.

Appendix B1: 260, 83
Appendix B2: 256, 255

21) *Salix alaxensis-S. arbusculoides*

This willow community is dominated by *S. alaxensis* ssp. *alaxensis*, *S. arbusculoides*, *S. hastata*, and *S. glauca*. The willows attain a height and vigor unapproached in any other community (Figure 2.21). The understory is relatively sparse, apparently due to heavy shading, with *Arctagrostis latifolia* var. *latifolia* and *Poa arctica* ssp. *arctica* having the most cover. Cryptogams are a minor component of this community. The community is found on some stabilized lake bluffs several kilometers from the Oumalik well and on the eroded side of the pingo east of the well.

Appendix B1: 241

22) *Arctagrostis latifolia*

This successional community (Figure 2.22) is strongly dominated by *A. latifolia* var. *arundinacea* or *A. latifolia* var. *latifolia*. It occurs on eroding lake bluffs on surfaces estimated to be one to several years old. The youngest surfaces support the simplest communities-- *A. latifolia* s.l., *Equisetum arvense*, and frequently seedlings of *Salix glauca*. Other species colonize as the surface age increases-- *Epilobium palustre*, *Draba borealis*, *Cardamine digitata*, *Saussurea angustifolia*, and *Senecio congestus*. This community presumably will become the *Salix glauca-Poa arctica*

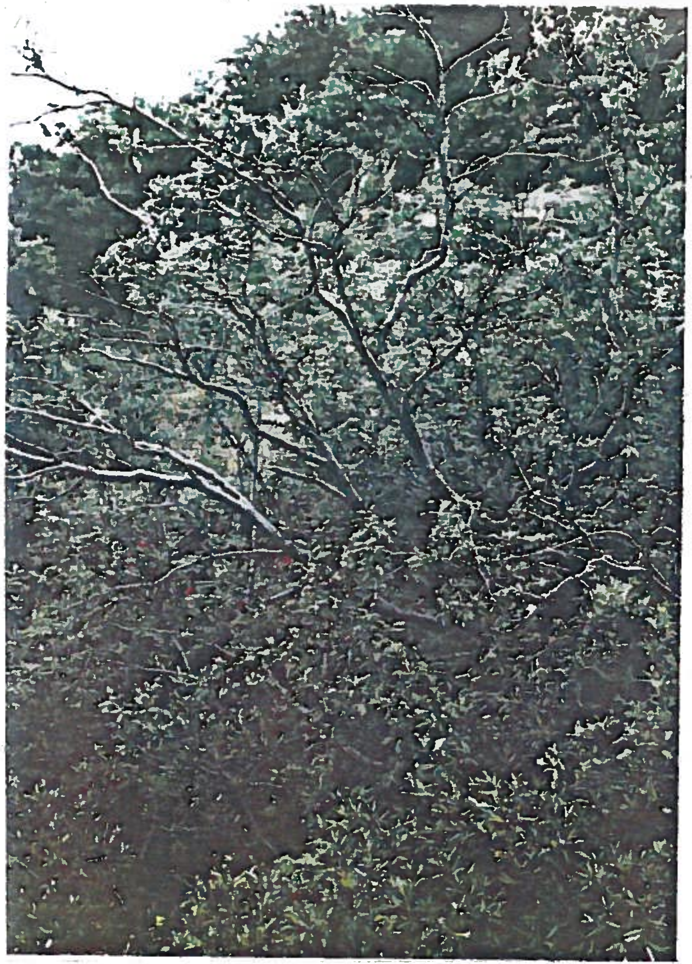


Figure 2.21. Community 21; *Salix alaxensis-S. arbusculoides*. Photo 105-25, 29 June 1981.

Figure 2.22. Community 22: *Arctagrostis latifolia*. Photo 79-33, 26 July 1980.

community if the surface remains stable long enough. Relevé 230 is wetter than most other examples of this community and includes *Eriophorum russeolum* var. *albidum* and *E. angustifolium* ssp. *subarcticum*.

Appendix B1: 225, 230, 233
Appendix B2: 226, 227, 228, 174, 231, 232

23) *Puccinellia borealis-Arctagrostis latifolia*

This infrequent successional community (Figure 2.23) occurs only on mounds isolated by thermokarst on eroding lake bluffs. The mounds are very well-drained, and the surface soil is dry. This is the only dry habitat in the Oumalik area. *P. borealis* and *A. latifolia* var. *arundinacea* dominate, with small amounts of *Descurainia sophioides* and a *Bryum* sp. present.

Appendix B1: 235

Ordination Results

Most ordinations produce axes that can be interpreted in terms of their underlying environmental variation only to 2 or 3 dimensions (Peet 1980). This is true of the Oumalik data set; the first two axes contain almost all the environmentally interpretable information, and only two axes are presented.

Sample Ordinations

The undisturbed sample positions in the ordinations of the undisturbed data set (U) and the undisturbed/natural disturbance

Figure 2.23. Community 23; *Puccinellia borealis-Arctagrostis latifolia*. Photo 81-26, 29 July 1980.

data set (UN) show similar patterns (Figure 2.24). This is expected since the UN set differs from the U set only by the addition of 14 samples of natural disturbance. However, these samples are quite different from the undisturbed vegetation and have increased the length of the axes markedly (that is, increased the beta diversity of the data set) as would be expected.

A disjunction of about 3 sd occurs in the UN ordination (Figure 2.24), caused by a successional *Arctophila* sample. This length approaches the longest disjunction that DECORANA can estimate accurately (Hill and Gauch 1980). The sample could have been eliminated from the analysis, but was retained to keep the data set complete, and because the ordination with it did not seem distorted relative to the U ordination and remained interpretable environmentally.

Environmental Interpretation of Ordination Spaces

In both ordinations moisture is very strongly associated with the first axis (Figures 2.25, 2.26, Tables 2.5, 2.6). In the U ordination, organic matter is also associated with the first axis as well as the second axis; that is, the main trend in organic matter is oblique to both axes. Organic matter and site moisture are positively correlated (Tables 2.5, 2.6), although not strongly so, because organic matter tends to accumulate in the marshes, which have low decomposition rates.

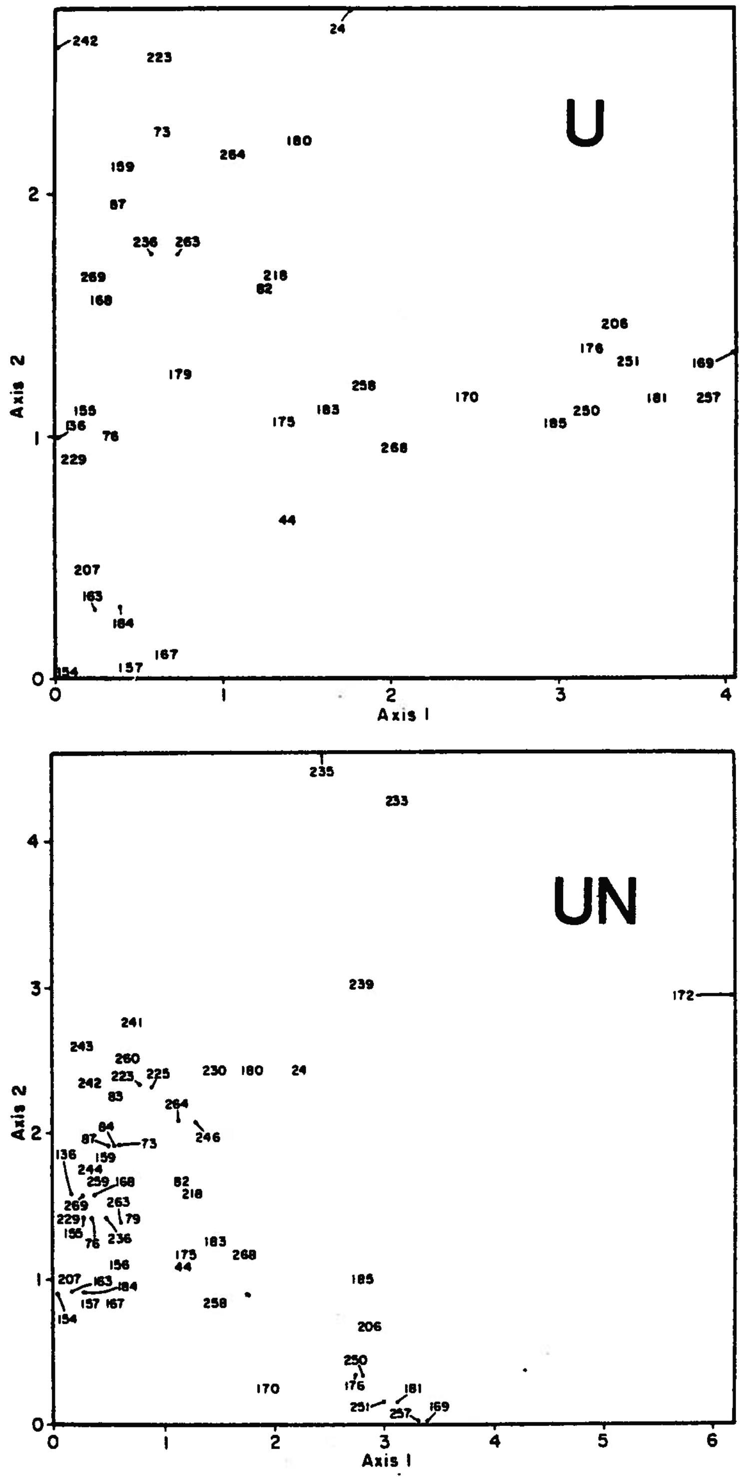


Figure 2.24. Sample ordinations of undisturbed vegetation (U) and undisturbed and naturally disturbed vegetation (UN). The axes are scaled in standard deviation units (see Methods). The species compositions of the samples are given in Appendices B1 and B2 and the site factors in Appendix C1 and C2.

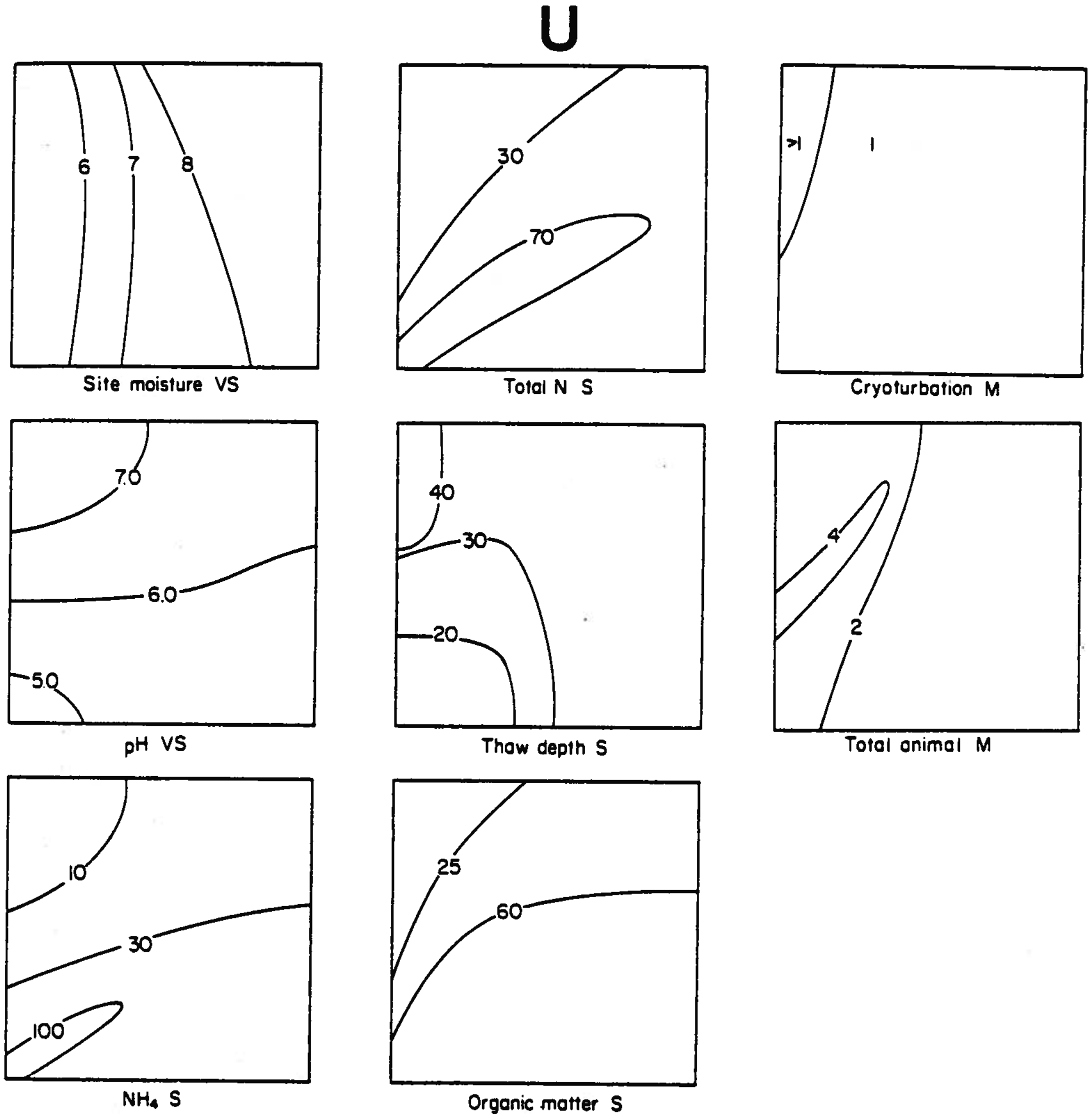


Figure 2.25 Environmental factors in ordination of undisturbed vegetation (U). The strength of the trends is given after the name of the site factor: very strong, strong, or moderate (see Table 2.4 for a more complete explanation)

Table 2.5. Spearman correlation coefficients for the first two axes and significant environmental factors of the ordination of undisturbed (U) samples. The environmental factors are those from Figure 2.26.

	axis 1	axis 2	site moisture	pH	NH_4	total N	thaw depth	organic matter	cryoturbation
axis 2	.16								
site moisture	.76**	-.05							
pH	-.05	.81**	-.23						
NH_4	.26	-.47**	.47**	-.50**					
total N	.28*	-.39**	.43**	-.43**	.96**				
thaw depth	.27	.52**	.15	.28*	-.35*	-.25			
organic matter	.56**	-.52**	.46**	-.56**	.63**	.59**	-.11		
cryoturbation	-.58**	.01	-.59**	.16	-.12	-.14	-.37*	-.31*	
total animal	-.57**	.03	-.35*	.06	-.22	.30*	-.06*	-.46**	.15

*$.01 < p \leq .05$

** $p \leq .01$

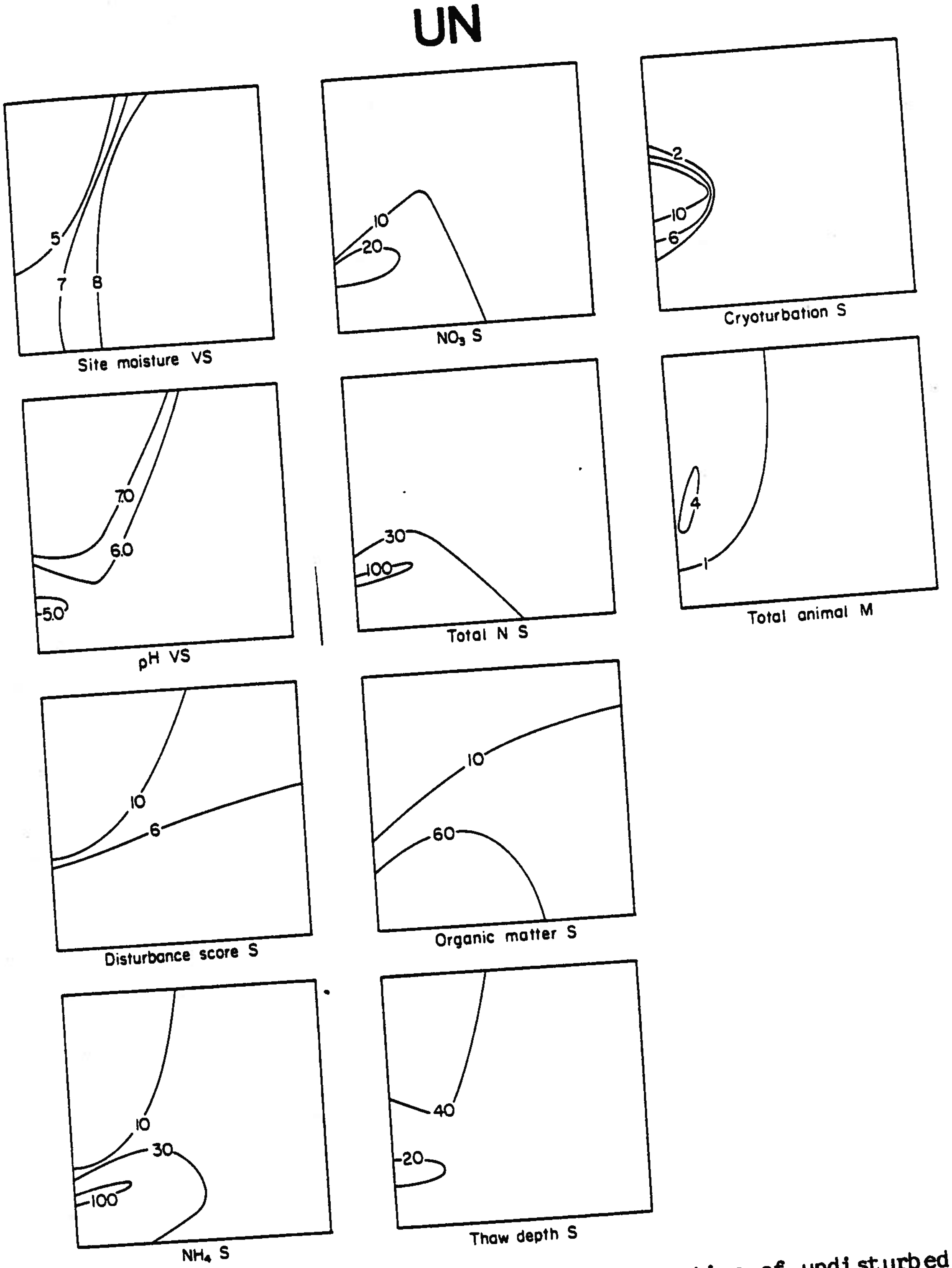


Figure 2.26. Environmental factors in ordination of undisturbed and naturally disturbed vegetation (UN). The strength of trends is given after the name of the site factor: very strong, strong, or moderate (see Table 2.4 for a more complete explanation).

Table 2.6. Spearman correlation coefficients for the first two axes and significant environmental factors of the ordination of undisturbed and naturally disturbed (UN) samples. The environmental factors are those from Figure 2.27.

	axis 1	axis 2	site moisture	pH	disturbance score	NH_4	NO_3	total N	organic matter	thaw depth	cryoturbation
axis 2	-.06										
site moisture	.60**	-.45**									
pH	.03	.61**	-.35**								
disturbance score	.17	.61**	.34**	.32**							
NH_4	.13	-.54**	.46**	-.58**	-.34**						
NO_3	.17	-.48**	.29**	-.20	-.30*	.68**					
total N	.14	-.54**	.41**	-.51**	-.32**	.96**	.85**				
organic matter	.25*	-.69**	.43**	-.66**	-.38**	.72**	.51**	.67**	-.34**		
thaw depth	.28*	.46**	-.21	.41**	.55**	-.51**	-.23	-.42**			
cryoturbation	-.54**	.11	-.39**	.23*	-.04	-.28*	-.21	-.27*	-.38**	-.16	
total animal	-.51**	.34**	-.41**	.06	.05	-.20	-.27*	-.24*	-.25*	.07	.13

*.01 $< p \leq$ .05

** $p \leq$ .01

Cryoturbation and total animal sign are also significantly correlated with the first axis of the U and UN ordinations. However, the influence of cryoturbation is significant in only a small part of the ordination space. Total animal sign seems to show the fairly weak trends that it does only because the scores tend to be high in samples positively correlated with willow abundance and samples with abundant willows are close together in the ordination space. Animal sign is more abundant there because both ptarmigan and caribou eat willow. Therefore it seems best, while recognizing the existence of trends in other environmental factors along the first axis, to consider and name the environmental gradient most strongly associated with the first axis in both ordinations as a complex moisture gradient.

In both ordinations, the second axis represents a complex gradient of interrelated, intercorrelated factors. None of the factors show significant variation in the wet samples, but they effectively associate with the floristic variation in the mesic samples. In the U ordinations, pH shows the strongest pattern of association with the second axis; and NH_4, total N, thaw depth, and organic matter also have their main variation in the direction of the second axis. The relationships of factors within this complex can be inferred by understanding some of the physical processes that operate in northern Alaska and by examining the correlation coefficients between factors (Tables 2.5, 2.6). Since the mineral soil of the area is moderately basic, if acidic organic matter is not present, the pH is moderately high. If there is a large amount of organic matter, the pH is lower. Negative Spearman correlation coefficients with a fairly high absolute value between pH and organic matter support this interpretation. Depth of thaw is also related to the amount of organic matter due to the insulating effect of the organic matter. The Spearman correlation coefficients between thaw and organic matter in the UN data set (-0.34, $p < 0.01$) supports this interpretation, but the U data set Spearman correlation coefficient (-0.11, ns) does not. At Prudhoe Bay Walker (1981) found a quite strong negative relationship between thaw and organic matter (-0.58 [Pearson's r], $p < 0.001$). The relationship of nitrogen to this complex in the Oumalik data may be due to the vastly increased exchange capacity of organic soils relative to mineral soils and their greater water-holding capacity, which allows them to hold more soil solution.

In addition to the factors important along the second axis in the U ordination, the second axis of the UN ordination also has NO_3 and disturbance score associated with it. NO_3 increases as organic matter increases (Table 2.6) and is probably causally related to it. Disturbance can be included in the pH/organic matter/thaw depth relation. Natural disturbances, such as slumping lake bluffs, frost boils, or ground squirrel mounds, are associated with low amounts of organic matter and therefore tend to have basic, deep-thawing substrates.

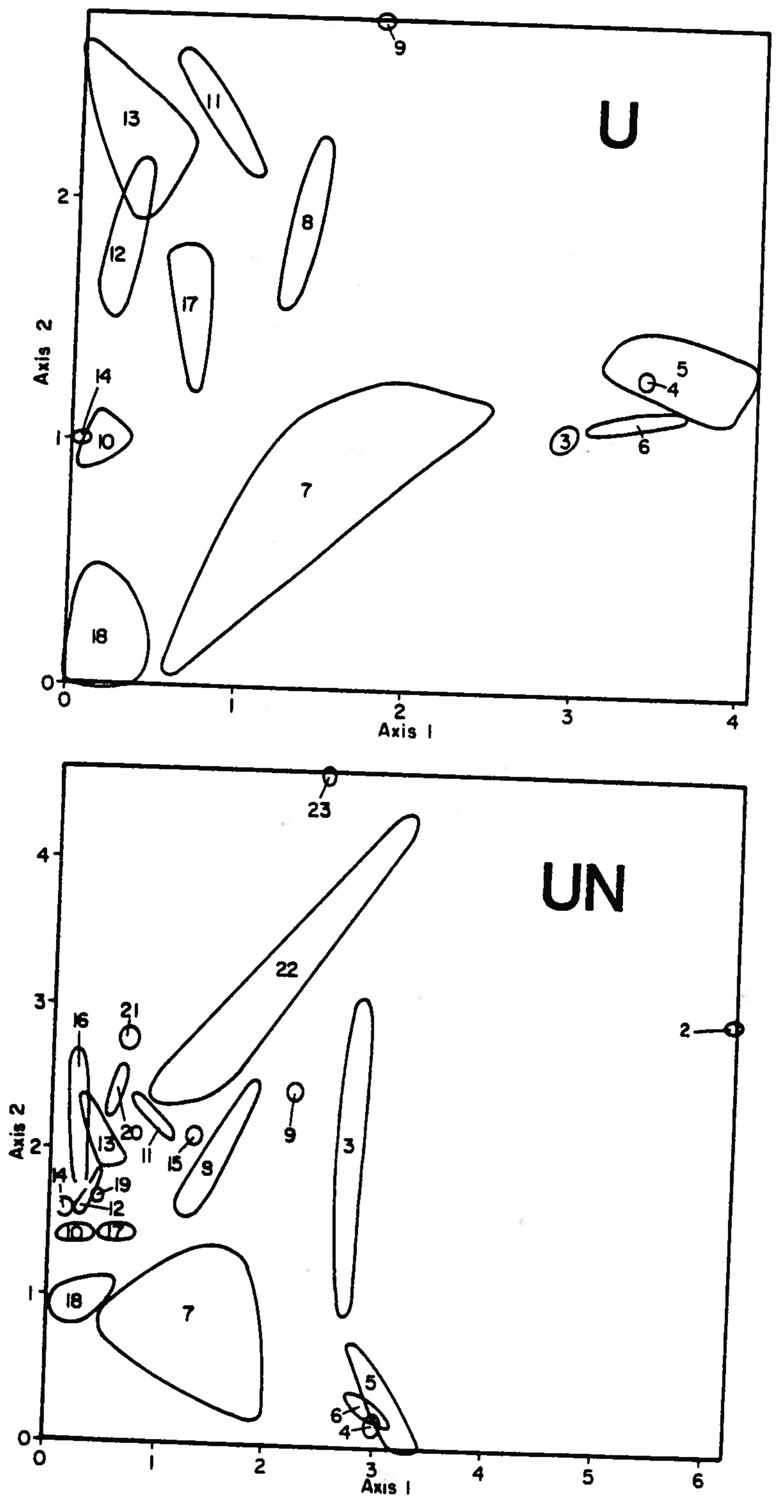
Community Patterns

The distribution of communities in the two ordinations shows quite interpretable patterns. In the U ordination (Figure 2.27), the sedge marshes with standing water (communities 3, 4, 5, 6) are at the high end of the first axis (moisture complex) and the somewhat less wet willow-sedge communities (communities 7, 8, 9) are just below the midpoint of the axis. At the low end of the moisture gradient are the remaining, mesic communities. The sedge-willow communities and the mesic communities are separated on the second (complex pH) gradient. Within the sedge-willow communities, the *Salix planifolia-Carex aquatilis* community is at the low (acid) end of the axis, the *S. lanata-S. planifolia* community toward the high end, and the *S. lanata-Equisetum arvense* community, which is somewhat of an outlier, at the high end.

Within the mesic communities, the *Betula nana-Ledum palustre* community is at the low (acid) end of the gradient, followed by the *Eriophorum vaginatum-Salix planifolia* tussock tundra and the closely related *Ledum palustre-Cassiope tetragona* community. The remaining four communities are at the basic end of the gradient and have *Dryas integrifolia* as the dominant plant. The *D. integrifolia-Salix glauca* community and the *Salix*

Figure 2.27. Communities in ordinations of undisturbed vegetation (U) and undisturbed and naturally disturbed (UN) vegetation. The communities are:

2 *Artophila fulva-Eriophorum scheuchzeri*
3 *Carex aquatilis-Eriophorum angustifolium*
4 *E. russeoleum-Hierochloë pauciflora*
5 *Carex chordorrhiza-C. rotundata*
6 *C. chordorrhiza-Salix planifolia*
7 *S. planifolia-C. aquatilis*
8 *S. lanata-S. planifolia*
9 *S. lanata-Equisetum arvense*
10 *Eriophorum vaginatum-S. planifolia*
11 *S. rotundifolia*
12 *Dryas integrifolia-E. vaginatum*
13 *D. integrifolia-S. glauca*
14 *Ledum palustre-Cassiope tetragona*
15 *E. angustifolium-Ochrolechia upsaliensis*
16 *D. integrifolia-O. upsaliensis*
17 *D. integrifolia-Carex* spp.
18 *Betula nana-Ledum palustre.*
19 *Hierochloë alpina-Arctagrostis latifolia*
20 *S. glauca-Poa arctica*
21 *S. alaxensis-S. arbusculoides*
22 *Arctagrostis latifolia*
23 *Puccinellia borealis-A. latifolia*



rotundifolia snowbed are at the far end of the gradient, and the *D. integrifolia-Eriophorum vaginatum* and *D. integrifolia-Carex* spp. communities are between those two and the tussock tundra.

In the UN ordination (Figure 2.27), the undisturbed communities show the same general arrangement as in the U ordination, but the naturally disturbed communities add a great deal of beta diversity to the data set. The *Arctophila fulva-Eriophorum scheuchzeri* community is at the high end of the first axis, well separated from the rest of the samples. On the second axis, samples of natural disturbances dominated by *Arctagrostis latifolia* s.l. (communities 22, 23) take up much of the high end of the gradient. Successional willow communities (20, 21) are more similar to some of the undisturbed communities and lie about at the midpoint of the second axis. The frost boil community (16) is quite similar to the *Dryas integrifolia-Salix glauca* community (13), and the ground squirrel mound community (19) is most similar to the *D. interifolia-Eriophorum vaginatum* community.

Taxa in the Ordination Spaces

Plotting abundance values of growth forms into the ordination space was not useful and no results are presented here. Patterns were present, but they were weak or not very interpretable ecologically. The problem is due to the widely different ecologies within a growth form, for example *Carex aquatilis* and *Arctagrostis latifolia* in the rhizomatous graminoids. In the case of rhizomatous graminoids in the UN ordination, high abundance values were found both at the high end of the first axis (very wet marshes) and at the high end of the second axis (moderately dry natural disturbances.

Figures 2.28 and 2.29 are the results of plotting taxa abundance values into the ordination space. The taxa are arranged by the position of their optima--from wet to mesic, and within mesic from acid to basic. The distributions tend to have less variation unexplained by the isolines that were drawn than the environmental factors. This is expected since the ordination spaces are constructed on the basis of species abundance values. However, a few taxa were not distributed as continuously as the majority were. That is, the nonzero abundance values showed a strong pattern, but a moderate number of zero values occur within this pattern. This may be due to dispersal, establishment, or competition factors preventing a taxon from occurring in every abiotically suitable site; or may be an artifact of the dimensional reduction of the ordination. Taxa that show this pattern are indicated in the diagrams.

Discussion

Flora

Oumalik could be expected to have a flora of over 200 vascular plants based on its location in floristic zone 4 of Young

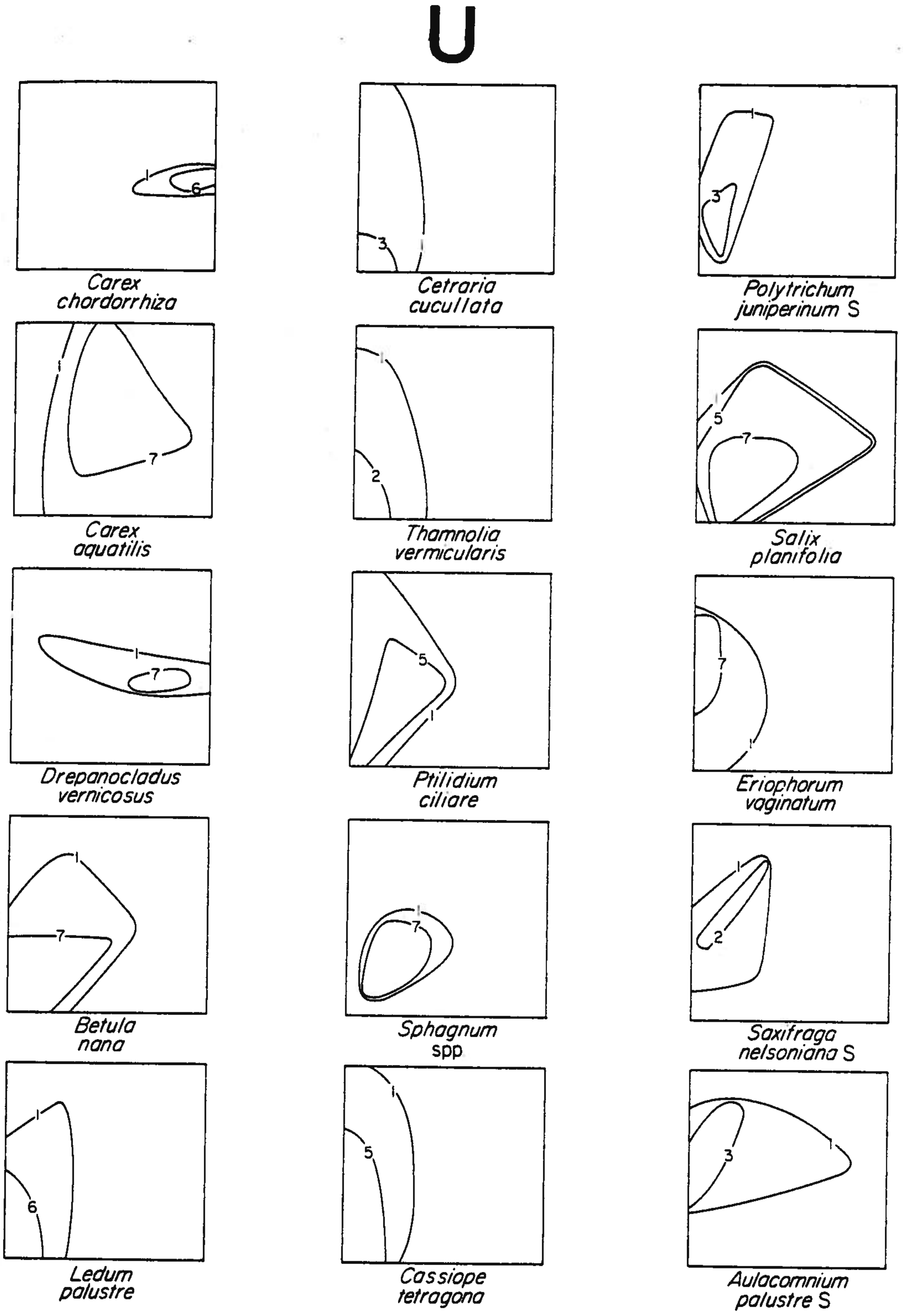
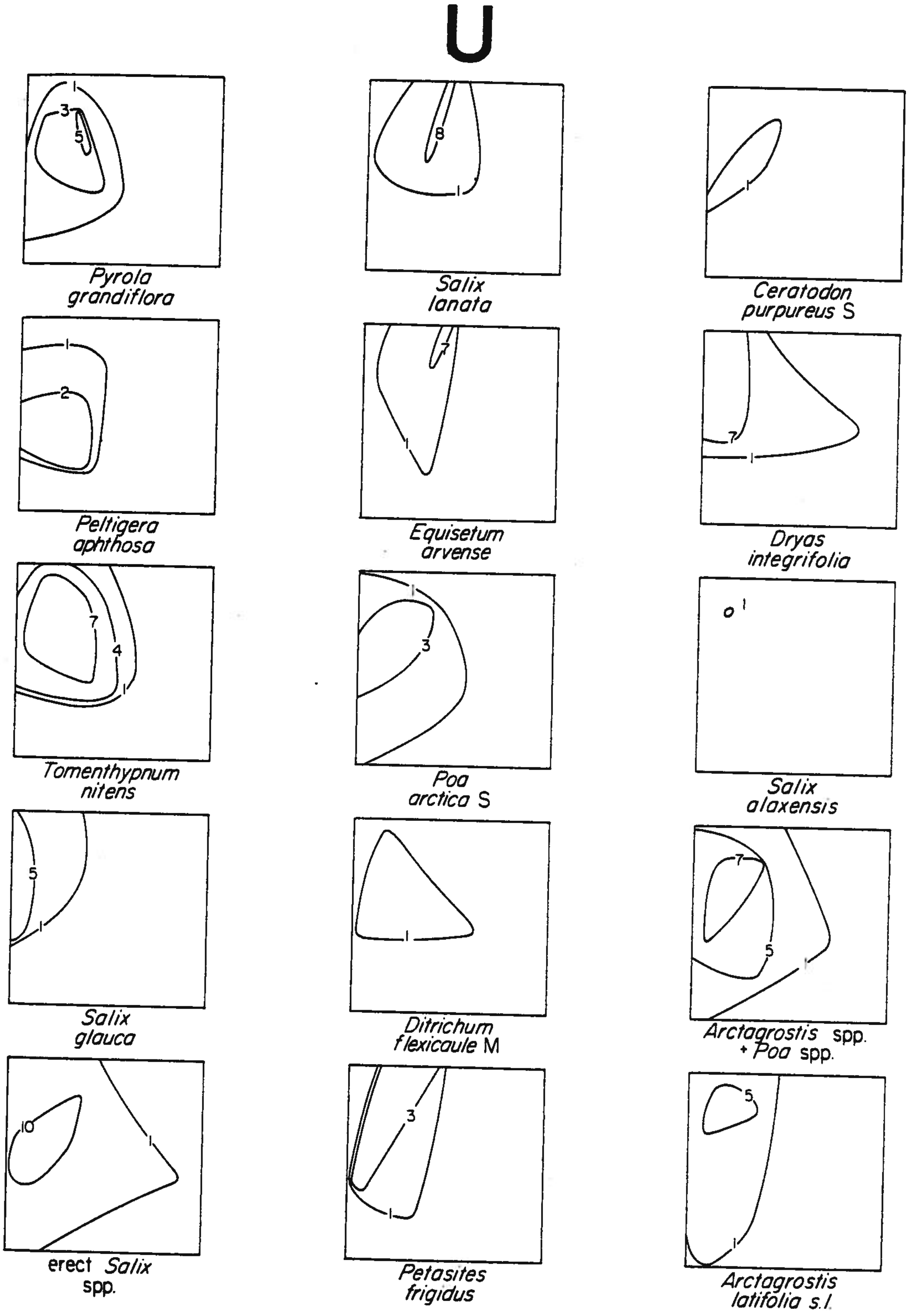


Figure 2.28. Taxa in ordination of undisturbed vegetation (U). Trends are very strong (Table 2.4) except when an "S" (strong) follows the taxon name; these taxa have zero values scattered among the nonzero values (see text). Figure continues on next page.



Pyrola grandiflora

Salix lanata

Ceratodon purpureus S

Peltigera aphthosa

Equisetum arvense

Dryas integrifolia

Tomenthypnum nitens

Poa arctica S

Salix alaxensis

Salix glauca

Ditrichum flexicaule M

Arctagrostis spp. + *Poa* spp.

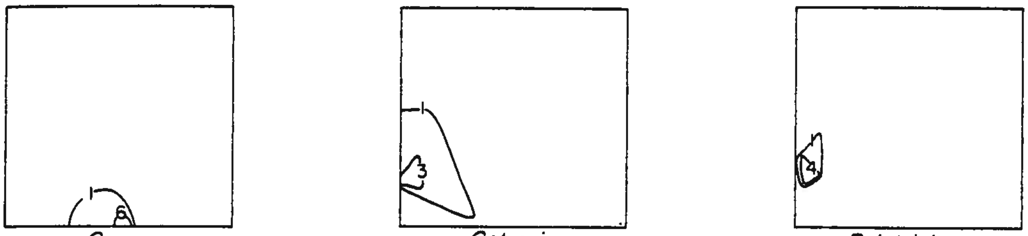
erect *Salix* spp.

Petasites frigidus

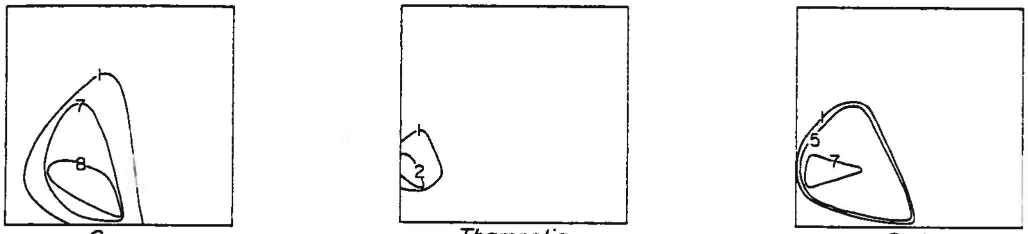
Arctagrostis latifolia s.l.

Figure 2.28 (continued).

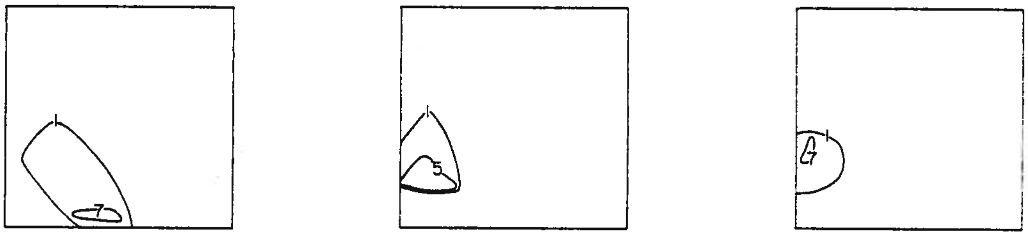
UN



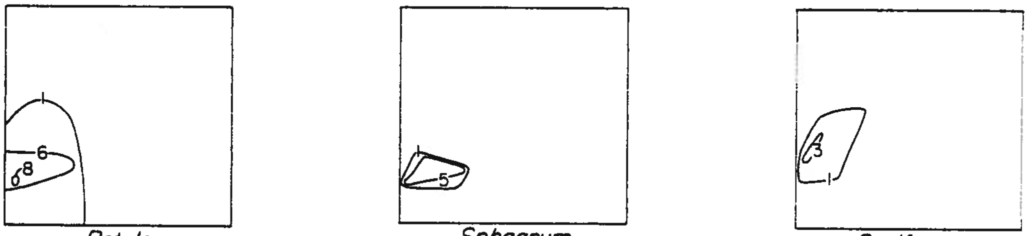
Carex chordorrhiza *Cetraria cucullata* *Polytrichum juniperinum*



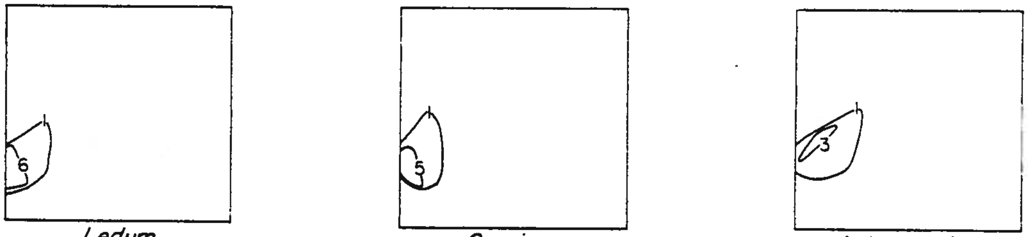
Carex aquatilis *Thamnolia vermicularis* *Salix planifolia*



Drepanocladus revolvens S *Ptilidium ciliare* *Eriophorum vaginatum*

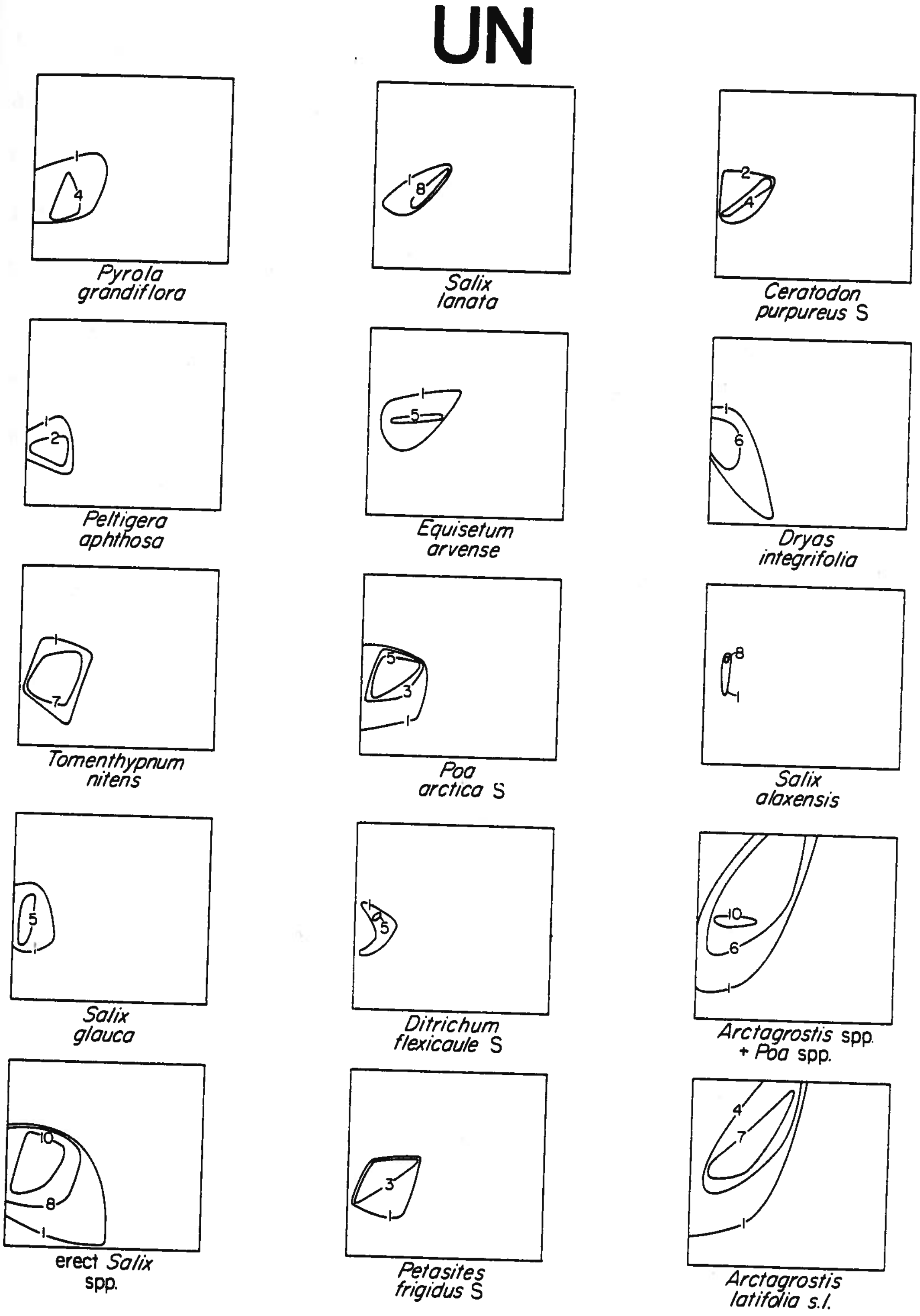


Betula nana S *Sphagnum* spp. *Saxifraga nelsoniana* S



Ledum palustre *Cassiope tetragona* *Aulacomnium palustre* S

Figure 2.29. Taxa in ordination of undisturbed and naturally disturbed vegetation (UN). Trends are very strong (Table 2.4) except when an "S" (strong) follows the taxon name; these taxa have zero values scattered among the nonzero values (see text). Figure continues on next page.



Pyrola grandiflora

Salix lanata

Ceratodon purpureus S

Peltigera aphthosa

Equisetum arvense

Dryas integrifolia

Tomenthypnum nitens

Poa arctica S

Salix alaxensis

Salix glauca

Ditrichum flexicaule S

Arctagrostis spp. + *Poa* spp.

erect *Salix* spp.

Petasites frigidus S

Arctagrostis latifolia s.l.

Figure 2.29. (continued).

(1971). Exceptionally rich areas in zone 4 can even have as many as 500 vascular species. The flora of 171 vascular plants collected at Oumalik is small for zone 4 because the area that was intensively collected was quite small and did not include the full habitat variation of the region. The substrate is uniform across the study site, and the topographic variability is low. Dry, well-drained sites and their associated flora are most notably missing. No major rivers are in the immediate area, so the floristically-rich, sandy, well-drained bank habitats were not included. Only one pingo is in the Oumalik area, and several species that are found nowhere else at Oumalik were collected from its well-drained habitats.

Classification

The Oumalik vegetation has components of both the Foothills and Coastal Plain regions. Tussock tundra typical of the Foothills covers the uplands, and the low areas are covered with marshes and other wet vegetation types characteristic of the Coastal Plain (Britton 1967). The variation in the vegetation is low relative to other northern Alaskan sites (Johnson et al. 1966, Komárková and Webber 1980, Walker 1981) for the same reasons cited for the small number of species found at Oumalik.

Ordinations

The ordinations were successful in separating the communities generated from the Braun-Blanquet tablework. In the few cases where communities overlap on the plane formed by the first two axes, they are usually separated on the third axis (not presented); only occasionally is the fourth axis necessary to separate them. This separation and the general tight clustering of samples within a community support the validity of the subjectively derived communities.

The difficulty in interpreting patterns of abundances of growth forms in the ordination space has significant implications for the modeling of vegetation. Models of arctic vegetation at Barrow (Tieszen 1978, Brown et al. 1980) have used growth forms as the basic unit of response. This was successful in that relatively simple, low-diversity system. However, the Oumalik ordination results seem to indicate that in more diverse systems species within a growth form have different enough ecologies so that the modeling by growth form includes a wide variety of responses to environmental influences. Modeling by growth form is valid if growth form categories correspond to ecological groupings, but will have severe limitations if this assumption is not met.

The ordinations showed that a complex moisture gradient is the most important environmental control on the vegetation. This agrees with the subjective interpretation that has been made many times about northern Alaskan vegetation. Ordinations done at Barrow (Webber 1978) and Atkasook (Webber unpublished) have also shown moisture to be the most important controlling factor of the vegetation. The moisture regime is obviously strongly linked to microrelief patterns at Oumalik as at other locations in northern Alaska (Wiggins 1951, Cantlon 1961, Britton 1967, Webber 1978, Walker and Webber 1980, Walker 1981).

However, ordinations should not only confirm field observations; to be useful, they should also provide additional insight into the relationships between the environment and vegetation. The ordinations were successful in this respect by revealing the importance of pH, organic matter, nitrogen, thaw depth, and disturbance in the mesic sites. The causal role vs. the concomitant variation role of these factors cannot be elucidated by indirect ordination. However, these results could profitably be used in subsequent experimental work to determine which factors to manipulate.

The important controlling nutrient at Oumalik turned out to be nitrogen. Phosphorus did not show even weak trends through the ordination space. Phosphorus was found to be the controlling nutrient in ordinations done on Barrow vegetation, which is primarily wet meadow (Webber 1978), and fertilization studies have shown that phosphorus is a limiting factor of productivity in wet sites in northern Alaska (G.R. Shaver, personal communication). Ordinations at Atkasook, where the surfaces are more mesic show nitrogen, and not phosphorus, to be an important controlling factor (P.J. Webber, unpublished). The same fertilization studies have shown that in mesic sites in northern Alaska nitrogen is a limiting factor of productivity (G.R. Shaver, personal communication). This suggests that the nutrient controls on vegetation at Oumalik are more similar to those at Atkasook than at Barrow, as one would expect. It is also interesting to note that within an area of broadly defined vegetation type, the nutrient controls on primary production and on vegetation composition are the same. The relationship between the two deserves further investigation.

Other environmental factors of note that did not show trends through the ordination space were soil particle size and snow. Particle size is important at Barrow (Webber 1978) and Atkasook (P.J. Webber unpub.), but did not emerge as a controlling factor at Oumalik because there is no variation in particle size there. Similarly, although time of meltout has been shown to be important in controlling arctic tundra vegetation composition (Webber 1971, Komârkovâ and Webber 1980), the Oumalik ordinations did not show this because the limited topographic variation generally makes the time of meltout quite uniform (Table C12).

Natural disturbance increases the beta diversity of the vegetation (Figures 2.24, 2.27). The natural disturbances have communities with fewer species than undisturbed communities, and tend to be dominated by one or a few species that are well-adapted for dispersal. Some of these species (e.g. *Salix glauca)* are important components of some mature undisturbed communities.

Others (e.g. *Arctagrostis latifolia)* are present in only small quantities in undisturbed communities, usually occurring in microsites that are disturbed.

CHAPTER III

DISTURBED VEGETATION

Introduction

Disturbed vegetation, as used here, means vegetation disturbed by man's activities. It does not include naturally disturbed vegetation unless this is specifically stated. Only the vegetation on sites that were disturbed during the 1949-50 exploratory drilling is discussed in this chapter. More recent disturbances are covered in Chapter VI. In this chapter the disturbed vegetation is classified and ordinated by itself, and then compared to the natural vegetation using ordination.

Methods

The sampling procedure, classification techniques, and ordination methods are the same as used for the natural vegetation (see Chapter II). Fifty-three relevés of disturbed vegetation were used to construct the classification, 34 with data for all plants and 19 with vascular plant data only. For the ordination the 34 relevés with data for all plants, which are also the relevés with soil analyses, were used to construct an ordination of disturbed vegetation. A second ordination, was made with the relevés of both natural disturbances (14 relevés) and man-caused disturbances (34 relevés) in order to compare the two types of disturbances.

Classification Results

The Braun-Blanquet tables for the disturbed vegetation are presented in Appendices B3 and B4 (in pocket). Appendix B3 contains the 34 relevés of disturbed vegetation that have vascular plants and cryptogam cover values, and Appendix B4 has the 19 relevés of disturbed vegetation with only vascular plants.

The descriptions of the disturbed communities follow below and are arranged from wettest to driest. They are named and described in the same way as for the natural vegetation. They are numbered starting after the natural vegetation communities.

24) *Arctophila fulva*

This community (Figure 3.1) occurs in areas where bulldozing and/or thermokarst created standing water more than about 40 cm deep. *A. fulva* dominates, and small amounts of *Carex aquatilis*, *Eriophorum angustifolium* ssp. *subarcticum*, and *Hippuris vulgaris* (in areas not sampled) occur. Floristically, this community is virtually indistinguishable from the *A. fulva-H. vulgaris* type (no. 1) found in the natural vegetation. In both cases the controlling environmental factor is the depth of water. This community is infrequent on the disturbance because sites with deep water are uncommon.

Appendix B4: 187

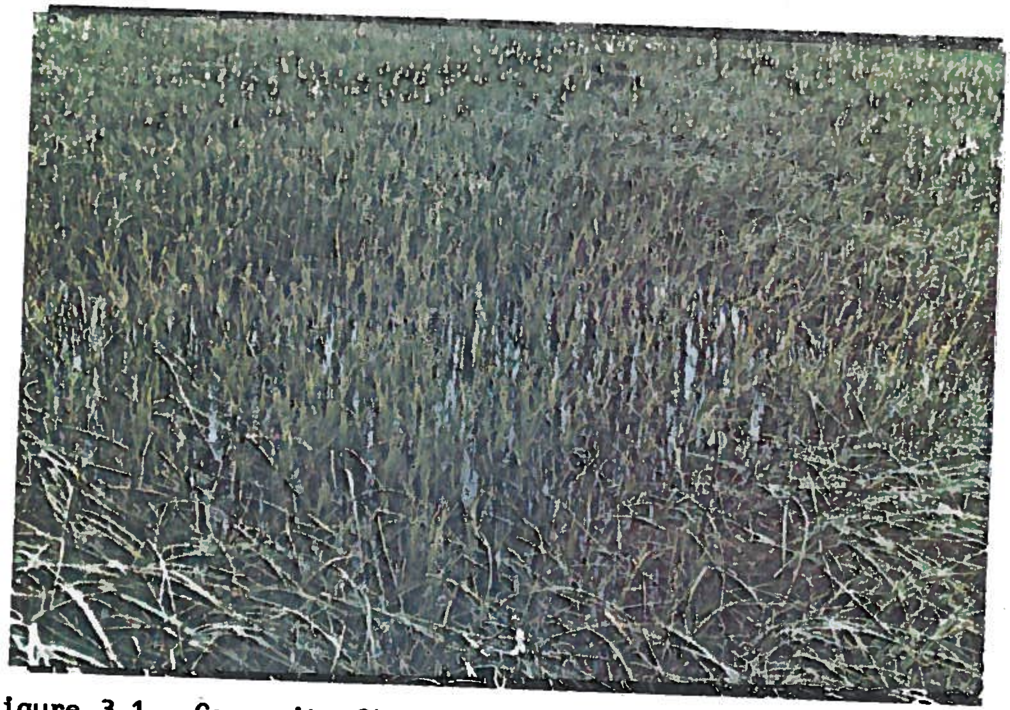


Figure 3.1. Community 24; *Arctophila fulva*. Photo 76-6, 14 July 1980.

Figure 3.2. Community 25; *Carex aquatilis-Eriophorum angustifolium* (disturbed). Photo 76-5, 14 July 1980.

25) *Carex aquatilis-Eriophorum angustifolium* (disturbed)

This floristically-poor community (Figure 3.2) is frequent on the disturbed area where the water is up to 40 cm deep. It occurs on bulldozed areas, in thermokarsts, and in multiple-pass vehicle trails in wet areas. Floristically, it is indistinguishable from natural vegetation community number 3 of the same name, which occurs in wet areas where the surface is apparently relatively young. The two species for which the type is named strongly dominate and are the only constantly-occurring taxa. Taxa that are present in small amounts in some examples of this type are *Salix planifolia* ssp. *pulchra, Poa arctica* ssp. *arctica,* and *Equisetum arvense.*

Appendix B3: 200, 186

Appendix B4: 213, 196, 201, 267, 221

26) *Eriophorum vaginatum-Salix planifolia* (disturbed)

This assemblage (Figure 3.3) was created by the partial disturbance of *Eriophorum vaginatum* tussock tundra (community 10). Multiple passes of vehicles churned the surface but did not totally destroy the vegetation. The site remains mesic, and many of the original species persist. Grasses and willows have increased in abundance. The present vegetation is dominated by the two species for which the type is named, along with moderate amounts of *Carex*

Figure 3.3. Community 26; *Eriophorum vaginatum-Salix planifolia* (disturbed). Photo 40-18, 7 July 1979.

Figure 3.4. Community 27; *Eriophorum vaginatum-Carex aquatilis*. Photo 49-26, 29 July 1979.

bigelowii, *Betula nana* ssp. *exilis*, *Poa arctica* ssp. *arctica*, *Arctagrostis latifolia* s.l., *Salix glauca*, and the mosses *Hylocomium splendens*, *Aulacomnium turgidum*, and *Polytrichum strictum*. This assemblage is uncommon at Oumalik because multiple-pass vehicle trails over tussock tundra are infrequent.

Appendix B3: 75, 81

27) *Eriophorum vaginatum-Carex aquatilis*

This is another community created by the partial disturbance of tussock tundra (community 10). The one sample representing this uncommon assemblage was taken from where the runway crosses an area of tussock tundra (Figure 3.4). No soil was added to this part of the runway, and compaction and/or subsidence has lowered the surface slightly (10 to 15 cm) and made the site wetter than the original mesic moisture regime. *E. vaginatum* and *Salix planifolia* persist but are less abundant, and many associated species such as the ericaceous shrubs, lichens, and forbs have been eliminated. Species characteristic of wet areas, especially the sedges *C. aquatilis*, *E. angustifolium* ssp. *subarcticum*, and *C. saxatilis* ssp. *laxa* have become dominant; and the forbs *Chrysosplenium tetrandrum*, *Saxifraga cernua*, *Epilobium palustre*, and *Comarum palustre* are now important.

Appendix B3: 90

28) *Saxifraga cernua-Marchantia polymorpha*

This unusual community grows in moist, relatively dark areas among stacked oil drums (Fig. 3.5). Total cover is low because much of the substrate was covered with oil drums and because of the low light levels. Other species are *Cardamine digitata, Saxifraga nelsoniana,* and a *Pohlia* sp. The assemblage no longer exists because the drums were removed in 1980 and the area was heavily trampled during the cleanup.

Appendix B3:78

29) *Betula nana-Carex aquatilis*

B. nana ssp. *exilis,* and *Salix planifolia* ssp. *pulchra* dominate the shrub layer of this community, while *C. aquatilis* and *Eriophorum angustifolium* ssp. *subarcticum* dominate the herb layer. (Figure 3.6). This assemblage occurs on two different types of disturbances. It is found occasionally on the wet bottoms of bulldozed trails (relevé 214) and on palsas formerly occupied by the *B. nana-Ledum palustre* community (no. 11), which were partially disturbed by multiple passes of vehicles (relevé 265). The partially disturbed palsa has *L. palustre* and *Vaccinium vitis-idaea,* which are remnants of the original community. The sample in the bladed trail includes substantial amounts of *Poa arctica* ssp. *arctica* and *Arctagrostis latifolia* var. *arundinacea,* which are both disturbance indicators. This assemblage is similar in dominant species to the undisturbed *S. planifolia-C. aquatilis* community (no. 7).

Appendix B3:214

Appendix B4:265

Figure 3.5. Community 28; *Saxifraga cernua-Marchantia polymorpha.* Photo 40-32, 8 July 1979.

Figure 3.6. Community 29; *Betula nana-Carex aquatilis.* Photo 71-10, 19 July 1980.

30) *Salix planifolia-Carex aquatilis* (disturbed)

S. planifolia ssp. *pulchra* and *S. lanata* ssp. *richardsonii* dominate the shrub layer, and *Carex aquatilis* and *Eriophorum angustifolium* ssp. *subarcticum* are the main components of the herb layer in this assemblage (Figure 3.7). Relevé 219 is on a multiple-pass vehicle trail through a *Salix lanata-S. planifolia* community (no.8), and relevé 266 was taken in an area disturbed by multiple passes of vehicles through an area whose original community is unknown, but probably included *B. nana* ssp. *exilis* and *C. aquatilis*. Both sites have saturated soil throughout the growing season. This assemblage is uncommon at Oumalik.

Appendix B4:266, 219

31) *Salix* spp.- *Arctagrostis latifolia-Eriophorum angustifolium*

This community (Figure 3.8) and the one following are the most visually conspicuous components of the recovering vegetation at Oumalik due to the tall, vigorous *Salix* spp. This community grows in somewhat moister, but still mesic, sites than community 32, and has an important component of *E. angustifolium* ssp. *subarcticum* and *Carex aquatilis* which differentiates it from community 32. The two do intergrade, however. The shrub dominants are *S. planifolia* ssp. *pulchra*, *S. glauca*, *S. alaxensis* ssp. *alaxensis*, *S. lanata* ssp. *richardsonii*, and often *Betula nana* ssp. *exilis*. The most important components of the herb layer are *Equisetum arvense*, *A. latifolia* s.l., *E. angustifolium* spp.

Figure 3.7. Community 30; *Salix planifolia-Carex aquatilis* (disturbed). Photo 79-18, 24 July 1980.

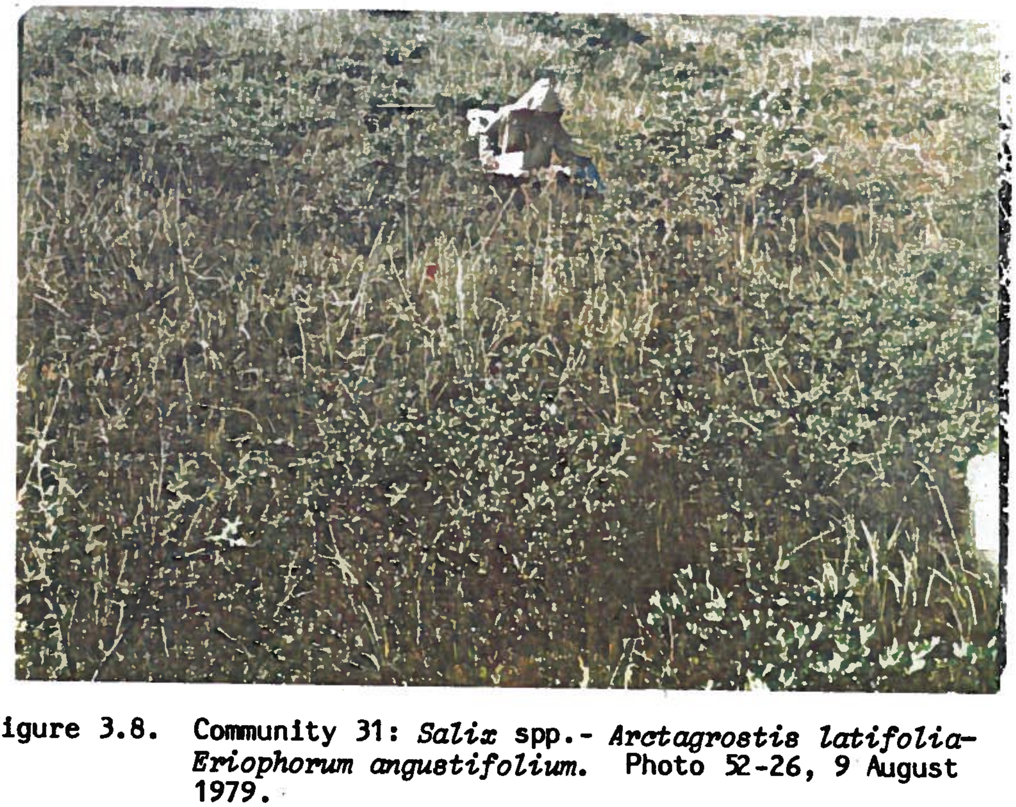


Figure 3.8. Community 31: *Salix* spp.- *Arctagrostis latifolia-Eriophorum angustifolium*. Photo 52-26, 9 August 1979.

subarcticum, and *C. aquatilis*. Important mosses are *Tomenthypnum nitens*, *Hylocomium splendens*, and *Ditrichum flexicaule*. This community is found in multiple-pass trails, thermokarsts in the camp area, and on some mounds of bladed material. Decomposition rates in the soils of this community and community 32 are very high compared to undisturbed areas (Chapter V).

Appendix B3:88, 89, 120, 86, 202, 72, 129, 126, 188, 193

Appendix B4:191

32) *Salix* spp.- *Arctagrostis latifolia*

This is similar to community 31, and the shrub layers of the two communities are indistinguishable. Since this community (Figure 3.9) occurs on slightly drier sites than community 31, it lacks *Carex aquatilis* and *Eriophorum angustifolium* ssp. *subarcticum* in the herb layer, and only some examples of it have the mosses that consistently occur in community 31. This assemblage is found on mounds of bladed material, slopes churned by vehicles and then smoothed by bulldozing, and multiple-pass trails.

Appendix B3:79, 80, 121, 77, 85, 71, 197, 70, 192, 102

Appendix B4:211

33) *Arctagrostis latifolia* (disturbed)

This community is composed mainly of *A. latifolia* var. *arundinacea* with some *A. latifolia* var. *latifolia* (Figure 3.10).

Figure 3.9. Community 32; *Salix* spp.- *Arctagrostis latifolia.* Photo 40-34, 9 July 1979.

Figure 3.10. Community 33; *Arctagrostis latifolia* (disturbed). Photo 52-36, 11 August 1979.

Equisetum arvense is also a dominant in some cases, and a variety of other plants, such as erect *Salix* spp., *Poa arctica* ssp. *arctica*, and *Stellaria laeta*, may be present. In wetter examples of this community (relevés 212 and 199) small amounts of *Carex aquatilis*, *Eriophorum angustifolium* ssp. *subarcticum*, and forbs characteristic of wetter areas are found. There is some floristic intergradation with the *Salix* spp.- *Arctagrostis latifolia* communities although physiognomically the communities are distinct, and the two types occur on the same general types of disturbances. The amount of organic matter in the soil seems to control which community develops. This community has a mean of 5%, compared to 30% for community 32 (Figure C8) and also less nitrogen (Figures C16-C18) and higher pH (Figure C14), which are both associated with the lower amount of organic matter. This community also has very high decomposition rates compared to undisturbed communities (Chapter V).

Appendix B3:127,137

Appendix B4:198, 194, 212, 199, 189

34) *Dryas integrifolia-Equisetum arvense*

This occurs in multiple-pass vehicle trails though *Dryas integrifolia-Salix glauca* or *Dryas integrifolia-Carex* spp. communites where the moisture regime has not been much changed (Figure 3.11). Many members of the original communities have persisted; and *Arctagrostis latifolia* var. *latifolia*, *Poa*

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Appendix B3:127,137

Appendix B4:198, 194, 212, 199, 189

34) *Dryas integrifolia-Equisetum arvense*

This occurs in multiple-pass vehicle trails though *Dryas integrifolia-Salix glauca* or *Dryas integrifolia-Carex* spp. communites where the moisture regime has not been much changed (Figure 3.11). Many members of the original communities have persisted; and *Arctagrostis latifolia* var. *latifolia*, *Poa*

Figure 3.11. Community 34; *Dryas integrifolia-Equisetum arvense.* Photo 76-10, 16 July 1980.

Figure 3.12. Community 35; *Betula nana-Arctagrostis latifolia.* Photo 71-11, 19 July 1980.

arctica ssp. *arctica*, and *Equisetum arvense*, which are minor components of the original communities, have greatly increased. In some cases *Salix lanata* ssp. *richardsonii* and *S. glauca* have become important components of the community. This assemblage occurs infrequently at Oumalik.

Appendix B3:124, 74

Appendix B4:190, 237

35) *Betula nana-Arctagrostis latifolia*

This community has a shrub layer of *B. nana* ssp. *exilis* and *Salix planifolia* ssp. *pulchra* and an herb layer of *A. latifolia* var. *arundinacea*, *Poa arctica* ssp. *arctica*, and the prostrate shrubs *Ledum palustre* ssp. *decumbens* and *Vaccinium vitis-idaea* ssp. *minus* (Figure 3.12). It is quite similar to the undisturbed *Betula nana-Ledum palustre* community (no. 19). Relevé 216 was done on a multiple-pass trail through that undisturbed community, and relevé 215 was done on a piece of turf inverted by bulldozing. The original community cannot be determined exactly, but also could be the *Betula-Ledum* community, with the present community arising from roots in the turf.

Appendix B3:215

Appendix B4:216

36) *Puccinellia borealis-Equisetum arvense*

This assemblage is rare on the Oumalik disturbance, occurring only on the tops of some mounds left by thermokarsting on the camp area and a small area of drilling mud in a mesic site (Figure 3.13). The mound is different from other similar mounds where no *P. borealis* grows and where *Arctagrostis latifolia* grows vigorously primarily in its higher carbonate content (Figure C15). The soil of the undisturbed *P. borealis-A. latifolia* community (no. 23) has a similarly high carbonate content (Figure C15). Species that occur in addition to the species for which the type is named are *A. latifolia* var. *arundinacea* and *Poa arctica* ssp. *arctica,* which occur in small amounts.

Appendix B3:195

Classification Discussion

The disturbed areas can be broadly classified into two types-- those where the original vegetation was entirely removed or killed (devastated sites) and those where disturbance left some of the original vegetation (partially disturbed sites). The vegetation on the devastated sites strongly intergrades, and therefore the communities derived from it also intergrade, e.g. communities 31, 32, and 33. The disturbed vegetation intergrades so strongly because many of the dominant species, such as *Salix* spp. and *Arctagrostis latifolia s.l.* have wide ecological amplitudes on the disturbance. Also, the disturbance is young enough that relatively few subordinate species have had time to colonize. Many species occur sporadically, but there has been insufficient time for species with narrower ecological tolerances,

Figure 3.13. Community 36; *Puccinellia borealis-Equisetum arvense*. Photo 76-15, 16 July 1980.

which differentiate communities in undisturbed vegetation, to colonize all the sites they can potentially occupy. Thus, the types of species that usually differentiate communities are not present consistently. This means that disturbed communities are often separated on the basis of relative abundance of dominant species rather than the presence/absence of species that characterize the type. Within the Braun-Blanquet system, anthropogenic communities of this type, which lack character and differential species at the association level and have them only for higher level syntaxa, have been called basal communities by Kopecky and Hejny (1974).

The partially disturbed vegetation was created by activities such as multiple passes of vehicles. Some of the original taxa remain on these sites, and some were eliminated, depending on which environmental factors were changed and the direction of the change. Other species, those responding favorably to the environmental changes and to disturbance in general, appeared or increased in abundance. There are many permutations of original community with type and intensity of disturbance so that this situation produced a large variety of communities, which are quite distinct from each other, e.g. communities 26, 27, 28, and 36. Not every one of these could be sampled and described, so some assemblages of very limited extent are not described here.

Some disturbed communities are very similar to natural vegetation communities. In some cases the similarity is between the vegetation on partially disturbed areas and their controls, e.g. communities 18 and 35, 13 and 34, 7 and 29. These communities are similar because of the persistence of original taxa as described above and will not be discussed further here. In other instances the similarity is because man-caused disturbances and natural disturbances of about the same age have created similar environments, which have been colonized by the same taxa. Strong similarity seems to occur only in cases where a single controlling environmental factor strongly dominates and overwhelms the effects of other environmental factors. The *Arctophila fulva* communities (nos. 1 and 24), which are essentially indistinguishable floristically, illustrate this well. The strongly dominating environmental factor in this case is water depth.

A second example of a high degree of similarity between man-disturbed and naturally disturbed vegetation is the two *Carex aquatilis-Eriophorum angustifolium* communities (nos. 3 and 25). Water depth/moisture regime is the prominent controlling factor for this pair of communities. The natural community (no. 3) occurs only in relatively recently disturbed wet sites, such as thermokarsts. In sites with similar moisture regime that have been stable much longer, e.g. bottoms of drained lake basins, the communities are floristically more complex, e.g. community 5.

Another case in which a man-disturbed community has a natural analog is the pair of *Arctagrostis latifolia* communities (nos. 22 and 33). They are quite similar floristically, and both occur on recently exposed mineral soil surfaces that have relatively warm soil temperatures. In one case this environment is created by the natural erosion of a lake bluff, and in the other by bulldozing.

There are two other pairs of natural disturbances and man-caused disturbances that illustrate this phenomenon, although the floristic similarities are not as strong. Communities 23 and 36 are both dominated by *Puccinellia borealis*, a plant which is absent in other communities at Oumalik. The important controlling environmental factor appears to be the high amount of carbonates (Figure C15). Communities 32 and 20 both have large components of *Arctagrostis latifolia* and willows, with the natural community having only *Salix glauca* while the disturbed community has several *Salix* species. The disturbed community occurs on bulldozed areas that are mesic with moderate amounts of organic matter and warm soil temperatures. The disturbed community occurs on temporarily stabilized parts of eroding lake bluffs that are environmentally similar to the bulldozed areas.

Recovering Vegetation by Disturbance Type and Original Community

This section describes the present vegetation on areas disturbed in 1949-1950 as a function of disturbance type and, where possible, original community. Much of the information in this section is presented in the descriptions of the disturbed communities. It is summarized here by disturbance type primarily to help land managers in making decisions on the acceptability of certain activities by providing information on the longer-term effects of certain types of disturbance. This information is applicable mainly to impacts of exploratory operations, such as the extensive off-road seismic work being done in the Arctic National Wildlife Refuge (Felix and Jorgenson 1984). It is not as generally applicable to development operations, such as the Prudhoe Bay and Kuparuk oil fields, because most activities are on gravel pads there. These Oumalik results are applicable to large areas of northern Alaska; see Chapter VII for a discussion of the limits of extrapolation.

The discussion is limited to recovery from physical disturbances since there are very few disturbances caused by chemical contaminations, such as spilled hydrocarbons. The only exception to this is a discussion of the effects of drilling mud. (For discussions of recovery of arctic terrain following hydrocarbon spills, see Everett [1978], Johnson et al. [1978], and Walker et al. [1978]). Not all types of disturbance occurred or were sampled in all the common vegetation types.

The majority of the disturbed area at Oumalik was affected by vehicles. In addition to the Caterpillar bulldozers, two types of vehicles, Weasels and LVT's, were on the site (U.S. Navy 1950). The Weasel is a small, light tracked vehicle. The LVT is an U.S. Navy amphibious assault vehicle rated at 2 tons. The tracks these two vehicles make are very distinct from each other.

Single passes of vehicles. Single passes of the Weasel probably produce very little impact (Abele et al. 1984), and none were identifiable 30 years later. Tracks of the LVT in the *Dryas integrifolia-Carex* spp. community (no. 17) are about 30 cm wide and depressed about 10 cm. Overall cover of the disturbed area is still complete and the dominant plants and overall physiognomy of the community are similar to the original. Several vascular species have been eliminated- *Salix arctica*, *Stellaria laeta*, *Eriophorum vaginatum*, *Arctous alpina*, *Pedicularis lanata*, *Carex misandra*, *Carex capillaris*, *C. bigelowii*, and *Saussurea angustifolia*. *C. scirpoidea* has increased from 25 to 50% cover. Moss cover and composition remain more or less the same, but lichens, except for *Cetraria cucullata* and *Dactylina arctica*, are eliminated.

In the *Betula nana-Ledum palustre* community (no. 18) a single-pass track has produced a lower and slightly wetter surface than the control. The original taxa have been reduced but not eliminated, and moderate amounts of *Carex aquatilis*, *Eriophorum angustifolium* ssp. *subarcticum*, and *E. russeolum* have also invaded.

In general, single-pass tracks after 30 years have complete cover, retain the dominants of the original community, lose some of the subordinate original taxa, lose most of their lichen cover, and may have taxa not present in the control which are favored by the new environment created by the disturbance.

The physical environment of these disturbances seems stable at this time. Abele et al. (1984) have shown that if vehicles do not break the organic mat, the surface can recover to its original level within 10 yr even if depressed as much as 15 cm. However, the tracks of LVT's apparently did break the organic mat at Oumalik, and it seems as if the present depressed microtopography is permanent.

Human trampling. The area in front of the 1949-1950 living quarters apparently was trampled by foot traffic off of the boardwalks that connected the buildings. The original community was *Dryas integrifolia-Salix glauca* (no. 13), and most of the original taxa, including forbs, that are minor components of the original remain. However, the overall appearance of the community (no. 34, Figure 3.11) is quite different from the original since *Equisteum arvense*, present in small amounts in the undisturbed community, has increased to 45% cover, and *Arctagrostis latifolia* and *Poa arctica*, also present in small amounts in the original, now have moderate covers. New species are *S. alaxensis* and *S. planifolia*. The trampling apparently was not severe enough to heavily damage the belowground perennating organs of the vascular plants or kill the cryptogams, but did create enough disturbance to make the site more favorable to the disturbance-responsive species *E. arvense*, *A. latifolia*, *and P. arctica*.

Compression from winter vehicle use. This disturbance occurred on parts of the winter runway where no soil was added to the surface (see Chapter I). Heavy vehicles compressed the surface 10-15 cm in an *Eriophorum vaginatum-Salix planifolia* community (no. 10). The soil was not churned however, and the compression may have occurred in the autumn when the lower part of the active layer was not yet frozen. The site is wetter than the adjacent control. The named dominants persist with reduced cover, but the ericaceous shrubs, lichens, and forbs characteristic of tussock tundra are essentially gone. Species characteristic of wet areas; *Carex aquatilis, C. saxatilis, Eriophorum angustifolium, Chrysosplenium tetrandrum, Saxifraga cernua,* and *Epilobium palustre;* are now present (community 27, Figure 3.4).

Multiple passes of vehicles. Several passes of vehicles (LVT's) over the same site break the organic mat in numerous places, and many passes churn the upper soil horizons. In gently sloping tussock tundra (community 10) a moderate number of passes that did not change the moisture regime eliminated essentially no species. However, the impact changed the physiognomy of the community to an almost closed dwarf shrub community by reducing the cover of *Eriophorum vaginatum,* increasing the cover of *Salix planifolia,* and allowing the invasion of *S. glauca* and *Arctagrostis latifolia.* In flat areas of tussock tundra where the depression caused by the impact became wetter, both the physiognomy and floristic composition were changed. *E. vaginatum* and *Betula nana* were reduced in cover, *Salix planifolia* was increased, the ericaceous shrubs were eliminated, and *E. angustifolium* and *Carex aquatilis* were increased (Figure 3.14). In parts of the multiple pass trails that underwent thermokarst, the community has little resemblance to the original. *E. angustifolium* and *C. aquatilis* dominate these sites, along with small amounts of forbs characteristic of wet, disturbed areas (community 25).

Multiple-pass trails in the *Dryas integrifolia-Salix glauca* community (no. 13) show much the same pattern as tracks through the tussock tundra. If damage was moderate and the moisture regime was little changed, many of the original species persist, and species which respond positively to disturbance *(Arctagrostis latifolia, Poa arctica, Salix* spp., *Equisetum arvense)* are prominent members of the disturbed community. If damage was more severe but the site is still mesic, many of the original species are gone and the disturbance species dominate (communities 31, 32). And in thermokarsts within the trails, the original species are essentially absent, and *Carex aquatilis* and *Eriophorum angustifolium* dominate (community 25).

In a multiple-pass track that caused moderate damage without changing the mesic moisture regime, in a *Betula nana-Ledum palustre* community, *B. nana, L. palustre,* and *Vaccinium vitis-idaea* decreased while *Poa arctica* and *Arctagrostis latifolia*

Figure 3.14. Multiple-pass vehicle tracks through tussock tundra. This area became wetter due to the disturbance, but did not thermokarst extensively. See text for description and list of taxa present. Photo 53-12.

Figure 3.15. Multiple-pass Weasel tracks through a drained lake basin. *Salix* spp. and other taxa have been eliminated. See text for description. Photo 79-20, 24 July 1980.

increased. The mosses remained about the same, as did the small amount of lichens.

Multiple-pass Weasel tracks are clearly visible in the *Salix lanata-S. planifolia* community (no. 8) (Figure 3.15). They are about 2 m wide and are depressed uniformly 15-20 cm across the track. Weasels were used through this area in the summer to transport personnel and supplies from the lake where float planes landed (J.F. Schindler, written communication). Shrubs were virtually eliminated, and broken pieces of stems were found in the soil. The moss *Tomenthypnum nitens*, dominant in the control, is gone, and total moss cover is much reduced. Most of the forbs in the community and the prostrate shrub *Dryas integrifolia* were eliminated, and *Carex aquatilis* and *Eriophorum angustifolium* now provide most of the cover.

In summary, if damage from multiple passes of vehicles in mesic sites is slight to moderate and the moisture regime is not changed, most of the original species persist, and species which respond positively to disturbance *(Arctagrostis latifolia, Poa arctica*, and *Equisetum arvense)* are increased. This community can have quite a different appearance from the original. If damage is more severe, most of the original species are lost, and the above disturbance species plus the erect *Salix* spp. dominate the site. If the tracks are much wetter than the original site due to subsidence and thermokarst, the original species are lost; and

Carex aquatilis and *Eriophorum angustifolium* provide a more-or-less complete cover.

Bulldozing. The bulldozing done at Oumalik had a variety of effects--from creating surfaces below water level to forming well-drained mounds of soil. In most cases the original community does not affect the vegetation found there now because the bulldozing totally destroyed the original vegetation and created an entirely new habitat. Only in a few cases, where more or less intact blocks of turf were pushed aside does the original vegetation have an effect. Because the original community is not important, this section is organized by the habitat created by the disturbance, from wettest to driest, rather than by original community.

In places where the surface was bulldozed and/or underwent thermokarst to leave water about 40-100 cm deep, the vegetation is now community 24 (Figure 3.1). *Arctophila fulva* dominates, with small amounts of *Eriophorum angustifolium* and *Hippuris vulgaris* present. This community is essentially indistinguishable from the natural community (no. 1) that grows in water of this depth. Most of the few places on the disturbance where water is deeper than about 1 m have no plants; one area has a large mass of floating *Scorpidium scorpioides*.

In bulldozed areas with shallower standing water than above, *Eriophorum angustifolium* and *Carex aquatilis* provide almost all the cover (community 25, Figure 3.2). This community is also essentially indistinguishable from a natural community (no. 3).

In a few cases bulldozing has left areas where soils are saturated, but have no standing water. These places are now covered with community 25 as described above or with community 29 (Figure 3.6) which has a shrub layer of *Salix planifolia* and *Betula nana* and herb layer of *Arctagrostis latifolia, Carex aquatilis, Eriophorum angustifolium,* and *Poa arctica.* The main mosses are *Aulacomnium palustre, A. turgidum,* and *Polytrichum juniperinum.* Except for the presence of some disturbance indicators, this community is similar to the undisturbed *Salix planifolia-Carex aquatilis* community (no.7).

Areas similar to the above but which are slightly less wet lack the prominent shrub layer, and have much more *Arctagrostis latifolia* and considerably less *C. aquatilis* and *E. angustifolium.* The forbs *Polemonium acutiflorum* and *Saxifraga cernua* are also important here.

Mounds of soil bulldozed up from adjacent areas are common in the drill site area. These mesic sites were colonized by varying amounts of erect *Salix* spp. *(S. alaxensis, S. glauca, S. lanata,* and *S. planifolia)* and *A. latifolia.* The communities dominated by *Salix* spp. (nos. 31, 32, Figures 3.8, 3.9) occur in sites with more soil organic matter than the *Arctagrostis* community (no. 33, Figure 3.10). These mounds are some of the places where the *Salix* spp. grow so vigorously (Chapter V).

The driest sites caused by bulldozing at Oumalik are pieces of turf pushed higher than their original position. These occur along a bulldozed trail (Figure 3.12) and in one mound of bulldozed material where turf pieces are intact. The turf pieces came from the *Betula nana-Ledum palustre* community (no. 18). Even if the pieces are upside down, they retain the name species plus *Salix planifolia* and *Vaccinium vitis-idaea.* The grasses *Arctagrostis latifolia* and *Poa arctica,* present in only small amounts in the undisturbed community, have 20-30% cover on the disturbed sites.

Drilling mud. The drilling mud and drill cuttings were dumped directly onto the tundra surfaces in a small area just north of the wellhead foundation (personal observation). They are on sites whose moisture regime ranges from mesic to deep water. In the standing water the vegetation is the same as areas where there is no drilling mud; the *Arctophila fulva* community (no. 24) occurs in deep water and the *Carex aquatilis-Eriophorum angustifolium* community (no. 25) occurs in shallow water. On the mesic area (Figure 3.16) cover is almost complete, and *Puccinellia borealis* dominates, with smaller amounts of a *Stellaria* sp., *Arctagrostis latifolia,* and *Poa arctica* (community 36). Adjacent disturbed areas with the same mesic moisture regime but no drilling mud are covered with the *Arctagrostis latifolia* (community no. 33). Thus, in wet sites the effect of the drilling mud is negligible compared to other disturbances, and in mesic sites plant cover is almost

Figure 3.16. Vegetation on drilling mud in mesic area. The dominant taxon is *Puccinellia borealis*. *Arctagrostis latifolia* dominates the vegetation in the background, on a site of similar moisture regime but no drilling mud. Photo 53-3, 11 August 1979.

complete although the community is quite different from undisturbed tundra and other disturbances with a similar moisture regime.

French (1978) looked at several other wells of the same age as Oumalik in the NPR-A and concluded that dumping drilling fluids directly onto the tundra did not have an adverse effect on the vegetation. He cautioned however, that the different chemical composition of modern drilling mud would probably make disposal onto the tundra surface today much less innocuous.

Comparison of recovery at Oumalik with other sites in the literature. The colonizers of the disturbances at Oumalik are similar to those at other sites in arctic Alaska and the Mackenzie Delta region of Canada. In wet sites, Hernandez (1973), who studied 5-6 year-old disturbances in the Mackenzie Delta area and Tuktoyaktuk Peninsula, and Johnson et al. (1978), who looked at 28-year-old disturbances at Fish Creek in northern Alaska, reported the same colonizers as found at Oumalik. In deep water created by bulldozing or thermokarst, *Arctophila fulva* is the dominant colonizer (Hernandez 1973), and in shallow water *Carex aquatilis* and *Eriophorum angustifolium* are the main colonizers (Hernandez 1973, Johnson et al. 1978).

On mesic devastated areas at Oumalik, the grasses that colonize are *Arctagrostis latifolia* and *Poa arctica*. These are also important colonizers of disturbances in the Mackenzie Delta area (Hernandez 1973, Younkin 1973) and at Fish Creek (Johnson et al. 1978, Komárková and Webber 1978). *A. latifolia* appears on disturbed areas in the first season after disturbance, and by the second year the plants are clumps of several shoots and produce seeds (Younkin 1973). *Calamagrostis canadensis* is an important colonizer on mesic areas at other sites in northern Alaska and Canada (Hernandez 1973 [MacKenzie Delta area], Racine 1979 [Seward Peninsula], C.H. Racine personal communication [Noatak drainage],). There is no *C. canadensis* at Fish Creek (Murray 1978) or Oumalik because these sites are north of its range (Hultén 1968). Younkin (1973) has shown that *C. canadensis* is not nearly so well-adapted as *A. latifolia* to cold soils in germination rate and seed output, which apparently limits it to warmer regions than *A. latifolia*.

In addition to grasses, willows are dominant colonizers of mesic, devastated areas at Oumalik. At other sites Hernandez (1973) found numerous *Salix* spp. seedlings and sprouts from roots on bulldozed areas 1-2 yr old in a *Salix-Alnus* community. Kershaw (1983) also found erect *Salix* spp. to be important components of the vegetation on 34-36 yr-old disturbances in the alpine of the Northwest Territories even though the substrate is very rocky compared to the silts and organic matter at Oumalik. At the cooler Fish Creek site (Johnson et al. 1978) willows are not conspicuous component of the recovering vegetation. (The importance of willows on disturbances at various sites is discussed further in Chapter VII).

Eriophorum vaginatum and *Carex bigelowii* are generally not colonizers of mesic sites at Oumalik or Fish Creek (Johnson et al. 1978, Komárková 1983) even though they dominate at other locations. At Eagle Summit in interior Alaska, *E. vaginatum* covered about 88% and *Carex bigelowii* 11% of an experimentally bulldozed site in the tussock tundra after 10 years (Chapin and Chapin 1980). McGraw (1980) has shown that the buried seed bank is probably the source of most of the colonizing individuals. In the northern foothills of the Brooks Range, Gartner et al. (1983) found that the colonizers of a 4-yr-old bulldozed site in tussock tundra were primarily *E. vaginatum* and *C. bigelowii* and that most of the individuals came from the buried seed bank. To explain the lack of *E. vaginatum* on upland disturbances at Fish Creek, Komárková (1983) cited decreased colonizing ability at the northern limit of its range and insufficient moisture on disturbed upland sites. At Oumalik the main disturbance is not in tussock tundra, and the soils of the disturbed area would not be expected to have a large number of *E. vaginatum* seeds. However, the almost complete lack of *E. vaginatum* on devastated sites means that individuals were not established by windblown seeds either. It is possible that viable seeds do not reach the disturbance or that the ones that did land on the site after disturbance did not have sufficient moisture or were out-competed by the very rapid growth of *Arctagrostis latifolia* (Younkin 1973) and the erect *Salix* spp.

Ordination Results and Discussion

Sample Ordinations

The sample ordinations for the disturbed vegetation (D) and for both natural and man-caused disturbances (DN) are in Figure 3.17. As with the natural vegetation, the third and fourth axes provided little additional information, and only the first two axes are presented. Relevé 172 is an outlier in the DN ordination as it was in the UN ordination, although by only about 2 sd, a distance readily handled by DECORANA (Hill and Gauch 1980). The remainder of the samples distribute well through the space. It should be noted that there are substantially fewer samples of wet vegetation than of mesic vegetation because the much higher variability in mesic vegetation required more samples than the relatively homogeneous wet vegetation and because many of the limited number of soil analyses were used for samples studied intensively in connection with the willows (see Chapter IV).

Environmental Interpretations of Ordination Spaces

The environmental factors that associate most strongly with the axes of the ordination of the disturbed vegetation are pH and moisture (Figure 3.18, Table 3.1). The first axis is associated most strongly with pH and the second axis with moisture. In the two ordinations of the natural vegetation (see

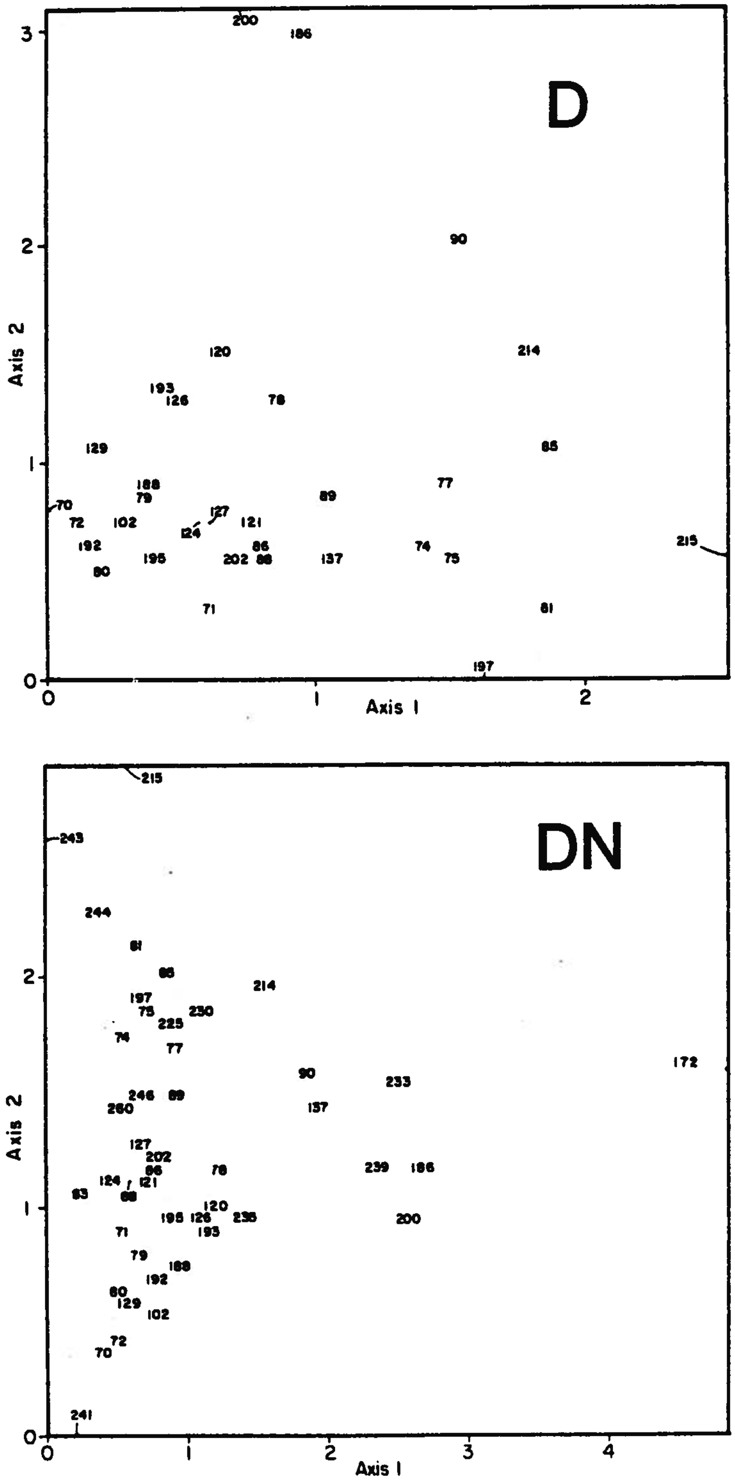
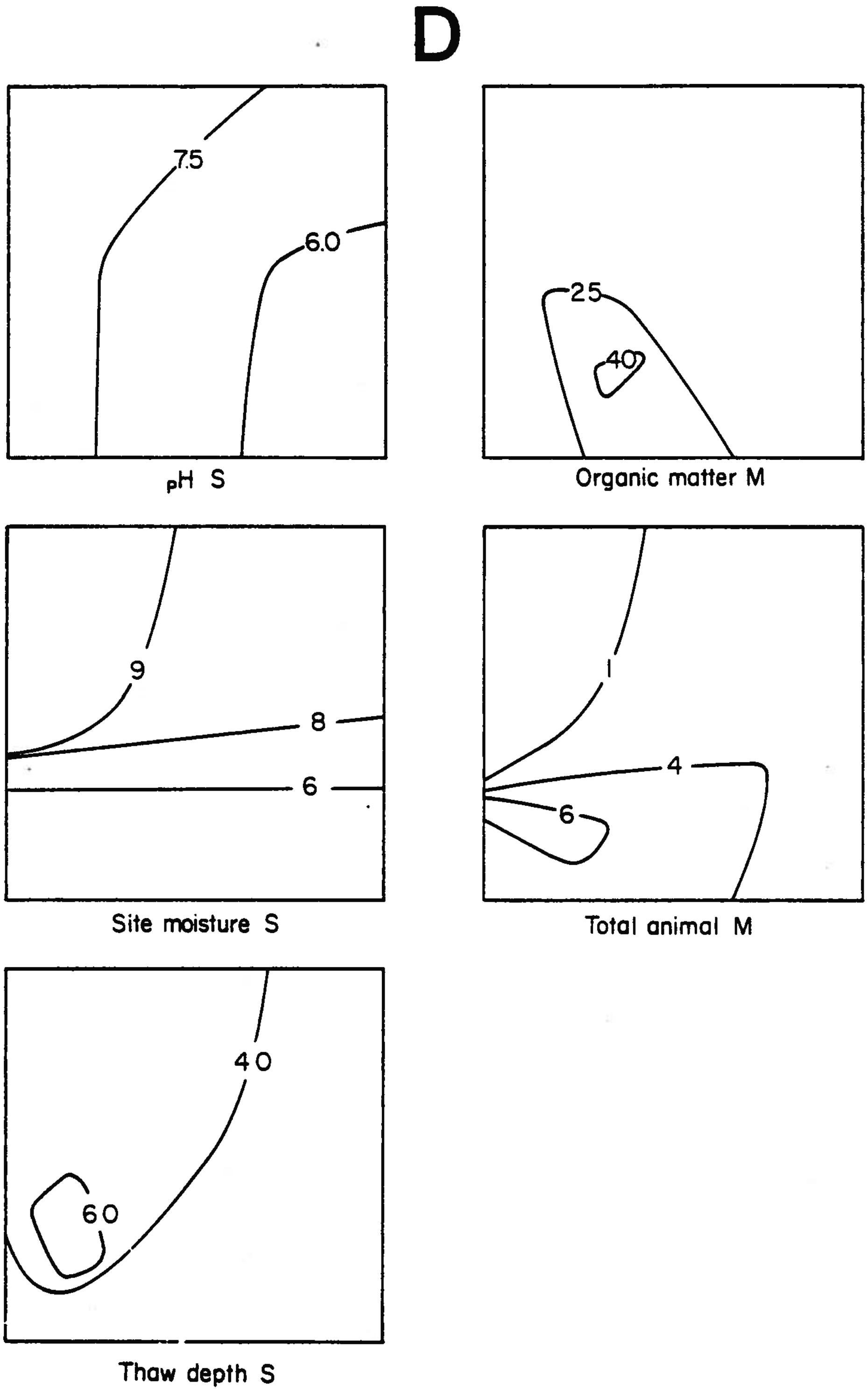


Figure 3.17. Ordinations of samples of human-disturbed vegetation (D) and human-disturbed and naturally disturbed vegetation (DN). Axes are scaled in standard deviation units (see Chapter II, Methods). Species compositions of the samples are in Appendices B3 and B4, and site factors are in Appendix C.



pH S

Organic matter M

Site moisture S

Total animal M

Thaw depth S

Figure 3.18. Trends of site factors through ordination space of disturbed vegetation (D). The strength of trends is rated as very strong (VS), strong (S), or moderate (M) (see Table 2.4 for complete descriptions of the categories.

Table 3.1. Spearman correlation coefficients for the first two axes and significant environmental factors of the ordination of disturbed (D) samples. The environmental factors are those from Figure 3.18.

	axis 1	axis 2	pH	site moisture	thaw depth	organic matter
axis 2	.17					
pH	-.70**	.07				
site moisture	.23	.60**	-.14			
thaw depth	-.53**	.17	.43**	-.16		
organic matter	.24	-.05	-.45**	.16	-.53**	
total animal	-.02	-.39*	-.18	-.33*	-.37*	.07

*.01 $< p \leq .05$
** $p \leq .01$

Chapter II) and the DN ordination (discussed below), the first axis associates primarily with moisture and the second with pH. The reversal of the associations in the D ordination seems to be an artifact caused by the small number of samples of wet disturbed areas. Only four disturbed samples were from wet areas while most of the remainder were mesic and a few were intermediate. The effects of the mesic samples dominate the analysis so that pH, which is the dominant controlling factor of the mesic vegetation, is shown to be the primary controlling factor overall, and moisture is the second-most important factor.

Other environmental factors that showed weaker trends through the ordination space were thaw depth, organic matter, and total animal sign. The greatest thaw depths are in the *Arctagrostis latifolia* community (no. 33) and the *Salix* spp.- *A. latifolia* communities (nos. 31, 32). The samples highest in organic matter are also from the *Salix* spp.- *A. latifolia* communities, though not those with the greatest thaw depth. Total animal sign was also highest in some of the *Salix* spp.- *A. latifolia* communities.

Factors of note that did not show trends were disturbance score, cryoturbation, and nutrients. Since disturbance score is quite uniform within this data set, it will not show trends even though its presence is one of the most important factors in determining the composition of vegetation on the disturbed areas.

Cryoturbation does not show trends because it is essentially not present on the young surfaces of the disturbance. Nutrient concentrations vary widely within community types (Figures C16 to C20), especially within the *Salix* spp. -*A. latifolia* communities, which are 20 of the 34 samples in this ordination. The heterogeneous jumble of materials comprising the soil of many of the disturbed samples causes the within sample and between sample variations of nutrient concentrations to be high and would tend to obscure trends, if they are indeed present.

Overall, the trends of environmental factors through the D ordination space are fewer and weaker than those in the U and UN data sets. Several plants, e.g. *Arctagrostis latifolia* and *Salix planifolia*, are common and dominant over a wide range of conditions on the disturbance. Thus, much or all of the cover of a disturbed sample may be composed of plants that indicate the environmental characteristics of that site only within broad limits. Conversely, there are many plants that occur infrequently on the disturbance. In undisturbed vegetation these less common plants are often the ones that are characterize communities. However, in disturbed vegetation, which is not yet in equilibrium with the site, the distribution of these plants is more random. They probably do not yet occupy all the sites within their ecological tolerance, and their present distribution within that tolerance is determined by the random factors of dispersal, germination, and establishment.

Thus, the assemblage of plants on a recently disturbed site gives a less precise indication of the environment at that site than the community on a site that has been undisturbed for some time.

However, overall the controlling environmental factors for the disturbed and natural vegetation were shown by the ordinations to be very similar. Moisture and pH are the two most important controlling factors in both cases, and thaw depth and organic matter are of secondary importance. Nitrogen is also of secondary importance in the U ordination, but not in the D ordination. These ordination results show that despite the differences in vegetation composition and age of the surface, the most important controlling factors are similar for mature and quite young vegetation at Oumalik.

In the ordination of man-disturbed and naturally disturbed vegetation (DN) there are more environmental factors that show significant trends with the axes than in the D ordination (Figure 3.19, Table 3.2). The first axis associates most strongly with moisture, and the second axis with pH and organic matter. This is quite similar to the U and UN ordinations (Figure 2.25 and 2.26); and implies that though the vegetation on substrates of different ages is very different, the dominant controlling factors remain the same.

Other environmental factors that showed association with the axes of the DN ordination are the three measures of nitrogen,

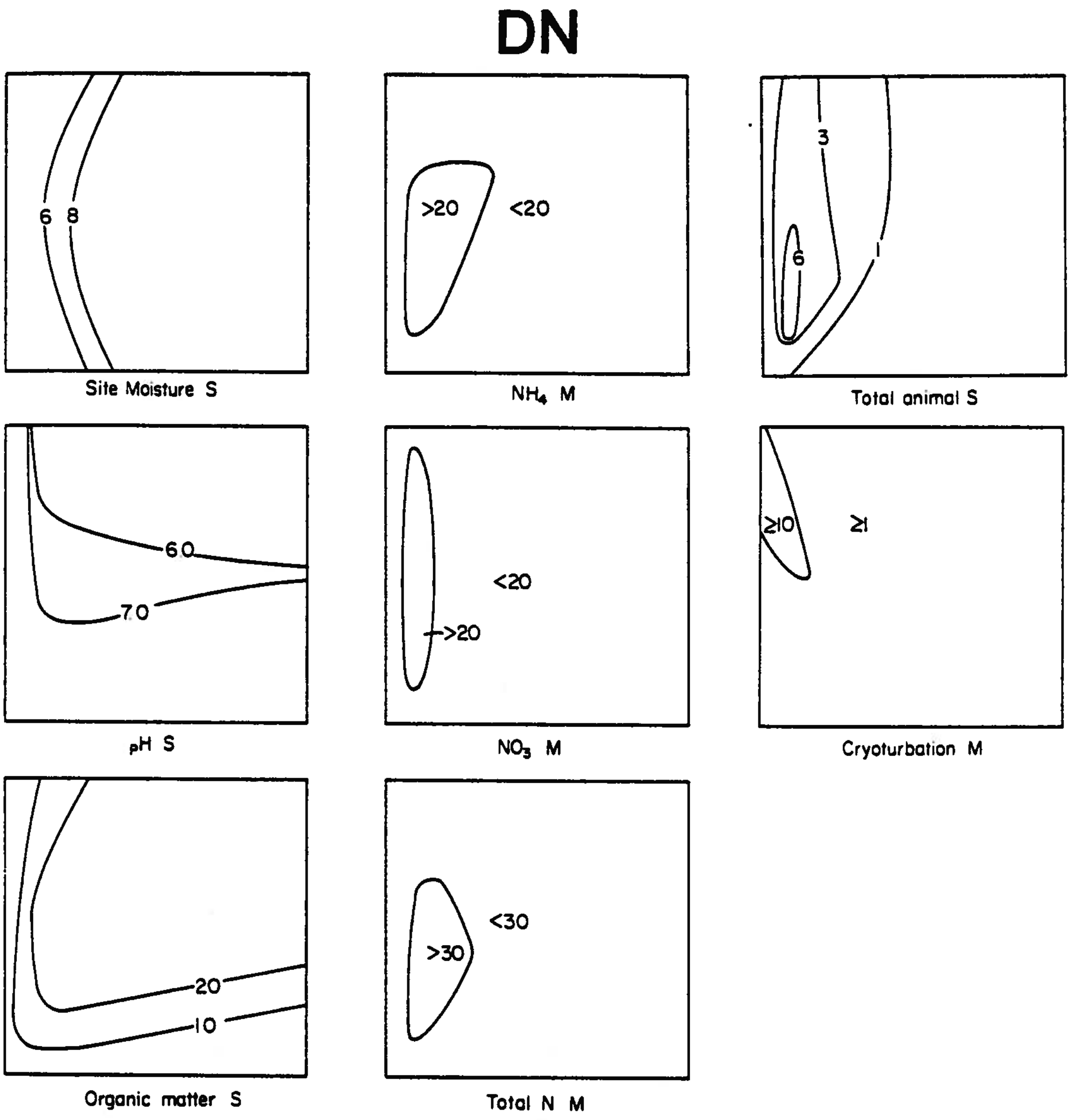


Figure 3.19. Trends of site factors through ordination of human-disturbed and naturally-disturbed vegetation (DN). The strength of the trends is rated as very strong (VS), strong (S), or moderate (M). See Table 2.4 for complete description of the categories).

Table 3.2. Spearman correlation coefficients for the first two axes and significant environmental factors of the ordination of samples of natural and man-caused disturbances (DN). The environmental factors are those from Figure 3.19.

	axis 1	axis 2	site moisture	pH	organic matter	NH_4	NO_3	total N	cryoturbation
axis 2	.04								
site moisture	.53**	-.05							
pH	-.12	-.50**	-.17						
organic matter	-.01	.10	.22	-.59**					
NH_4	.08	.07	.28*	-.58**	.81**				
NO_3	-.28*	-.11	-.08	-.26*	.53**	.60**			
total N	-.05	-.04	.16	-.49**	.77**	.93**	.81**		
cryoturbation	-.46**	.09	-.24	.32*	-.34**	-.36**	-.07	-.28*	
total animal	-.54**	-.09	-.25*	-.17	.15	.27*	.33*	.33*	.00

*$.01 < p \leq .05$

** $p \leq .01$

cryoturbation, and total animal sign. The three measures of nitrogen concentration show similar, relatively weak patterns in the ordination, and in general are higher in the two *Salix* communities (nos. 31 and 32). The patterns shown by cryoturbation only separate frost boils from the rest of the vegetation, and total animal sign seems closely related to the abundance of willows.

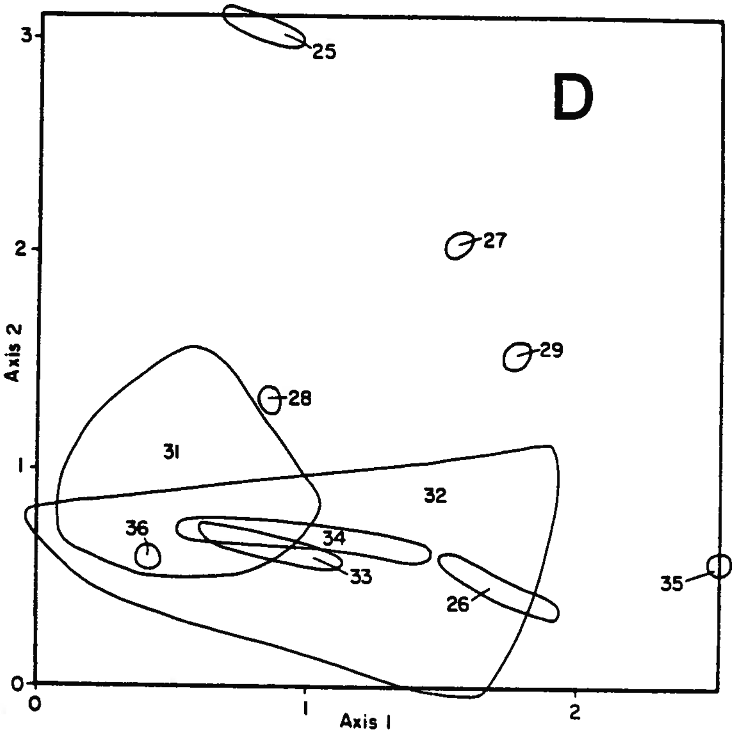
Community Patterns

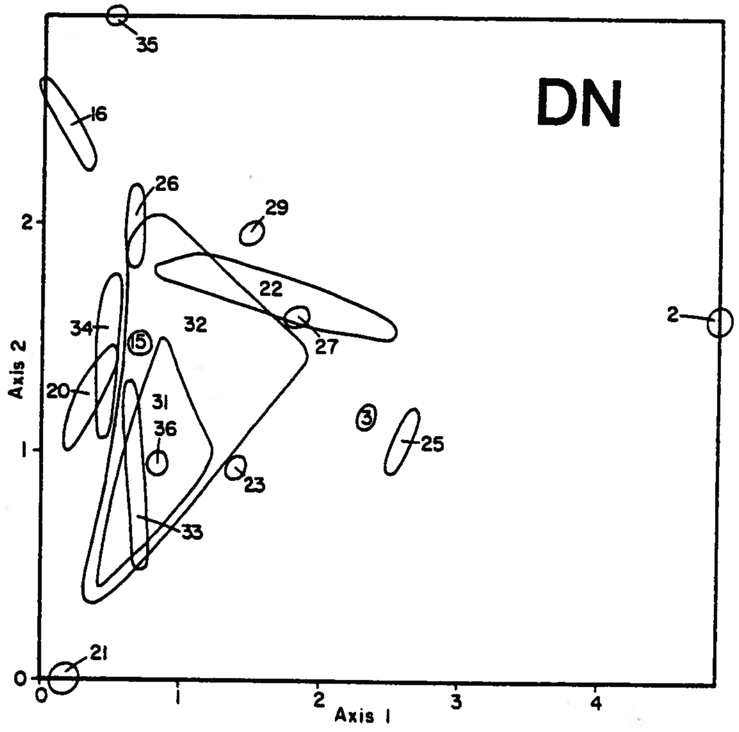
The disturbed communities in the D and DN ordinations (Figure 3.20) do not separate as well as those in the U and UN ordinations. Even on the third and fourth axes (not presented), many of the communities still overlap. A few, such as the very unusual *Saxifraga cernua-Marchantia polymorpha* (no. 28), do separate out on subsequent axes. The communities intergrade for the same reasons as discussed in the classification of disturbed vegetation.

In the D ordination, the *Betula nana-Arctagrostis latifolia* community (no. 35) is well-separated on the acid end of axis 1 (Figure 3.20). The two partially-disturbed *Eriophorum vaginatum* communities (nos. 26 and 27) and the *Betula nana-Carex aquatilis* community (no. 29) are also toward the acid end. The rest of the communities are not well separated on axis 1. Some of them are resolved on the second axis (moisture). At the high (wet) end of axis 2 is community 25, the *Carex aquatilis-Eriophorum*

Figure 3.20. Communities in the ordination of human-disturbed (D) and human-disturbed and naturally disturbed vegetation (DN). The communities are:

2 *A. fulva-Eriophorum scheuchzeri*
3 *Carex aquatilis-E. angustifolium*
15 *E. angustifolium-Ochrolechia upsaliensis*
16 *D. integrifolia-O. upsaliensis*
20 *S. glauca-Poa arctica*
21 *S. alaxensis-S. arbusculoides*
22 *Arctagrostis latifolia*
23 *Puccinella borealis-A. latifolia*
25 *C. aquatilis-E. angustifolium* (disturbed)
26 *E. vaginatum-S. planifolia* (disturbed)
27 *E. vaginatum-C. aquatilis*
28 *Saxifraga cernua-Marchantia polymorpha*
29 *Betula nana-C. aquatilis*
31 *Salix* spp. -*A. latifolia-E. angustifolium*
32 *Salix* spp. -*A. latifolia*
33 *A. latifolia* (disturbed)
34 *D. integrifolia-Equisetum arvense*
35 *B. nana-A. latifolia*
36 *Puccinellia borealis-E. arvense*


D
Axis 2
Axis 1
0
1
2
3
25
27
29
28
31
32
36
34
33
26
35


DN
Axis 2
Axis 1
0
1
2
3
4
35
16
26
29
22
2
34
15
32
27
20
31
36
3
25
23
33
21

angustifolium marsh. Communities 27 and 29 again separate from the other communities by being in the moderately wet portion of axis 2.

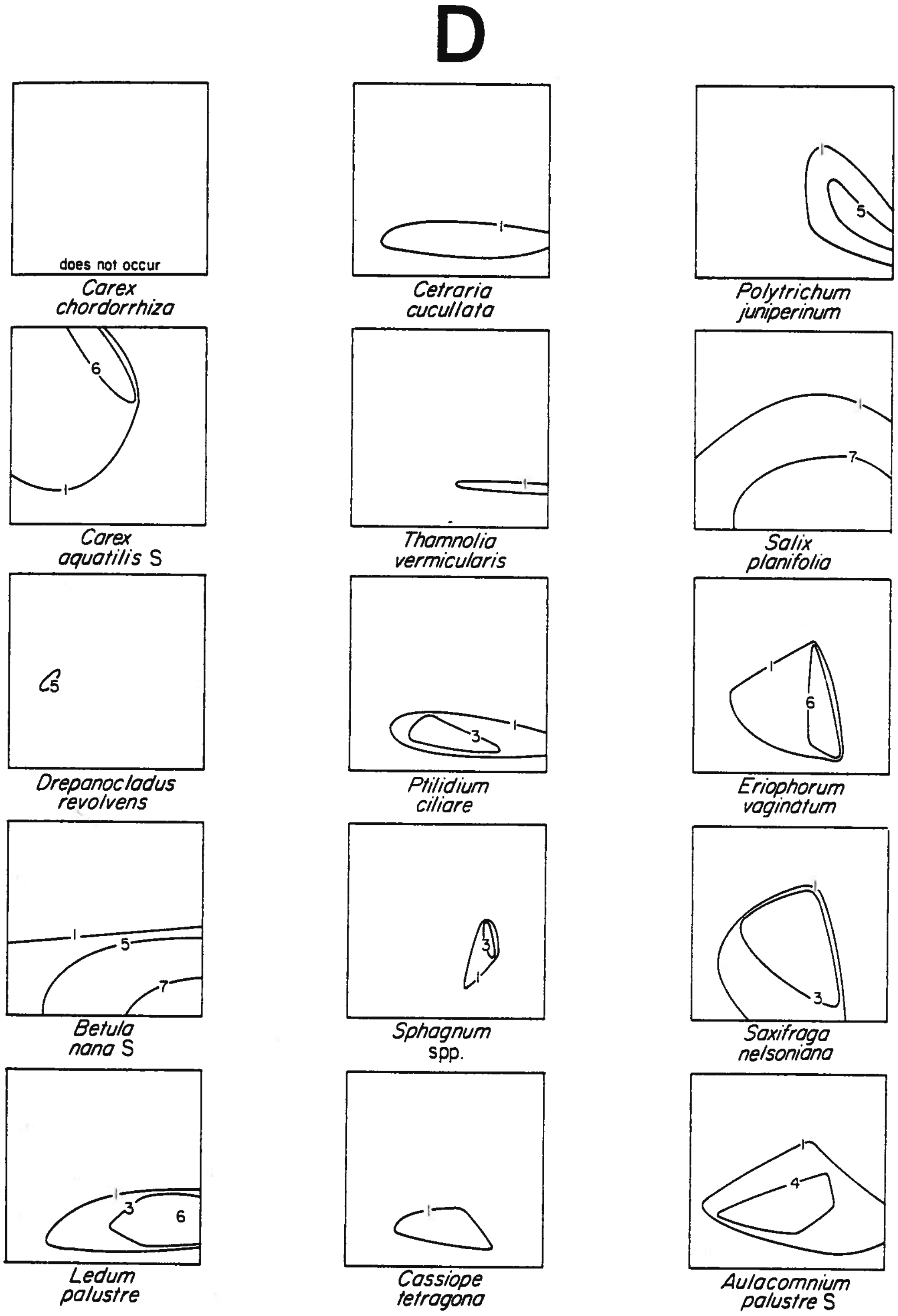
The communities that do not separate in the D ordination are those on mesic sites that are circum-neutral to basic. Many of these have *A. latifolia* and *Salix* spp. as important components or dominants and differ in the degree of their dominance or in the addition of other species, e.g. *Eriophorum angustifolium* to separate community 31 from 32.

In the DN ordination the disturbed communities have much the same configuration as in the D ordination except the arrangement is rotated 90° because the axes are reversed as discussed above (Figure 3.20). The successional *Arctophila* community (no. 2) is at the high (wet) end of axis 1. The disturbed (no. 25) and undisturbed (no. 3) *Carex aquatilis* and *Eriophorum angustifolium* communities lie about the center of axis 1. The remainder of communities are crowded into the mesic portion of the ordination.

Some of these mesic communities are separated by their position on axis 2, which in this ordination is most strongly related to pH. The *Betula nana-Arctagrostis latifolia* community (no. 35) is at the acid end of the gradient as it is in the D ordination. The *Dryas integrifolia-Ochrolechia upsaliensis* community (no. 16), which occurs on quite basic frostboils, occupies an anomalous position next to it. At the opposite (basic) end of axis 2 is the *Salix alaxensis-S. arbusculoides* community (no. 21). As in the D ordination, the mesic, circum-neutral to basic portion of the space is occupied by many communities that do not separate well.

Taxa in the Ordination Spaces

The distribution of taxa in the D and DN ordinations are given in Figures 3.21 and 3.22. The taxa are arranged in the same order as for the U and UN ordinations (Figures 2.28 and 2.29), that is by position of their modes in the natural vegetation--from wet to mesic, and within mesic from acid to basic. The strength of trends is somewhat less in the D and DN data sets than in the U and UN data sets. The D and DN data sets have 9 and 10 taxa, respectively, whose abundance trends are weaker rather than very strong. For the UN and U data sets, the numbers are 4 and 6, respectively. The weaker trends in data sets with disturbed vegetation is probably due to the random factors of dispersal, germination, and establishment already discussed.



Carex chordorrhiza

Cetraria cucullata

Polytrichum juniperinum

Carex aquatilis S

Thamnolia vermicularis

Salix planifolia

Drepanocladus revolvens

Ptilidium ciliare

Eriophorum vaginatum

Betula nana S

Sphagnum spp.

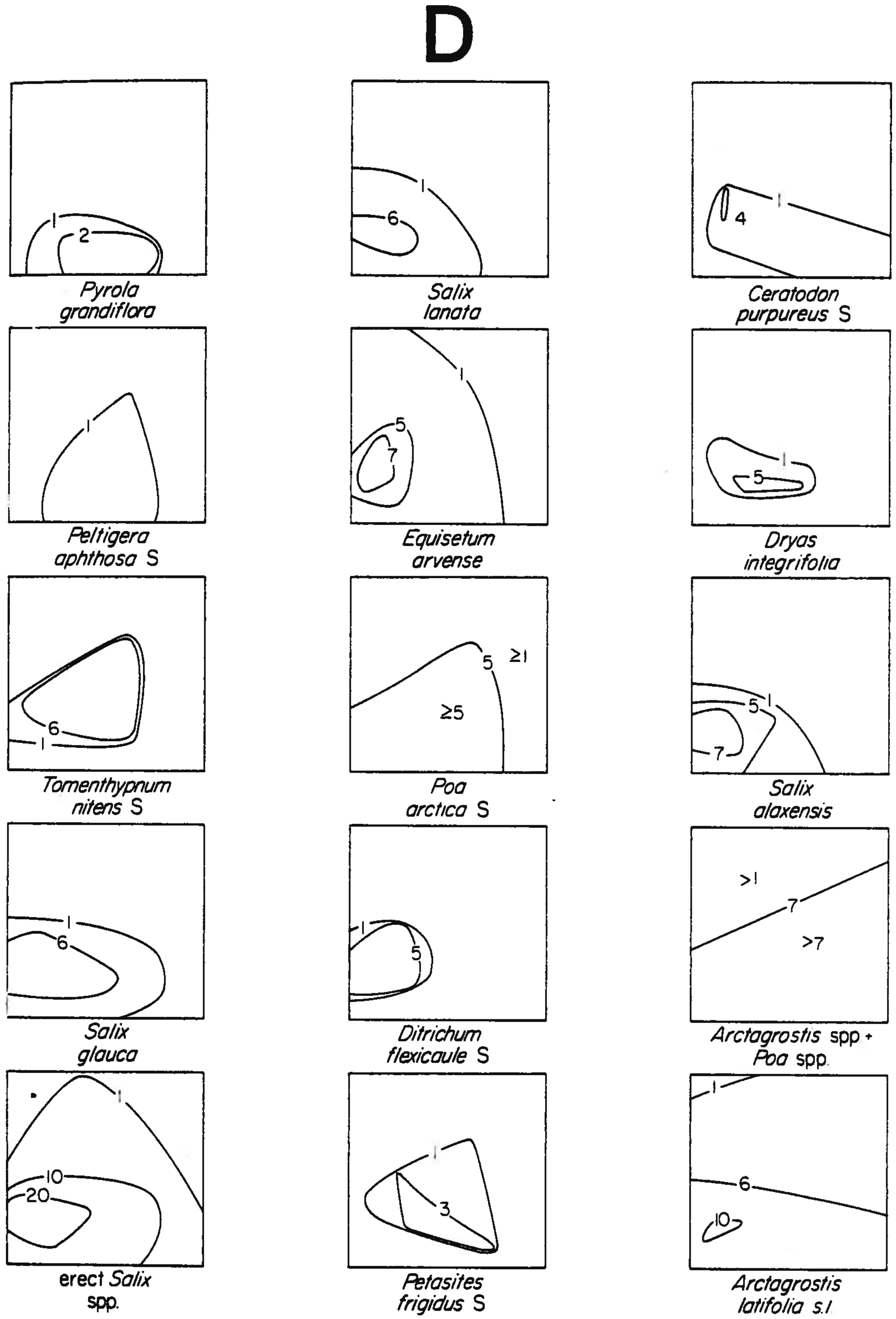
Saxifraga nelsoniana

Ledum palustre

Cassiope tetragona

Aulacomnium palustre S

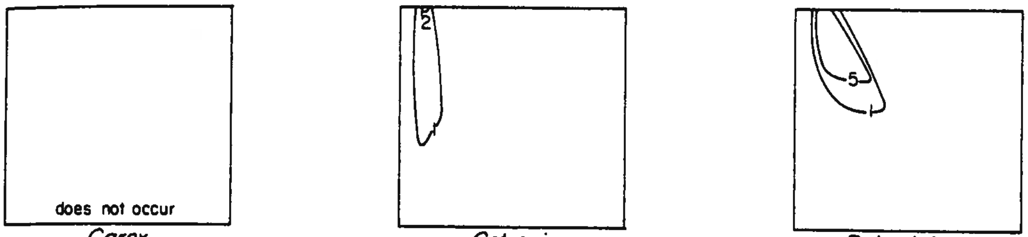
Figure 3.21. Taxa in ordination of human-disturbed vegetation (D). Trends are very strong except when an "S" follows the taxon name; these taxa have zero values scattered among the nonzero values (see text).



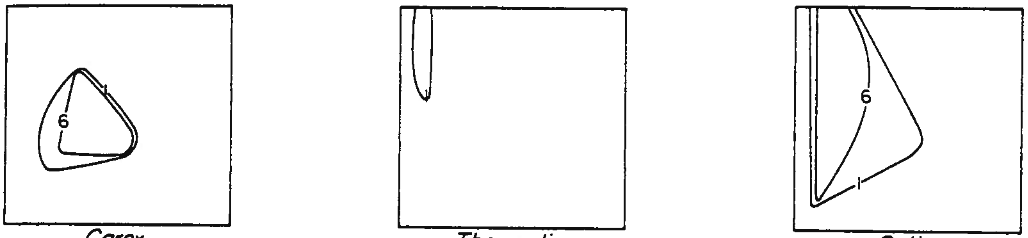
Pyrola grandiflora
Salix lanata
Ceratodon purpureus S
Peltigera aphthosa S
Equisetum arvense
Dryas integrifolia
Tomenthypnum nitens S
Poa arctica S
Salix alaxensis
Salix glauca
Ditrichum flexicaule S
Arctagrostis spp + *Poa* spp.
erect *Salix* spp.
Petasites frigidus S
Arctagrostis latifolia s.l

Figure 3.21. (Continued).

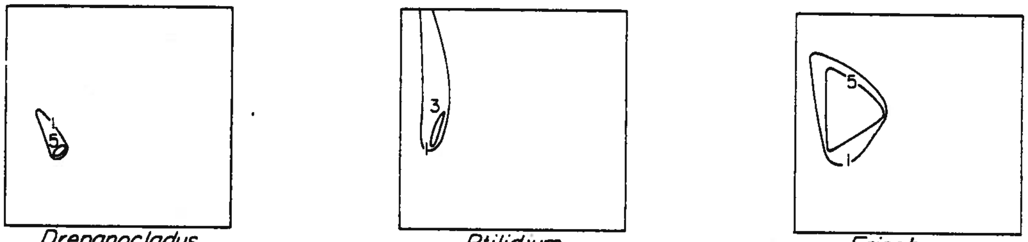
DN



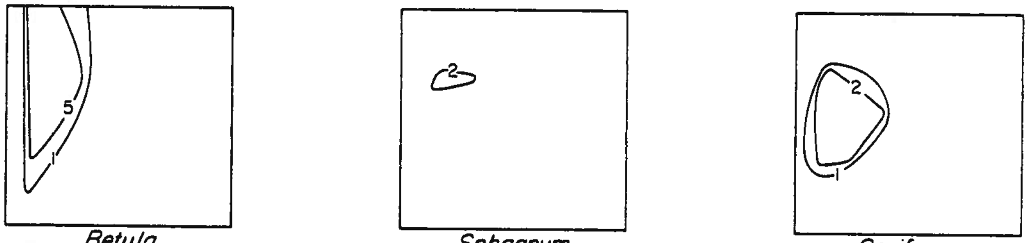
Carex chordorrhiza | *Cetraria cucullata* | *Polytrichum juniperinum* S



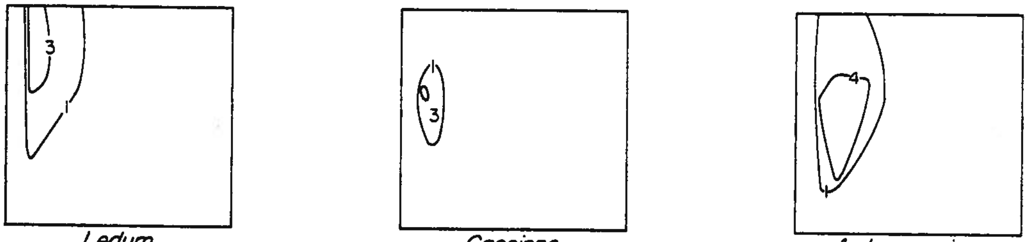
Carex aquatilis | *Thamnolia vermicularis* | *Salix planifolia*



Drepanocladus revolvens | *Ptilidium ciliare* | *Eriophorum vaginatum* S



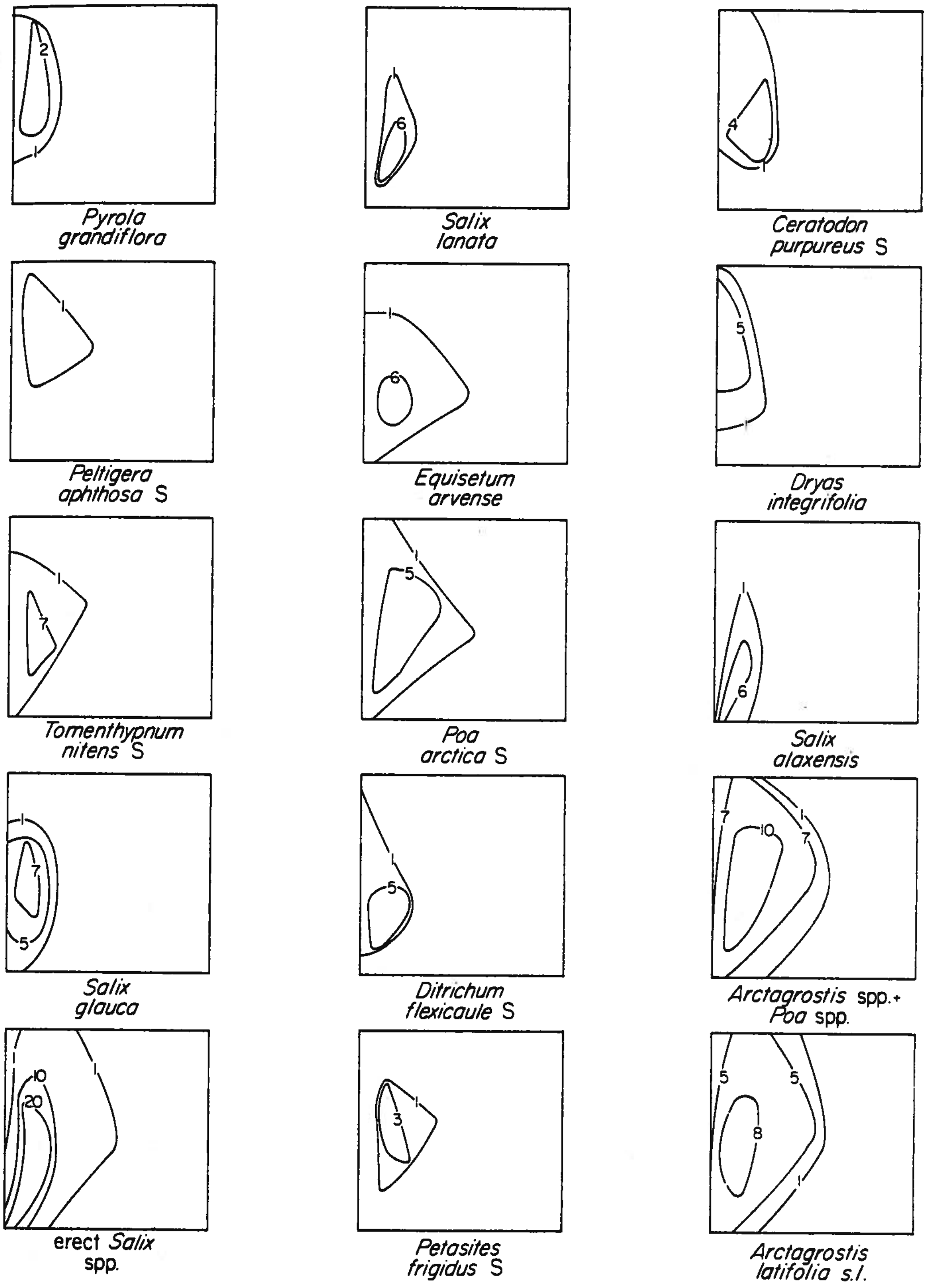
Betula nana | *Sphagnum* spp. | *Saxifraga nelsoniana* S



Ledum palustre | *Cassiope tetragona* | *Aulacomnium palustre* S

Figure 3.22. Taxa in the ordination of human-disturbed and naturally disturbed vegetation (DN). Trends are very strong except when an "S" follows the taxon name; these taxa have zero values scattered among the nonzero values (see text).

DN



Pyrola grandiflora

Salix lanata

Ceratodon purpureus S

Peltigera aphthosa S

Equisetum arvense

Dryas integrifolia

Tomenthypnum nitens S

Poa arctica S

Salix alaxensis

Salix glauca

Ditrichum flexicaule S

Arctagrostis spp.+ *Poa* spp.

erect *Salix* spp.

Petasites frigidus S

Arctagrostis latifolia s.l.

Figure 3.22. (Continued).

CHAPTER IV

SEEDBANK

Introduction

Plants that colonize disturbances can originate in several ways. Plants and plant parts may survive the disturbance and spread vegetatively, seeds may disperse to the site after disturbance to germinate, or seeds may germinate from reserves in the soil of the disturbed site. At Oumalik rhizomes and roots undoubtedly did survive and sprout in partially disturbed sites following the 1949-1950 disturbance. But many of the dominant colonizers of the disturbed areas were not present or were present in only small amounts in the pre-disturbance communities. They apparently began from seeds, but the relative importance of seeds from the seedbank and seeds dispersed to the area after disturbance was unknown. In order to infer the importance of the seedbank in providing colonizers for the 1949-1950 disturbance, I evaluated the size and composition of the seedbank in several of the common communities at Oumalik.

The few seedbank studies done in northern Alaskan plant communities have shown that the size of the seedbank, and presumably its importance in providing colonizers, varies a great deal. Two studies in *Eriophorum vaginatum* tussock tundra have shown that the seedbank is large (McGraw 1980, Gartner et al. 1983) and important in providing colonizers of disturbances (Chapin and Chapin 1980, Chester and Shaver 1982, Gartner et al. 1983). In a *Carex aquatilis* meadow at Barrow, Leck (1980) found only small numbers of *Chrysosplenium tetrandrum.* Roach (1983) found seedbanks of moderate size that were mainly *Carex bigelowii (C. aquatilis* was not separated from *C. bigelowii* in this study) and *Polygonum viviparum* (= *Bistorta vivipara)* (presumably from bulbils) in a wet meadow and seedbanks of moderate size composed primarily of *C. bigelowii, Saxifraga punctata* (= *S. nelsoniana),* and *P. viviparum* in a moist *C. bigelowii* meadow.

The specific questions that I attempted to answer were:

1) Is *Eriophorum vaginatum* in the seedbank at Oumalik? Even though it is a dominant colonizer of other disturbances in similar types of tundra (Chapin and Chapin 1980, Chester and Shaver 1982, Gartner et al. 1983), it has not colonized the devastated sites at Oumalik. It occurs on partially disturbed sites, but may have survived the disturbance in these cases. Is it not in the seedbank as it is at other tussock tundra locations (McGraw 1980, Gartner et al. 1983), or are other factors preventing it from colonizing?

2) *Arctagrostis latifolia* s.l. and the erect *Salix* spp. are dominant colonizers of the mesic sites at Oumalik. *S. alaxensis, S. lanata,* and *S. planifolia* have short-lived seeds (Densmore and Zasada 1983) that are not expected to be present in the seed bank. But do *A. latifolia* and *S. glauca* colonize from seeds in the

seedbank or from seeds dispersed to sites after disturbance?

3) *Carex aquatilis* and *Eriophorum angustifolium* are the dominant colonizers of wet sites at Oumalik. Are they present in the seedbank or did they colonize from seeds dispersed to sites after disturbance?

Methods

Soils were collected in the summer of 1981 and germinated over the following winter. The results were different than those obtained in other similar studies (McGraw 1980, Gartner et al. 1983), and it was unclear whether this was caused by differences among sites or differences in storage and germination conditions of the samples. Therefore, soils were collected again in summer 1983, and germinated. The differences from the other studies persisted, and results from both years are reported because the differences between them are interesting and help to interpret the results of McGraw (1980) and Gartner et al. (1983).

The 1981 samples were collected on 23 July. This is probably after *E. vaginatum* had dispersed seeds for that year (Gartner et al. 1983), but before most other species dispersed seeds. The three primary communities that were affected by the 1949-1950 disturbance (*Dryas integrifolia-Salix glauca* [community 13], *Carex chordorrhiza-C. rotundata* [no. 5], and *Betula nana-Ledum palustre* [no. 18]) were sampled as was the *E. vaginatum-Salix planifolia community* (no. 10) for comparison with seed bank data from other tussock tundra sites. Samples from the *E. vaginatum* community were from between tussocks.

Five replicate blocks 15 x 15 x 10 cm deep were sampled in each community. Sampling to a depth of 10 cm was judged adequate to represent the seedbank because McGraw (1980) and Gartner et al. (1983) found that the number of seeds in tussock tundra declined rapidly with depth and that there were no seeds in mineral soil. At Oumalik the mineral horizon is 13-18 cm below the surface.

The blocks were cut out by digging a trench on one side of the 15 x 15 cm area to be removed and cutting around the boundaries of the block with a knife. From the trench a horizontal cut at a depth of 10 cm was made under the block to separate it from the adjacent soil. This procedure was possible because the organic horizons and even the silts below them hold together very well. The blocks were cut in half vertically so that they could be placed into plastic bags, and were shipped to the lab in Boulder. The time from sampling to arrival in Boulder was 4-5 days. Upon arrival they were stored at 2°C. On 19 January 1982, about 6 months after sampling, the blocks were placed into the greenhouse. Each half block (15 x 7.5 x 10 cm deep) was spread out over vermiculite in a 25 x 25 cm greenhouse flat, which produced a soil depth of 1.5 cm or less. One of the two halves of each block was fertilized with a solution of 15-30-15 NPK fertilizer once per month and the other half recieved just tap water. All flats were watered at least once a day to keep them moist. They received natural light and the prevailing greenhouse temperature, which ranged from a low of about 20°C to over 30°C in bright sun in late spring and summer. The high temperatures did not likely reduce germination because most arctic plants have optimal germination between 20 and 30°C (Billings and Mooney 1968, Wein and MacLean 1973, Gartner 1983).

The flats were observed 1-2 times weekly through 21 May 1982 (4 months) so that seedlings could be detected even if they died soon after germinating. Data collected for each seedling were the date first seen, approximate location in the flat, and tentative identification. Tentative identifications were checked throughout this observation period and corrected as necessary. The flats were observed again on 4 August 1982 (6 1/2 months after being put out to germinate) and on 8 October 1982 (9 1/2 months) to check for newly germinated plants and to check identifications made when the plants were young. Four new seedlings were found on 4 August and one on 8 October.

Some individuals of *Carex aquatilis*, *C. bigelowii*, *C. capillaris*, *Ranunculus gmelini*, and *Juncus biglumis* flowered. Other plants were identified vegetatively on the basis of extensive field experience, except for *Eriophorum triste* which could not be differentiated vegetatively from *E. angustifolium* ssp.

subarcticum. Both were grouped as *E. angustifolium*. Non-flowering *C. aquatilis* and *C. bigelowii* were differentiated by color and growth habit as seen in the flowering individuals. Common greenhouse weeds such as *Oxalis* sp. and ferns were easily recognized and were removed as they appeared.

The same communities were sampled again in 1983 on 15 July using similar techniques as in 1981. In 1983 only four soil blocks were taken from each community and these were cut horizontally to divide the sample into 0-5 cm and 5-10 cm depths. This allowed some differentiation on the depth of germinable seeds. The soils were stored at 0-5°C for two days, were at ambient temperature for about one day while being transported to Fairbanks, were stored frozen there for four days, and were at ambient temperature for about a day while being transported to Boulder. They were then stored at about -18°C from 23 July to 22 October 1983 when they were put into the greenhouse to germinate. The samples were treated the same as the 1981 samples except that all were fertilized, and after 2 1/2 months the light regime was changed from natural to continuous light using supplemental incandescent night lighting. All were fertilized because there was not sufficient greenhouse space to have both depth and fertilizer treatments, and because in the soils collected in 1981, seedlings in the fertilized flats were much larger and easier to identify. Fertilization also generally caused greater numbers of seedlings and a greater number of species to germinate (see Results). The light regime was changed from that used with the 1981 samples in an attempt to simulate arctic conditions more closely in order to promote germination, and to encourage more vigorous growth for easier identification of seedlings.

The best greenhouse/growth chamber conditions to use in a seedbank experiment vary with the site the soils are collected from and the species of interest. Ideally, one would create the conditions in the greenhouse that duplicate those in the field precisely, and thus the seeds that would germinate in the field would germinate in the greenhouse. Since duplicating field conditions is impossible, I chose to treat the soils so that the maximum number of species and total numbers of seedlings would germinate. This estimates the maximum potential seed reserves in the soil; whether or not these numbers are realized in the field depends on conditions.

The germination of seedlings from soils collected in 1983 was followed using a mylar sheet for each flat. The mylar was placed on a piece of plexiglass which was laid on top of the flat. For each new seedling, its position, date first seen, and tentative identification were marked onto the mylar. Seedlings that germinated previously were checked to see if they still survived and if the identification could be refined or changed. The soils were checked about weekly for 7 months and then again after a total of 11 months. No plants from the 1983 soils flowered; all were identified vegetatively.

Tests for significance on the numbers of seedlings m^{-2} between fertilized and unfertilized soils collected in 1981, between the top five and lower five cm in 1983, and between fertilized 1981 soils (0-10 cm) and fertilized 1983 soils (0-10 cm) were done using t-tests. Before doing the t-tests, the variances were tested for equality using an F test. If they were not significantly different, a standard t-test was used. In the one case where the variances were significantly different, a t-test which does not assume equal variances was used (Sokal and Rohlf 1981:411).

Results and Discussion

Eriophorum Tussock Tundra

Eriophorum vaginatum tussock tundra had the highest density of total germinable seeds of the four communities, about 300 seeds m^{-2} in unfertilized soils and about 600 seeds m^{-2} in fertilized soils (Table 4.1). The soils were taken from mossy areas between tussocks. At Kuparuk Ridge this microsite had about 1.8 times the number of germinable seeds as the tundra average (calculated from Gartner et al. [1983]) and at Eagle Creek intertussock areas had about 1.3 times as many seeds as tussocks (calculated from McGraw [1980]). Therefore the results probably

Table 4.1. Seedbank size by community. Data are in seedlings per m^2 ($\bar{X}$ ± S.E.). For details on species composition, see Tables 4.2, 4.3, 4.5, and 4.6. Differences between unfertilized and fertilized 1981 results, fertilized 1981 and 1983 results, and the two depths were tested for significant differences using t-tests (see text). All are nonsignificant at $p \leq 0.05$, but the depths are different in the *Carex* marsh at $p < 0.09$ and in the *Dryas* community at $p < 0.06$. For complete community descriptions see text.

	1981		1983 Fertilized		
	Unfertilized	Fertilized	Total	5-10 cm	0-5 cm
Eriophorum tussock tundra	302 ± 96	587 ± 124	610 ± 86	310 ± 159	300 ± 90
Dryas tundra	284 ± 130	462 ± 147	400 ± 159	80 ± 52	320 ± 111
Carex marsh	409 ± 124	338 ± 121	450 ± 126	50 ± 33	400 ± 128
Betula-Ledum community	142 ± 82	160 ± 52	66 ± 13	22 ± 13	44 ± 18

represent maximum seedbank densities for the Oumalik tussock tundra.

The seedbank in tussock tundra at Oumalik is dominated by *Carex bigelowii* (Table 4.2), as it is at Eagle Creek and Kuparuk Ridge. At Oumalik *C. bigelowii* is a fairly constant component of tussock tundra, but has a low cover, generally 2 to 10%. The small numbers of seeds *of C. aquatilis* and *Eriophorum angustifolium*, species characteristic of wet areas, probably came from seeds blown short distances from marshes near the areas sampled. The other species in the seedbank are present in the community, but have low covers.

The total number of distinct taxa found in all treatments of the Oumalik tussock tundra soils (eight) is greater than that at Eagle Creek or Kuparuk Ridge. At Eagle Creek McGraw (1980) found five species, *C. bigelowii*, *Eriophorum vaginatum*, *Ledum palustre*, *Empetrum nigrum*, and *Betula nana* (in decreasing order of importance). At Kuparuk Ridge Gartner et al. (1983) found only *C. bigelowii*, *E. vaginatum*, and unidentified dicots.

Several of the species in the seedbank at Oumalik but not at these two other sites such as *Saxifraga nelsoniana*, *Stellaria* sp., and probably the *Luzula* spp., do occur in the vegetation there. Roach (1983) also found *S. nelsoniana(=S. punctata)*, *Stellaria* sp., and a different *Luzula* sp. in the seedbank in a *Carex bigelowii-Salix reticulata* community just north

Table 4.2. Seedbank composition of *Eriophorum* tussock tundra. Data are in seedlings per m^2 ($\bar{X}$ ± S.E.). To determine the actual total number of seeds that germinated in the five 7.5 x 15 x 10 cm deep blocks in each of the 1981 treatments, divide the seeds m^{-2} by 17.8. For each of the 1983 treatments, divide by 11.1 to obtain the total number of seeds that germinated in the four 15 x 15 x 5 cm deep blocks.

species	1981			1983 fertilized	
	unfertilized	fertilized	total	5-10 cm	0 - 5 cm
Arctagrostis latifolia	71 ± 52		66 ± 13		66 ± 13
Carex aquatilis		107 ± 86			
C. bigelowii		128 ± 65	444 ± 101	244 ± 129	200 ± 69
Carex sp.	107 ± 65	36 ± 22	66 ± 39	55 ± 42	11 ± 11
*Eriophorum angustifolium**	18 ± 18				
Luzula confusa	71 ± 71	18 ± 18	11 ± 11		11 ± 11
L. kjellmaniana		18 ± 18			
Saxifraga nelsoniana		53 ± 53			
Stellaria sp.		18 ± 18			
unknown dicot	36 ± 22	231 ± 72	22 ± 22	11 ± 11	11 ± 11
total seedlings	302 ± 96	587 ± 124	610 ± 86	310 ± 159	300 ± 90
number of distinct taxa	5	6	4	2	4

*includes *E. triste*

of the Brooks Range at the Atigun River crossing. The reasons for the absence of these species in the seedbank at Eagle Creek and Kuparuk Ridge is unknown. It is possible that the storage and germination conditions used in those studies were sufficiently different from those used in this study to produce the different results. The above species germinated only in the 1981 fertilized soils from Oumalik, which were stored at above-freezing temperatures for several months. In contrast, the Eagle Creek, Kuparuk Ridge, and 1983 Oumalik soils were stored frozen. Perhaps the above-freezing temperatures allowed dormancy mechanisms to be broken.

The numbers of seeds at 0-5 cm and 5-10 cm in tussock tundra are about equal at Oumalik (Table 4.1), primarily due to the approximately equal distribution of the dominant *C. bigelowii*. McGraw (1980) and Gartner et al. (1983) also found *C. bigelowii* strongly represented at greater depths. *A. latifolia* seeds were restricted to the upper 5 cm at Oumalik.

Small numbers of *Arctagrostis latifolia* seeds germinated from the Oumalik tussock tundra soils, but not from soils in the three above studies, although *A. latifolia* occurs constantly but with low abundance in tussock tundra and in the moist tundra of Roach's (1983) study. Its presence in the seedbank is significant because *A. latifolia* is one of the dominant colonizers of mesic disturbed areas at Oumalik. The few seeds in the seedbank may be an artifact of the vast amount of *A. latifolia* on the disturbance. Even though the tussock tundra sampled is about 1 km from the disturbance, it is possible that the *A. latifolia* seeds that germinated were transported by wind from the disturbance, since they are very light, averaging 0.25 mg (Mitchell 1979). It seems likely that the *A. latifolia* on the disturbance originated from seeds dispersed to the area after disturbance, rather than from the seedbank. Gartner et al. (1983), using seed exclosure experiments, also concluded that the seedbank is not a source of the colonizing grasses, including *A. latifolia*.

The numbers of seeds found in Oumalik tussock tundra soils are less than found in tussock tundra at Eagle Creek where there were 3370 seeds m^{-2} total and ~~1170~~ 2830 JJE seeds m^{-2} in the top 10 cm (calculated from McGraw [1980]). It is also less than the 1170 seeds m^{-2} total at Kuparuk Ridge, but the fertilized number is about the same as the 590 seeds m^{-2} found in the top 10 cm there (calculated from Gartner [1982]). However, the Eagle Creek and Kuparuk Ridge cores were not fertilized, and the 300 seeds m^{-2} in the unfertilized Oumalik soils are about half the number found in the top 10 cm at Kuparuk Ridge. It is difficult to know whether to compare the data from Oumalik (0-10 cm) to the top 10 cm or the full profile at the other two sites. All three studies found essentially no seeds in mineral soil; but at Eagle Creek and Kuparuk Ridge the organic horizon is about 30 cm deep, while at

Oumalik it is only 13-18 cm thick. Thus, the top 10 cm at Oumalik probably contains most of the germinable seeds present.

With the limited data available (3 sites) there appears to be a northward decrease in the numbers of buried seeds in tussock tundra. Johnson (1975) showed a latitudinal decrease in seed bank size in subarctic spruce forests in Canada, and Milton (1939) showed an altitudinal decrease in graminoid-dominated vegetation. Thus, there appears to be a decrease in the size of the seedbank within a vegetation type as climate becomes more severe. This is a hypothesis that needs further testing.

The decrease with latitude in the germinable seed bank of tussock tundra is caused by some species dropping out of the seedbank as latitude increases and the numbers of seeds of the species that do persist declining in numbers. At Eagle Creek *Ledum palustre* ssp. *decumbens* is an important component of the seedbank with 1300 seeds m^{-2} and *Betula nana* is a minor component (McGraw 1980). At the more northern Kuparuk Ridge (Gartner et al. 1983) and Oumalik sites, these two species are not in the seed bank. At Eagle Creek and Kuparuk Ridge *Eriophorum vaginatum* is an important component of the seedbank, but at Oumalik it is absent. *Carex bigelowii* is present at all three sites, but declines from 1665 seeds m^{-2} at Eagle Creek (McGraw 1980) to 683 seeds m^{-2} at Kuparuk Ridge (Gartner et al. 1983) to 128-444 seeds m^{-2} at Oumalik (Table 4.2).

The reasons for the absence of *E. vaginatum* in the seedbank at Oumalik are unclear. It grows vigorously and flowers at Oumalik,and some seedlings are present in recently disturbed areas (Chapter VI). Oumalik apparently has somewhat cooler and shorter summers than Kuparuk Ridge, where *E. vaginatum* is abundant in the seedbank (Gartner et al. 1983), although the temperature data are short-term and somewhat fragmentary (1979 from Haugen [1982] [Kuparak Ridge is called Toolik River station by Haugen], 1980 from R.K. Haugen [written communication], and 1981 Oumalik data compared to Galbraith Lake data as a substitute for Kuparuk Ridge from R.K.Haugen [written communication]). However it seems unlikely that the slightly cooler summers are responsible for the lack of *E. vaginatum* in the seedbank.

At Oumalik none of the 1949-1950 disturbances occurred in tussock tundra, so the lack of *E. vaginatum* in the buried seedbank cannot be used to explain its lack as a colonizer. However, at Fish Creek (Figure 1.1) where some of the disturbances occurred in tussock tundra, its lack as a colonizer (Komárková 1983) could be due to its absence in the seedbank. Another explanation could be the lack of sites that are sufficiently wet, but not water-covered (Komárková 1983).

Whenever comparing the results of different seedbank germination studies, the explanation of differences in results will always be uncertain. The lack of a species can always be attributed to differences in methods. It is possible that *E. vaginatum* is in the seedbank at Oumalik, but was unable to germinate under the storage and greenhouse conditions that were used. However, it is also possible that it is not present in the seedbank at Oumalik, and perhaps other sites north of the Foothills. Since the seedbank is potentially important in rehabilitating disturbed areas in northern Alaska (Shaver et al. 1983), more research is needed with uniform methods along the latitudinal gradient in Alaska to look at trends in colonizing ability and seedbank of *E. vaginatum* and to understand reasons for changes in these life history characteristics.

Dryas Tundra

The seedbank in the *Dryas integrifolia-Salix glauca* community (no. 13) ranged from 284 to 462 germinable seeds m^{-2} depending on the treatment (Table 4.3). This is somewhat smaller than the seedbank in tussock tundra (Table 4.1). Ten species of seedlings were identified in the soils, more than in the other communities sampled at Oumalik (Table 4.4). This community is also more species-rich than the other communities sampled for the seedbank.

The seedbank is dominated by *Carex bigelowii* and *Saxifraga hieracifolia*. *C. bigelowii* is a constant component of this community, and usually occurs with a cover of 10 to 20%.

Table 4.3. Seedbank composition of *Dryas* tundra. Data are in seedlings per m^2 ($\overline{X} \pm S.E.$). To determine the actual number of seeds that germinated in the five 7.5 x 15 x 10 cm deep blocks in each of the 1981 treatments, divide seeds m^{-2} by 17.8. For each of the 1983 treatments, divide by 11.1 to obtain the total number of seeds that germinated in the four 15 x 15 x 5 cm deep blocks.

species	1981		1983 fertilized		
	unfertilized	fertilized	total	5-10 cm	0 - 5 cm
Arctagrostis latifolia		53 ± 53			
Carex aquatilis	18 ± 18				
C. bigelowii	124 ± 87	124 ± 87	144 ± 55	33 ± 33	111 ± 22
Carex capillaris		36 ± 36			
Carex sp.		53 ± 36	88 ± 54	44 ± 26	44 ± 32
*Eriophorum angustifolium**	18 ± 18				
Juncus biglumis		18 ± 18			
Luzula kjellmaniana	18 ± 18				
Saxifraga hieracifolia			167 ± 92		167 ± 92
S. nelsoniana		18 ± 18			
Stellaria sp.		36 ± 36			
unknown sedge	18 ± 18	18 ± 18			
unknown dicot	89 ± 56	107 ± 71			
total seedlings	284 ± 130	462 ± 147	400 ± 159	80 ± 52	320 ± 111
number of distinct taxa	4	6	2	1	2

*includes *E. triste*

Table 4.4. Number of distinct taxa in the seedbank by community. *Carex* sp., unknown sedge, and unknown dicot were not counted if there were other members of these groups identified to species. For complete community descriptions see text.

community	1981			1983 fertilized			grand total
	unfertilized	fertilized	total	total	5-10 cm	0 - 5 cm	
Eriophorum tussock tundra	5	6	8	4	2	4	8
Dryas tundra	4	7	9	2	1	2	10
Carex marsh	4	4	4	3	2	3	4
Betula–Ledum community	3	4	4	2	2	1	5

S. hieracifolia is also usually found in this community, but with very low cover. The other species that germinated are subordinate species in the community (the plant I have called *Eriophorum angustifolium* is probably the vegetatively indistinguishable *E. triste)*, except for *C. aquatilis*, which occurs in nearby thermokarsts. Despite the presence of large amounts of *Arctagrostis latifolia* on the disturbed area about 100 m away, *A. latifolia* germinated in only small numbers from the seedbank. The dominants in the community, *Dryas integrifolia* and *Salix glauca*, did not germinate from the soils.

The soils that were collected in 1981 and fertilized had the largest total seedbank (this difference was not statistically significant) and the most species. The 1981 unfertilized soils had fewer total numbers of seedlings but more species than the species-poor 1983 germination results.

There were more seeds at the 0-5 cm depth (320 ± 111) than at 5-10 cm (80 ± 52) ($p < 0.06$). This was due to differences in numbers with depth for both the dominants, *C. bigelowii* and *S. hieracifolia*.

No other work in Alaska has evaluated the seedbank in this community. In a related community, a moist meadow dominated by *C. bigelowii* with smaller amounts of *Salix alaxensis*, *S. reticulata*, and *D. octapetala*, Roach (1983) collected soils that germinated a great deal of *C. bigelowii*, *S. punctata (= S.*

nelsoniana), and *Polygonum viviparum*. One seed of *D. octopetala* and several seeds of *Stellaria laeta* also germinated. The other species she found do not occur in the Oumalik community. The total number of seeds (740-820 m^{-2}) and the number of species (13) that germinated is greater than from the Oumalik community.

Carex Marsh

Soils from the *Carex chordorrhiza*-*C. rotundata* community had 338-450 seeds m^{-2} that germinated (Table 4.5), a number comparable to the *Dryas* community (Table 4.1). Of the four communities in which the seedbank was evaluated at Oumalik, the *Carex* marsh had the fewest taxa germinate--four identified to species, an unidentified *Carex* sp. that could be one of the other species and an unknown dicot. Most of the seedlings were *C. aquatilis* and *C. chordorrhiza*, both dominants in the community. *Eriophorum angustifolium* and *Ranunculus gmelini* also germinated; *E. angustifolium* is a constant and common component of the community while *Ranunculus gmelini* occurs only rarely in this community.

The *Carex* marsh had the fewest differences among treatments of the four communities sampled (Table 4.5). The fertilized and unfertilized soils from 1981 were different only in having *Ranunculus gmelini* in the fertilized treatment and an unknown dicot in the unfertilized treatment. These were present in

Table 4.5. Seedbank composition of the *Carex* marsh. Data are in seedlings per m^2 $(\overline{X} \pm \text{S.E.})$. To determine the actual total number of seeds that germinated in the five 7.5 x 15 x 10 cm deep blocks in each of the 1981 treatments, divide the seeds m^{-2} by 17.8. For each of the 1983 treatments, divide by 11.1 to obtain the total number of seeds that germinated in the four 15 x 15 x 5 cm deep blocks.

species	1981			1983 fertilized	
	unfertilized	fertilized	total	5-10 cm	0 - 5 cm
Carex aquatilis	160 ± 99	107 ± 86	267 ± 101	33 ± 33	233 ± 102
C. chordorrhiza	71 ± 44	107 ± 52	144 ± 115	22 ± 22	122 ± 93
Carex sp.			33 ± 21		33 ± 21
*Eriophorum angustifolium**	124 ± 60	71 ± 33	11 ± 11		11 ± 11
Ranunculus gmelini		53 ± 36			
unknown dicot	53 ± 36				
total seedlings	409 ± 124	338 ± 121	450 ± 126	50 ± 33	400 ± 128
number of distinct taxa	4	4	3	2	3

*includes *E. triste*

small numbers, and the differences could be due to patchiness of seeds in the soil. The 1983 soils lacked any dicots, but since these are only a minor component of the seedbank in this community, the 1983 results are not significantly different from 1981.

Germinable seeds are more frequent in the upper 5 cm than at the 5-10 cm depth (Table 4.5), although the difference was not statistically significant. All species that germinated from the 1983 soils showed this trend.

In the only other seedbank work in Alaska in a similar community, Leck (1980) found only one species in 16 cm cores from a *Carex aquatilis* community at Barrow. *Chrysosplenium tetrandrum* germinated from the cores and had a patchy distribution that averaged 40-205 seeds m^{-2}. The dominant graminoids *C. aquatilis*, *Eriophorum angustifolium*, and *Dupontia fisheri* did not germinate from the cores, which were frozen for 6 yr before being tested for germination.

Betula-Ledum Community

The *Betula nana-Ledum palustre* community (no. 18) had the lowest density of germinable seeds (66 to 160 m^{-2}) of the communities sampled (Table 4.1). It is the only community in which the composition of the seedbank is markedly different from the actual community. The composition (Table 4.6) is similar to marsh vegetation. The samples were taken from palsas, which are part of

Table 4.6. Seebank composition of the *Betula-Ledum* community. Data are in seedlings per m^2 ($\overline{X}$ ± S.E.). To determine the actual total number of seeds that germinated in the five 7.5 x 15 x 10 cm deep blocks in each of the 1981 treatments, divide the seeds m^{-2} by 17.8. For each of the 1983 treatments, divide by 11.1 to obtain the total number of seeds that germinated in the four 15 x 15 x 5 cm deep blocks.

species	1981		1983 fertilized		
	unfertilized	fertilized	total	5-10 cm	0 - 5 cm
Carex aquatilis	18 ± 18	71 ± 18	55 ± 11	11 ± 11	44 ± 18
C. chordorrhiza	36 ± 36	18 ± 18			
C. rotundata			11 ± 11	11 ± 11	
Carex sp.	18 ± 18		11 ± 11		11 ± 11
*Eriophorum angustifolium**		18 ± 18			
unknown sedge	36 ± 36	18 ± 18			
unknown dicot	36 ± 22	36 ± 22			
total seedlings	142 ± 82	160 ± 52	66 ± 13	22 ± 13	44 ± 18
number of distinct taxa	3	4	2	2	1

*includes *E. triste*

the vegetation complex disturbed in the drill site area. The palsas are 3-5 m in their long diameter and are surrounded by marsh, so that the marsh species would need to disperse only a few m to reach the areas sampled. *B. nana* and *L. palustre*, the dominants of the community, are not in the seedbank although they are present in tussock tundra soils at Eagle Creek (McGraw 1980).

The fertilized and unfertilized soils from 1981 had quite similar seedbanks, except that more *Carex aquatilis* germinated from the fertilized soils. The 1983 soils had fewer total germinable seeds and a slightly different composition than the 1981 soils, although the numbers of seeds are very small and the differences could be due to random variation. There was an insignificant tendency for there to be more germinable seeds in the top 5 cm than in the 5-10 cm layer.

Overall Trends

The communities varied 3- to 9-fold in the density of seeds that germinated (Table 4.1). In general, tussock tundra > *Carex* marsh, *Dryas* tundra > *Betula-Ledum* community. The numbers in tussock tundra were less than found by Gartner et al. (1983) and McGraw (1980) in the same community further south and suggest a decrease in seed bank size with latitude in this community as discussed earlier. The number of seeds in *Dryas* tundra was less than Roach (1983) found in a related community in the foothills of the Brooks Range.

Thompson (1978) suggests that the size of the seedbank across vegetation types increases as natural disturbance increases. The Oumalik data follow this generalization to some extent since *Eriophorum* tussock tundra probably experiences the most disturbance (due to frost action), followed by *Dryas* tundra, with the other two communities having little disturbance at this time scale. However, Fox (1983) postulates that the seedbank size increases with productivity. The size of the seedbanks in the four Oumalik communities follows productivity trends to some extent, showing that productivity is a factor that might need to be included in generalizations about seedbank size in relation to disturbance.

The number of species that germinated from the Oumalik samples followed the general pattern of tussock tundra, *Dryas* tundra > *Carex* marsh, *Betula-Ledum* community (Table 4.4). This trend generally corresponds with the number of species in the community. The tussock tundra soils germinated more species than obtained by McGraw (1980) or Gartner et al. (1983). Fewer species germinated from the *Dryas* tundra than found by Roach (1983).

The top 5 cm generally had more species and more total seeds than the 5-10 cm depth (Table 4.1). Tussock tundra was an exception, having about equal numbers at the two depth intervals. The greater number of seeds in the upper layer is caused by some species being restricted to the top 5 cm and because species that do occur in both depth intervals generally have fewer seeds at the deeper interval. This decrease with depth is a trend found in most seedbanks (Harper 1977).

The storage and germination conditions affected the results quite markedly (Tables 4.1-4.6). There was a nonsignificant tendency in the 1981 soils for more seedlings to germinate from the fertilized soils than the unfertilized, although the *Carex* marsh showed the opposite trend. All communities had more species in the fertilized soils. There were generally fewer total seedlings (nonsignificant statistically) but a greater number of species in the 1981 fertilized soils than in the 1983 fertilized soils. The dominants of the seedbank generally were in soils sampled in both years, but in reduced amounts in the 1981 soils. The greater number of species in the 1981 soils was due to species that germinated in relatively small numbers. Perhaps stratifying the seeds by storing the 1981 soils at above-freezing temperatures broke dormancy in the seeds of these species, but this did not occur in the 1983 soils, which were stored at below-freezing temperatures. The smaller number of species germinating from the soils which were not stratified suggests that more species might have germinated from the Eagle Creek (McGraw 1980) and Kuparuk Ridge (Gartner et al. 1983) tussock tundra soils if they had been stratified rather than stored frozen. The different results among treatments of the Oumalik soils emphasize the difficulties in comparing different seedbank studies and in choosing the proper storage and germination conditions for a study.

The species that germinated from the seedbank are generally present in the community, or, if not in the community, are found within several tens of m from the sampling site. The one exception may be *Ranunculus gmelini*, which had several seeds in soils from the *Carex* marsh. In the *Betula-Ledum* community the difference of the seedbank from the present vegetation and its resemblance to marsh vegetation could be partly due to the past vegetation of the site (palsas are thrust up from marshes) as well as current dispersal onto the area.

Not all of the species that occur in the seedbank are colonizers of disturbances. *Carex chordorrhiza* in the *Carex* marsh has moderately high density in the seedbank but is not a colonizer of disturbances. Other non-colonizing species that occur in low densities in the seedbank are *Luzula confusa*, *L. kjellmaniana*, and *Saxifraga nelsoniana*. It is difficult to imagine the evolutionary advantage of developing the capacity for seeds to persist in the seedbank in non-colonizing species; very likely the persistence is incidental. These species, which disperse seeds late in the season, needed to develop seeds that could persist through the winter to germinate the following spring. If they do not germinate the first year, no special adaptation may be required to persist for moderately long periods of time in the cold, wet soils. The fact that when these species germinated in the 1983 soils, they came almost exclusively from the upper 5 cm, indicates that they don't persist in the soil as long as some of the other species, and supports this explanation.

These results are able to answer some of the questions that prompted this study and that are asked in the Introduction but leave other questions unanswered. *Eriophorum vaginatum* did not germinate from the Oumalik soils and does not appear to be in the seedbank there. Since the failure of a species to germinate in a seedbank evaluation cannot prove its absence or lack of importance, soils from sites where it has been shown to occur, Oumalik, and tussock tundra sites further north should be collected and treated similarly in germination tests. Other factors, such as distance of the disturbance from an *Eriophorum vaginatum* seed source, insufficient moisture, and vigorous competition may also be factors for the lack of *E. vaginatum* on devastated areas of the disturbance.

The dominant colonizers of the mesic areas of the 1949-1950 disturbance and mesic natural disturbances, *Arctagrostis latifolia* and the erect *Salix* spp. apparently do not originate from the seedbank. Only a few seeds of *A. latifolia* germinated and no seeds of *S. glauca,* the only erect willow at Oumalik with seeds long-lived enough to possibly be in the seedbank (Densmore and Zasada 1983). Both the grasses and the willows have very light seeds and are well-adapted to wind dispersal. They apparently depend on dispersal to areas after disturbance rather than germinating from the seedbank.

Seeds of the colonizers of the wet sites on the 1949-1950 disturbance do occur in the seedbank in the communities that occupied the area before the disturbance. *Carex aquatilis* has many seeds in the seedbank of the marsh community sampled (and also palsas), and *Eriophorum angustifolium* has a smaller number of seeds. The seedbank may be important in providing *C. aquatilis* colonizers to disturbances in these communities. Wind dispersal may also be important for *C. aquatilis* since Billings and Peterson (1980) observed it colonizing recently drained lake basins, and it seems likely that it originated from wind-dispersed seeds, although the possibility of seeds germinating from lake sediments cannot be ruled out. *E. angustifolium* is obviously well-adapted to wind dispersal and may depend more on this than persistence in the seedbank for colonization. Although seeds of these species are in the seedbank, it is unknown whether or not they could survive through the 1949-1950 disturbance (one full growing season) to germinate on the disturbed areas.

CHAPTER V

THE RESPONSE OF WILLOWS TO DISTURBANCE

Introduction

One of the most striking aspects of the recovery of vegetation since the 1949-1950 disturbance at Oumalik is the vigorous growth of erect willows on some mesic disturbed areas (Figure 5.1). Dense stands occur, composed of *Salix alaxensis* ssp. *alaxensis*, *S. glauca*, *S. lanata* ssp. *richardsonii*, and *S. planifolia* ssp. *pulchra*. *S. arbusculoides* and *S. hastata* also occur infrequently. Individuals on these sites grow taller and with greater rates of shoot elongation and produce more catkins than individuals of the same species in the surrounding, undisturbed tundra. Kershaw (1983) observed similar responses in Northwest Territories.

The disturbed areas where the willows grow vigorously are well-drained, mesic sites where the soil was highly disturbed. These sites were created by two main types of disturbances. The first was the bulldozing of soil into mounds that are elevated above the surrounding marshes 40-80 cm. This occurred in the drill area and on the site of the winter runway. The second occurs on the sloping sides of the knoll on which the camp was built. Here, the soil was apparently disturbed to a depth of 40 cm or more and resmoothed by bulldozers. Both disturbances create the same

Figure 5.1. Vigorous *Salix* spp. on the disturbance. These willows are growing on mounds of bulldozed material in the drill area. Photo 70-33, 9 July 1981.

Figure 5.2. Uniform height of willows on the disturbance. The evenness is controlled by winter snow depth. Photo 39-28, 3 July 1979.

effect--soils that are warm because the insulating moss and organic soil horizons are gone and that are well-drained because they are elevated or on slopes. This contrasts sharply with the cold, waterlogged soils of undisturbed tundra. The willows also grow vigorously in multiple pass vehicle trails, although not so vigorously as in the two above situations. The vehicles churned the upper soil horizons, which makes the sites somewhat warmer and better drained and therefore more suitable for willow growth.

In undisturbed sites in the Oumalik area, willows are generally low-growing (<50 cm) and have low rates of shoot elongation. In special situations such as along rivers or on slumping lake banks, they do grow taller and have greater rates of shoot elongation. In these sites, soils thaw more deeply and are warmer than in other undisturbed tundra. The riparian sites may also have higher soil nutrient concentrations because of material brought in by seasonal flooding. In both of these natural disturbances, nutrient turnover may be faster since decomposition is favored in the warm, well-drained soils compared to the cold, waterlogged soils of much of the area.

Another interesting feature of the willows on the disturbance is their uniform height within a local area (Figure 5.2). At this height, there are clusters of dead shoots (Figure 5.3), which seem to indicate that their height corresponds to winter snow depth and that shoots which extend above the snow are killed. Shoots above the snow are subject to severe cold and

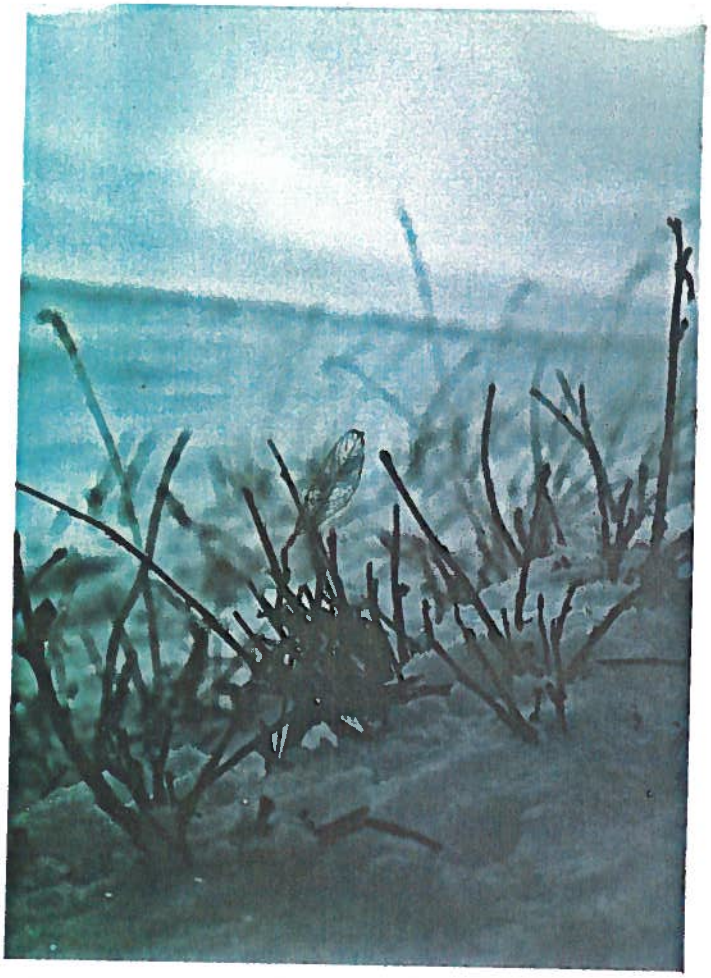


Figure 5.3. Clusters of dead willow shoots at snow level. Repeated winter kill occurs as shoots that grow above the snow are killed by snow abrasion and desiccation. The next growing season lateral buds below the dead portion send up shoots that are killed the following winter. Photo 58-27.

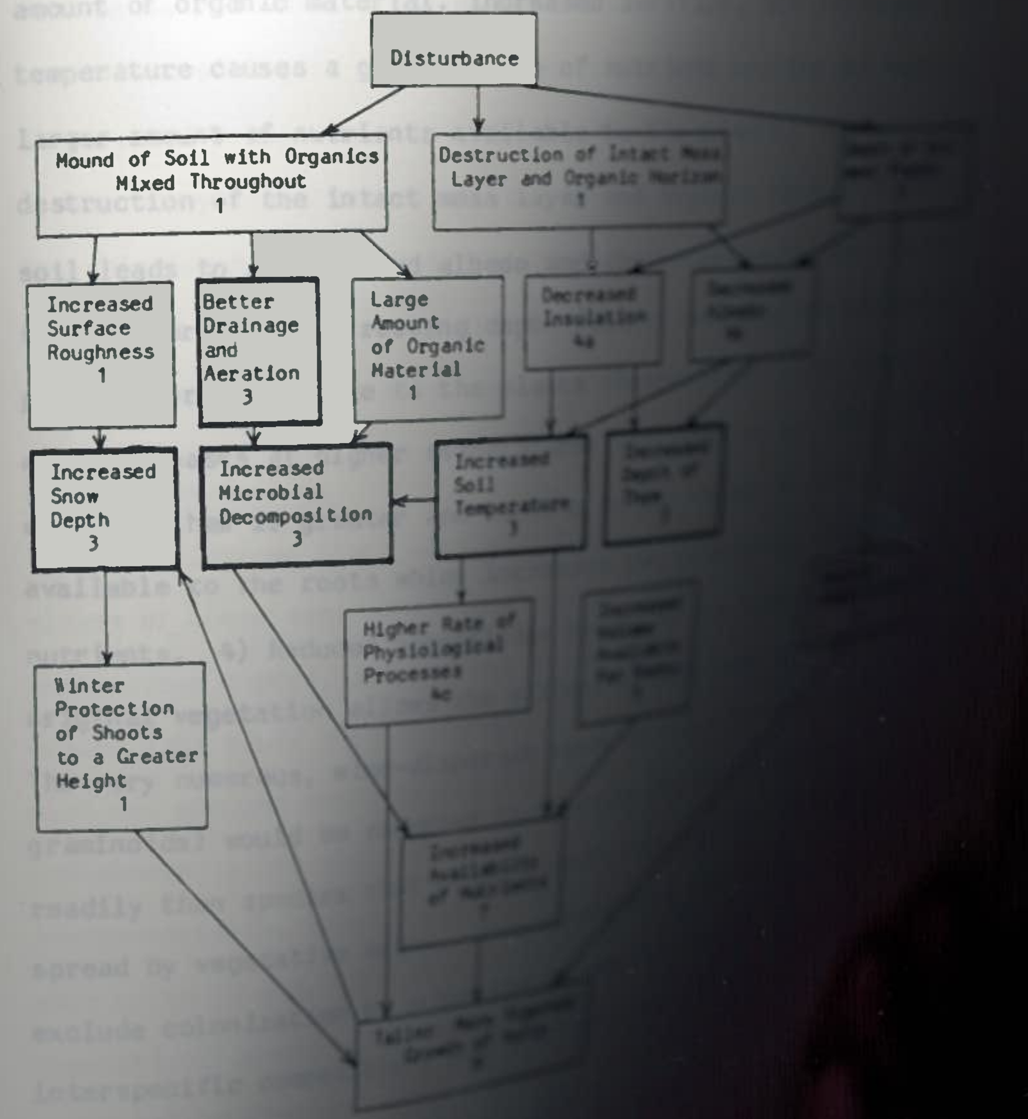
strong winds carrying snow and ice particles. The winds are strongly desiccating and their effect would be increased by abrasion damage caused by the windblown ice and snow. When the ground is frozen, replacing water lost to the atmosphere is impossible, and enough water can be lost to kill shoots above the snow (Daubenmire 1974, Wardle 1974, Tranquillini 1979). One species of willow, *S. alaxensis*, is an exception to the above pattern. Although it also often shows evidence of repeated winter kill at the trimline, in some cases it reaches heights of over 1.5 m, which is far above the trimline. Apparently, *S. alaxensis* does survive above the snow in some cases.

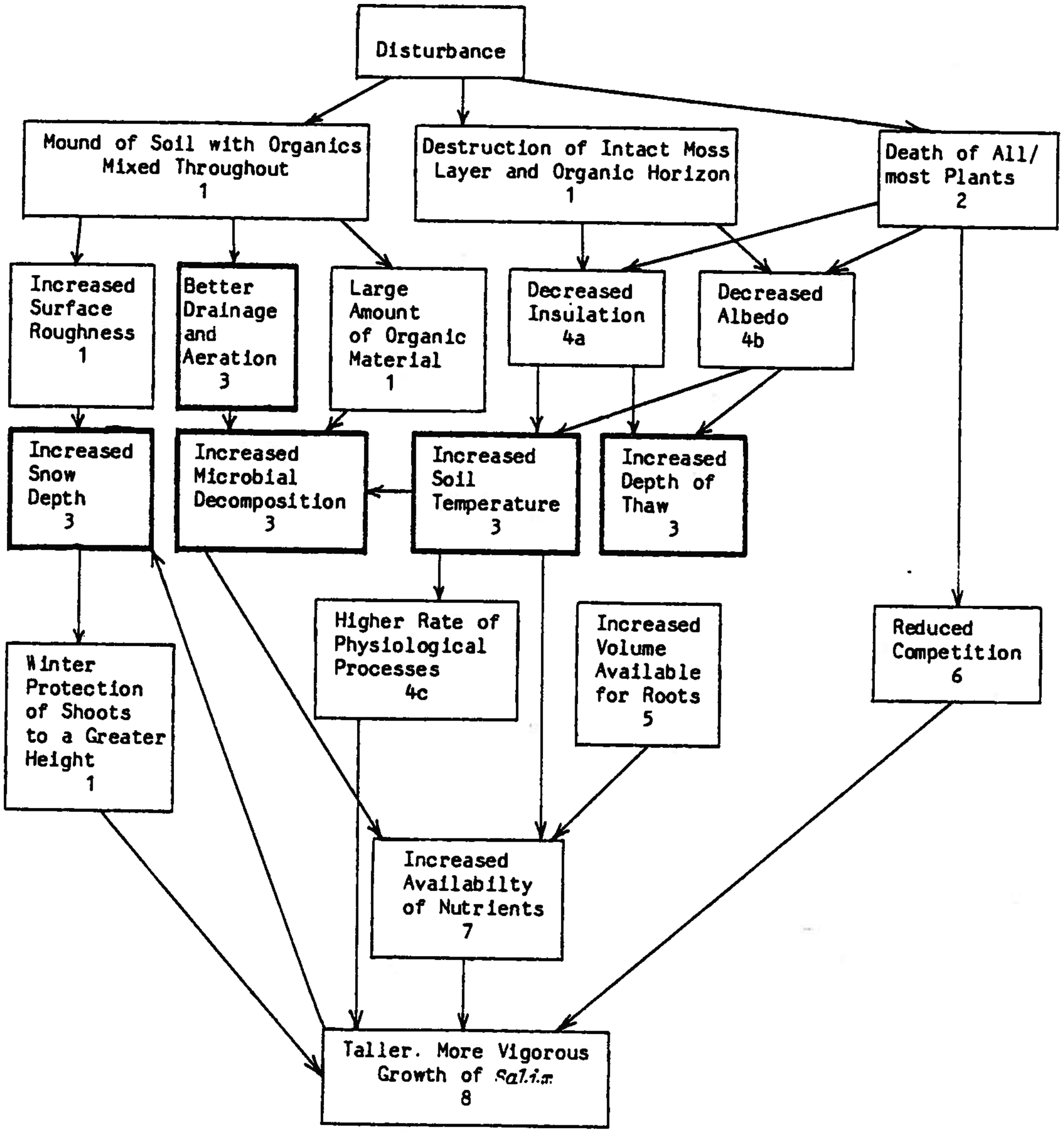
An extensive study was done on these willows in order to understand the changes in the environment caused by disturbance that allow the willows to grow so vigorously. Disturbance has changed factors which limit the growth of willows in undisturbed sites so that these factors are no longer limiting or are limiting at higher levels. Understanding these changes will allow better predictions to be made about the effects of future disturbances in similar terrain and vegetation types, and permit a better understanding of the factors that limit willow growth in undisturbed situations.

Other taxa, especially the grasses *Arctagrostis* spp., respond to disturbance in a similar vigorous manner on the mesic sites. The willows were chosen for study because growth measurements are easier and could be repeated over several years on the same individuals. The understanding gained from the willow study of the changes caused by disturbance to factors important to plant growth can be extrapolated to other taxa if this is done with knowledge of the differences in the ecologies of the taxa involved.

An hypothesis to explain the vigorous growth of the erect *Salix* spp. on these disturbed mesic sites is given as a box-and-arrow diagram in Figure 5.4. It proposes three primary direct effects of disturbance on the areas where the willows grow so vigorously: 1) creation of mounds with a high proportion of organics, 2) destruction of the intact moss layer and organic horizons, and 3) the elimination of most or all of the plants previously growing there. These primary effects lead to several more or less interacting pathways that affect the growth of the willows: 1) The mounds of bladed material increase the surface roughness which causes a greater depth of snow to accumulate during the winter. This protects the willows to a greater height and enables them to grow taller than those on control areas. A feedback loop operates in this snow depth-height relationship. If shoots that grow above the previous year's snow depth are dense, they will collect snow to a greater depth the next year and provide mutual protection for each other to increasingly greater heights (Savile 1972). The increased snow depth also causes a later meltout of snow which retards phenology of the *Salix* on the

Figure 5.4. Box and arrow diagram showing hypothesis to explain vigorous growth of *Salix* spp. on certain areas of the disturbance. Factors outlined in darker lines were tested for significant differences between disturbed and undisturbed sites.
1 - observed
2 - inferred
3 - tested statistically
4 - known from other research
    a) e.g. Brown and Grave 1979
    b) e.g. Brown and Grave 1979
    c) Billings et al. 1978 (increased root growth)
    d) Savile 1972
    e) Chapin and Bloom 1976 (for phosphate)
5 - mathematical relationship
6 - test attempted, but failed; inferred
7 - follows if arrows pointing to this box are justified
8 - at least partially explained if the remainder of the diagram is justified




Disturbance
Mound of Soil with Organics Mixed Throughout 1
Destruction of Intact Moss Layer and Organic Horizon 1
Death of All/most Plants 2
Increased Surface Roughness 1
Better Drainage and Aeration 3
Large Amount of Organic Material 1
Decreased Insulation 4a
Decreased Albedo 4b
Increased Snow Depth 3
Increased Microbial Decomposition 3
Increased Soil Temperature 3
Increased Depth of Thaw 3
Winter Protection of Shoots to a Greater Height 1
Higher Rate of Physiological Processes 4c
Increased Volume Available for Roots 5
Reduced Competition 6
Increased Availabilty of Nutrients 7
Taller. More Vigorous Growth of Salix 8

disturbed areas and delays the thawing of the soil. These negative effects on the growth of the *Salix* are far outweighed by the other factors. 2) Increased microbial activity due to the large amount of organic material, increased aeration, and increased soil temperature causes a greater rate of nutrient cycling and makes a larger amount of nutrients available to the plants. 3) The destruction of the intact moss layer and organic horizon of the soil leads to a decreased albedo and decreased insulation. Higher soil temperatures at rooting depth result, and make the nutrients present more available to the plants (Brady 1974). Root growth also increases at higher temperatures (Billings et al. 1978). The depth of thaw is greater and makes a larger volume of soil available to the roots which increases the potentially available nutrients. 4) Reduced competition caused by the destruction of the original vegetation allows the willows to grow more vigorously. The very numerous, wind-dispersed seeds of the willows (and the graminoids) would be expected to colonize the bare areas more readily than species that produce seeds less profusely or that spread by vegetative means. Once established, they would tend to exclude colonization by other species and, relieved of interspecific competition, they could grow more vigorously.

Methods

The approach to the willow study was to measure several growth responses on four willow species in both disturbed and undisturbed sites. The measurements were tested for significant differences between disturbed and undisturbed sites in order to provide evidence for or against the subjective observation that willows on disturbed sites grow more vigorously. Support for the hypothesis of Figure 5.4 was sought by testing for significant differences between disturbed and undisturbed sites for the factors in the heavy-lined boxes. Winter observations were made to study the relationship of snow depth and willow height, and multiple regression was used to explain the variation in growth responses with the variation in site factors that were measured.

Growth Measurements

Eighteen plots were established for the willow study; eleven of these were on areas disturbed in 1949-50, six were in undisturbed tundra, and one was in the natural disturbance of an eroded lake bluff that had stabilized. The naturally disturbed plot was grouped with the man-disturbed plots for comparison to undisturbed plots since it is more like the disturbed plots environmentally, vegetationally, and in growth rates. The plots were up to 10 m by 10 m in size, but were smaller if a vegetationally and environmentally homogeneous area this large could not be found. *Salix alaxensis*, *S. glauca*, *S. lanata*, and *S. planifolia* were measured in each plot if they were present. Table 5.1 lists the numbers of disturbed and undisturbed plots in which the four species were found. The plots were also selected to have

Table 5.1. Numbers of disturbed and undisturbed plots for each species of willow

species	disturbed	undisturbed
S. alaxensis	8	0
S. glauca	9	3
S. lanata	9	1
S. planifolia	11	4
Total	12	6

five or more individuals of the species that were to be measured. The only exception to this was one plot in which there were only four *S. alaxensis* individuals.

Twig measurements were collected in a nested design of shoots within shrubs within plots within disturbance type (disturbed, undisturbed). In 1979, five shrubs of each of the four species that were present were randomly selected in each plot. The sex of these dioecious shrubs was recorded, but not used in the analysis because the sample size could not accommodate another independent variable. On each shrub, five shoots were randomly selected. In selecting the shoots, the sampling universe was defined as the shoots on the periphery of the shrub that became progressively one year older proximally. Shoots of the current year originating from much older branches were not included because they were distinctly different in size and form. The chosen shoots were marked and numbered with surveyor's flagging.

In 1980 and 1981 growth measurements were made on the marked shoots. To estimate primary productivity, twigs were measured on 5-7 August in both years. Bliss (1956) found at Umiat that *S. lanata* and *S. planifolia* stopped growth by 27 July in 1953, apparently due to intrinsic factors since environmental conditions were still suitable for growth. When the twigs were measured at Oumalik, there were also full-size or near full-size terminal buds, further indicating that elongation had ended. For each twig, the length of the current year's growth and its proximal diameter were recorded. In 1981, if several shoots were growing from the 1980 growth, the most distal one was measured. Some twigs measured in 1980 died before the 1981 measurements, but the number was small and did not create statistical problems.

The measurements were used to calculate a twig "volume" using the formula for the volume of a cylinder

$$V = (1/2\ D)^2\ (L)\ (3.14)$$

where V is the volume, D is the proximal diameter in mm, and L is the length in mm. This calculation ignores the tapering of the twig and assumes that the actual dry weight is proportional to the calculated volume. Linear measurements were done rather than collecting the twigs and determining the dry weight so that the same individuals could be remeasured again and so that the plots were not destroyed for future follow-up. A measure proportional to the actual desired quantity is adequate since analysis of variance and standardized regression results are the same with the proportional measurements.

The assumption that the calculated volume is proportional to the dry weight was tested by collecting 25 twigs of the four species from both disturbed and undisturbed areas (only disturbed areas for *S. alaxensis)*. These were dried in plant presses in the field, and then measured, oven-dried at 105°C, and weighed in the laboratory. The measurements were the same as those taken in the field and the weights were of the catkins, leaves, and twig separately. Volume and dry weight were correlated using Pearson's product-moment correlation.

The number of catkins on each of the marked shoots was counted as a measure of the reproductive output. For *S. glauca* the counts were made at the same time as the twigs measurements since the catkins occur on the current year's growth and mature late in the summer. For the other three species the counts were done as soon as we arrived on the site in the spring (mid to late June) since the catkins occur on the previous year's growth and may absciss by late June. In cases where the catkins had abscissed (mainly *S. alaxensis),* abcission scars were still obvious and could be counted.

The maximum height of each shrub was also measured when the twig measurements were done.

Stem sections were taken to determine the ages of the willows and to measure the ring widths as another growth measurement that potentially held different information than the shoot measurements. In addition to the four species above, stems of *S. arbusculoides* were collected and aged. The sections were collected in 1979 from immediately outside the plots in areas environmentally and vegetationally similar to the plot. They were taken from outside the plots so that shrubs inside the plot were not destroyed. The stems were thin-sectioned on a microtome, mounted on microscope slides, and stained by Tom Bolden, University of Colorado Health Sciences Center in Denver. The slides were placed into a Leitz Wetzlar Prado microscope slide projector and projected onto a wall. The boundaries between rings were marked on strips of paper for two radii for each sample. Walker (1981) also used this technique. Two radii are considered sufficient to account for the within section variation (Fritts 1976). Incomplete rings (Fritts 1976) occurred occasionally and could often be detected in the projected image if the entire section was on the slide. Others were found when the two radii were compared; if a discrepancy was found, the slide was reexamined to resolve it. No false rings were found, and missing rings could not be detected since the specimens were not cross-correlated. Cross-correlation was not considered necessary since the sections were used to obtain the average increment rather than to construct a chronology.

Rings of willows from the disturbance were wide, well-defined and almost always complete. Rings of willows from undisturbed areas were narrow, sometimes incomplete, and often difficult to differentiate. On the difficult sections, the entire circumference was examined for clues to determine boundaries between rings, and higher powers used to look at the problem areas in more detail. With this care good results were obtained.

The age of each stem was determined by counting the number of rings from the strips of paper. The ages were used to calculate the length of time that it took for the willows to colonize the disturbed areas, and to get an idea of the longevity of the willows in undisturbed areas. The width of each ring was calculated by measuring the width on the paper strips and converting it to the actual width using a factor obtained by projecting a stage micrometer with the microscope slide projector. There is a strong pattern of wide growth increments when the stems are young and decreasing ring widths as the stems become older; this is the usual pattern in woody plants (Fritts 1976). This posed a problem in comparing ring widths from individuals growing in disturbed vs. undisturbed sites since the willows in undisturbed sites are markedly older. In one sense it would be desirable to compare rings of the same calendar year so that climatic variation between the compared samples would be zero. However, the variation due to differences in age overwhelms the variation due to climate. Therefore, I used the average of 10 years of the same ages of willows. Averaging 10 years will minimize differences due to year-to-year climatic fluctuations, but will not correct for longer-term climatic change among willows that are different ages.

The ages for averaging were chosen independently for each species. Scattergrams of ring width as a function of age were done for each sample to help choose the ages to use. The ages chosen were those whose ring widths did not show a decreasing or increasing trend with age. The choice was limited, of course, by the age of the youngest section. The ages that were chosen are given in Table 5.2, along with the numbers of sections from disturbed and undisturbed areas. The sample numbers are slightly smaller than those in Table 5.1 for *S. lanata* and *S. planifolia* because some of the stems collected could not be successfully sectioned.

Winter Observations and Follow-up

I visited Oumalik twice in the winter, on 16-22 April 1980 and 12-16 April 1981, in order to look at the relationship of snow depth to willow height and to do a snow survey for the Cold Regions Research and Engineering Laboratory (CRREL). The snow survey results are in a May 1981 internal report to CRREL and will not be presented here. April was chosen as the time of maximum snow depth (Dingman et al., 1980) and as a time when weather and light made it reasonable to live in and work from a snow cave.

The primary questions to be answered by the winter observations were whether snow depth corresponded to the trimline in the willow stands, whether the tall *S. alaxensis* were above the snow in winter, and whether shoots of other species that were above the snow could survive. To help answer the question of whether species other than *S. alaxensis* can survive above the snow, in summer 1979 I moved some barrel piles that had unusually tall and vigorous willows growing by them, presumably because of the winter snow protection the barrels caused. This created an

Table 5.2. Ages of rings and sample sizes used to calculate mean growth increments.

species	ages used for averaging	sample size	
		disturbed	undisturbed
S. alaxensis	7-16	8	0
S. glauca	9-18	9	3
S. lanata	10-19	7	1
S. planifolia	11-20	9	2

experiment of putting willow species that apparently do not survive above the snow at Oumalik into the above-snow winter environment. During the April visits, I noted where snow depth was in relation to the trimline in each of the willow plots. I also marked some shoots that were above the snow with surveyor's flagging placed at snow level. Notes were made if the shoots above the snow were broken or had buds missing. The following summer I noted the survival of shoots and buds in relation to the previous winter's snow depth.

Environmental Measurements

All the site factors listed in Tables 2.1 and 2.2 were estimated or measured at the willow plots since they were also used as vegetation samples. In addition, the date of meltout (time of 0% snow cover) was recorded in 1980, gravimetric soil moisture was determined from samples collected at 10 cm on 15 July 1980, and soil temperature was calculated as the mean of three replicate readings with a thermistor probe at 10 cm on 14 July 1983.

Measures of decomposition were also obtained. The decomposition work was reported in Ebersole and Webber (1983) as a way to account for the abundance of willows and grasses on the mesic areas of the disturbance. In this chapter, the decomposition results will be used to test the hypothesis (Figure 5.4) that decomposition rates (and therefore nutrient availability) are greater in disturbed willow plots than in undisturbed willow plots and to help explain the variation in willow growth responses.

Three types of decomposition samples were placed into 9 disturbed and 16 undisturbed plots selected to represent the range of decomposition environments at Oumalik. Eleven of these plots were willow plots--five undisturbed, and six disturbed. For the willow plots without decomposition samples, substitutions were made from plots that were classified in the same community (Chapters II and III) and were similar environmentally. In all cases, results from plots that are strongly similar were available. The three types of decomposition samples were (1) 2.00 g (all weights are oven dry) of *Agropyron cristatum* stems from a disturbed area in Boulder, Colorado, in a 10 x 10 cm nylon net bag whose largest holes were about 0.7 x 0.3 mm, (2) one cellulose filter paper weighing about 0.56 g in a similar bag, and (3) birch wood tongue depressors weighing 2.4-3.1 g. On July 6, 1980, samples were placed into each of the plots at a depth of 10 cm. The samples were placed at depth because the decomposition of interest occurs in the organic matter mixed into the soil by disturbance rather than in litter on the surface. Ten cm was chosen as the depth of most abundant roots. Each plot contained four replicates of each of the three types of decomposition samples. Two replicates of each type were removed 1 yr after emplacement, and two were retrieved at the end of the maximum time available for the experiment on August 3, 1981, which was equivalent to approximately 1.5 growing seasons.

After removal, the samples were dried in the field. In the laboratory the tongue depressors and filter papers were rinsed with cold running water to remove adhering mineral soil. The grass was not washed because of the significant water-soluble fraction (15-19%) it contains. The samples were oven dried and weighed to determine weight loss. Representative used and unused samples of each type of sample were ashed (450°C for 2 hr). The differences in the weight of ash between used and unused samples were used to correct weight loss of all samples for adhering soil. After correction, the percent weight loss for each of the three types of samples for both time periods was calculated. For use as an independent variable in multiple regressions, these six rates for each plot were combined into a decomposition index by expressing each as a percentage of the maximum rate for that sample type and time period and then averaging these six numbers.

All the site factors were tested for significant differences between disturbed and undisturbed plots to determine what factors might be important in differentiating the two types of plots, and specifically, to test for differences in the factors that are part of the hypothesis of Figure 5.4. The Kruskal-Wallis test was used so that the parametric assumptions did not need to be tested. If the results were suggestive but not significant at the $p \leq 0.05$ level, a oneway ANOVA was done after testing its assumptions. See the Results section for which test was used in each specific case.

The multiple regressions that explain the variation in decomposition rates with the variation in measured site factors were recalculated from those reported in Ebersole and Webber (1983). Soil temperatures measured in 1983 were used because there were data from every plot and because they were subject to very little diurnal and no among-day variation, while the soil temperatures used in the first analysis were missing for some plots and were measured over several days. Fewer independent variables (6) were used and only the first two variables entered are reported. The details of the multiple regression analysis are the same as for the growth response analysis (next section).

Competition Experiment

The hypothesis of Figure 5.4 suggests that the lack of competition on the bare areas created by the 1949-1950 disturbance might be part of the explanation for the vigorous growth of the willows on these sites. Because willow seeds are abundant and wind-dispersed, some seeds usually arrive on open areas. Without competition from many other species, they might be able to grow more vigorously than in a closed community. Thus, a measure of the relative competition levels of bare and undisturbed tundra was desired. It was also of interest to know the current relative level of competition in the willow communities on the disturbance compared to bare areas and undisturbed areas.

I attempted to test the relative levels of competition by planting cuttings of *S. alaxensis* and *S. planifolia* into undisturbed tundra; a bare, recently disturbed area; and a willow community on the 1949-1950 disturbance. *S. planifolia* cuttings about 20 cm long were taken on 19 July 1981 from three sites: the *Salix-Arctagrostis* community (number 32) that occurs on the area disturbed in 1949-1950, tussock tundra (community 10), and a drainage coming off the uplands (community 7). *S. alaxensis* cuttings about 30 cm long were taken from community 32. Lateral branches were clipped off the cuttings and catkins were removed, but emerging leaves were allowed to remain. The cut ends were dipped into Rootone 10 (a powder that is 0.4% 1-naphthaleneacetamide), tapped to knock off excess powder, and placed about 5 cm deep into slits made with a shovel. Twenty-five cuttings of each species from each of the collection sites were placed into three planting sites: undisturbed tussock tundra (community 10), the approximately thirty-year-old *Salix-Arctagrostis* community (number 32), and the site where the debris that was collected from the site in 1980 was buried in March 1981. This bare, highly disturbed site was used to simulate the conditions immediately after the Oumalik well was abandoned in 1950.

I hoped to be able to test the growth (dry weight) of the current year for differences between the disturbed and undisturbed planting sites, and then to see how the current level of competition in the willow community (number 32) compared to these other two communities. However, less than 5% of the cuttings survived, and the experiment produced no usable results.

Statistical Methods for the Growth Response Analysis

For each species the growth reponses were correlated using Pearson's product-moment correlation to determine if the various measures contained different information. (All statistical analyses were done using SPSS-6000 version 8.3 [Statistical Package for the Social Sciences] [Nie et al. 1975, Hull and Nie 1981, Benson 1982] on the University of Colorado Cyber.) Correlations were generally low; where high correlations (>0.80) between 2 response variables occurred, they were not consistent across all four species except for the heights measured in 1980 and 1981. Thus, the response variables, except for the heights, contained different information, and all were retained for the analysis. Inspection of the two year's measurements of heights showed that they were very similar, as would be expected, and these were averaged to obtain a single height response.

The growth measurements were tested statistically for differences between disturbed and undisturbed plots in order to provide evidence for or against the subjective observation that willows on disturbed sites grow more vigorously. *(S. alaxensis* was not tested since it does not occur on undisturbed sites in the

Oumalik area.) The volume and catkin measurements are in a three-level nested design, shoots within shrubs within plots within disturbance type. The heights are in a two-level nested design, shrubs within plots within disturbance type; and the ring widths are in a simple oneway design. Parametric analysis of variance (ANOVA) (nested and oneway designs) was used when the assumptions of normality and homoscedasticity were met since they are more powerful than nonparametric tests and since there are not nonparametric techniques for nested designs. The Kolmogorov-Smirnov test was used to test for normality and Bartlett's Box F was used to test for homoscedasticity. These tests were done at the disturbance type level. If these tests showed that the assumptions were violated, transformations (ln, square root, Box-Cox) were tried. If the data still did not meet ANOVA assumptions, the responses were averaged within the lowest level of the nested design (this tends to make the variables more normally distributed according to the central limit theorem [Sokal and Rohlf 1981]), and the normality and homoscedasticity were tested again. In the three-level nested designs, averaging was also done at the plot level if necessary. If the parametric assumptions could not be met, the nonparametric Kruskal-Wallis test was used at the disturbance type level by pooling all observations within a disturbance type. One final choice on the type of test to use was made for the analysis of *S. glauca* catkins. The number of catkins averaged within shrubs met the assumptions for a two-level nested ANOVA, but did not show differences between disturbed and undisturbed plots. The nested design was sacrificed and a oneway ANOVA was done in order to gain more degrees of freedom. See the Results section for the test used in each specific case.

Stepwise multiple regression was chosen to explain the variation of willow growth rates with the variation in site factors. The goal was to determine which site factors were most important in controlling willow growth. For each growth response of each species, a separate regression was done (24 regressions total). Other statistical techniques that were considered for this analysis were canonical correlation and simple correlation. Canonical correlation would have the advantage of summarizing the relationships between growth responses and site factors for each species in just one solution rather than six as for the multiple regression. However, the canonical variates can be quite difficult to interpret since they are linear combinations of the original variables. In addition, correlation procedures are less appropriate to use than regression when trying to explain the variation of one variable or a set of variables as opposed to establishing how two variables vary jointly. Calculating simple correlations of all environmental variables and response variables for each species is less appropriate than regression for the same reason as above, and also has the major disadvantage of not achieving a reasonable level of data reduction and not accounting for intercorrelations of site factors. Multiple regression has the advantage of attaining a reasonable level of data reduction while keeping the solution in the original variates.

The forward method of stepwise multiple regression was used (Cohen et al. 1977, Draper and Smith 1981). At each step, the one predictor variable that would reduce the residual sum of squares the most if chosen is entered into the equation if it meets certain criteria. That is, the variable is chosen that explains the greatest amount of variance unexplained by the variables already in the equation. After each step, each of the variables in the equation is tested to determine if it still explains a significant part of the variance. If not, it is removed. The criteria for entering and removing variables were set at F-values significant at $p \leq 0.10$ for entering and $p > 0.10$ for removal as recommended by Draper and Smith (1981.) Draper and Smith (1981) note that the F-distribution does not give the actual probability levels, but that they are useful for internal comparisons and for constructing the most useful set of predictors. In this case, where hypotheses are not being tested and the regressions are used for descriptive purposes, this does not create a problem at all. Model I regression techniques were used even though the data are Model II (predictor variables measured with error) because there are no Model II techniques for multiple regression. This is justified because the regressions are used for descriptive purposes rather than hypothesis testing.

For each response variable, a single value per plot was obtained by averaging the growth responses. This was necessary because the site factors were taken at the plot level.

As predictor variables, six site factors were chosen--total N, P, K, soil temperature, decomposition rate, and soil moisture. These were chosen subjectively as the most important factors for willow growth. It is necessary to limit the number of possible predictor variables because multiple regression is a powerful technique and can assign random variation that is left unexplained by the first one or two predictors to other predictors that may explain this variation only due to chance. Such results are unstable with slight changes in the data or set of predictors, and it is best to reduce the number of predictors (Draper and Smith 1981). This instability of the solution was seen when larger sets of predictors were tried. For the same reason, only the first two predictor variables entered are reported. In most cases, only one or two were entered by the procedure, but in a few cases, there were three or four entered.

Plots of the regression residuals against the predicted Y values for the regressions with the untransformed data (Draper and Smith 1981, Sokal and Rohlf 1981) and scattergrams of the growth responses against the site factors both indicated that ln transformations of the dependent and predictor variables would help to meet the regression assumptions of linearity and equal variances of Y values for a given X. Regressions using these transformations were done, and plots of residuals and scattergrams of the transformed data showed little evidence that the assumptions were not met. These are the regressions that are reported.

Principal components analysis (PCA) on the site factors was attempted so that all the site factors could be retained without having the problems caused by too many predictor variables. A PCA was run on 21 of the site factors and then regressions were done using the principal components (PC's) as predictor variables. PCA's were also done on three subsets of the 21 site factors; nutrient variables, moisture variables, and soil temperature/snow variables; and regressions were done for each of the subsets. With the PC's as predictors, there were a higher number of growth responses that had no predictors entered into the equation, and the r^2 values for the equations that did have predictors were lower than with the original data. The interpretation of the PC's was uncertain in many cases. Because of these poorer results with the PC's as predictors, the transformed original data were used as predictors.

Results and Discussion

Ecologies of the Studied Willow Species

The four willow species *S. alaxensis*, *S. glauca*, *S. lanata*, and *S. planifolia* are all found with abundance on some of the mesic, circum-neutral areas of the disturbance (Appendices B3 and B4), but they generally do not occur together as major components of undisturbed communities, except for *S. lanata* with *S. planifolia* (Chapter II, Appendices B1 and B2). In undisturbed and naturally disturbed areas, *S. alaxensis*, *S. glauca*, and *S. lanata* have fairly narrow ecological amplitudes (Figures 2.30 and 2.31). *S. alaxensis* is almost exclusively limited to stabilized lake bluffs, which are basic and xero-mesic and is essentially absent from undisturbed areas (Appendices B1, B2; Figures 2.30 and 2.31) It also occurs along major rivers, which are some distance from Oumalik. Apparently some type of disturbance is needed to provide a suitable habitat for it. *S. glauca* occurs only in mesic, relatively basic sites; while *S. lanata* is found in moderately wet, circum-neutral sites. *S. planifolia* has a wide ecological amplitude with its highest abundance in acidic sites that are mesic to somewhat wet. It occurs with a moderate abundance even in relatively basic mesic sites and in areas that are quite wet.

Times of Willow Establishment

The oldest willows on each of the devastated sites, where the vegetation was totally destroyed, became established from 5 to 9 yr (mean 7.7 yr) after the disturbance ended (Table 5.3). The ages determined from the stem sections are minimum ages since some of the earliest rings could have been missed by sampling the stem too high, and since other willows might have become established before the sampled willow. This would mean the time needed for colonization might be overestimated by several years. The different species showed some differences in colonization times, but these were not significant as determined with a one-way ANOVA. These times needed for willows to establish are similar to those found by Kershaw (1983) on similar disturbances in the Northwest Territories, Canada, where willows took from 4-15 yr (average 11) to establish. The greater variability and somewhat greater mean are caused by Kershaw's wider range of disturbances sampled and his larger sample size.

The partially-disturbed sites had some willow stems that survived the disturbance (Table 5.3). In some cases, e.g. *S. glauca*, the apparent rapid establishment could be caused by sampling a stem that sprouted from a willow that survived the disturbance.

The establishment of willows on disturbed sites favorable to them is rapid for all the species studied. *S. planifolia* tended

Table 5.3. Time, in years after disturbance, of willow establishment. All willows refers to the oldest willow on each plot, regardless of species. The means for the five species on devastated sites were tested for differences with a oneway ANOVA and found not to be significantly different ($p > 0.05$). The means for the partially disturbed sites were not tested because of small sample size. The ages of the willows are minimum ages so these times may be somewhat overestimated (see text).

	S. alaxensis			*S. arbusculoides*			*S. glauca*			*S. lanata*		
	n	min.-max.	mean	n	min.-max.	mean	n	min.-max.	mean	n	min.-max.	mean
devastated sites	6	6-16	9.8	3	10-11	10.3	7	9-15	11.1	6	8-11	9.2
partially-disturbed sites	2	7	7.0				1*		2	1		7

	S. planifolia			All willows		
	n	min.-max.	mean	n	min.-max.	mean
devastated sites	5	5-9	7.6	7	5-9	7.7
partially-disturbed sites	3**	8-10	9.3	3	0-2	0.7

* another individual that became established in 1921 survived the disturbance and was 59 yr old when sampled.

** another individual that became established in 1949 survived the disturbance and was 31 yr old when sampled.

to become established most quickly; this may be because it is more abundant than the other species in the surrounding, undisturbed tundra. However, even *S. alaxensis* and *S. arbusculoides*, which ar relatively rare in the undisturbed tundra and whose nearest known individuals are some distance (about 1 km) from the disturbance, became established within about 10 yr after the disturbance ended. Willows obviously have a large capacity for dispersal and for quic colonization of disturbances.

The number of rings of willows on undisturbed sites (Tabl 5.4) gives a minimum age as described above, and in addition the ages are minimum stem ages, rather than shrub ages, since stems ca die while the shrub survives (Beschel and Webb 1963). The ages ranged from 19 yr for *S. glauca* on the natural disturbance of a lake bluff to over 70 yr for *S. planifolia* in tussock tundra and i a drained lake basin. *S. lanata* in the same drained lake basin plot was 57 yr old, and *S. glauca* in the *Dryas integrifolia-S. glauca* community ranged from 26 to 49 yr old. Due to the small sample sizes, these results are only preliminary indications of willow ages in undisturbed communities.

Snow Depth and Willow Heights

The winter observations showed that snow depth in April corresponded essentially exactly with the trimline of willow stands. The stands without trimlines were in topographic location where the snow depth was much greater than the willow heights.

Table 5.4. Ages in years of willows on undisturbed sites. The ages are given by community name and number with associated landform. *S. alaxensis* and *S. arbusculoides* are rare in undisturbed tundra and were not sampled. The ages of willows are minimum ages (see text).

	S. glauca			*S. lanata*		*S. planifolia*	
	n	min.-max.	mean	n	mean	n	mean
Dryas integrifolia-Salix glauca (13) knoll (upland remnant modified by thaw lake processes)	3	26-49	40.3				
Eriophorum vaginatum-Salix planifolia (10) upland unaffected by thaw lake cycle						1	74
S. lanata-S. planifolia (8) older drained lake basin				1	57	1	73
S. glauca-Poa arctica (20) stabilized lake bluff	1		19				

The observations also showed that the tall *S. alaxensis* shrubs do survive above the snow through the winter, as expected (Figure 5.5).

Summer observations of bud survival of shoots marked at snow level showed the reasons for the trimline. Bud survival above the snow in undisturbed areas was negligible, and in disturbed areas only an occasional lateral bud survived. The only exception is *S. alaxensis*, which experienced severe kill in the approximately 30 cm above the snow, but a moderate to high winter survival of buds above this height. No other species had shoots more than 30 cm above the snow. This pattern of bud survival produces *S. alaxensis* shrubs with a distinct trim line at snow level and several shoots extending above this level that have no leaves for about 30 cm above the snow and abundant leaves above this zone (Figure 5.6).

The cause of the low survival of buds just above the snow is postulated to be the abrasion caused by the snow and ice particles carried by the wind. Most of these particles are carried at and just above the snow surface. Continual abrasion or intensive abrasion during periods of strong winds and/or low temperature when the particles are hardest can damage tissues and buds leading to desiccation and death. *S. alaxensis* buds higher than approximately 30 cm above the snow are above the zone of most intense abrasion and have a moderately high winter survival.

Figure 5.5. *Salix alaxensis* above the snow in winter. The tallest shoots and most of the shorter ones are *S. alaxensis*. A few of the shorter shoots are other *Salix* spp. Photo 97-3, 13 April 1981.

Figure 5.6. *Salix alaxensis* without leaves in intense snow abrasion zone. Winter snow depth is at lower boundary of leafless zone. Photo 41-20, 12 July 1979.

Where above-snow *S. alaxensis* shoots are very dense, this leafless zone does not occur. Apparently the shoots mutually protect each other by decreasing the wind speed and the speed of the snow and ice carried by the wind (Savile 1972).

Other factors that could conceivably create the well-defined trimline are the effects of caribou and ptarmigan. *Salix* spp. leaves are a significant part of the caribou diet (White and Trudell 1980). But caribou are infrequent in the Oumalik area and eat only a few mouthfuls before moving at least several meters before stopping to eat again. These erratic eating habits could not explain the uniform trimline. In addition, many buds remain through the winter but do not survive, as opposed to twigs which do not survive because no buds remain. The significance of the effect of ptarmigan picking off buds that are just above the snow is not considered to be an important factor for the same reason, as well as the fact that very few ptarmigan remain on the Coastal Plain through the winter (NPRA Task Force 1978b). Matthews (1983) also observed *S. alaxensis* above winter snow depth in arctic Quebec, and Edlund and Egginton (1984) inferred that it must be above the snow in western Victoria Island. Tall *S. planifolia* also survive above the snow in northern Quebec (Matthews 1983), indicating that other species have this capacity, perhaps if they grow fast enough to extend above the zone of most intense snow abrasion or if winds in the region are light.

Some of the willows whose snow protection was eliminated by moving the barrels that caused snow to drift over them were exceptions to the low survival of buds above the snow, although there was wide variation in this characteristic. These shrubs were growing quite vigorously due to surface disturbance by the barrel piles. Some *S. glauca* individuals had a high survival of above-snow buds while nearby individuals with apparently very similar environments had almost no buds that survived above the snow. Buds of *S. lanata* had very poor survival rates. *S. planifolia* terminal buds rarely survived above the snow but lateral buds frequently did. Comparing the occasional bud survival of these individuals which are growing vigorously in favorable environments and the negligible survival of above-snow buds in the more limiting undisturbed areas leads to the hypothesis that hardiness to the above-snow environment varies with the vigor of the individual.

Bud survival of the four willow species below April snow depth was moderate to high although *S. arbusculoides* seemed to be somewhat less winter-hardy than the other species. Even below the snow, terminal buds rarely survived, and lateral buds continued twig elongation the next year. In some places where survival of buds over the winter was quite high in the two years of observations, dead older twigs showed moderate to severe kill over the winter in other years. An exception to the high winter bud survival below the show was *S. planifolia* in tussock tundra in a snow accumulation area. These shrubs would be completely covered very early in the season, yet had many buds killed over the winter. Perhaps willows stressed during the growing season by factors such as low nutrient availability are more susceptible to winter kill of buds regardless of snow protection.

Winter observations at Oumalik were made only in April and one can question the importance of snow depths earlier in the winter. Dingman et al. (1980) show that at Barrow in the winter of 1970-1971, 20 cm of the 35 cm maximum snow depth was on the ground by 10 October. There was then a gradual increase in snow depth through the winter until a plateau was reached at the end of February, which lasted through May. It seems reasonable to assume that the same pattern of most of the snow accumulating very early in the winter occurs at Oumalik as well. In addition, the dense stands of willows would collect snow carried by the wind and have a tendency to fill up with snow to the height of the willows relatively early in the winter. This suggests that in these dense stands, the willows could gradually increase in height over several years by growing taller than the previous year's trimline and collecting protective snow to a greater height.

Differences in Site Factors Between Disturbed and Undisturbed Plot

Table 5.5 gives the means and results of the tests for differences in site factors between disturbed and undisturbed willow plots. The disturbed plots are significantly drier than undisturbed plots, although they are still mesic. Soil temperatures are warmer in disturbed plots, and decomposition rates are greater. Thaw depths are not significantly different. Snow for both years was deeper in the disturbed plots, and as a result the time of meltout was later.

It is interesting to note that there is a nonsignificant tendency for the concentration of nutrients to be less in disturbed plots than in undisturbed plots. The greater rates of decomposition show that there is a higher rate of turnover, however, and reveal information about nutrient differences between the two types of plots that would not be seen by determining just nutrient concentrations. Apparently, the nutrients are taken up by plants and microorganisms as soon as they are released by decomposition.

Decomposition results. The decomposition results are given in Figure 5.7. For all three substrates, over both time periods, weight losses were greater in disturbed plots than in undisturbed plots ($p < 0.02$). The plots with the highest decomposition rates are bulldozed slopes and mounds of bladed material dominated by *Salix* spp. and/or *Arctagrostis*

Table 5.5. Means of site factors and tests for significant differences between disturbed and undisturbed willow plots.

site factor	means		tests for differences	
	undisturbed	disturbed	method	sig.
soil moisture, ordinal scale	7.0	6.5	K-W	*
pH	6.68	6.96	oneway	ns
N-NH4, ppm	41.97	21.78	K-W	ns
N-NO3, ppm	18.13	21.78	K-W	ns
total N, ppm	60.10	43.57	K-W	ns
P, ppm	3.52	3.15	K-W	ns
K, ppm	172.17	84.33	K-W	ns
Ca, ppm	7383	4802	oneway	ns
Mg, ppm	728.8	596.9	K-W	ns
organic matter, %	41.35	26.88	K-W	ns
available water, %	22.17	24.93	K-W	ns
carbonates, %	3.55	2.67	K-W	ns
decomposition, %	48.8	64.8	K-W	*
thaw depth, cm	50.5	51.8	K-W	ns
soil temperature, °C	3.0	4.7	K-W	*
snow depth, 1980, cm	50.5	78.2	K-W	*
snow depth, 1981, cm	39.7	73.2	K-W	**
meltout, day in June	10.0	16.1	K-W	*

* $0.01 < p \leq 0.05$; ** $0.001 < p \leq 0.01$; ns nonsignificant

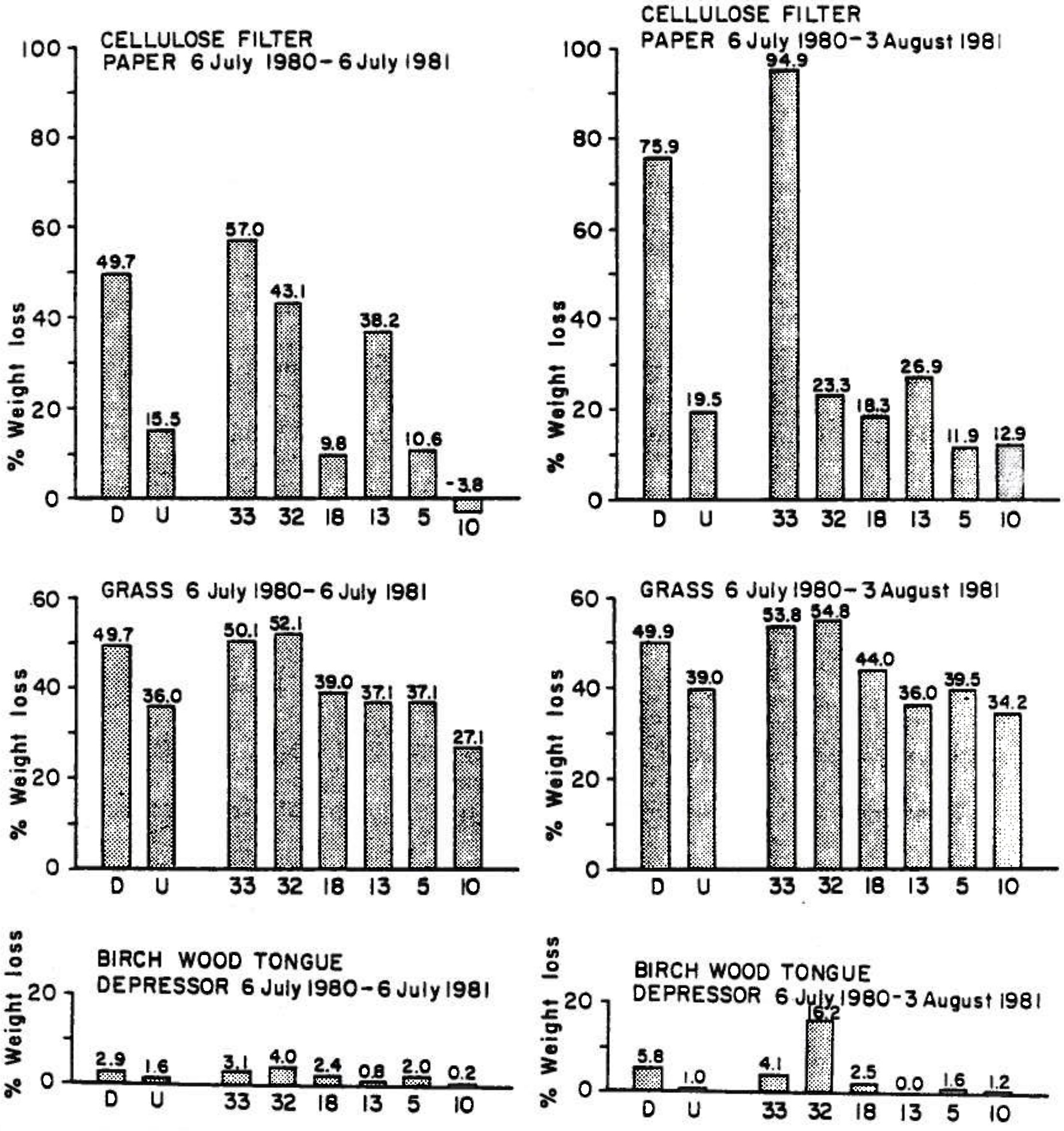


Figure 5.7. Percent weight loss of decomposition substrates. For all substrates, weight losses are significantly greater ($p<0.02$) in disturbed plots (D) than in undisturbed plots (U). The code numbers are community numbers: 32 *Salix* spp.- *Arctagrostis latifolia;* 33 *Arctagrostis latifolia* (the two disturbed communities); 18 *Betula nana-Ledum palustre;* 13 *Dryas integrifolia-Salix glauca;* 5 *Carex chordorrhiza-C. rotundata;* 10 *Eriophorum vaginatum-S. planifolia* (the four undisturbed communities).

latifolia (communities 32, 33) (Figure 5.7). These sites have relatively warm soil temperatures, and due to their good drainage the soils of these sites are also well aerated, as indicated by the soil color. The sites with the slowest rates of decomposition are undisturbed tussock tundra (community 10), which has cold soil temperatures and anaerobic soil as evidenced by the strong gleying. The greater rates of decomposition in marshes, which also have highly anaerobic soils, are probably due to their higher soil temperatures. Communities 18 and 13 are intermediate in decomposition rates, aerobicity as judged from soil color and moisture, and soil temperatures.

Differences between the 12- and 13-month losses varied with the type of decomposition sample (Figure 5.7). The grass showed only slightly greater losses over the longer time period, apparently because the easily leached or decomposed fraction was gone within the first year, leaving only the more resistant components. Filter paper and birch wood losses tended to increase slightly to substantially in the additional month. Colonization by decomposers may have taken longer in these substrates compared to the grass in which decomposers were probably already resident.

The results of the stepwise linear multiple regressions show that soil temperature is the most important environmental factor in explaining the variation in decomposition rates (Table 5.6) and that it correlates positively with decomposition rate.

Table 5.6. Results of multiple regressions on decomposition rates. Coefficients of the independent variables are positive unless followed by a negative sign. The first r^2 value is for the equation with only the first independent variable entered, and the second r^2 value is for the equation with both variables in it. Only the first two independent variables entered are reported.

	grass stems		filter paper		tongue depressor	
	variables	adjusted r^2	variables	adjusted r^2	variables	adjusted r^2
12 months 6 July 1980-6 July 1981	soil temperature	0.21	soil temperature	0.22	soil temperature	0.10
	soil moisture (-)	0.29	soil moisture	0.29	soil moisture	0.19
13 months 6 July 1980-3 August 1981	soil moisture (-)	0.27	soil moisture (-)	0.31	soil moisture	0.25
	soil temperature	0.47	soil temperature	0.49	soil temperature (-)	0.39

Other investigations in the arctic have also shown that soil temperature is the major limiting factor (Heal and French 1974). Soil moisture is the second most important limiting factor at Oumalik and is negatively correlated with decomposition. No samples were in the rare dry sites in which the lack of moisture is limiting so decomposition shows a negative, essentially linear relationship with soil moisture. In studies covering the complete moisture gradient, the response curve of decomposition as a function of moisture reaches a maximum in the mesic sites and declines in both dry and wet sites (Heal and French 1974).

Depth of thaw and pH also appear as important factors in the regressions; both are positively correlated with decomposition. The interpretation of thaw depth is uncertain. An increase in pH tends to increase decomposition rates in tundra sites because a greater variety of decomposer organisms can function in less acid sites (Heal and French 1974).

The r^2 values for the regressions are small, ranging from 0.19 to 0.49. They are greater for the longer period of time, perhaps indicating that the longer period of time gave a more accurate measure of decomposition potentials of the plots. However, a large amount of variation in the weight losses cannot be explained by the linear, additive regression model. Possible sources of the variation unaccounted for are nonlinear responses of decomposition rate to variation in environmental factors, interactions among environmental factors in their effect on decomposition rate, changes in decomposition patterns within and between seasons (site factors were measured only once), and random variation in decomposition potential or measured environmental factors on a microscale within a plot or habitat type.

The r^2 values for the regressions reported in Ebersole and Webber (1983) are larger than the ones reported here, although the important explanatory variables are generally the same. Differences in the procedures used are that fewer independent variables were used in this analysis, more plots are included here since soil temperature is not missing in any plots, and the soil temperature used is from 1983 rather than 1981. Using fewer independent variables is better for reasons explained in the Methods sections. However, even considering only the first two variables from Ebersole and Webber (1983), the r^2 values are still larger. The larger number of plots in this analysis may add more variation that cannot be explained as well with the multiple regression model. Another reason for the differences may be that soil temperatures in 1983 were taken during a cooler period than those in 1980. During this cooler period, soil temperature differences between disturbed and undisturbed plots were less distinct. During warm periods, such as those when the 1980 soil temperatures were taken, the disturbed soils warm up more than undisturbed soils because they are not insulated as well. This greater temperature difference during warmer times may be more responsible for the increased decomposition rates in the disturbed sites than the slight temperature difference during cooler periods.

The greater decomposition rates in disturbed areas presumably create a higher availability of nutrients in a system in which production is limited by nutrients, especially nitrogen and phosphorus (Haag 1974, McKendrick et al. 1978, Ulrich and Gersper 1978, Chapin and Van Cleve 1978, Shaver and Chapin 1980). Other studies in the Alaskan arctic have shown that enhancing the nutrient regime also changes species composition by differentially favoring the growth of high-turnover species, which include willows and grasses. (McKendrick and Mitchell 1978, McKendrick et al. 1978, 1980, Shaver and Chapin 1980, Chapin and Shaver 1981, Shaver et al. 1983). Thus, the enhanced nutrient regime at Oumalik seems to provide a partial explanation for the presence and production vigor of the willows on the disturbance.

Analysis of Growth Measurements

For *S. glauca, S. lanata,* and *S. planifolia* (the three measured species that occur in both disturbed and undisturbed plots) twig volumes are significantly different in disturbed plots and undisturbed plots, and are greater in disturbed plots (Table 5.7, Figure 5.8). The volumes are highly correlated with weights of the twigs and weights of the twigs plus leaves (Table 5.8), and

Table 5.7. Twig volumes of *Salix* spp. on disturbed and undisturbed sites.

species		undisturbed		disturbed			
		n	$\overline{X}$ (mm^3) ± S.E.	n	$\overline{X}$ (mm^3) ± S.E.	sig.	test
S. alaxensis	1980		-	195	1360 ± 116		-
	1981		-	163	640 ± 63		-
S. glauca	1980	75	70 ± 7.8	220	213 ± 21.8	***	Kruskal-
	1981	66	36 ± 5.2	200	126 ± 15.3	***	Wallis
S. lanata	1980	25	149 ± 22.3	225	460 ± 34	***	Kruskal-
	1981	21	32 ± 4.2	188	143 ± 12.0	***	Wallis
S. planifolia	1980	100	58 ± 6.8	275	184 ± 16.6	***	Kruskal-
	1981	86	23.9 ± 2.77	232	52 ± 5.0	***	Wallis

*** $p < 0.001$

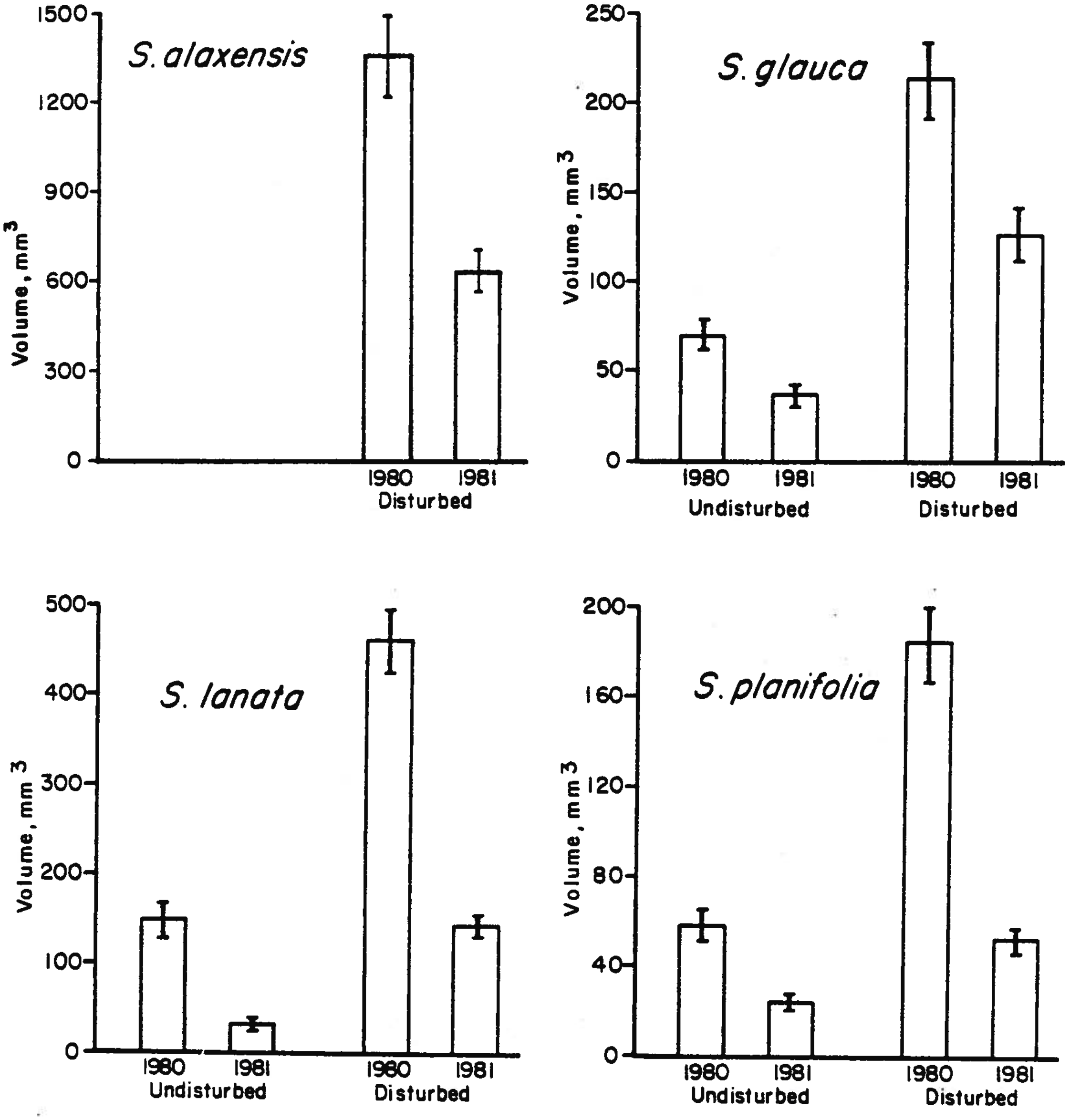


Figure 5.8. Twig volumes of *Salix* spp. on disturbed and undisturbed sites. See Table 5.7 for tests of significance.

Table 5.8. Pearson correlation coefficients of twig weights with twig volume and number of catkins with catkin weight. Sample size for the first two columns is 25, and for the third column is in parentheses. D = disturbed, U = undisturbed.

species		volume with total weight[1]	volume with twig weight	catkin number with catkin weight
S. alaxensis	D	0.85	0.97	[1.00] (2)
S. glauca	U	0.75	0.87	0.79 (8)
	D	0.91	0.95	0.49 (17)
S. lanata	U	0.87	0.96	-
	D	0.92	0.96	-
S. planifolia	U	0.77	0.90	0.17 (7)
	D	0.92	0.95	0.55 (5)

[1] Total weight is the sum of the weight of the twig itself and the weight of the leaves.

thus are good, nondestructive, surrogate measures for actual primary productivity measurements. In all cases, 1980 volumes are markedly greater than 1981 volumes. Heights of willows on disturbed sites are also significantly different from and greater than those on undisturbed sites (Table 5.9, Figure 5.9). For the two species for which nested ANOVA's could be done, there were also significant differences among plots within a disturbance type. Differences in ring width between disturbed and undisturbed sites are not as sharp (Table 5.10, Figure 5.10). *S. glauca* shows significant differences, *S. planifolia* has results that are strongly suggestive of significance, and *S. lanata* (with only one sample from undisturbed areas) does not show significant differences.

The results from these three growth measurements support the subjective observations that the willows on disturbed sites generally grow taller, with greater annual increments in the stems, and with greater twig production than willows on undisturbed sites.

The results also show that there is a great deal of variation of growth responses of willows growing in similar sites. The heights show significant variations among plots within disturbance type. And results of a three-level nested ANOVA on the volume measurements of *S. glauca* and *S. planifolia* (which are not presented to formally test hypotheses because of heteroscedasticity

Table 5.9. Heights of *Salix* spp. on disturbed and undisturbed sites. Significance levels are given for disturbance type and, where possible, plot within disturbance type.

species		undisturbed		disturbed		significance tests		
		n	$\overline{X}$ (cm) ± S.E.	n	$\overline{X}$ (cm) ± S.E.	dist.	plot w/in dist	test
S. alaxensis	1980		-	39	143 ± 9.7			
	1981		-	39	148 ± 10.6			
S. glauca	1980	15	36 ± 3.2	45	75 ± 3.6	**	***	2-level nested ANOVA
	1981	15	35 ± 3.4	44	74 ± 3.3	**	***	
S. lanata	1980	5	45.8 ± 2.44	45	77 ± 3.9	**	-	Kruskal-Wallis
	1981	5	46.6 ± 2.42	45	78 ± 4.0	**	-	
S. planifolia	1980	20	37.7 ± 2.61	55	60 ± 3.1	*	***	2-level nested ANOVA
	1981	20	38.4 ± 2.63	55	56.4 ± 2.73	*	***	

* $0.01 < p \leq 0.05$
** $0.001 < p \leq 0.01$
*** $p < 0.001$

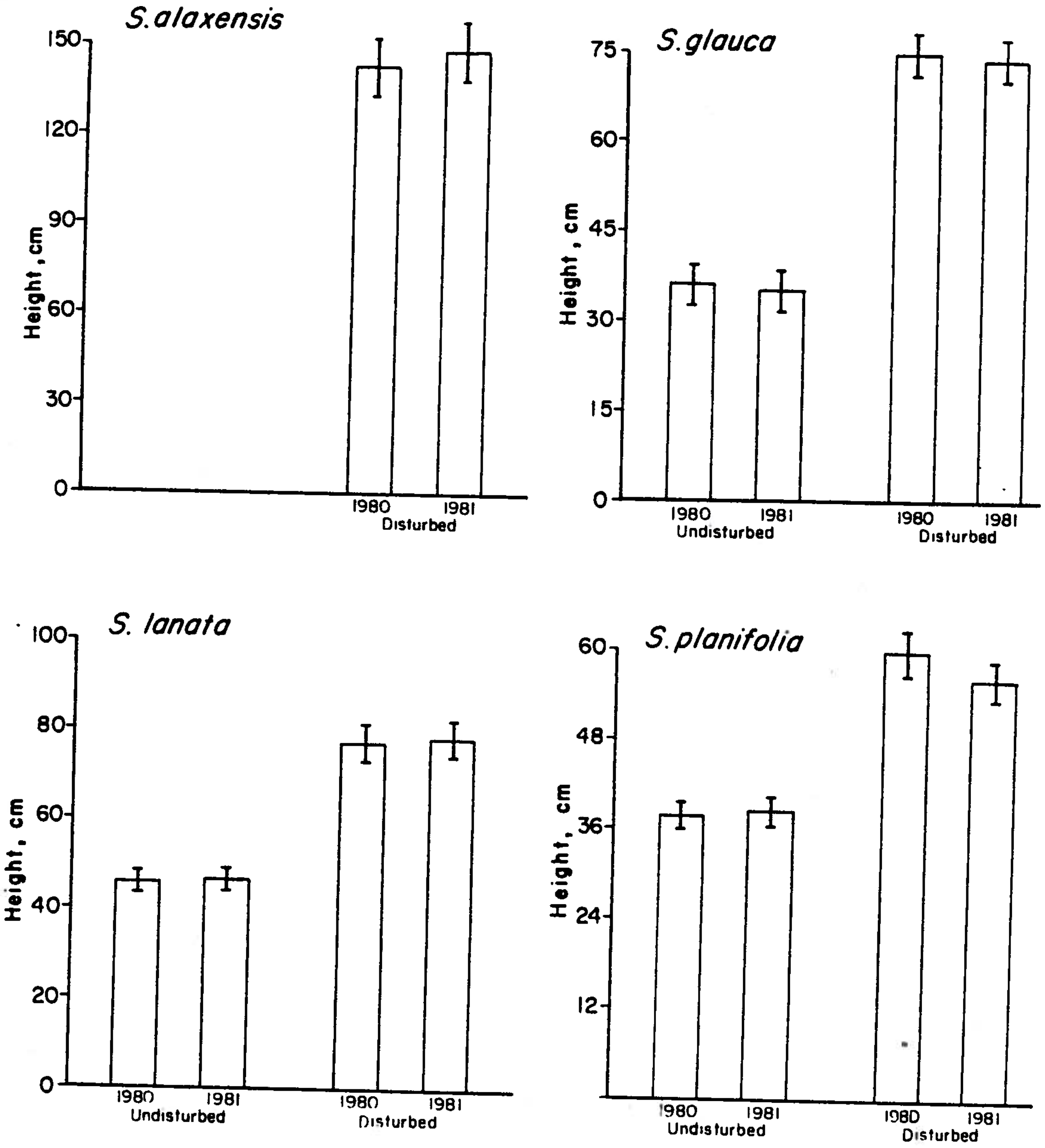


Figure 5.9. Heights of *Salix* spp. on disturbed and undisturbed sites. See Table 5.9 for tests of significance.

Table 5.10. Ring widths of *Salix* spp. on disturbed and undisturbed sites. Measurements are the average of 10 years (see Table 5.2).

	undisturbed		disturbed		significance of difference	
species	n	$\overline{X}$ (cm) ± S.E.	n	$\overline{X}$ (cm) ± S.E.	sig.	test
S. alaxensis		-	8	660 ± 74		-
S. glauca	3	130 ± 39	9	380 ± 47	**	oneway ANOVA
S. lanata	1	214	7	380 ± 66	ns	t-test[1]
S. planifolia	2	112 ± .5	9	250 ± 41	[0.16][2]	one way ANOVA

** $0.001 < p \leq 0.01$; ns nonsignificant

[1] t-test that compares a single observation to a sample mean (Sokal and Rohlf 1981:231).

[2] The variances are significantly different (Bartlett's Box-F test), and a Kruskal-Wallis test is not able to show that disturbed and undisturbed plots are different. However, Scheffé (1959) shows that with the given sample sizes and ratio of variances, when an alpha of 0.05 is specified, the actual alpha is about 10^{-5}. The probability of 0.16 therefore strongly suggests a significant difference.

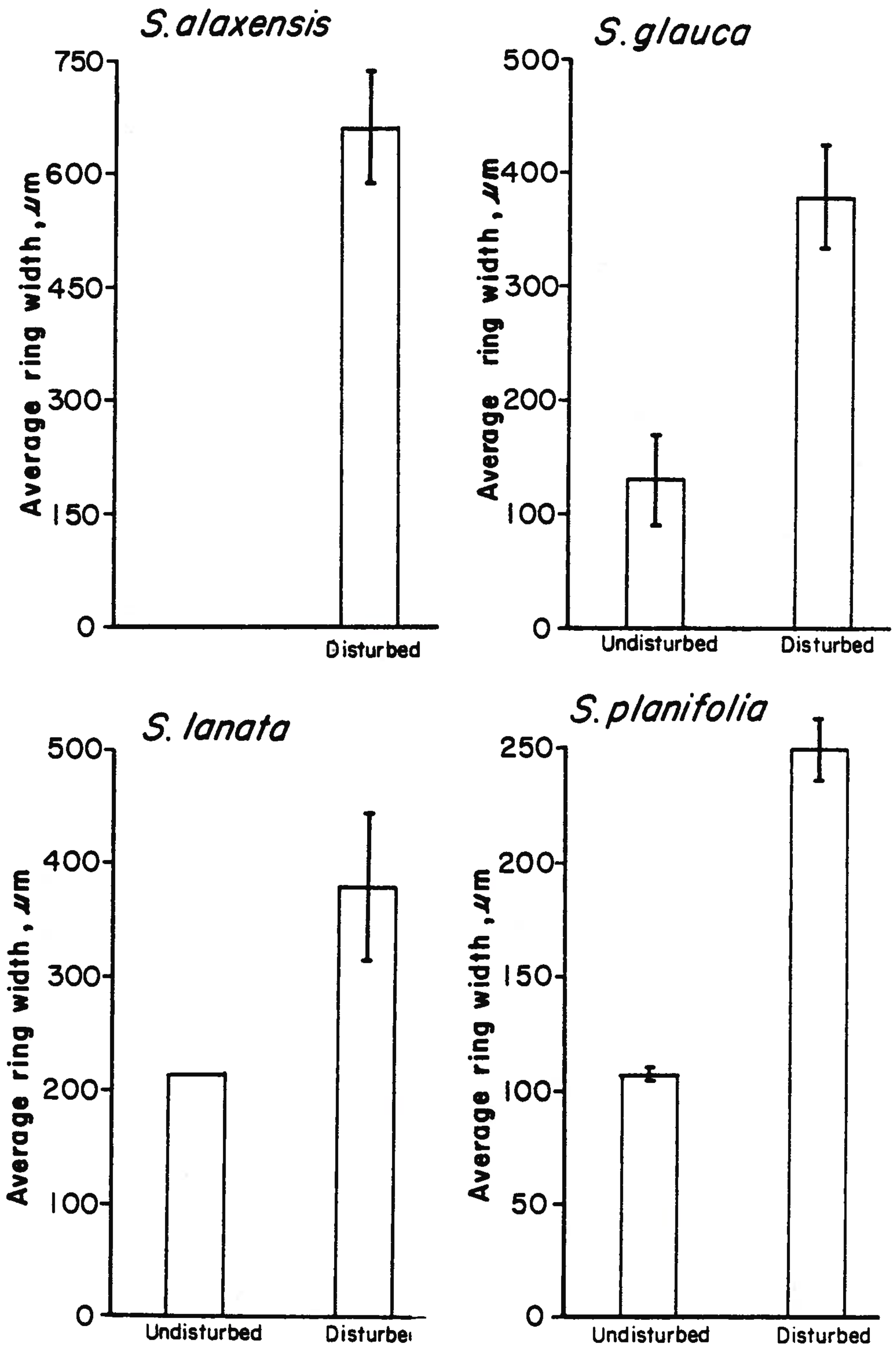


Figure 5.10. Average ring widths of *Salix* spp. on disturbed and undisturbed sites. See Table 5.10 for tests of significance.

at the disturbance type level) also show significant differences among plots within disturbance types and among shrubs within plots.

For the reproductive measures, the number of catkins is a reasonably good to poor predictor of catkin weight (Table 5.8). The poor correlations are due to a fairly wide variation in catkin-size, especially the presence of very small, poorly developed catkins. Despite this, the higher number of catkins in disturbed sites is significantly different from the numbers in undisturbed sites for two of the three species in 1980 and highly suggestive for the third (Table 5.11, Figure 5.11). In 1981, the counts are not significantly different for any of the species, but the results for *S. lanata* are strongly suggestive. In 1981, *S. planifolia* reverses the pattern of growth and reproductive responses being greater in disturbed sites, although the greater number of catkins in undisturbed sites is not significantly different from the number in disturbed sites. I do not have an explanation for this reversal, but it may relate to the compensatory relationship between shoot growth and reproductive output discussed below.

Twig volume (vegetative growth) and number of catkins (reproductive output) show compensation between years (Figures 5.8, 5.11). Shoot growth is greater in 1980 while catkin production is greater in 1981 (except for *S. glauca* and *S. planifolia* on

Table 5.11. Numbers of catkins per shoot of *Salix* spp. on disturbed and undisturbed sites.

		undisturbed		disturbed		significance tests	
Species		n	$\overline{X}$ (cm) ± S.E.	n	$\overline{X}$ (cm) ± S.E.	sig.	test
S. alaxensis	1980		-	195	0.30 ± 0.055		-
	1981		-	179	0.50 ± 0.093		-
S. glauca	1980	75	0.41 ± 0.087	221	0.99 ± 0.091	*	oneway ANOVA[1]
	1981	71	0.69 ± 0.120	207	0.93 ± 0.093	ns	
S. lanata	1980	25	0.04 ± 0.040	220	0.21 ± 0.036	$p = 0.08$	Kruskal-Wallis
	1981	24	0.17 ± 0.078	218	0.45 ± 0.055	$p = 0.14$	
S. planifolia	1980	100	0.18 ± 0.046	275	0.40 ± 0.045	*	oneway ANOVA[2]
	1981	93	0.32 ± 0.074	248	0.22 ± 0.037	ns	

* $0.01 < p \leq 0.05$
ns nonsignificant

[1] To make the data normal and homoscedastic, the number of catkins per shoot was averaged within shrubs and treated with a ln transform. The oneway ANOVA was done on shrub measurements grouped by disturbance type with plot being ignored.

[2] To make the data normal and homoscedastic, the number of catkins per shoot was averaged within plots and treated with a ln transform. The oneway ANOVA was done on these averages grouped by disturbance type.

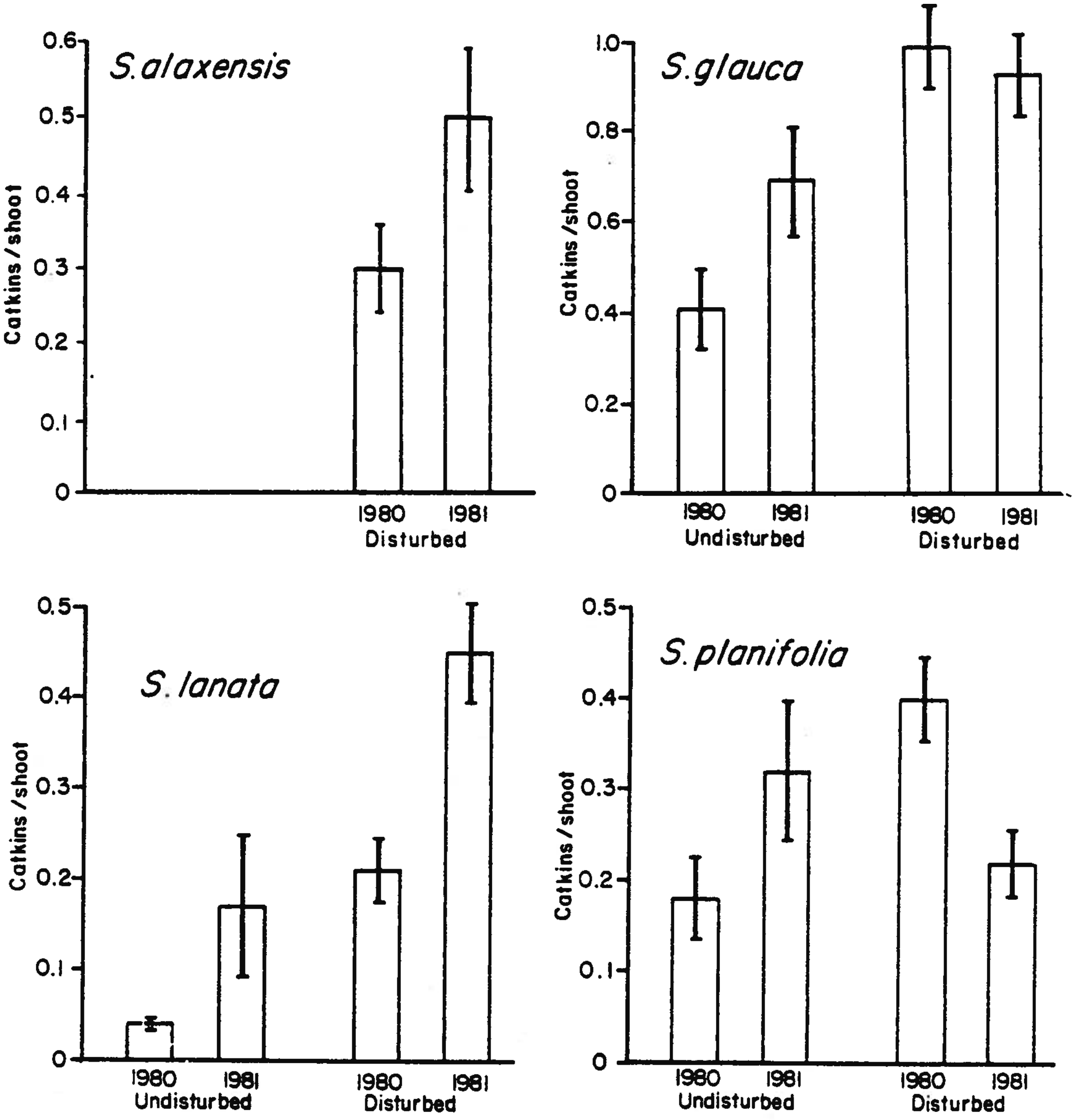


Figure 5.11. Numbers of catkins per shoot of *Salix* spp. on disturbed and undisturbed sites. See Table 5.11 for tests of significance.

disturbed sites). The resources (energy, nutrients) available to these plants are apparently allocated differently in various years. Perennial, polycarpic plants often show a negative relationship between vegetative growth and reproductive output (Harper 1977). The compensation in the willows could be due to intrinsic controls, such as those operating in mast years of high seed production in forest trees (Harper 1977), or the willows could be responding to climate differences among years.

I attempted to relate the differences in shoot growth and reproductive effort to summer air temperature at Oumalik 1979-1981 in a qualitative way. Summer 1979 was an exceptionally warm summer and June 1980 was also unusually warm. The remainder of the summer of 1980 and summer 1981 seem to be more average for Oumalik although without long-term records, it is difficult to know. Bliss (1966) found that annual production of several alpine species on Mt. Washington correlated with summer heat sums and that three-day shoot elongation correlated with heat sums during those periods. In addition, Bliss shows that June growth uses reserves from previous years. It seems reasonable to assume that the willows at Oumalik show similar patterns and that the large 1980 shoot elongation is a response to the warm temperatures in summer 1979 and June 1980. The opposite pattern in reproductive output could be explained if reproductive output is suppressed during and after years of favorable growing conditions when vegetative growth is favored, and rises during climatically less favorable years.

Explanation of Willow Growth Variation with Environmental Measurements

Table 5.12 gives the results of the multiple regressions. Seventeen of the 24 response variables had regressions significant at the $p \leq 0.10$ level. The species differed in the number of response variables that had significant regressions, in the site factors that were entered into the equations, and in the magnitude of the r^2 values for the equations. *S. lanata* growth responses were the best explained, with soil temperature by far accounting for the most variation in the growth responses. *S. alaxensis* and *S. planifolia* had an intermediate amount of variation explained. Soil temperature was the sole site factor entered into the significant equations for *S. planifolia*. For *S. alaxensis* soil temperature was the most important factor in two equations, while phosphorus and potassium were the most important factors in the two other significant equations. *S. glauca* responses were the least explained by the regressions; only three responses had significant regressions, and the r^2 values for these were quite low.

The differences among species are difficult to interpret. Some of the differences are probably due to random variation in growth responses and site factors and differences among plots where the different species occur. Other differences may be real, and

Table 5.12. Multiple regression results of willow growth responses related to site factors. Coefficients of the independent variables are positive unless followed by a negative sign. The first r^2 value is for the equation with only the first independent variable entered, and the second r^2 value is for the equation with both variables in it. Only the first two independent variables entered are reported.

	S. alaxensis		*S. glauca*		*S. lanata*		*S. planifolia*	
	variables	adjusted r^2	variables	adjusted r^2	variables	adjusted r^2	variables	adusted r^2
twig volume, 1980	soil temperature	0.60	-		soil temperature	0.81	soil temperature	0.47
	soil moisture	0.72			P (-)	0.90		
1981	-		-		soil temperature	0.77	soil temperature	0.18
					decomposition	0.84		
no. of catkins, 1980	-		decomposition	0.30	soil temperature	0.31	soil temperature	0.34
1981	P	0.35	-		soil temperature	0.37	-	
height	soil temperature	0.62	soil temperature	0.35	soil temperature	0.96	soil temperature	0.54
ave. ring width	K(-)	0.31	soil moisture (-)	0.27	total N (-)	0.49	-	
					soil temperature	0.88		

some may be due to differences in the appropriateness of the model for the different species (discussed below).

In looking at the regression results (Table 5.12) by growth response rather than by species, additional patterns can be seen. Height, 1980 twig volume, and to a lesser extent, 1981 twig volume, have similar results. Soil temperature is the site factor that is most important in explaining the variation in the responses for the species that have significant regressions. Soil temperature is also the most significant factor for 1980 catkins for *S. lanata* and *S. planifolia* and for 1981 catkins for *S. lanata* . Phosphorus and decomposition are each the most important factor one time for the catkin responses, perhaps indicating that nutrient flux and phosphorus concentration may also be important controlling factors in willow reproductive output. The results from the ring width regressions are the least consistent across species and the most different from all other responses. Soil moisture (negative relationship) is the most important site factor in explaining the variation in *S. glauca* ring width, and potassium (negative relationship) is the most important for *S. alaxensis*. Nitrogen (negative relationship) is the most important for *S. lanata*, with soil temperature second and a strong contributor to the r^2 value. The negative relationship of these nutrient concentrations to ring width is the opposite of what one might expect. However, the lack of differences in nutrient concentrations between disturbed and undisturbed willow plots despite greater decomposition rates in disturbed plots (Table 5.5) seems to indicate that nutrients are taken up as soon as they are released and that concentration of nutrients in the soil may be a poor measure of the nutrient status of a plot. The negative relationship with soil moisture is expected since the sites where the willows grow most vigorously are somewhat drier than the places where *S. glauca* grows in undisturbed areas.

Soil temperature is by far the most important factor in explaining the variation in growth responses of the willows. Low soil temperature is one of the several factors that has been cited in limiting production in arctic tundra (Dennis and Johnson 1970, McCown 1978). Kummerow and Ellis (1984) also found that in a controlled environment *Carex bigelowii* and *Eriophorum vaginatum* produced greater total biomass at higher soil temperatures with constant air temperature. The limiting effects of low soil temperature seem to be indirect rather than direct effects since arctic plants are fairly well adapted to absorption of nutrients and root growth at low soil temperatures (Chapin 1983). The most significant indirect effect of low soil temperature is its effect on nutrient cycling. Permafrost is associated with the low soil temperatures and creates poor drainage and often anaerobic soils. The low oxygen concentrations and the cold soil temperatures result in low decompostion rates (Heal and French 1974), and create a situation in which decomposition is the major bottleneck in nutrient supply to plants (Dowding et al. 1981, Chapin et al. 1980). At Oumalik, the sites where the willows grow most vigorously have relatively high soil temperatures and are well-oxygenated as judged by soil color. They were expected to and did have higher rates of decomposition than other sites (see Decomposition results). Chapin and Bloom (1976) found that microbial activity was also increased in an experimentally heated soil at Barrow and resulted in increased plant size on the area.

Chapin and Shaver (1981) looked at vehicle trail disturbances and rejected their hypothesis that the temperature effects on root growth, nutrient absorption, and organic matter mineralization account for the increased biomass in the disturbed areas. They concluded that factors, perhaps related to soil water and nutrient movement accounted for the increase in production. At Oumalik, the sites where the willows grow most vigorously are mounds of bulldozed material, and therefore movements of soil water and nutrients are not important factors. It seems quite possible that the willow species of this study respond differently to the changes caused by disturbance, particularly soil temperature, than the *Carex* spp. and *Eriophorum* spp. studied by Chapin and Shaver (1981). The dominant grass on mesic disturbed areas at Oumalik, *Arctagrostis latifolia,* seems to respond to disturbance similar to the willows. Apparently, these plants have a higher capacity to respond to the favorable conditions caused by disturbance than most other species.

At Umiat, Bliss (1956) found that the growth responses of *A. latifolia* through the season reflected air temperature remarkably closely, while other species' responses were dampened or quite unresponsive to air temperature changes. Walker (1981) showed that *S. lanata* height, biomass, and average ring width increase with increasing temperature away from the coast south from Prudhoe Bay. McKendrick et al. (1978) found that *A. latifolia* was more responsive to fertilization at Barrow than *Dupontia fisheri*, and several studies have found that *A. latifolia* responds strongly to fertilization (McKendrick and Mitchell 1978, McKendrick et al. 1980). Shaver and Chapin (1980) have suggested that it is the rapid-growing, high-turnover species that are favored by the factors changed by disturbance.

Thus, there is evidence to support the hypothesis that the growth of some of the willows and *A. latifolia* are more responsive to changes in the environment than most other species. They are opportunistic and respond in a positive way to the changes created by disturbance. Soil temperature might be able to explain a larger amount of the variation in growth responses for these species on disturbed and undisturbed areas than for the species studied by Chapin and Shaver (1981).

The lack of the importance of decomposition rates in explaining the willow growth responses was somewhat surprising. The general absence of nutrient concentrations as explanatory factors is understandable since concentrations did not differ between disturbed and undisturbed sites (Table 5.5), and the concentration of nutrients in the soil may be a poor indication of the rate at which nutrients are available. However, I expected the increased decomposition rates to be important in explaining variation in the growth responses since nutrients limit productivity in arctic tundra (Haag 1974, McKendrick et al. 1978, Ulrich and Gersper 1978, Shaver and Chapin 1980). The absence is puzzling and it is difficult to conceive that the nutrient flux is not an important factor in accounting for the variation in willow growth responses.

CHAPTER VI

SHORT-TERM RECOVERY

Introduction

The debris left at the Oumalik site from the 1949-1950 drilling was cleaned up in summer 1980 (Schindler 1983, Schindler and Smith 1983, Tetra Tech 1983). Boards, crates, pieces of canvas, and other combustibles were removed from the places where they had lain for 30 years and were burned. Fifty-five gallon fuel drums were removed, crushed, and buried with other noncombustibles. The U.S. Geological Survey, who sponsored the cleanup, was interested in studying the response of the vegetation to the cleanup. In 1979 I began a study in which I removed debris from the tundra surface and followed the colonization of the new bare surfaces. Komárková (1985) did a similar study at Fish Creek. The goal was to describe the patterns of colonization of these sites in terms of the species that colonized, the means of colonization (vegetative or from seed), and the rate that a vegetation cover returned to the sites. Damage caused by the cleanup work was also observed immediately after the cleanup ended and in following visits.

The results of this study are useful for evaluating the effects of the cleanup at Oumalik and for extrapolating to other sites that have been or will be cleaned up. They are useful for understanding how various taxa and communities at Oumalik respond to disturbance in general. The results are also helpful in reconstructing the colonization of the bare areas in the first several years after the 1949-1950 disturbance. This reconstruction must be done with care, however, since the bare areas of the present study are smaller than those of the 1949-1950 disturbance and, in some cases, were already surrounded by vigorously growing, propagule-producing taxa that are responsive to disturbance.

Methods

Eighty-four short-term recovery plots were established 18-29 July 1979 by removing boards, crates, pieces of canvas, 55-gallon drums, and other debris from the places where they had lain since the well was abandoned in 1950. The debris was present in otherwise undisturbed vegetation and in vegetation on the devastated sites. The pieces of debris and the bare places they covered were small; removal of drums left bare areas approximately 40 x 90 cm, boards 15-30 x 80-150 cm, crates about 40 x 60 cm, and pieces of canvas up to 1 x 1.5 m. At the time the debris was removed, the vascular species within 1 m of the bare area were listed, and any rhizomes or other living plant parts in the plot were recorded. The plots were marked with a numbered stake, and a photo was taken from a photo stake.

Three large plots were established after the cleanup in late July 1980. These were under large piles of debris that were impractical for me to remove in 1979, and are 3 x 4 m, 12 x 12 m, and 50 x 55 m.

The smaller plots were observed twice the following two summers and once four years after the debris was removed. The observation dates were 26 June 1980, 8-12 August 1980, 24-25 June 1981, 23-25 July 1981, and 11-13 July 1983. The larger plots were followed on the 1981 and 1983 dates.

At each observation time, the species present and the means of colonization (vegetative expansion or by seed) were noted. In the earlier observations (through June 1981) individual colonizing plants were followed by marking their locations on sketch maps of the plots. As the number of plants increased, this became impractical, and in July 1981 and in 1983, cover values for each vascular taxon were estimated. Total vascular cover was also recorded, as was total moss cover in 1983. Lichens did not appear as colonizers. This chapter emphasizes the cover value data from 1983 and discusses the total vascular covers for July 1981 briefly.

Seedling survival was followed for about one year from the late season 1980 to the late season 1981 observations. Seedlings were marked with toothpicks. In plots with few seedlings, all were marked. If there were many seedlings, random sets of ten were chosen. If the toothpicks were heaved out by frost action and the seedling they had marked could not be determined with certainty, that seedling was omitted from the counts. Attempts to follow seedlings for longer periods failed because too many toothpicks were heaved out and the original positions could not be determined.

For analysis the plots were grouped by the vegetation that surrounded them since this was expected to and did affect colonization patterns more than any other factor. A few plots were discarded because the surrounding vegetation was heterogeneous or because they were not described by any of the classification units. The types were: 1) undisturbed marsh. This was generally the *Carex rotundata-C. saxatilis* community (no. 5), but in a few cases was *C. aquatilis-Eriophorum angustifolium* (no. 3). Colonization patterns were quite similar for these two communities, and they were combined for this analysis. 2) disturbed marshes with deep water; the *Arctophila fulva* community (no. 24). 3) disturbed marshes with shallow water; the *C. aquatilis-E. angustifolium* community (no. 25). 4) *Salix* -sedge community; more or less the *Salix* spp.- *Arctagrostis latifolia-Eriophorum angustifolium* disturbed community. These plots tended to be wetter than average examples of this community, with less *A. latifolia* and more *E. angustifolium* and *Carex* spp. that are characteristic of wet areas. 5) tussock tundra; the undisturbed *Eriophorum vaginatum-Salix planifolia* community (no. 10). 6) *Betula-Ledum* community; the undisturbed *Betula nana-Ledum palustre* community (no. 18). 7) *Dryas* tundra; the undisturbed *Dryas integrifolia-Salix glauca* community (no. 13). 8) *Arctagrostis;* the disturbed *A. latifolia* community (no. 33). and 9) *Salix-A. latifolia;* the disturbed *Salix* spp.- *A. latifolia;* community (no. 32).

The large plots were all surrounded by the *Salix-* sedge community. Due to their topographic position, they have soils that are saturated or almost saturated throughout the growing season. In contrast, the smaller plots in the *Salix* -sedge community are mesic. Two of the three plots were used as burn sites for combustibles removed from the Oumalik site. Most of the ashes and other unburned debris were removed and buried, but some nutrient enrichment probably occurred. Because of the differences in size, moisture regime, and burning, these large plots were analyzed separately from the other debris plots in the *Salix* -sedge community.

The recovery of the burial site was followed in the same way as the debris plots. The site was on a previously undisturbed tussock-covered upland about 2 km west of the well (Figure 1.9). Noncombustibles were stacked there during the 1980 summer cleanup and buried in March 1981. A pit was dug with D-8 Caterpillar bulldozers, the debris pushed into the pit, compacted, and the soil spread back over the site. The following summer Tetra Tech (1983) verified that the minimum overburden was 0.61 m, as required by contract. Fertilizer and seed were spread with hand spreaders before the burial crew left the site. Fertilizer was a 10-20-10 mixture applied at 672-728 kg ha^{-1}. The seed mixture was 30% glaucous bluegrass *(Poa glauca)*, 30% arctared red fescue *(Festuca rubra)*, 20% boreal red fescue *(F. rubra)*, and 20% annual rye *(Lolium multiflorum)* spread at about 56 kg ha^{-1} (Schindler and Smith 1983, Tetra Tech 1983).

Damage caused by cleanup activities, such as trampling around the campsite and place where the barrels were crushed and diesel spills in the crushing area caused by dumping small amounts of fuel remaining in the barrels to be crushed were also observed and photographed immediately after the cleanup ended and in 1981 and 1983.

Results

Marsh Communities

In the three marsh communities, cover from plants colonizing via vegetative means was greater than 99% of the vascular cover, and seedlings had only a very small cover (Table 6.1). Vascular cover ranged from 6 to 20% after 2 yr and 11 to 26% after 4 yr (Table 6.1). In all three communities the primary means of colonization is tillers from graminoids on the edges of the plots (Figure 6.1). *Carex aquatilis* and *Eriophorum angustifolium* provided the most cover in all three communities (Table 6.2). In the disturbed marsh with deep water *Arctophila fulva* was also

Figure 6.1. Recovery in an undisturbed marsh after debris removal. On the left is the plot immediately after removal of a 55-gal. drum in 1979, and on the right is the plot 4 yr later. Much of the apparent decrease in size of the bare area is due simply to sedges bending over the plot. Cover of plants rooted in the plot is 12%, mostly from *Carex aquatilis* and *Eriophorum angustifolium*. Plot D-64 in community 5. Photos 47-29 on 24 July 1979 and 157-14 on 11 July 1983.

Table 6.2. Vascular taxa present by community in debris plots four years after debris removal. The number of plots in each community is in parenthesis after the community name. For each species the frequency and average percent cover in all plots are given; "-" means one individual and <1% cover, "+" means <1% cover but several individuals.

from seed	freq.	average cover	from rhizomes	freq.	average cover
		undisturbed marsh (6)			
Carex aquatilis	1	-	*Carex aquatilis*	6	6.5
			Eriophorum angustifolium	5	3.2
			C. rotundata	2	3.0
			C. chordorrhiza	2	2.5
			Comarum palustre	1	1.0
		disturbed marsh, deep water (5)			
Epilobium palustre	1	-	*Eriophorum angustifolium*	5	7.6
			Carex aquatilis	4	3.2
			Arctophila fulva	4	2.0
			Arctagrostis latifolia	1	-
			Hippuris vulgaris	1	-
		disturbed marsh, shallow water (7)			
*Saxifraga cernua**	2	+	*E. angustifolium*	7	17.4
Fpilobium palustre	1	+	*Carex aquatilis*	7	8.7
			Arctophila fulva	1	0.6
			Equisetum arvense	2	0.3

Table 6.2. Continued.

from seed	freq.	average cover	from rhizomes	freq.	average cover
		disturbed marsh, shallow water (continued)			
			Arctagrostis latifolia	2	+
			Ranunculus gmelini	1	+
		Salix -sedge(6)			
Carex aquatilis	3	+	*Eriophorum angustifolium*	4	7.2
Poa cf. *arctica*	3	+	*Carex aquatilis*	4	2.0
Salix cf. *lanata*	2	+	*Equisetum arvense*	3	2.3
Salix sp.	2	+	*Stellaria* sp.	3	+
Epilobium palustre	2	+	*Juncus castaneus*	1	3.3
S. planifolia	2	+	*Carex holostoma*	1	0.5
Eriophorum angustifolium	2	+	*Cardamine digitata*	1	+
Pedicularis langsdorffii	1	+	*Equisetum variegatum*	1	+
*Saxifraga cernua**	1	+	*E. scirpoides*	1	+
Senecio congestus	1	+	*Carex rotundata*	1	+
Pedicularis capitata	1	+	*Eriophorum russeolum*	1	+
Betula nana	1	+			
		tussock tundra (10)			
Salix planifolia	5	0.2	*Vaccinium vitis-idaea*	8	3.2
Eriophorum vaginatum	5	+	*Eriophorum vaginatum*	3	0.6
Cardamine digitata	4	+	*Carex bigelowii*	3	0.6
S. glauca	1	+	*Rubus chamaemorus*	3	0.3
Poa sp.	1	+	*Arctagrostis latifolia*	3	0.1
Dryas integrifolia	1	+	*Cardamine digitata*	3	+

Table 6.2. Continued.

from seed	freq.	average cover	from rhizomes	freq.	average cover
			tussock tundra (continued)		
Carex aquatilis	1	+	*Petasites frigidus*	2	2.0
*Saxifraga cernua**	1	+	*Eriophorum angustifolium*	2	1.0
Salix lanata	1	+	*Pyrola grandiflora*	2	0.4
Eriophorum cf. *triste*	1	+	*Stellaria* sp.	2	0.1
			Ledum palustre	2	0.1
			Saxifraga nelsoniana	2	+
			Carex aquatilis	1	0.3
			Salix reticulata	1	0.2
			S. planifolia	1	0.1
			Pedicularis capitata	1	+
			Anemone cf. *parviflora*	1	+
			Arctous rubra	1	+
			Betula-Ledum (4)		
Eriophorum vaginatum	1	+	*Vaccinium vitis-idaea*	3	5.8
Senecio congestus	1	+	*Ledum palustre*	1	3.0
Salix planifolia	1	+	*Rubus chamaemorus*	1	1.2
unknown dicot	1	-	*Carex aquatilis*	1	1.0
			Eriophorum angustifolium	1	0.2
			E. vaginatum	1	+

Table 6.2. Continued.

from seed	freq.	average cover	from rhizomes	freq.	average cover
		Dryas tundra (5)			
Lupinus arcticus	4	+	*Equisetum arvense*	5	4.8
Salix glauca	4	+	*Pyrola grandiflora*	3	0.4
Carex bigelowii	1	0.2	*Eriophorum triste*	2	0.8
Poa cf. *arctica*	1	+	*Arctagrostis latifolia*	2	0.6
Dryas integrifolia	1	+	*Saussurea angustifolia*	2	+
Epilobium palustre	1	+	*Cardamine digitata*	2	+
			Stellaria sp.	2	+
			Lupinus arcticus	1	4.0
			Equisetum scirpoides	1	0.2
			Astragalus umbellatus	1	+
			Luzula confusa	1	+
			Arctous rubra	1	+
		Arctagrostis (17)			
Epilobium palustre	8	0.4	*Arctagrostis latifolia*	13	6.4
Poa cf. *arctica*	7	0.2	*Equisetum arvense*	11	9.9
*Saxifraga cernua**	5	1.5	*Carex aquatilis*	7	1.2
Draba sp.	4	+	*Cardamine digitata*	6	+
Senecio congestus	2	+	*Eriophorum angustifolium*	4	1.2
Arctagrostis latifolia	1	0.3	*Stellaria* sp.	4	0.3
Festuca sp.	1	+	*Saussurea angustifolia*	2	+
Gastrolychnis apetala	1	-	*Epilobium angustifolium*	1	0.1

Table 6.2. Continued.

from seed	freq.	average cover	from rhizomes	freq.	average cover
			Arctagrostis (continued)		
			Salix reticulata	1	0.1
			Astragalus umbellatus	1	0.1
			Pedicularis capitata	1	+
			Saxifraga nelsoniana	1	+
			Poa cf. *arctica*	1	+
			Bistorta plumosa	1	+
			Eriophorum triste	1	+
			Salix-Arctagrostis (14)		
Poa cf. *arctica*	7	+	*Equisetum arvense*	11	7.4
Salix sp.	6	+	*Arctagrostis latifolia*	9	1.0
*Saxifraga cernua**	3	0.3	*Carex aquatilis*	8	2.0
Salix glauca	3	0.3	*Stellaria* sp.	5	+
Chrysoplenium tetrandrum	3	+	*Eriophorum angustifolium*	3	0.3
Juncus castaneus	2	+	*Cardamine digitata*	3	+
Draba cf *glabella*	2	+	*Poa* cf. *arctica*	2	0.1
Epilobium palustre	2	+	*Salix reticulata*	1	0.4
Salix lanata	2	+	*S. planifolia*	1	0.2
Salis alaxensis	1	+	*Dryas integrifolia*	1	0.1
Carex capillaris	1	+	*Astragalus umbellatus*	1	0.1
Arctagrostis latifolia	1	+	*Carex* sp.	1	0.1
Lupinus arcticus	1	+	*Petasites frigidus*	1	0.1

Table 6.2. Continued.

from seed	freq.	average cover	from rhizomes	freq.	average cover
		Salix–Arctagrostis (continued)			
Salix planifolia	1	+	*Salix glauca*	1	+
S. reticulata	1	+	*Vaccinium vitis-idaea*	1	+
Betula nana	1	+	*Pyrola grandiflora*	1	+
Senecio congestus	1	-	*Betula nana*	1	+
			Equisetum variegatum	1	+
			E. scirpoides	1	+

*from bulbils

important, and in the undisturbed marsh *C. rotundata* and *C. chordorrhiza* were important in some plots. Seedlings (Table 6.2) occurred only on the edges of some plots where there was no standing water; none germinated in standing water.

Moss cover was absent to low in these three communities. The vascular cover in the plots in the disturbed marsh with shallow water is substantially greater than those in the undisturbed marsh, which is similar abiotically and floristically. This suggests that the same species on the disturbed areas are growing and tillering more vigorously than those in undisturbed areas.

Salix- Sedge Community

In the *Salix* -sedge community (Figure 6.2), vegetative colonization provides more cover than seedlings, but seedlings provide about 5% of the vascular cover (Table 6.1). *E. angustifolium*, *C. aquatilis*, and *Equisetum arvense* are the most frequent vegetative colonizers and provide the most cover (Table 6.2). The two sedges colonize via tillers from nearby plants, and *E. arvense* from rhizomes, some of which were present beneath the debris when it was removed. *Juncus castaneus*, an infrequent plant on disturbed and undisturbed areas at Oumalik, was adjacent to one plot and covered 20% of it after 4 yr (Table 6.2). Seedlings from numerous species occurred in these plots. Species of *Salix* occurred in almost every plot, and *C. aquatilis* and *Poa* cf. *arctica* were also frequent. Mosses had 10% cover after 4

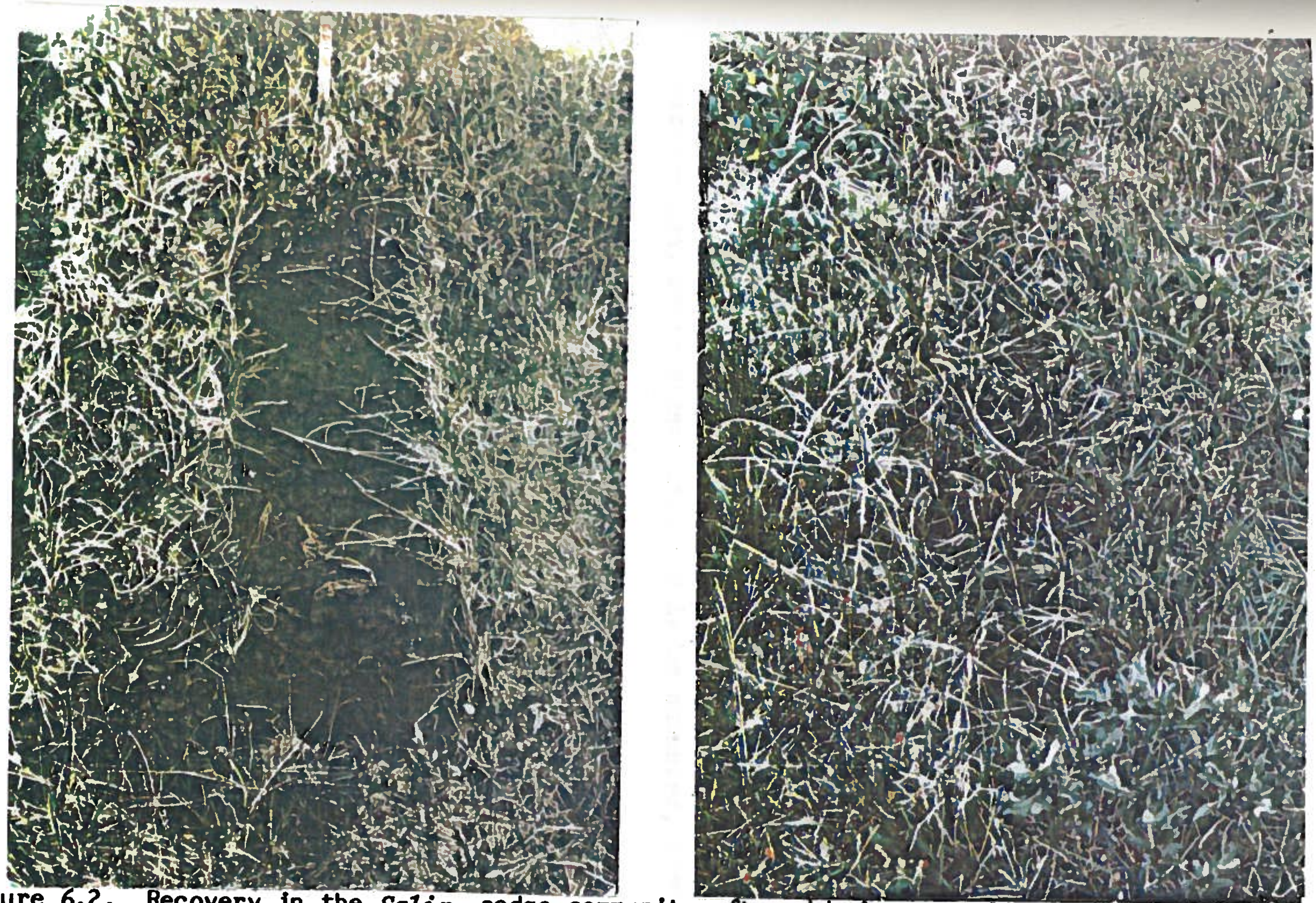


Figure 6.2. Recovery in the *Salix* -sedge community after debris removal. On the left is the plot immediately after removal of a board in 1979, and on the right is the plot four years later. Vascular cover in 1983 was 40%, the highest value for plots in this community, and is mainly from *Eriophorum angustifolium*. Plot D-1 in community 31. Photos 42-31 on 18 July 1979 and 158-26 on 12 July 1983.

yr, and vascular cover was about 13% after 2 yr and about 20% after 4 yr (Table 6.1).

Eriophorum Tussock Tundra

The tussock tundra plots had a large number of species present (Table 6.2), but vascular cover was the lowest of any of the vegetation types and moss cover was also low (Table 6.1, Figure 6.3). Vegetative colonizers composed about 95% of the vascular cover and seedlings 5% (Table 6.1). *V. vitis-idaea* is the most frequent colonizer and has the highest cover (Table 6.2). The other vegetative colonizers have fairly low frequencies and covers. Some of the vegetative colonizers, e.g. *Vaccinium vitis-idaea, Salix planifolia,* and *Ledum palustre,* grew from roots that remained viable under the debris. Species such as *Rubus chamaemorus* and *Pyrola grandiflora* came from rhizomes from plants growing outside the plot. *Eriophorum vaginatum* sprouted from sides of tussocks that were pushed aside by sides of drums and were killed on that side.

Frequent seedlings were *Salix planifolia, E. vaginatum,* and *Cardamine digitata.* More than one or two *S. planifolia* seedlings were present only in plots with a flowering *S. planifolia* individual immediately adjacent or hanging over the plot. In some of these cases *S. planifolia* seedlings were numerous and had appreciable cover. The presence of *E. vaginatum* seedlings is significant because it shows that *E. vaginatum* produces viable

Figure 6.3. Recovery in tussock tundra after debris removal. Immediately after removal of a drum in 1979, the plot was bare (left). Four years later (right) vascular cover was 12%, mainly from *Vaccinium vitis-idaea*, and moss cover was 3%. Plot D-59 in community 10. Photos 47-19 on 23 July 1979 and 157-7 on 11 July 1983.

seeds at Oumalik even though it is not a colonizer of devastated areas of the 1949-1950 disturbance (Chapter III) and is not in the seedbank (Chapter IV).

The *E. vaginatum* seedlings appear to originate from seeds dispersed to the area after the debris was removed rather than from the seedbank, based on the position of the seeds relative to the surface. This contrasts with other tussock tundra disturbances at sites further south (Chapin and Chapin 1980, Chester and Shaver 1982, Gartner et al. 1983), where the seedbank was the source of the *E. vaginatum* seedlings. *Carex bigelowii* seedlings were not present even though its seeds are abundant in the seedbank (Chapter IV). Apparently, its seeds in the seedbank did not survive 30 yr of being covered with debris, or else could not germinate in the xero-mesic surfaces of the plots.

Betula-Ledum Community

The colonization patterns in the *Betula-Ledum* community were similar to tussock tundra. Covers were similar (Table 6.1), and all species that colonized in the *Betula-Ledum* community, except *Senecio congestus*, also colonized plots in tussock tundra. *Vaccinium vitis-idaea* was the most frequent vegetative colonizer and had the most cover, as in tussock tundra, and was the only species that occurred in more than one plot (Table 6.2).

The fewer species colonizing in the *Betula-Ledum* community, even considering the smaller number of plots, reflects the smaller number of species in the surrounding community. Moss cover was also low, only 4% (Table 6.1).

Dryas Tundra

In the *Dryas* community seedlings contributed only about 1% of the vascular cover (Table 6.1). *Lupinus arcticus* and *Salix glauca* seedlings were in four of the five plots. Of the vegetative colonizers, *Equisetum arvense* occurred in every plot with an average cover of almost 5% (Table 6.2). Its rhizomes were often abundant under debris when it was removed, and within 3 to 4 wk after removal, these produced stems 15 cm tall. *Pyrola grandiflora* also colonized via rhizomes in more than half the plots. Moss cover varied widely, from 3 to 40%.

Arctagrostis and Salix-Arctagrostis Communities

In the *Arctagrostis* and *Salix-Arctagrostis* communities similar species colonized, (Table 6.2), although cover was higher and proportionally more of the cover was from seedlings in the *Arctagrostis* community (Table 6.1). Vegetatively, *A. latifolia* and *Equisetum arvense* were most frequent and had high covers in the two communities. *A. latifolia* was more abundant in the Arctagrostis community (Figure 6.4). *E. arvense* colonized from rhizomes present when the debris was removed, as it did in *Dryas* tundra, and *A. latifolia* colonized via tillers from plants just outside the plot. The sedges *Carex aquatilis* and *Eriophorum angustifolium*, plants of wet areas, occurred with significant abundance when these debris plots in mesic areas were adjacent to wet areas. *Poa* cf. *arctica* was a common colonizer as a seedling in both communities. *Salix* spp. were common in the *Salix-Arctagrostis* community, but did not occur in the *Arctagrostis* community. *Epilobium palustre* and *Saxifraga cernua* occurred with moderate frequency and abundance in the two communities. Moss cover was substantially higher in the *Arctagrostis* community.

In both communities for the first two seasons after debris was removed, seedlings were abundant in many plots. But in the *Arctagrostis* community a thick accumulation of *A. latifolia* litter (Figure 6.4) killed young seedlings, mainly *A. latifolia.* And in the *Salix-Arctagrostis* community, heavy accumulation of *Salix* spp. leaves killed seedlings, mainly *Salix* spp.

Large Plots

On the large plots cleared of debris in 1980, the thermal regime is greatly changed from the undisturbed control. In one of the plots, the average thaw on 14 July 1983 was 36.7±1.27 cm ($\bar{x}$ ± S.E., n = 10), which was significantly different (t-test, $p < 0.01$) from the 15.4 ± 1.35 cm (n = 10), in the adjacent, undisturbed control area. The increased depth of thaw has caused subsidence of 30-35 cm over ice wedges. In the lower part of the plot these troughs are filled with water. This subsidence may increase until the thermal regime recovers as vegetation cover, litter, and the thickness of the organic horizon increase.

Figure 6.4. Recovery in the *Arctagrostis* community after debris removal. Two short pieces of piling were removed in 1979 (left). Four years later (right) vascular cover, mainly *A. latifolia*, was 18% and moss cover 5%. The cover appears greater because of the angle of the photo and the large amount of litter on the formerly bare surface. Plot D-9 in community 33. Photos 43-24 on 18 July 1979 and 159-17 on 13 July 1983.

Vegetation recovery on these large plots is rapid. In 1983 vascular cover ranged from 10 to 60% and averaged 32%. Almost all of the vascular cover was from seedlings, and rhizomes contributed only a small amount of cover at the plot edges. *Arctagrostis latifolia* seedlings covered the most area (16%), followed by seedlings of *Senecio congestus* (8%) (Table 6.3). Twenty-two other taxa were present as seedlings in these plots (Table 6.3), including a moderate number of *Salix* spp. seedlings greater than one year old. Taxa that colonized vegetatively and that were present in small amounts at the edges of the plot were *Equisetum arvense*, *A. latifolia*, *Eriophorum angustifolium*, and *E. russeolum*. The cover of mosses was also high, averaging 37% and ranging from 15 to 65%. Most of the bryophyte cover was from *Bryum* spp. and *Ceratodon purpureus*. *Marchantia polymorpha* had 8-10% cover in two plots.

In the two plots that were used as burn sites, the rapid recovery (Figure 6.5) may be partly due to the nutrients that were released from the burned debris. Even though the bulk of the ashes were removed from these sites, there was still probably a pulse of nutrients into the system. These added nutrients may be more important for the mosses than vascular plants since the unburned plot had comparable responses by vascular plants, but a markedly less vigorous response by the mosses. Gartner et al. (1983) noted a similar luxuriant moss growth on fertilized compared to unfertilized areas of a bulldozed disturbance. Although the added

Table 6.3. Taxa present as seedlings in large debris plots 3 yr after debris removal. There were three plots in this category.

	frequency	average cover
Arctagrostis latifolia	3	16.0
Senecio congestus	3	8.0
Epilobium palustre	3	2.0
*Saxifraga cernua**	3	0.3
Puccinellia borealis	3	0.3
Draba cf. *glabella*	3	+
Poa cf. *arctica*	2	1.3
Eriophorum angustifolium	2	0.3
Chrysosplenium tetrandrum	2	+
Gastrolychnis apetala	2	+
Ranunculus gmelini	2	+
Carex aquatilis	1	0.3
Salix glauca	1	+
Eriophorum vaginatum	1	+
Stellaria sp.	1	+
Pedicularis langsdorffii	1	+
Carex scirpoidea	1	+
Eriophorum russeolum	1	+
Salix planifolia	1	+
S. alaxensis	1	+
Juncus castaneus	1	+
Descurainia sophioides	1	-
Polemonium acutiflorum	1	-
Luzula confusa	1	-

*from bulbils

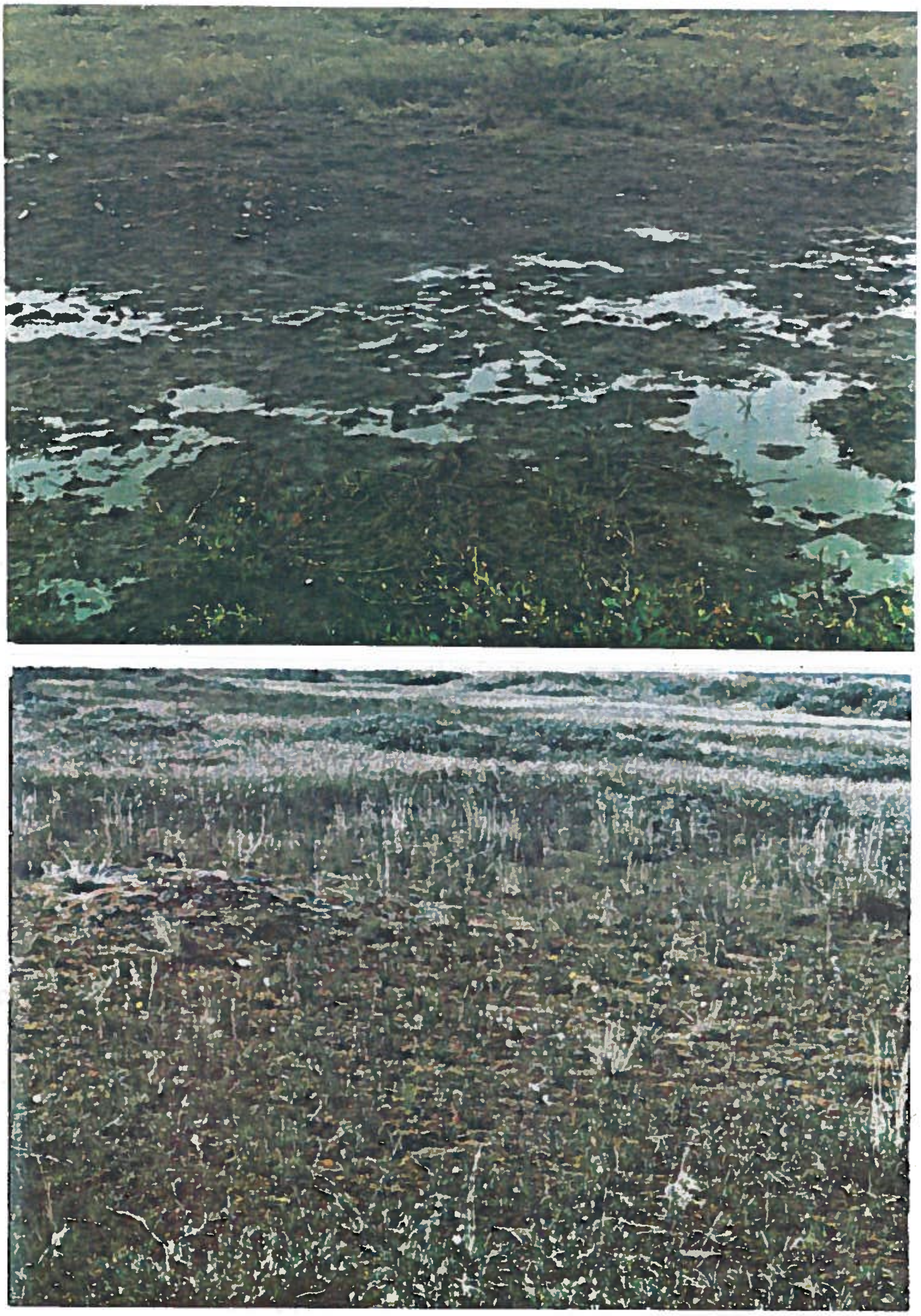


Figure 6.5. Recovery on a site where debris was burned. Immediately after burning (1980) the site was bare (above). Three years later moss cover was 65% and vascular cover 25% (below). Plot D88. Photos 88-11 on 13 August 1980 and 159-37 on 14 July 1983.

nutrients may play a part in the abundance of seedlings, the numerous seedlings on the plot where debris was not burned seem to indicate that this is not the primary factor. The most obvious factor is the moisture regime. The saturated or near saturated soils of these plots seem more favorable for seedling establishment than the mesic or water-covered soils of the small debris plots, and are probably optimal.

1980 Cleanup Camp

At the site of the 1980 cleanup camp (Figure 1.9) lasting damage was minimal. One year after removal of the camp the area covered by tents was browner because of more standing and prostrate dead. There was also more bare soil from scuffing and trampling, especially on revegetated frost boils, where the vegetation is thinnest. Three years after abandonment the area was quite inconspicuous in general appearance. There were some shallow depressions, apparently over ice wedges, but these were not prominent. Compositionally, *Arctagrostis latifolia* had increased somewhat, but otherwise the community was not perceptibly changed by the presence of the camp for about 1 1/2 summer months.

Burial Site

The burial site had a total vegetation cover of 60% in July 1983, in its third season (Figure 6.6). Vascular plant cover averaged 50% and moss cover 15%, although the distribution of

Figure 6.6. Burial site three years after burial (in March 1981). Total cover was 60% (above). Some subsidence had occurred along the east side (below) and in other places. See Figure 1.20 for an aerial view. Photos 160-27 and 160-29 on 14 July 1983.

plants was patchy (personal observation, Tetra Tech [1983]) (Figure 1.20), presumably due to uneven spreading of the seed.

About two-thirds of the vascular cover was apparently from the sown *Lolium multiflorum* and one-third from *Poa glauca* and *Festuca rubra.* These identifications are tentative since the plants were all vegetative and difficult to identify. Other plants that were not seeded were present in small quantities, including *Eriophorum vaginatum* sprouting from tussocks on the surface. The main mosses were *Bryum* spp. and *Ceratodon purpureus.*

In its third season the burial site was still fairly stable. Sheet erosion and gullying were not problems. However, some subsidence had occurred, mainly along the edges (Figure 6.6). At the northwest corner and in places along the east side the surface was about 1 m lower than the original surface. A few small areas in the middle of the area were also starting to subside.

Other Areas Damaged by Cleanup

Other than the burial site, the greatest damage caused by the cleanup was where the drums were crushed (Figure 6.7). The area was formerly covered with the *Dryas integrifolia-Salix glauca* community (no. 13) (Figure 2.13) and the microrelief was reticulate-patterned ground (Everett 1980a) with cells 1 to 1.5 m across. The site was used intensively by cleanup crews during the 1 1/2 mo they worked at Oumalik. Severe trampling in the approximately 25 x 30 m area completely eliminated the vegetation

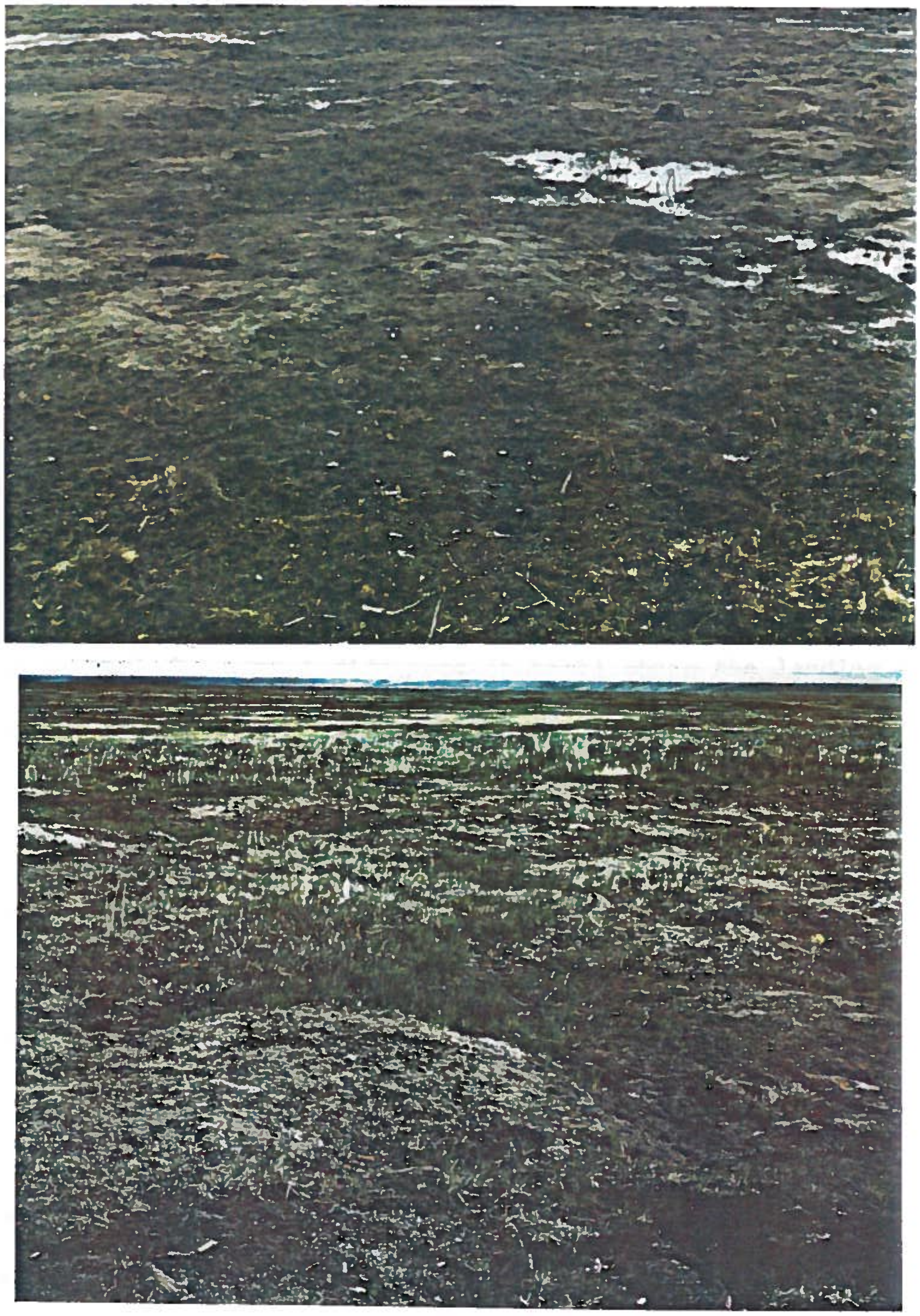


Figure 6.7. Crushing site immediately after disturbance and three years later. Photos are from the same point and looking the same direction, after the cleanup crew left (above) and three years later (below). See text for more complete description. Photos 87-15 on 12 August 1980 and 161-2 on 14 July 1983.

and organic horizon from the centers of hummocks and severely damaged it in the shallow troughs between hummocks (Figure 6.7, top). In some of the wetter areas the approximately top 10 cm were thoroughly churned by trampling. These areas had standing water after the cleanup crews left in 1980.

During the cleanup landing mats (interlocking sheets of metal) found on the site were laid down in some places to provide a firm surface as the area became increasingly muddy and difficult to work in. Loss of vegetation cover under these mats was less than where there were no mats. Depth of thaw on 12 August 1980 after the crews left was not different (t-test) where the landing mats were used and where they were not. Depth of thaw in the centers of cells in the intensively disturbed areas (69.7 ± 1.55 cm, $n = 10$) was significantly different (t-test, $p < 0.001$) than thaw in a control area adjacent to the disturbance (59.1 ± 1.39 cm, $n = 10$).

In addition to the mechanical damage to this area, small amounts of hydrocarbons, mostly diesel fuel, were dumped onto the ground. This occurred when water, which sometimes included hydrocarbons, was dumped from drums before they were crushed. These spills complicate the description of the recovery since their exact extent is impossible to determine in the heavily trampled area. These spills will also slow the recovery of vegetation since the effects of diesel fuel on vegetation are severe and long-lasting (Everett 1978, Walker et al. 1978).

There were also small (20-40 cm x 40-60 cm) diesel spills in otherwise undisturbed vegetation just outside of the trampled area. These had very little living cover in 1980, except for small amounts of *Carex bigelowii* and to a lesser extent other species, which were rooted mainly outside the spill and extended into the spill area from rhizomes. The remainder of the vegetation was brown and appeared dead.

One year after the crushing site was used, the heavily damaged areas still had little vegetation. *Carex bigelowii* and *Arctagrostis latifolia* were somewhat more resistant to trampling than other species, and some individuals had resprouted from rhizomes. The diesel spills in the otherwise undisturbed vegetation had brown and desiccated surfaces although the soil was moist below 0.5 cm. The smell of diesel fuel was strong, and the vegetation was not noticeably different from 1980.

In 1983, three years after the disturbance occurred, subsidence was minimal despite the increased depth of thaw on the disturbed area. On the disturbed area thaw averaged 61.0 ± 3.21 cm in the centers of the cells (on 14 July 1983, $n = 10$ in all cases), which was significantly different (t-test, $p < 0.01$) than thaw in the same microsite in the adjacent undisturbed control area (37.0 ± 3.39 cm). In the troughs, the disturbed area thawed to an average of 39.6 ± 4.39 cm, significantly different from the control area, 14.8 ± 1.16 cm (t-test, $p < 0.001$).

Vegetation recovery varied with the microsite (Figure 6.7). On the tops of hummocks that had the vegetation essentially removed, the only cover after 3 yr was small amounts of *Equisetum arvense* and secondarily *Carex bigelowii*, which grew from rhizomes that survived the disturbance. On hummocks where some vegetation and organic matter remained after disturbance, *Arctagrostis latifolia* increased, and there were small amounts of *Eriophorum angustifolium* s.l., *Carex* spp., and *Senecio congestus*. *S. congestus* is a weedy species in the natural vegetation; the other plants are part of the original community. Cover is higher in the wetter troughs (Figure 6.7). The most common species there are *C. bigelowii* and *E. angustifolium* s.l.

The small diesel spills in otherwise undisturbed vegetation changed very little in 3 yr. No new plants had appeared by 1983. The plants from rhizomes outside the plots which were present in 1980 were still alive and generally were somewhat larger.

Seedling Survival

Seedling survival for the three taxa most commonly found as seedlings in the debris plots is given in Table 6.4. *Salix* spp. could not be identified to species when they first appeared and are lumped together. *Salix* spp., *Arctagrostis latifolia* and *Carex aquatilis* all had high survival rates over one year, although the sample sizes for *A. latifolia* and *C. aquatilis* are small.

Table 6.4. Seedling survival in debris plots. This is one-year survival from 8-12 August 1980 to 23-25 July 1981. Not all communities had enough seedlings to follow seedling survival.

species / community	*Salix* spp.			*Arctagrostis latifolia*			*Carex aquatilis*		
	number of plots	survival	%	number of plots	survival	%	number of plots	survival	%
disturbed marsh, shallow water	1	0/10	0*						
Salix- sedge	2	11/15	73				1	17/18	94
tussock tundra	3	23/28	82						
Dryas tundra	2	11/15	73						
Arctagrostis	4	27/28	96	1	9/9	100			
Salix-Arctagrostis	10	73/90	81						
total	22	145/176	82	1	9/9	100	1	17/18	94

*Omitted from totals. Plot was mesic in 1980, and seedlings apparently died when plot was flooded in 1981.

Discussion

The bare areas created by the 1980 cleanup are all becoming revegetated. Rates range from rapid to fairly slow. Vegetation cover after 2 and 4 yr does not show a consistent relationship with moisture (Table 6.1). This is different from the pattern found by Komárková (1985) at Fish Creek, where cover was highest in mesic plots and negligible in dry plots and in plots with deep water. Within wet sites and within mesic sites at Oumalik, bare areas surrounded by disturbed vegetation are revegetating faster than those surrounded by undisturbed vegetation. This apparently occurs because plants of the same taxon are growing more vigorously on disturbed areas than on undisturbed areas, and because the taxa on disturbed areas tend to be more opportunistic than taxa of undisturbed areas.

Revegetation by Seedlings

Seedlings are an important means of colonization. They are most abundant on the larger bare areas, apparently due to the favorable moisture regime there. These saturated or almost saturated soils appear more conducive to germination and establishment than mesic areas or very wet sites.

Among the smaller debris plots, seedlings were most common and had the highest cover in the *Arctagrostis* community; there were somewhat fewer in the *Salix-Arctagrostis*, *Salix*- sedge, and tussock tundra communities. Only a small amount were present in the

Betula-Ledum and *Dryas* tundra communities, and they were rare in all three marsh communities. The number of species found as seedlings in the communities generally followed the same pattern.

Many taxa, 35, were seen as seedlings. Based on the position of the seedling and the seed coat, if present, these came from seeds dispersed to the site after the debris was removed rather than from the seedbank. Apparently, the seeds of the seedbank, in at least the top several cm, did not survive the 30 yr beneath debris. In many cases temperatures beneath the debris were probably high, which may have caused death of the seeds or germination when the seedlings could not survive. Seeds buried more deeply were not a factor because there was no churning of the soil associated with this type of disturbance and the depth from which a seed can germinate is limited.

The dominant colonizers of the mesic areas of the 1949-1950 disturbance such as *Salix glauca, S. planifolia, Arctagrostis latifolia,* and *Poa* cf. *arctica* were also common as seedlings in the debris plots. Other frequent taxa on the 1949-1950 mesic disturbances, such as *S. alaxensis,* and *S. lanata* were found occasionally as seedlings in the debris plots. Even though in many cases there were more seed-producing plants of these taxa near the debris plots than near the 1949-1950 disturbance, the presence of these taxa as seedlings demonstrates that they had the potential to colonize the 1949-1950 disturbances by seed. Other taxa that are common on the 1949-1950 disturbance and were found as seedlings in the mesic debris plots are *Saxifraga cernua* (from bulbils) and *Epilobium palustre*. These are common on the 1949-1950 disturbance on areas that are wet but do not have standing water.

The presence of occasional *Eriophorum vaginatum* seedlings in the debris plots is significant because it shows that *E. vaginatum* produces viable seeds at Oumalik. However, *E. vaginatum* is not in the seedbank at Oumalik (Chapter IV) as it is tussock tundra further to the south in Alaska (McGraw 1980, Gartner et al. 1983). Apparently, there is some factor preventing the seeds from persisting in the seedbank at Oumalik.

The lack of *E. vaginatum* seedlings on the 1949-1950 disturbance is apparently due to its absence in the seedbank (Chapter IV) and the lack of sites that are sufficiently wet without having standing water. Chapin and Chapin (1980), Chester and Shaver (1982) and Gartner et al. (1983) concluded that most of the *E. vaginatum* seedlings on disturbances in tussock tundra came from the seedbank rather than seeds dispersed to the site after disturbance. However, the presence in some debris plots of *E. vaginatum* seedlings that are apparently not from the seedbank shows that *E. vaginatum* does germinate in at least low densities from currently dispersed seeds. *E. vaginatum* is common in the debris plots only on moisture-saturated soils. The mesic areas of the 1949-1950 disturbance were probably not wet enough for germination in anything but low densities, and the few individuals that did germinate were probably out-competed by the vigorously-growing grasses and willows.

The presence in the debris plots of a moderate number of seedlings of *Carex aquatilis* and *Eriophorum angustifolium*, the dominant colonizers of wet areas on the 1949-1950 disturbance, shows that they may have colonized these older disturbances by seed. However, seedlings of these species were not found in standing water in the debris plots, and their origin in areas of standing water on the older disturbance is unclear. It seems necessary that the seedlings of *Arctophila fulva*, another taxon present in standing water on the disturbance, can establish underwater since vegetative colonization is not possible because the nearest other plants of this species are about 1 km away. Perhaps under some conditions *C. aquatilis* and *E. angustifolium* can establish as seedlings in standing water, or perhaps they colonized standing water on the 1949-1950 disturbance vegetatively.

Seedling survival in the debris plots of *Salix* spp., *Arctagrostis latifolia*, and *Carex aquatilis* was high. On disturbances in tussock tundra Gartner et al. (1983) also found high survival rates for seedlings of *Eriophorum vaginatum*, *Carex bigelowii*, and several grasses taken collectively; and Chester and Shaver (1982) found high survival of *E. vaginatum* and C. *bigelowii*. The low level of competition on bare areas seems to allow a high survival rate since in undisturbed tussock tundra, McGraw and Shaver (1982) found markedly lower seedling survival rates for *E. vaginatum* as well as low rates for *Empetrum nigrum* and for *Ledum palustre* in the first three years.

In the *Arctagrostis* and *Salix-Arctagrostis* communities, the elimination of seedlings by litter accumulation seems to indicate that these communities are following Connell and Slatyer's (1977) inhibition model of succession. In the classic model of succession (Connell and Slayter's [1977] facilitation model) only early successional species are able to establish themselves initially, and these species modify the environment to be less favorable for themselves and more favorable for later successional species. In the *Arctagrostis* and *Salix-Arctagrostis* communities it seems as if the plants which have established themselves initially have modified the environment so that it is less suitable for recruitment of individuals of any species. This follows Connell and Slayter's (1977) inhibition model. Only when early colonizers are damaged or killed due to physical extremes, disease, or herbivores can other individuals invade. It appears that the *Arctagrostis* and *Salix-Arctagrostis* communities may persist for a long time on the mesic areas of the disturbance.

Vegetative Revegetation

Many taxa in the Oumalik vegetation are well-adapted for vegetative invasion of open areas. Most of the taxa that were around the debris plots invaded these bare areas vegetatively (40 taxa were observed doing this). The taxa colonizing vegetatively that were most common and provided the most cover were *Equisetum arvense* in the *Dryas*, *Arctagrostis*, and *Salix-Arctagrostis* communities, *A. latifolia* in the *Arctagrostis* community, and *Carex aquatilis* and *Eriophorum angustifolium* in the marsh communities. Taxa colonized via long underground rhizomes (e.g. *Pyrola grandiflora, Petasites frigidus, Rubus chamaemorus)*, from roots (e.g. *Salix glauca, Ledum palustre, Vaccinium vitis-idaea)* or by tillering (e.g. *Arctagrostis latifolia, Carex aquatilis)*. *Equisetum arvense* originated from rhizomes under the debris when it was removed.

Moss Colonization

Moss cover was highest in the large debris plots, and seemed to be increased by the nutrient enrichments caused by the burning of debris on some of these plots. Of the small debris plots, cover after 4 yr was highest in the *Arctagrostis* community (23%). Other mesic communities ranged from 4 to 17% moss cover. Debris plots in marsh communities had low moss covers. Much of the moss cover in all communities was *Bryum* spp. and *Ceratodon purpureus*.

Cleanup Recommendations

The overall effect of the cleanup program was to make the site stand out markedly less from its surroundings. Before cleanup the site was conspicuous from the air, but after removal of the debris and natural revegetation of the large bare areas, the site blends in fairly well with the surrounding terrain. On the ground the thermokarsts and effects of bulldozing will remain visible indefinitely, and the vegetation will be different from undisturbed vegetation for many human generations. However, removing the debris will hasten the recovery of the site toward a state closer to undisturbed vegetation.

The significant additional damage caused by cleanup operations was confined to two small areas, the burial site and the drum crushing site; the camp site is recovering with essentially negligible long-term effect. On the burial site there has not been any sheet erosion or gullying as occurred at a few other NPR-A burial sites (Tetra Tech 1983). However, the burial site, located in a landform with high ground ice content (Lawson 1983), has experienced some minor subsidence. Even though subsidence was not a problem in the NPR-A burial sites in the first two years after burial (Schindler and Smith 1983, Tetra Tech 1983), it is possible that the extremely high ice content at Oumalik in the upland surfaces chosen for the burial site (Lawson 1983), may create problems over the longer term. The burial sites at Oumalik and other cleanup locations should be followed in the future to look at longer term stability of these sites. If these future observations find thermal erosion problems, sites with lower ice content (Lawson 1983) may be better for similar activities in the future. If appropriate, areas that are already disturbed should be chosen for similar activities to avoid disturbing additional areas as at Oumalik. This will also reduce the cost of transporting the debris to the burial site.

The rehabilitation of the burial site has effectively produced a fairly high vegetation cover. However, rather than introducing *Lolium multiflorum* to areas where it does not occur, it seems better to replace it in future seedings with *Arctagrostis latifolia*, a native plant that vigorously and rapidly colonizes disturbed areas and whose seed is available.

Damage caused at small, intensive work sites like the site where the drums were crushed can be minimized by avoiding hydrocarbon spills and protecting the surface. Placing landing mats or other platforms in areas of intensive use will make work easier and minimize vegetation damage and loss.

CHAPTER VII

EXTRAPOLATION OF OUMALIK RESULTS

Introduction

It is important to know the validity and limitations of extrapolating the disturbance and recovery patterns at Oumalik to other areas, since disturbances are occurring in northern Alaska in locations that are different in climate, substrate, and vegetation from Oumalik to greater or lesser extents. This problem was approached by making observations at several other test wells across the NPR-A that were drilled during the Naval exploration (Reed 1958). Because these sites are similar in age to Oumalik and had similar activities, comparing their disturbance and recovery patterns to Oumalik should provide a good indication to what extent the results obtained at Oumalik can be extrapolated to other parts of northern Alaska.

Five of these 1947-1952 test wells in the eastern part of the NPR-A (Figure 1.1) were visited for two to three days to describe the general patterns of recovery for comparison to Oumalik. The sites were chosen on the basis of logistics and to represent both the cooler coastal areas and the Foothills province.

Description of Other Sites

East Oumalik

East Oumalik Test Well No. 1 was drilled in 1950 (Reed 1958) and is located about 18 km ESE of Oumalik (Figure 1.1). It is different from Oumalik in being on an upland surface that was originally covered with tussock tundra. Disturbances to the surface caused more severe thermokarsting than at Oumalik; subsidence up to 5 m has occurred because the area is exceptionally ice-rich (Lawson 1982, 1983). Essentially all the disturbed area has a plant cover. Even though the original vegetation is different from Oumalik, the recovering vegetation is quite similar because the environments created by disturbance are similar. Mounds left by thermokarsting are dominated by vigorously growing willows and grasses (*Salix* spp. -*Arctagrostis latifolia* community [no. 32]), and the *Carex aquatilis-Eriophorum angustifolium* community (no. 25) is in the wet bottoms of thermokarsts.

Wolf Creek

Wolf Creek Test Well No. 3 was drilled in 1952 (Reed 1958) on sloping tussock tundra in the Northern Foothills (Figure 1.1). There was little thermokarsting, apparently because the amount of ground ice is low due to the proximity of bedrock to the surface, and the disturbed area is generally flat and lacks the thermokarst topography that Oumalik has. Most of the disturbed surface is xero-mesic, and the soil is about 5-10% small rocks. The dominant colonizers are the same as those at Oumalik. The same erect *Salix* spp. as at Oumalik *(S. alaxensis, S. glauca, S. lanata,* and *S. planifolia)* grow vigorously and are the most prominent colonizers. Arctagrostis latifolia *and* Equisetum arvense *are the dominant members of the herb layer, which is less dense than that at Oumalik.* Senecio lugens, *Antennaria* cf. *alpina,* and *Saxifraga oppositifolia* spp. *oppositifolia* occur with moderate abundance at Wolf Creek, but do not occur on the disturbance at Oumalik. These taxa may be present because the Wolf Creek substrate is more basic. The few mounds of bulldozed soil are dominated by *Arctagrostis latifolia.* The occasional wet areas have a complete cover of *Carex aquatilis* and *Eriophorum angustifolium.* Bulldozed trails on slopes off the main disturbance have experienced gullying, some of which is still active. The plants listed above have colonized the stabilized portions, and *Equisetum arvense* has colonized the bare mineral soil of parts that are still stabilizing.

Knifeblade Ridge

Near the 1951 Knifeblade Wells (Figure 1.1) is a bulldozed area presumably of the same age. Formerly covered with tussock tundra, the surface of this area is now composed of small, flat pieces of shale (Figure 7.1). Recovery is slower on this Foothills site than at Wolf Creek, and total cover is 20-25%. The same

Figure 7.1. Disturbed area at Knifeblade Ridge. *Salix* spp. are the dominant colonizers of this rocky surface. The herb layer is sparse, and much bare soil is present. Photo 49-8, 26 July 1979.

Figure 7.2 Disturbed area at Simpson. The wet areas have revegetated well except where the water is too deep, but the mesic to dry areas have sparse vegetation. Photo 78-32, 21 July 1980.

erect *Salix* spp. as at Oumalik are the dominant colonizers, and they grow more vigorously than in undisturbed control areas. An occasional *Alnus crispa* ssp. *sinuata* shrub is present, and the sparse herb layer is composed of 21 forbs with ≤1% cover. There are no wet areas at this site.

Simpson

Simpson Test Well No. 1 was drilled in 1947-1948 about 3 km from the Arctic Ocean (Figure 1.1). It experiences the very cool, short summers described by Haugen (1982) for coastal sites. The well and associated disturbances are located in a high-centered polygon complex. Polygon troughs on the disturbance are deeper than those in adjacent undisturbed areas, apparently due to subsidence. These wet areas have revegetated well except for very deep water (Figure 7.2). *Arctophila fulva* grows in moderately deep water, and *Carex aquatilis, Eriophorum scheuchzeri,* and *Dupontia fisheri* ssp. *fisheri* dominate shallow water. Recovery on the dry to mesic centers of the high-centered polygons varies, and cover ranges from 0-60% (Figure 7.2). The poor revegetation seems to be due to the organic mat on the surface, which is dry at the very top and makes a poor site for seedling establishment (Johnson et al. 1978). The higher covers occur where the organic mat is somewhat broken up. The most important colonizers, are *Luzula confusa, Arctagrostis latifolia, Stellaria* spp., and *Poa arctica.* Small amounts of about 10 other taxa were seen on these sites.

Salix spp. are unimportant on the disturbance, probably because the summer climate is too severe.

Fish Creek

Fish Creek Test Well No. 1, drilled in 1949 (Reed 1958), is about 13 km from the Arctic Ocean (Figure 1.1). The lower amount of ground ice than at Oumalik (Lawson 1983) has caused less subsidence (Lawson 1983, Lawson and Brown 1978). The mesic disturbed areas are dominated by *Arctagrostis latifolia* and *Poa arctica*, and the wet areas by *Carex aquatilis* and *Eriophorum angustifolium* (Johnson et al. 1978, Komárková and Webber 1978, Komarkova 1983). *Salix planifolia* is a common colonizer of mesic areas (Komárková and Webber 1978), but it is the only willow that is important and does not grow unusually tall except in the protection of debris before the 1979 cleanup. Areas of hydrocarbon spills have very low plant cover (Johnson et al. 1978).

Discussion

The dominant colonizers across all the disturbed sites that I studied were quite similar. This pattern was very strong in wet sites; colonizers of mesic areas were somewhat more varied. In deep water *Arctophila fulva* colonizes, and in shallower water *Carex aquatilis* and *Eriophorum angustifolium* provide most of the cover. Near the coast *E. scheuchzeri* and *Dupontia fisheri* are also important in at least some sites with shallow water. On mesic sites *Arctagrostis latifolia* and *Poa arctica* are important at all sites. *Salix alaxensis, S. glauca, S. lanata,* and *S. planifolia* are also important colonizers except near the coast, and usually grow taller and more rapidly than in undisturbed control areas. *S. planifolia* seems to be a colonizer at more northern sites than the other willows. On mesic sites near the coast *Luzula confusa,* in addition to the grasses *A. latifolia* and *P. arctica,* is a colonizer with relatively high cover on mesic areas. Colonization of any hydrocarbon spill is very slow.

The pattern of wet areas being more resilient to disturbance than drier sites (see Chapter VIII), i.e. returning more quickly to a state approximating the original, seems to be true at all sites that had both wet and mesic disturbed areas. Approximately 30 years after disturbance, wet sites generally had a complete vegetation cover unless the water was too deep for any plants.

On mesic sites the recovery after 30 years is quite variable. Recovery is optimal in locations represented by Oumalik and East Oumalik, where cover is essentially complete and the colonizers are growing vigorously. As far north as Fish Creek cover on mesic sites is also almost complete although willows are not as dominant. At sites very near the coast, such as Simpson, recovery is slower. In the Foothills the colonizing willows and grasses grow vigorously, but cover, especially of the herb layer, seems to be reduced as the rockiness of the substrate increases.

With care, the observations made at Oumalik on the recovery of vegetation from disturbance can be extrapolated to large areas of the northern Alaska. Disturbed sites on fine-grained sediments in the northern part of the Foothills and on the Coastal Plain except near the coast will show patterns of recovery quite similar to Oumalik. The Oumalik results are less useful in predicting response to disturbances along rivers, on sand dunes, and other places that have markedly different substrates than Oumalik. At sites near the coast colonizers will grow less vigorously although cover may still be high, and some additional colonizing species may be present. (See also Lawson et al. [1978] and Komárková [1983] for description and analysis of the recovery at the more coastal Fish Creek site.)

The Oumalik results are also useful for prediction of the response to disturbance in the more southern parts of the Foothills although on rocky substrates or on dry ridge tops there will be more differences.

The Oumalik results are not applicable to sites in the mountains, and should be used with more caution in the western and eastern parts of the Arctic Coastal Plain and Foothills, since I did not make any comparison to sites there. The similarity of the responses to disturbance will relate most closely to the similarity of the environments created by the disturbance.

CHAPTER VIII

RESISTANCE AND RESILIENCE OF OUMALIK VEGETATION

Compositional Recovery

Two important, distinct properties of ecosystems relative to disturbance are the ability to withstand displacement from a given state and the ability to return to the original state after displacement. In this discussion, the ability to withstand displacement is called resistance, after Webster et al. (1974). Systems with high resistance will tolerate a higher intensity of disturbance before being changed and will change less for a given intensity of disturbance than systems with low resistance. This property has also been called inertia (Orians 1975, Cairns and Dickson 1977, Westman 1978) and resilience (Holling 1973). The ability to return to the original state after disturbance and the rate of the return are referred to as resilience after Webster et al. (1974). Holling (1973) called this property stability. A system that returns to its original state rapidly after disturbance has high resilience, and a system that returns slowly or not at all has low resilience.

Although these terms have been applied previously mainly to ecosystems, I will use them more narrowly to describe the response of vegetation to disturbance, since vegetation is the focus of this dissertation. The resistance and resilience of the entire system are strongly related to the amount of ground ice. This has been discussed extensively (e.g. Brown and Grave 1979, Lawson 1983), and I will emphasize vegetation here and will discuss the geomorphic resistance and resilience and the importance of ground ice briefly.

Research in northern Alaska and Canada, including that at Oumalik, has shown that different Low Arctic vegetation types differ in their resistance and resilience to disturbance. I devised graphic models showing the resistance and resilience of three broad vegetation types defined by moisture regime. The models show the generalized or average resistance and resilience of each type. They were constructed based on the response to physical disturbances, such as vehicle passage, and apply to physical disturbances rather than contamination disturbances such as hydrocarbon spills. These models are an improvement over other similar models (Komárková 1983) because they are three-dimensional, and show resistance and resilience on orthogonal axes, allowing these distinct properties to be shown independently of each other.

Information on the relative resistance thresholds of the vegetation types and the relative intensity of disturbance necessary to totally destroy them came from results of experimental and construction-related vehicle disturbances reported in Hok (1969), Bellamy et al. (1971), Radforth (1972), Hernandez (1973), Walker et al. (1977). Information on rates of recovery following disturbance (resilience) is not as common in the literature, and the resilience portion of the diagrams was made mainly on the basis of my own observations. Supporting observations come from Hernandez (1973), who makes general statements comparing vegetation types, and Komárková (1983), who compares the recovery of wet and mesic sites at Fish Creek 30 yr after disturbance.

At Oumalik, quantitative measures of the extent of recovery after 30 years were made using Sorenson's community coefficient (Muller-Dombois and Ellenberg 1974). Percent similarity using taxa cover values was calculated between vegetation samples from control areas and disturbed sites on which the vegetation was presumably totally destroyed. The control vegetation was in nearby undisturbed areas with the same moisture regime as the disturbed vegetation, and the communities chosen for controls were those that were on the disturbed site before disturbance, as interpreted from predisturbance aerial photographs and landform-vegetation associations. Disturbed wet areas are about 50% similar to the original vegetation, and mesic areas 1-15% similar. There are no dry sites at Oumalik and information for the dry resilience curve came from other sites (Chapter VII). These values were used to draw the initial portion of the resilience curves of Figure 8.1. Beyond 30 years, the rate of recovery and shape of the resilience curve are conjectures based on rates and patterns in the first 30 years and general knowledge of the vegetation.

The models have a number of assumptions. They show the response to a single disturbance, and do not treat the effects of additional disturbances during recovery. No random variation around the deterministic surface is shown, but this is assumed to be present. That is, the state of the system through time oscillates about the smooth curve that is shown. It is also assumed that climate has not changed so much that the vegetation cannot recover to its predisturbance state. It is possible that vegetation is not in equilibrium with the prevailing climate. It may be changing very slowly to another state but lagging behind climate change, or it may be able to persist under the present climate, but not able to reestablish itself. In either case, if the system is disturbed, it may return to a different state (Webber and Ives 1978, Komárková and Webber 1978).

Compositional similarity to the original community was chosen as the criterion on which to judge resistance and resilience. This is a more stringent evaluation than using percent cover, growth form similarity, or productivity comparisons; and was used to describe the response relative to total recovery, in which the system is floristically, physiognomically, and functionally

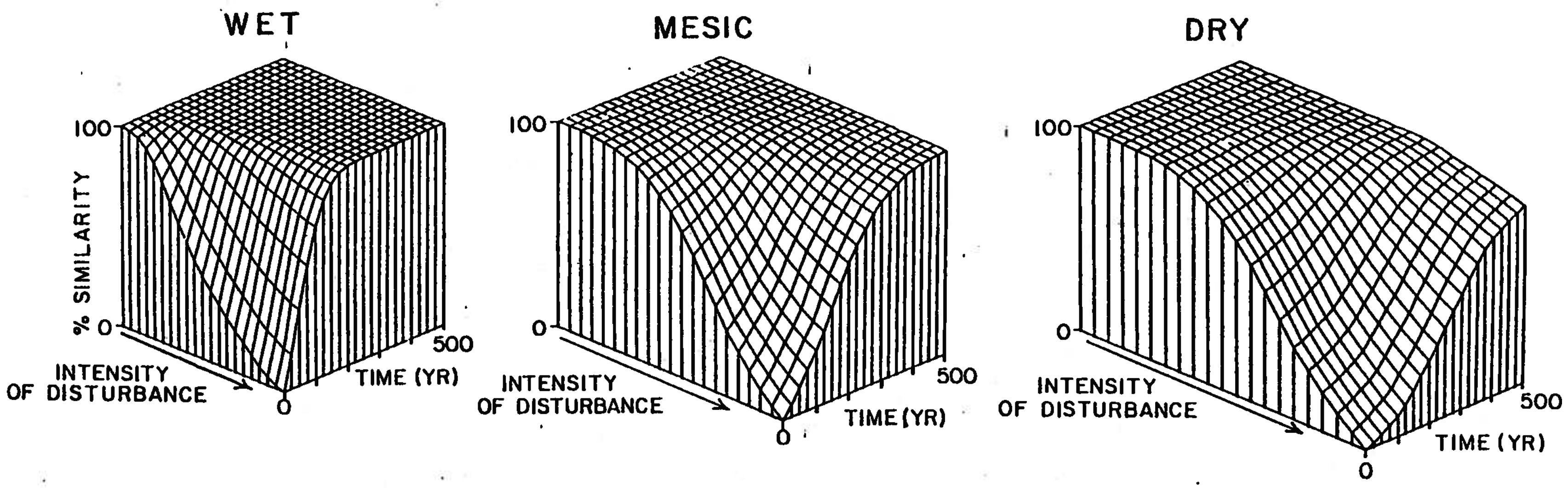


Figure 8.1. Resistance-resilience models for wet, mesic, and dry vegetation. The height of the surface is percent compositional similarity to the original vegetation. See text for more complete explanation.

indistinguishable from the original vegetation. Functional recovery, based on primary productivity, is discussed later in this chapter.

The height of the surfaces (Figure 8.1) is the percent similarity to the original community, and is shown as a function of the intensity of disturbance and time since disturbance. The left face, that is when time = 0, is the resistance of the vegetation to disturbance. The vegetation can tolerate some disturbance without changing, but as intensity increases, the resistance threshold (Komárková 1983) is reached, and, the community begins to change.. With increasing disturbance intensity the community is damaged more (is less similar to the original), until it is totally destroyed (similarity of zero). After the disturbance ends, the vegetation begins to recover. The models assume that the substrate stabilizes relatively quickly; if it does not, then there will be a time lag before recovery begins.

If the site, especially the moisture regime, is permanently and significantly changed by disturbance, (that is, if the geomorphic resilience threshold is exceeded) the vegetation that recovers on the site will be different from the original. This situation is fairly frequent in ice-rich permafrost areas such as Oumalik. As a result of disturbance, sites frequently change from mesic or dry to wet due to subsidence, and the vegetation that recovers on these sites will be characteristic of wet areas. The creation of mesic mounds by bulldozing in wet areas is another example of a geomorphic resilience threshold being exceeded, and the recovered vegetation will be different from the original. In these cases, the system follows the resistance curve for the original vegetation type, and the resilience curve for the moisture regime of the new site. However, if the site characteristics, particularly the moisture regime, are not much changed, I agree with Komárková (1983) that climate has not changed enough to prevent the original communities from reestablishing themselves. If a totally foreign substrate, such as a gravel pad, is created by disturbance, then these models do not apply.

According to the hypothesized models, wet sites have the lowest resistance of the three vegetation types. Only a low intensity of disturbance is needed to alter the vegetation from the original and only a relatively moderate disturbance will completely destroy the community. Dry sites are the most resistant and will tolerate a moderate amount of disturbance before being changed. Mesic sites are intermediate in this respect. Wet sites are the most resilient (recover most quickly), and dry sites are the least resilient. Mesic sites are again intermediate. Thus, in these Low Arctic vegetation types, resistance and resilience are inversely related. Webster et al. (1974) also concluded from a theoretical, nutrient cycling perspective that among biomes resistance and resilience were inversely related.

The time needed for complete recovery to the original communities is unknown, but is estimated in a general way in the models. Vegetation on wet disturbed sites after 30 yr is about 50% similar to the original vegetation at Oumalik. The similarity is due mainly to the quick colonization by *Carex aquatilis* and *Eriophorum angustifolium*, which are also important components of the undisturbed community. Subordinate species of the control community have not colonized the wet disturbed sites in 30 years. The rate of change back to the original community could be slower than suggested by the model's smooth resilience curve, which is based on the rates of the first 30 years. Recovery to the original community following total destruction of a wet community is hypothesized to take 75-200 years based on assumptions that the rate of return will be similar to that shown in Figure 8.1.

Thirty years after disturbance, vegetation on mesic sites at Oumalik has low similarity with vegetation on undisturbed, mesic control sites. Recovery of these sites will take much longer than wet sites, especially if they are following the inhibition model of succession (Connell and Slatyer 1977) (Chapter VI), in which change toward later successional stages can be quite slow. In estimating time needed for mesic upland sites to recover from disturbance, Komárková (1983) noted that complex *Eriophorum vaginatum* communities occupy river meanders near Atkasook, Alaska, that are 600-800 years old (Everett 1979, 1980c, Komárková and Webber 1980). With this one data point, I hypothesize that recovery of disturbed mesic sites at Oumalik where the vegetation was totally destroyed will take roughly 500-800 years. Some of the mesic disturbed areas may never return to the original vegetation. The mounds of bladed material and mounds created by thermokarsting may have environments different enough from the original mesic sites (better drained and warmer soils with higher decomposition rates) that they may always have a different vegetation.

Dry sites are the slowest to recover. There are no dry sites at Oumalik, and the relative rates of recovery shown in the model come from observations at Knifeblade Ridge and Simpson (see Chapter VII). Since after 30 years dry disturbed sites have recovered slower than mesic sites, the time for complete recovery of dry sites where the vegetation was totally destroyed is hypothesized to be several hundred years longer than for the mesic sites.

Functional Recovery

Another perspective on recovery is functional (Webber and Walker, in prep.), which emphasizes the role of vegetation in preventing substrate erosion, as cover and forage for wildlife, and as the energy-fixing component of the ecosystem. Since this criterion is much less stringent than compositional recovery because it ignores species composition, functional recovery is faster than compositional recovery. A functional perspective is probably the only reasonable perspective for some severely disturbed sites, such as gravel pads and runways of some of the abandoned, exploratory 1970's and 1980's NPR-A wells. These sites are so drastically different from the original site or other natural sites and are such severe environments for plant establishment and growth that just establishing vegetation cover can be considered a success.

In this discussion, a site will be considered to be functionally recovered when its primary productivity is equal to or greater than the original. Figure 8.2 shows resilience from a functional perspective for the three major vegetation types. No data are available on primary productivity, so these models are based on subjective estimates and predictions. The resistance responses are considered to be the same as in Figure 8.1 since primary productivity immediately following disturbance will be close to proportional to the the compositional similarity of the disturbed community to the original. In disturbed wet sites at Oumalik, productivity probably exceeded the original in less than 30 yr after disturbance. Production will probably decline with time to the same level as the original site. On mesic sites where grasses and willows grow vigorously because of a nutrient subsidy (sensu Odum et al. 1979), functional recovery is very rapid and production probably exceeds that of the original in the early stages of recovery (curve a in Figure 8.2). Without a nutrient subsidy the return of productivity to its original level is much slower (curve b in Figure 8.2). Functional recovery is slowest in

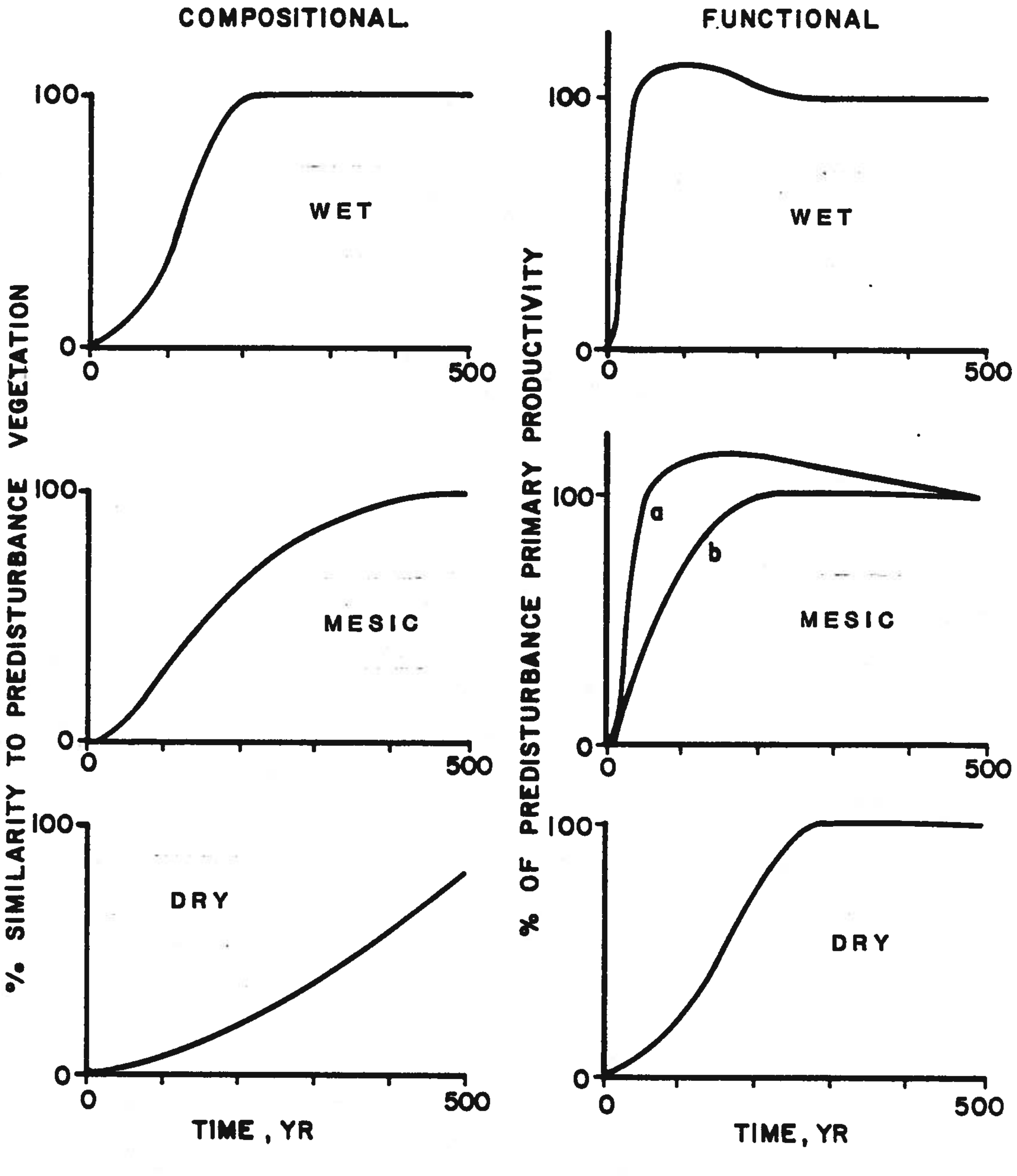


Figure 8.2. Functional resilience of wet, mesic, and dry vegetation. Compositional resilience curves from Figure 8.1 are given for comparison. Curve a is with nutrient subsidy, and curve b is without nutrient subsidy. See text for more complete explanation.

dry sites, and productivity is hypothesized to take several hundred years to return to predisturbance levels.

Minimizing Effects of Human Activities

Several measures would have kept the 30-year effects of drilling the 1949-1950 Oumalik well to an extremely low level. The most obvious would have been to remove the debris that was left on the site after it was abandoned. The most important action to prevent damage to the surface and vegetation would have been restricting activities to the wet areas, such as the area where the well head is located, and avoiding the upland mesic areas. This would have prevented disturbance of surfaces where the amount of ground ice is high (Lawson 1983) and avoided thermokarsting, which is an essentially permanent landform change. Avoiding mesic areas also prevents disturbance of mesic vegetation, which is relatively slow to recover. The wet areas where activity occurred would have been intensively damaged, but would recover much more quickly than mesic areas. Another action to minimize impacts would have been to bulldoze the disturbed wet areas smooth when the well was abandoned. This would avoid the creation of mesic mounds where the vegetation is quite different from the undisturbed area, and left the entire disturbed area with a surface that was saturated or had standing water. If these actions had been taken, the disturbed area would probably now have a complete cover of vegetation, a productivity nearly as high or higher than the original, a physiognomy similar to the predisturbance marshes and a species composition reasonably similar to the original. The palsas and small areas of tussock tundra which, along with the predominant marshes, were part of the predisturbance vegetation complex would be lacking, but the overall effect of the well would be extremely minimal 30 yr later.

The above conclusions and the many observations made at Oumalik and other NPR-A sites lead to the recommendation that if damage to the vegetation and surface is going to be caused by an activity, it is often preferable from the perspective of vegetation recovery to disturb a wet area rather than a mesic or dry area. Even though the initial impact will be greater, the wet area will recover much faster. In general, after a short period of time, disturbance in a wet area will be less noticeable and the vegetation more similar to the original vegetation functionally, structurally, and compositionally than in a mesic or dry area. Within wet areas, it is best to choose areas with less microrelief. Wet areas with greater microrelief are damaged more (Walker et al. 1977), and the disturbance will be more visible through time if the microrelief is altered.

CHAPTER IX

SUMMARY AND CONCLUSIONS

The 1949-1950 Oumalik Test Well offers an excellent opportunity to study recovery of vegetation in the Low Arctic since the disturbances are older than those of most previous studies, occurred at a known time, and are uncomplicated by repeated disturbance. The three-decade perspective provides longer-term information on recovery that was rare before this study and is needed to make sound management decisions as development in northern Alaska continues.

A classification using Braun-Blanquet methods of the natural vegetation around the Oumalik well defined 23 communities. DECORANA ordinations of samples of undisturbed vegetation and samples of undisturbed and naturally disturbed vegetation combined were interpreted to indicate that moisture is the most important controlling factor of the vegetation. Within the mesic vegetation the most important control is a complex gradient of pH, organic matter, nitrogen and thaw depth. In the ordination of undisturbed and naturally disturbed vegetation, disturbance intensity is also included in this complex.

Vehicle passage and bulldozing were the actvities that disturbed the majority of the area affected by the 1949-1950 disturbance. In areas with large amounts of ground ice, deep thermokarsts were caused by the disturbance. After about 30 years the area affected by the 1949-1950 disturbance has an essentially complete and vigorous plant cover. A few taxa provide most of the cover: *Carex aquatilis* and *Eriophorum angustifolium* in wet sites and *Arctagrostis latifolia* s.l., *Poa arctica, Salix alaxensis, S. glauca, S. lanata,* and *S. planifolia* on mesic areas.

Classification of the man-disturbed vegetation defined 13 communities. These communities intergrade strongly because only a few taxa with wide ecological amplitudes have colonized most of the disturbed areas. Some of the disturbed communities are quite similar to communities on natural disturbances. Strong similarity occurs in cases where a single controlling factor strongly dominates. Examples are *Arctophila fulva* communities in deep water, *Carex aquatilis-Eriophorum angustifolium* communities in shallower water, and *Arctagrostis latifolia* communities on mineral soil surfaces with warm soil temperatures.

In the ordination of the disturbed vegetation, pH and moisture are shown as the most important controlling factors. Trends of site factors in this ordination are weak compared to the ordinations of natural vegetation since the taxa on the disturbed sites are broad-ranging and do not indicate environmental characteristics of the sites as precisely as many more narrowly distributed taxa in undisturbed areas.

The size and composition of the seedbank as determined by germination varied widely in the four communities tested. In

Eriophorum vaginatum-Salix planifolia tussock tundra there were 300-610 seeds m^{-2} of nine species with *Carex bigelowii* dominant; the *Dryas integrifolia-Salix glauca* community had 284-462 seeds m^{-2} of ten species with *C. bigelowii* and *Saxifraga hieracifolia* dominant, the *C. chordorrhiza-C. rotundata* community had 338-450 seeds m^{-2} of five species with *C. aquatilis* and *C. chordorrhiza* dominant; and the *Betula nana-Ledum palustre* community had 66-160 seeds m^{-2} of four species with *C. aquatilis* dominant. Comparing the tussock tundra results with other published studies suggests that there is a decrease in the number of species and total number of seeds with latitude in this community. The number of species found in the seedbanks of the four Oumalik communities follows the same pattern as the number of species in the actual communities. The species in the seedbank generally occurs in the present, mature vegetation, except in the seedbank of the *Betula-Ledum* community which has marsh species whose seeds have dispersed short distances.

Storage and germination conditions affected the seedbank results a great deal. Fertilization appeared to increase the number of seeds that germinated (although this was not statistically significant) and the number of species. More species but fewer total seeds germinated from soils stored for several months at 2°C than from those stored at -18°C for about the same time. Some of the seeds of the dominant species of the seedbank apparently lost viability by being stored at 2°C but the stratification also apparently broke dormancy in some species.

The general lack of *Arctagrostis latifolia* and *Salix* spp. in the seedbank suggests that they colonized the 1949-1950 disturbance from seeds dispersed to the areas after disturbance rather than seeds from the seedbank. *Carex aquatilis* on the disturbance may have originated from the seedbank, but *Eriophorum angustifolium* probably did not. The lack of *Eriophorum vaginatum* in the seedbank may be a partial cause of its absence on the 1949-1950 disturbance.

The erect willow species *S. alaxensis, S. glauca, S. lanata,* and *S. planifolia* are abundant and grow unusually vigorously on mesic disturbed areas at Oumalik. They were established within a maximum of 5 to 9 yr after the disturbance ended. In general, on the disturbance they are significantly taller, have greater annual increments and twig production, and produce more catkins than in undisturbed areas. There is compensation between shoot growth and reproductive effort, that is, a year of high shoot growth is a year of lower reproductive output and vice versa. Height is limited by winter snow depths because buds, except those of *S. alaxensis,* generally cannot survive the abrasion of snow and ice and subsequent desiccation by the wind in the above-snow environment. In some cases, *S. alaxensis* survives above the snow because it grows fast enough to put buds above the zone of most intense abrasion just above the snow.

Characteristics of disturbed willow plots that are significantly different from undisturbed plots and may account for some of the greater growth rates are warmer and somewhat drier soils, greater snow depths, and greater decomposition rates. The depth of thaw and concentrations of N, P, and K in the soils are not different between disturbed and undisturbed plots. Multiple regression shows that soil temperature is the site factor that accounts for the greatest amount of variation in the growth responses. The regressions do not show decomposition rates to be important, although it seems highly likely that the increased rate of turnover of nutrients in disturbed sites is an important factor in allowing the greater growth of willows.

Small bare areas similar to those created by the 1980 cleanup of solid debris are becoming revegetated at rates that range from rapid to fairly slow depending primarily on the vegetation that surrounds them. After 4 yr bare areas in various communities have vascular plant covers of 10-29% and moss covers of 0-23%. There is no consistent pattern of cover with moisture, but within wet sites and within mesic sites, bare areas surrounded by disturbed vegetation have greater covers than those surrounded by undisturbed vegetation.

Most of the cover is from plants that colonized vegetatively. Most of the taxa that were around the bare areas did invade vegetatively (40 were observed). Seedlings were also an important means of colonization, and 35 taxa were seen as seedlings. They were rare to abundant in bare areas of the various communities, but even if abundant, provide only a small amount of cover relative to vegetative colonizers, 4 yr after the bare areas were created. They were most abundant on areas with saturated soil, and nutrient enrichment from debris that was burned on some of the plots seemed to promote seedling germination and establishment. Litter on bare areas in the *Arctagrostis* and *Salix-Arctagrostis* communities on the 1949-1950 disturbance generally strongly inhibited seedling establishment. These communities seem to be following Connell and Slayter's (1977) inhibition model of succession, in which later successional species can invade only when early colonizers are damaged or killed. It appears as if these communities may persist for a long time.

The effects of the 1980 cleanup of solid debris were to make the site stand out markedly less from its surroundings and to hasten recovery of the site toward a state closer to undisturbed vegetation. Additional damage caused by the cleanup was fairly minimal.

Observations at five disturbed areas of similar age and disturbance history as Oumalik across the NPR-A from the Foothills to the coast allows general statements on regional recovery patterns to be made. The dominant colonizers of wet areas are similar at all sites: *Arctophila fulva* in deep water and *Carex aquatilis* and *Eriophorum angustifolium* in shallower water. Dominant colonizers of mesic areas are more varied. *Arctagrostis* *latifolia* and *Poa arctica* are important at all sites visited. *Salix alaxensis*, *S. glauca*, *S. lanata*, and *S. planifolia* are also important colonizers except near the coast, and where present usually grow taller and more rapidly than in undisturbed control areas. On dry sites *A. latifolia*, *P. arctica*, and *Luzula confusa* are the most important colonizers.

Recovery in wet sites is rapid at all disturbances visited; about 30 years after disturbance, wet sites generally had a complete vegetation cover unless water was too deep for any plants. On mesic sites recovery after 30 years is quite variable. Recovery is optimal in locations represented by Oumalik and East Oumalik, which represent the Arctic Coastal Plain away from the coast and the northern portion of the Foothills. At sites very near the coast and on rocky sites in the Foothills recovery is slower, and a moderate amount of bare ground is present.

With care, observations at Oumalik on the recovery of vegetation from disturbance can be extrapolated to large areas of northern Alaska. Sites on fine-grained sediments on the Coastal Plain except near the coast and in the northern part of the Foothills will be most similar. Coastal sites, rocky sites, sand dunes, and other sites that have different substrates or are climatically fairly different will have different patterns.

The vegetation of wet sites has less resistance (ability to withstand displacement from a given state) and greater resilience (ability to return to the original state following displacement) than dry vegetation. Mesic vegetation is intermediate, but more like dry vegetation. These patterns hold for compositional recovery (return to the original taxa) and functional recovery (return to the original productivity). Because of these properties, if damage to the vegetation is going to be caused by an activity, it would usually be preferable to disturb a wet area rather than a mesic or dry area. Even though the initial impact will be greater, the wet area will recover much faster and is less likely to be changed so much that it cannot return to the original vegetation.

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APPENDIX A

LIST OF PLANTS COLLECTED AT OUMALIK

The plants listed here were collected within 4 km of Oumalik Test Well No. 1 or at one location along Ishuktak Creek, about 7 km to the northwest of the well. The numbers of taxa in each group are: 172 vascular plants, 19 hepatics (and several more identified only to genus or growth form, 82 mosses (and several more identified only to genus), and 58 lichens. Nomenclature follows Murray and Murray (1978) for vascular plants, Steere and Inoue (1978) for hepatics, Steere (1978) for mosses, and Thomson (1979) for the lichens except for the Cladoniaceae which follow Hale and Culberson (1970). Voucher specimens for vascular plants are at the University of Colorado, Boulder (COLO) and the University of Alaska, Fairbanks (ALA), with additional specimens of the *Salix* at the National Museums of Canada, Ottawa (CAN). Specimens for some of the lichens are at the University of Wisconsin, Madison (WIS) and for some of the bryophytes at Memorial University, St. John's, Newfoundland (NFLD).

The 4 range extensions, all vascular plants, are indicated by asterisks. These were determined by comparison with Hultén (1968, 1973), Argus (1973), Komárková and Webber (unpublished data), and Murray (unpublished data). Finally, since I am a beginner with the cryptogams, some of these identifications should be considered tentative.

VASCULAR PLANTS

Andromeda polifolia L.
Anemone parviflora Michx.
Anemone richardsonii Hook.
Antennaria friesiana (Trautv.) Ekman
  = *A. alpina* (L.) Gaertn. *pro parte*
Arabis lyrata L. ssp. *kamchatica* (Fisch.) Hult.
Arctagrostis latifolia (R. Br.) Griseb. var. *arundinacea* (Trin.) Griseb.
Arctagrostis latifolia (R. Br.) Griseb. var. *latifolia*
Arctophila fulva (Trin.) Anderss.
Arctous alpina (L.) Neid.
  = *Arctostaphylos alpina (L.)* Spreng.
Arctous rubra (Rehd. & Wilson) Nakai
  = *Arctostaphylos rubra* (Rehd. & Wilson) Fern.
Arnica frigida C.A. Mey.
Artemisia tilesii Ledeb. *ssp.* tilesii
Artemisia tilesii *Ledeb.* ssp. *unalaschensis* (Bess.) Hult.
Aster sibiricus L.
Astragalus alpinus L. ssp. *alpinus*
Astragalus alpinus L. ssp. *arcticus* (Bunge) Hult.
Astragalus umbellatus Bunge
Betula nana L. ssp. *exilis* (Sukatsch.) Hult.
Bistorta plumosa (Small) Greene
  = *Polygonum bistorta* L. ssp. *plumosum* (Small) Hult.
Bistorta vivipara (L.) S.F. Gray
  = *Polygonum viviparum* L.
Bromus pumpellianus Scrib. var. *arcticus* (Shear) Pors.
  = *Bromopsis pumpelliana* (Scribn.) Holub ssp. *arctica* (Shear) Löve & Löve
Calamagrostis stricta (Timm.) Koel.
  = *C. neglecta* (Ehrh.) Gaertn.
Caltha palustris L. ssp. *arctica* (R.Br.) Hult.
  = *C. minor* Mill. ssp. *arctica* (R. Br.) Löve and Löve
Cardamine digitata Richards.
  = *C. hyperborea* O.E. Schulz
Cardamine pratensis L. ssp. *angustifolia* (Hook.) O.E. Schulz
Carex aquatilis Wahlenb.
Carex atrofusca Schkuhr
Carex bicolor All.
Carex bigelowii Torr.
Carex capillaris L.
  = *C. capillaris* L. ssp. *fuscidula* (V. Krecz.) Löve and Löve
Carex chordorrhiza Ehrh.
**Carex holostoma* Drej.
  Range extension - The Oumalik collections add a location to a spotty circumpolar distribution; the only other known occurrence on the North Slope is one record at Atkasook (Komárková and Webber, unpublished data).
Carex krausei Boeck.

Carex marina Dew.
Carex membranacea Hook.
Carex misandra R. Br.
  = *C. fuliginosa* Schhuhr ssp. *misandra* (R. Br.) Löve and Löve
Carex rariflora (Wahlenb.) J.E. Sm.
Carex rotundata Wahlenb.
Carex saxatilis L. ssp. *laxa* (Trautv.) Kalela
Carex scirpoidea Michx.
Carex vaginata Tausch
Carex williamsii Britt.
Cassiope tetragona (L.) D. Don ssp. *tetragona*
Castilleja caudata (Pennell) Rebr.
Cerastium beeringianum Cham. and Schlecht. ssp. *beeringianum*
Chrysosplenium tetrandrum (Lund) T. Fries
Comarum palustre L.
  = *Potentilla palustris* (L.) Scop.
Delphinium brachycentrum Ledeb.
Descurainia sophioides (Fisch.) O.E. Schulz
Draba alpina L.
Draba borealis DC.
Draba cinerea Adams
Draba fladnizensis Wulf.
Draba glabella Pursh
Draba lactea Adams
Dryas integrifolia M. Vahl ssp. *integrifolia*
Dupontia fisheri R. Br. ssp. *psilosantha* (Rupr.) Hult.
Eleocharis acicularis (L.) Roem. and Schult.
Empetrum nigrum L. ssp. *hermaphroditum* (Lange) Bocher
Epilobium angustifolium L.
Epilobium palustre L.
Equisetum arvense L.
**Equisetum fluviatile* L. *ampl.* Ehrh.
  Range extension from Umiat.
Equisetum scirpoides Michx.
Equisetum variegatum Schleich.
Erigeron humilis Grah.
Eriophorum angustifolium Honck. ssp. *subarcticum* (Vassil.) Hult.
Eriophorum russeolum E. Fries var. *albidum* Nyl.
Eriophorum scheuchzeri Hoppe var. *scheuchzeri*
Eriophorum scheuchzeri Hoppe var. *tenuifolium* Ohwi
Eriophorum triste (T. Fr.) Hadac and Löve
  = *E. angustifolium* Honck. ssp. *triste* (T. Fr.) Hult.
Eriophorum vaginatum L.
Eutrema edwardsii R. Br.
Festuca altaica Trin.
Festuca baffinensis Polunin
Festuca brachyphylla Schult.
Festuca rubra L.
Gastrolychnis affinis (Vahl) Tolm. and Kozh.
  = *Melandrium affine* J. Vahl
Gastrolychnis angustiflora ssp. *tenella* (Tolm.) Tolm. and Kozh.

= *Melandrium taylorae* (Robins) Tolm.
= *M. taimyrense* Tolm.
Gastrolychnis apetala (L.) Tolm. and Kozh.
= *Melandrium apetalum* (L.) Fenzl.
Gastrolychnis triflora (R. Br.) Tolm. and Kozh.
= *Melandrium triflorum* R. Br.
Gentianella propinqua (Richards.) J.M. Gillet ssp. *arctophila* (Griseb.) Hult.
= *Gentiana propinqua* Richards. ssp. *arctophila* (Griseb.) Hult.
Hedysarum alpinum L. ssp. *americanum* (Michx.) Fedtsch.
Hierochloë alpina (Sw.) Roem. and Schult.
Hierochloë pauciflora R. Br.
Hippuris vulgaris L.
Huperzia selago (L.) C.F.P. Martius ssp. *appressum* (Desv.) D. Löve
= *Lycopodium selago* L. ssp. *appressum* (Desv.) Hult.
Juncus arcticus Willd. ssp. *alaskanus* Hult.
Juncus biglumis L.
Juncus castaneus Sm. ssp. *castaneus*
Juncus triglumis L. ssp. *albescens* (Lange) Hult.
Kobresia myosuroides (Vill.) Fiori and Paol.
Lagotis glauca Gaertn. ssp. *minor* (Willd.) Hult.
Ledum palustre L. ssp. *decumbens* (Ait.) Hult.
Lloydia serotina (L.) Rchb.
Lupinus arcticus S. Wats.
Luzula arctica Blytt
Luzula confusa Lindeb.
Luzula kjellmaniana Miyabe and Kudo
= *L. tundricola* Gorodk.
Menyanthes trifoliata L.
Minuartia arctica (Stev.) Aschers. and Graebn.
Minuartia rossii (R. Br.) Hiern
= *Arenaria rossii* R. Br.
Minuartia rubella (Wahlenb.) Graebn.
= *Arenaria rubella* (Wahlenb.) Sm.
Orthilia secunda (L.) House ssp. *obtusata* (Turcz.) Böcher
Pyrola secunda L. ssp. *obtusata* (Turcz.) Hult.
Papaver macounii Greene
Parnassia kotzebuei Cham. and Schlecht.
Parnassia palustris L. ssp. *neogaea* (Fern.) Hult.
Parrya nudicaulis (L.) Regel ssp. *septentrionalis* Hult.
Pedicularis capitata Adams
Pedicularis labradorica Wirsing
Pedicularis lanata Cham. and Schlecht.
= *P. kanei* Durand ssp. *kanei*
Pedicularis langsdorffii Fisch. ssp. *arctica* (R. Br.) Pennell
Pedicularis lapponica L.
Pedicularis parviflora J.E. Sm. ssp. *pennellii* (Hult.) Hult.
Pedicularis sudetica Willd. ssp. *albolabiata* Hult.
Pentaphylloides floribunda (Pursh) A. Löve
= *Potentilla fruticosa* L.

Petasites frigidus (L.) Franch.
Poa alpigena (Fr.) Lindm. ssp. *vivipara* Hult.
Poa arctica R. Br. ssp. *arctica*
Poa glauca M. Vahl
Poa lanata Scribn. and Merr.
Polemonium acutiflorum Willd.
Primula egaliksensis Wormskj.
Puccinellia borealis Swallen
Pyrola grandiflora Radius
Ranunculus gmelinii DC.
Ranunculus hyperboreus Rottb.
Ranunculus lapponicus L.
Ranunculus pallasii Schlecht.
Ranunculus pedatifidus Sm. ssp. *affinis* (R. Br.) Hult.
Rhododendron lapponicum (L.) Wahlenb.
Rubus chamaemorus L.
Rumex arcticus Trautv.
Salix alaxensis (Anderss.) Cov. ssp. *alaxensis*
**Salix arbusculoides* Anderss.
Range extension from Umiat.
Salix arctica Pall.
**Salix arctophila* Cockerell
Range extension of about 400 km from northeast Alaska.
Salix fuscescens Anderss.
Salix glauca L.
Salix hastata L.
Salix lanata L. ssp. *richardsonii* (Hook.) A. Skvortz
Salix phlebophylla Anderss.
Salix planifolia Pursh. ssp. *pulchra* (Cham.) Argus
Salix reticulata L. ssp. *reticulata*
Salix rotundifolia Trautv. ssp. *rotundifolia*
Saussurea angustifolia (Willd.) DC.
Saxifraga cernua L.
Saxifraga foliolosa R. Br.
Saxifraga hieracifolia Waldst. and Kit.
Saxifraga hirculus L.
Saxifraga nelsoniana D. Don
= *S. punctata* L. ssp. *nelsoniana* (D. Don) Hult.
Saxifraga oppositifolia L. ssp. *oppositifolia*
Senecio atropurpureus (Ledeb.) Fedtsch. ssp. *frigidus* (Richards.) Hult.
Senecio congestus (R. Br.) DC.
Senecio lugens Richards.
Silene acaulis L. ssp. *arctica* Löve and Löve
Sparganium hyperboreum Laest.
Stellaria edwardsii R. Br.
Stellaria laeta Richards.
Stellaria longipes Goldie
Stellaria monantha Hult.
Taraxacum alaskanum Rydb.
Taraxacum ceratophorum (Ledeb.) DC.

Tofieldia pusilla (Michx.) Pers.
Trichophorum caespitosum (L.) Hartm.
Triglochin maritima L.
Trisetum spicatum (L.) Richter
Vaccinium uliginosum L. ssp. *microphyllum* Lange
Vaccinium vitis-idaea L. ssp. *minus* (Lodd.) Hult.
Valeriana capitata Pall.
Wilhelmsia physodes (Fisch.) McNeill

HEPATICS

Anastrophyllum minutum (Schreb.) Schust.
Aneura pinguis (L.) Dum.
Blepharostoma trichophyllum (L.) Dum.
Calypogeia integristipula Steph.
Cephalozia bicuspidata (L.) Dum.
Cephalozia lunulifolia (Dumort.) Dumort.
Cephaloziella byssacea (Roth) Warnst.
Gymnocolea inflata (Huds.) Dum.
Jungermannia pumila With.
Lejeunea alaskana (Schust. and Steere) Inoue and Steere
Lophozia barbata (Schmid.) Dumort.
Lophozia binsteadii (Kaal.) Evans
Lophozia excisa (Dicks.) Dumort.
Lophozia latifolia Schust.
Lophozia ventricosa (Dicks.) Dum.
Lophozia sp.
Marchantia polymorpha L.
Ptilidium ciliare (Web.) Hampe
Scapania gymnostomophila Kaal.
Tritomaria quinquedentata (Huds.) Buch
unknown leafy liverworts
unknown thalloid liverworts

MOSSES

Amblystegium serpens (Hedw.) B.S.G.
Aulacomnium palustre (Hedw.) Schwaegr.
Aulacomnium turgidum (Wahlenb.) Schwaegr
Barbula convoluta Hedw.
Barbula sp.
Brachythecium salebrosum (Web. and Mohr) B.S.G.
Brachythecium sp.
Bryum archangelicum B.S.G.
Bryum argenteum Hedw.
Bryum caespiticium Hedw.
Bryum knowltonii Barnes
Bryum pallescens Schleich. *ex* Schwaegr.
Bryum stenotrichum C. Muell.

Bryum turbinatum (Hedw.) Turn.
Bryum sp.
Calliergon cordifolium (Hedw.) Kindb.
Calliergon giganteum (Schimp.) Kindb.
Campylium chrysophyllum (Brid.) J. Lange
Campylium hispidulum (Brid.) Mitt.
Campylium polygamum (B.S.G.) C. Jens.
Campylium sommerfeltii (Myrin) J. Lange
Campylium stellatum (Hedw.) C. Jens.
Ceratodon purpureus (Hedw.) Brid.
Cinclidium latifolium Lindb.
Cinclidium subrotundum Lindb.
Cirriphyllum cirrosum (Schwaegr. *ex* Schultes) Grout
Cynodontium sp.
Cyrtomnium hymenophylloides (Heub.) Kop.
Dicranella cerviculata (Hedw.) Schimp.
Dicranum angustum Lindb.
Dicranum elongatum Schleich *ex* Schwaegr.
Dicranum spadiceum Zett.
Distichium capillaceum (Hedw.) B.S.G.
Distichium inclinatum (Hedw.) B.S.G.
Ditrichum flexicaule (Schwaugr.) Hampe
Drepanocladus badius (C.J. Hartm.) Roth
Drepanocladus lycopodioides (Brid.) Warnst.
Drepanocladus revolvens (Sw.) Warnst.
Drepanocladus uncinatus (Hedw.) Warnst.
Drepanocladus vernicosus (Lindb.) Warnst.
Encalypta alpina Sm.
Encalypta procera Bruch
Encalypta rhaptocarpa Schwaegr.
Encalypta vulgaris Hedw.
Encalypta sp.
Fissidens adiantoides Hedw.
Fissidens osmundoides Hedw.
Hygrohypnum alpestre (Hedw.) Loeske
Hylocomium splendens (Hedw.) B.S.G.
Hypnum bambergeri Schimp.
Hypnum callichroum Funck *ex* Brid.
Hypnum cupressiforme Hedw.
Hypnum lindbergii Mitt.
Hypnum pratense Koch *ex* Brid.
Isopterygiopsis muelleriana (Schimp.) Iwats.
Leptobryum pyriforme (Hedw.) Wils.
Mnium blyttii B.S.G.
Mnium thomsonii Schimp.
Mnium sp.
Myurella julacea (Schwaegr.) B.S.G.
Oncophorus wahlenbergii Brid.
Philonotis fontana (Hedw.) Brid.
Plagiomnium ellipticum (Brid.) Kop.
Pohlia andrewsianum J. Shaw

Pohlia bulbifera (Warnst.) Warnst.
Pohlia cruda (Hedw.) Lindb.
Pohlia drummondii (C. Muell.) Andr.
Pohlia elongata Hedw.
Pohlia nutans (Hedw.) Lindb.
Polia schleicheri Crum
Pohlia sp.
Polytrichastrum longisetum (Sw. *ex* Brid.) G. L. Smith
Polutrichum commune Hedw.
Polytrichum hyperboreum R. Brown
Polytrichum juniperinum Hedw.
Polytrichum strictum Brid.
Pottia heimii (Hedw.) B.S.G.
Psilopilum laevigatum (Wahlenb.) Lindb.
Rhacomitrium lanuginosum (Hedw.) Brid.
Rhizomnium andrewsianum (Steere) Kop.
Rhizomnium pseudopunctatum (Bruch and Schimp.) Kop.
Rhytidium rugosum (Hedw.) Kindb.
Scorpidium scorpioides (Hedw.) Limpr.
Sphagnum squarrosum (Crome)
Sphagnum sp.
Splachnum vasculosum Hedw.
Tetraplodon mnioides (Hedw.) B.S.G.
Timmia norvegica Zett.
Tomenthypnum nitens (Hedw.) Loeske
Trematodon brevicollis Hoppe and Hornsch.
unknown acrocarpous moss

LICHENS

Alectoria nigricans (Ach.) Nyl.
Alectoria ochroleuca (Hoffm.) Mass.
Caloplaca cinnamomea (Th. Fr.) Oliv.
Cetraria cucullata (Bell.) Ach.
Cetraria ericetorum Opiz
Cetraria islandica (L.) Ach.
Cetraria nivalis (L.) Ach.
Cetraria richardsonii Hook.
Cladina aberrans (Abb.) Hale and W. Culb.
  = *Cladonia aberrans* (Abb.) Stuck.
Cladina alpestris (L.) Harm
  = *Cladonia stellaris* (Opiz) Pouz. and Vezda
Cladina arbuscula (Wallr.) Hale and Culb.
  = *Cladonia arbuscula* (Wallr.) Rabenh.
  = *Cladonia sylvatica* (L.) Hoffm.
Cladina mitis (Sanst.) Hale and W. Culb.
  = *Cladonia mitis* Sandst.
Cladina rangiferina (L.) Harm.
  = *Cladonia rangiferina* (L.) Wigg.
Cladonia amaurocraea (Floerke) Schaer.

Cladonia bacilliformis (Nyl.) Vain
Cladonia chlorophaea (Floerke *ex* Somm.) Spreng.
Cladonia coccifera (L.) Willd.
Cladonia cornuta (L.) Hoffm.
Cladonia deformis (L.) Hoffm.
Cladonia ecmocyna (Ach.) Nyl.
Cladonia fimbriata (L.) Fr.
Cladonia gracilis (L.) Willd.
Cladonia norrlini Vain.
Cladonia pleurota (Floerke) Schaer.
Cladonia pocillum (Ach.) O. Rich.
Cladonia pyxidata (L.) Hoffm.
Cladonia subfurcata (Nyl.) Arn.
Cladonia sulphurina (Michx.) Fr.
= *C. gonecha* (Ach.) Asah.
Cladonia uncialis (L.) Wigg.
Cornicularia divergens Ach.
Dactylina arctica (Hook.) Nyl.
Dactylina beringica Thoms. & Bird
Hypogymnia subobscura (Vain.) Poelt
Lecanora epibryon (Ach.) Ach.
Lobaria linita (Ach.) Rabenh.
Nephroma arcticum (L.) Torss.
Nephroma expallidum Nyl.
Ochrolechia androgyna (Hoffm.) Arn.
Ochrolechia frigida (Sw.) Lynge
Ochrolechia upsaliensis (L.) Mass.
Parmelia fraudans Nyl.
Peltigera aphthosa (L.) Willd.
Peltigera canina (L.) Willd.
Peltigera canina (L.) Willd. var. *rufescens* (Weis.) Mudd.
Peltigera canina (L.) Willd. var. *spuria* (Ach.) Schaer. f. *sorediata* Schaer.
Peltigera polydactyla (Neck.) Hoffm.
Pertusaria bryontha (Ach.) Nyl.
Physconia muscigena (Ach.) Poelt
Polyblastia sendtneri Kremph.
Psoroma hypnorum (Vahl) S. Gray
Rinodina turfacea (Wahlenb.) Koerb.
Solorina octospora (Arn.) Arn.
Solorina saccata (L.) Ach.
Solorina spongiosa (Sm.) Anzi
Sphaerophorus globosus (Huds.) Vain.
Stereocaulon paschale (L.) Hoffm.
Thamnolia subuliformis (Ehrh.) W. Culb.
Thamnolia vermicularis (Sw.) Ach. *ex* Schaer.

APPENDIX B

VEGETATION TABLES

Appendices B1 to B4, the Braun-Blanquet tables used to define the communities described in Chapters II and III, are in the pocket at the back of this volume.

B1 Samples of natural vegetation from the all-plant data set.

B2 Samples of natural vegetation from the vascular-plant-only data set.

B3 Samples of disturbed vegetation from the all-plant data set.

B4 Samples of disturbed vegetation from the vascular-plant-only data set.

APPENDIX C

SITE FACTORS

Abbreviations, Units, and Code Values for Appendices C1 and C2

sample	sample number
cmty	community number (see Chapters 2, 3; Appendix B
dist	disturbance type
	1=undisturbed
	2=naturally disturbed
	3=anthropogenically disturbed
thaw	depth of thaw in mid-August, cm
aspect	direction faced by the plot slope, degrees from true north
incl	average inclination of the plot slope, degrees
watdep	average depth of water, cm
stmois	site moisture, ordinal scale
slmois	soil moisture, ordinal scale
temp	summer air temperature, ordinal scale
snow	duration of snow cover, ordinal scale
wind	wind regime, ordinal scale
age	surface age, ordinal scale
stability	surface stability, ordinal scale
cryoturb	cryoturbation, ordinal scale
bsoil	cover of bare soil, %
watcov	cover of water, %
caribou	caribou sign, ordinal scale
mcrtn	microtine sign, ordinal scale
grdsq	ground squirrel, ordinal scale
ptarm	ptarmigan sign, ordinal scale
birds	other bird signs, ordinal scale
insects	insect sign, ordinal scale
othanml	sign of other animals, ordinal scale
totanml	total animal sign, sum of all animal scores
microty	microrelief type
	1 featureless, flat
	2 tussocks
	3 reticulate-patterned ground
	4 low-centered polygon center
	5 low-centered polygon rim
	6 low-centered polygon trough
	7 high-centered polygon center
	8 high-centered polygon trough
	9 palsa
	10 irregular
	11 mounds of bladed material
	12 ruts of multi-pass trail
	13 thermokarst
	14 irregularly rough, caused by moderate surface disturbance leaving surface changed but not removed
	15 bladed and smoothed
	16 area bladed below original surface
	17 graveled area

microht	microrelief height, cm
sand	Wentworth scale, %
silt	Wentworth scale, %
clay	Wentworth scale, %
hygmois	hygroscopic moisture, %
orgmat	organic matter, %
watabs	water absorption, %
fldcap	field capacity, %
wltpt	wilting point, %
avwat	available water, %
carb	carbonates, %
pH	pH
NH4	total available ammonium nitrogen, ppm
NO3	total available nitrate nitrogen, ppm
Ntot	total available nitrogen, ppm
P	total available phosphorus, ppm
K	total available potassium, ppm
Ca	calcium, ppm
Mg	magnesium, ppm
CEC	cation exchange capacity, meq/100 g

APPENDIX C1. ENVIRONMENTAL FACTORS FOR THE ALL-PLANT DATA SET

SAMPLE	CMTY	DIST	DISINT	DSCORE	THAW	ASPECT	INCL	WATDEP	STMOIS	SLMOIS	TEMP	SNOW	WIND	AGE	STABLTY	CRYOTRB	BRSOIL	WATCOV	CARIBOU	MCRTN	GRDSQ	PTARM	BIRDS	INSECTS	OTHANML	TOTANML	MICROTY	MICROHT
24	9	1	1	2	38	360	1	5	9	9	3	4	5	5	8	1	1	15	0	1	0	1	0	0	0	2	10	8
44	7	1	1	2	20	70	1	5	6	8	3	4	6	5	8	1	0	2	0	1	0	0	0	0	0	1	10	20
70	32	3	6	9	31		0		5	6	3	4	6	4	8	2	1	0	0	2	0	3	1	1	0	7	11	15
71	32	3	6	9	24		0		5	6	3	4	6	4	8	1	0	0	0	1	0	3	1	1	0	6	11	15
72	31	3	6	9	32	170	5		5	7	3	4	5	4	8	1	2	0	0	2	0	3	1	1	0	7	11	20
73	13	1	1	2	20		0		5	7	3	5	6	6	9	1	1	0	1	1	0	0	0	1	0	3	3	16
74	34	3	5	8	22	75	4		5	6	3	4	6	4	8	2	1	0	0	1	0	1	0	1	0	3	12	12
75	26	3	2	3	20	60	1		6	7	3	5	4	6	9	1	0	0	1	3	0	1	0	0	0	5	2	10
76	10	1	1	2	22	58	1		6	7	3	4	7	6	9	1	0	0	1	2	0	1	0	0	0	4	2	20
77	32	3	6	9	28	70	2		5	7	3	4	3	4	6	1	1	0	0	1	0	0	1	0	0	2	14	58
78	28	3	7	10	22	70	2		6	7	3	4	1	4	4	1	0	0	0	1	0	0	1	0	0	2	14	130
79	32	3	6	9	50	110	3		5	6	3	4	6	4	6	1	10	0	0	2	0	1	1	1	0	5	15	15
80	32	3	6	9	50	276	2		5	6	3	4	7	4	6	1	8	0	1	2	0	2	0	0	0	5	15	
81	26	3	5	8	33	50	4		5	6	3	4	6	4	7	1	0	0	1	1	0	1	0	0	0	3	12	15
82	8	1	1	2	25		0		6	7	3	4	6	6	9	1	0	0	0	1	0	1	0	1	0	3	1	10
83	20	2	7	10	45	250	5		5	6	4	5	7	4	6	1	8	0	1	1	2	0	1	0	0	5	10	20
84	13	2	3	5	30	160	10		5	6	5	4	7	5	8	1	0	0	1	0	0	1	1	0	0	3	10	30
85	32	3	6	9	25		0		5	6	3	4	6	4	9	1	0	0	0	2	0	0	2	0	0	4	11	12
86	31	3	6	9	32		0		5	6	3	4	6	4	9	1	1	0	1	1	0	1	2	1	0	6	11	
87	13	1	1	2	32	150	4		5	7	4	4	6	6	8	1	0	0	1	1	0	1	1	0	0	4	3	15
88	31	3	5	8	25		0		6	7	3	4	5	4	9	1	0	0	0	0	0	1	1	0	1	3	14	
89	31	3	5	8	25		0		6	7	3	4	5	4	9	1	0	1	0	1	0	1	1	0	1	4	14	20
90	27	3	4	7	51		0		8	7	3	4	5	4	9	1	2	0	1	2	0	0	0	0	0	3	14	10
102	32	3	6	9	62		1		5	5	3	4	6	4	8	1	3	0	0	1	0	1	0	0	0	2	11	
120	31	3	5	8	54	70	3	20	9	9	3	4	3	4	6	1	5	60	1	1	0	0	0	0	1	3	13	170
121	32	3	3	6	55	80	3		5	6	3	4	5	4	7	1	5	0	0	1	0	1	0	1	0	3	5	12
124	34	3	4	7	65		3		5	6	3	4	6	4	6	1	8	0	0	1	0	2	0	0	0	3	3	15
126	31	3	5	8	68		1	1	6	6	3	4	5	4	9	1	2	1	0	1	0	0	0	0	1	2	13	
127	33	3	6	9	92		18		5	5	3	4	6	4	6	1	35	0	0	0	0	0	0	1	0	1	14	
129	31	3	6	9	85	100	3		5	6	3	4	6	4	8	1	2	0	1	0	0	1	0	1	0	3	15	
136	14	1	4	6	32		6		5	6	3	4	6	5	8	1	3	0	1	0	0	1	0	0	0	2	5	12
137	33	3	6	9	40		0		5	4	3	4	6	4	9	1	0	0	0	2	0	0	0	0	0	2	11	
154	18	1	1	2	15	180	2		5	7	3	4	7	5	9	1	0	0	0	0	0	2	0	0	0	2	9	12
155	10	1	1	2	18	270	10		6	7	3	4	7	6	8	5	0	0	1	2	0	2	0	0	0	5	2	20
156	18	1	1	2	13	270	30		5	6	3	4	7	5	8	1	0	0	0	0	0	0	0	0	0	0	16	5
157	18	1	1	2	17		0		4	6	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	2	10
159	12	1	1	2	22	270	2		5	7	3	4	7	6	9	6	0	0	0	0	0	0	0	0	0	0	2	15
163	18	1	1	2	17	180	1		5	6	3	4	7	6	9	1	0	0	2	0	0	1	0	0	0	3	2	10
167	7	1	1	2	17		0		5	7	3	4	7	6	9	1	0	0	2	0	0	0	0	0	0	2	2	10
168	12	1	1	2	21	225	5		5	7	3	4	7	6	8	6	0	0	0	0	0	0	0	0	0	0	2	15
169	5	1	1	2	28		0	11	9	10	3	4	7	6	10	1	35	100	0	0	0	0	0	0	0	0	1	
170	7	1	3	6	36		0		7	8	3	4	7	4	9	1	0	0	0	0	0	0	0	0	0	0	5	4
172	2	2	6	9	32		0	6	8	9	3	4	7	4	10	1	0	60	0	0	0	0	0	0	0	0	1	
175	7	1	4	7	23	270	1	40	8	8	3	4	7	4	9	1	0	20	0	0	0	0	0	0	0	0	8	15
176	4	1	1	2	34		0	7	9	10	3	4	7	6	10	1	0	95	0	0	0	0	0	0	0	0	4	10
179	17	1	1	2	22		0		5	6	3	4	7	6	10	6	0	0	0	0	0	0	0	0	0	0	1	10
180	8	1	1	2	32	270	2		6	7	3	4	7	4	10	1	5	0	0	2	0	1	0	2	0	5	10	5
181	6	1	1	2	40		0	5	9	10	3	4	7	6	10	1	0	100	0	0	0	0	0	1	0	1	1	
183	7	1	1	2	32		0		7	8	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	5	15
184	18	1	1	2			0		6	7	3	4	7	5	10	1	0	0	0	0	0	0	0	0	0	0	9	10
185	3	1	1	2			0		9	10	3	4	7	6	10	1	0	100	0	0	0	0	0	0	0	0	1	

APPENDIX C1. (CONT.)

SAMPLE	CMTY	DIST	DISINT	DSCORE	THAW	ASPECT	INCL	WATDEP	STMOIS	SLMOIS	TEMP	SNOW	WIND	AGE	STABLTY	CRYOTRB	BRSOIL	WATCOV	CARIBOU	MCRTN	GRDSQ	PTARM	BIRDS	INSECTS	OTHANML	TOTANML	MICROTY	MICROHT
186	25	3	1	2			0		9	10	3	4	7	4	1	1	0	100	0	0	0	0	0	0	0	0	16	
188	31	3	6	9			0		5	6	3	4	7	4	9	1	2	0	0	0	0	0	0	0	0	0	11	
192	32	3	6	9	58	0	5		5	6	3	4	7	4	4	1	10	0	0	0	0	0	0	0	0	0	14	20
193	31	3	5	8	65	0	2	8	6	6	3	4	7	4	4	1	5	20	0	0	0	0	0	0	0	0	13	10
195	36	3	7	10	75	135	10		4	5	3	4	7	4	4	1	60	0	0	0	0	0	0	0	1	1	14	30
197	32	3	6	9	35		25		5	6	3	4	7	4	6	1	0	0	0	0	0	0	0	2	2	4	11	
200	25	3	7	10	47		0	24	9	10	3	4	7	4	10	1	0	100	0	0	0	0	0	0	0	0	16	
202	31	3	6	9	30	112	2		6	7	3	4	7	4	8	1	0	0	0	0	0	0	0	0	1	1	11	5
206	5	1	1	2	37		0	11	9	10	3	4	7	6	10	1	0	100	0	0	0	0	0	0	0	0	1	
207	18	1	1	2	23	0	1		5	5	3	4	7	6	9	2	0	0	1	0	0	2	0	0	0	3	7	
214	29	3	6	9	27	315	2		8	9	3	4	7	4	10	1	0	0	0	0	0	0	0	0	0	0	16	7
215	35	3	6	9	28		0		5	6	3	4	7	4	8	1	0	0	0	0	0	3	0	0	0	3	11	15
218	8	1	1	2	22		0		6	7	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	1	5
223	11	1	3	5	47	90	20		5	6	3	6	7	5	6	5	1	0	2	0	0	0	0	0	0	2	10	15
225	22	2	7	12	50	45	45		4	6	3	5	7	3	4	1	2	0	0	2	0	0	0	0	0	2	10	20
229	10	1	1	1	32		0		6	7	3	4	7	7	10	1	0	0	2	0	0	2	0	0	0	4	2	15
230	22	2	7	12	80	270	30		4	6	3	6	7	3	4	1	2	0	0	0	0	0	0	0	0	0	10	20
233	22	2	7	12		270	4		5	6	3	5	6	3	6	1	15	0	0	0	0	0	0	0	0	0	10	2
235	23	2	7	12	95	270	15		4	4	3	4	7	3	3	1	70	0	0	0	1	0	1	0	0	2	10	5
236	17	1	1	2	44	0	2		5	6	3	4	7	6	9	1	0	0	2	0	0	0	0	0	0	2	2	10
239	3	1	6	9	35		0		8	9	3	4	7	4	10	1	0	0	0	0	0	0	0	0	0	0	1	
241	21	2	7	10	55	270	45		4	5	3	5	7	4	6	2	5	0	0	0	0	0	0	0	1	1	10	15
242	13	1	1	2	44	225	30		4	5	3	4	7	5	6	4	3	0	0	0	0	1	0	0	0	1	3	15
243	16	2	7	12	48		0		4	4	3	4	7	3	7	10	20	0	0	0	0	1	1	0	0	2	1	3
244	16	2	7	10	35		0		4	4	3	4	7	4	7	10	8	0	2	0	0	1	0	0	0	3	1	2
246	15	2	7	10	47		0		8	7	3	3	7	4	7	10	15	0	0	0	0	0	0	0	0	0	1	2
250	6	1	1	2	32		0		8	8	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	1	2
251	4	1	1	2	32		0		8	8	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	1	7
257	5	1	1	2	37		0	1	8	9	3	4	7	6	10	1	0	20	0	0	0	0	0	0	0	0	4	1
258	7	1	1	2	37		0		5	4	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	5	10
259	19	2	4	7	38	0	5		3	4	3	4	7	4	6	1	0	0	0	0	1	0	3	0	0	4	5	50
260	20	2	5	10	60	0	5		3	4	3	4	7	3	6	1	0	0	1	0	3	1	1	0	0	8	10	70
263	17	1	1	2			0		5	6	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	1	4
264	11	1	2	3		90	15		5	6	3	6	7	5	6	1	2	0	1	0	0	0	0	0	0	1	10	20
268	7	1	1	2	30		0		7	8	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	1	20
269	12	1	1	1	45	90	10		4	5	3	4	7	7	9	7	0	0	0	2	0	0	0	0	0	2	2	20

APPENDIX C1. (CONT.)

SAMPLE	SAND	SILT	CLAY	HYGMOIS	ORGMAT	WATABS	FLDCAP	WLTPT	AVWAT	CARB	PH	NH4	NO3	NTOT	P	K	CA	MG	CEC
24				10.69	61.3	429.3	176.5	147.4	29.0	.9	6.35	41.2	26.4	67.6	4.0	370	12820	1132	
44				12.46	84.1	443.1	172.5	152.9	19.6	2.0	5.68	157.0	54.5	211.5	1.1	494	6450	875	111.96
70	2.4	79.0	18.6	3.19	16.9	116.9	44.9	24.4	20.5	4.1	7.79	618.	240.	858.	6.8	80	3100	374	82.18
71				7.76	53.5	322.8	110.3	88.5	21.8	1.1	6.71	36.8	77.5	114.3	.6	66	7180	1158	84.12
72	3.0	79.9	17.1	2.47	11.9	92.2	36.8	18.4	18.4	5.9	7.57	15.7	24.7	40.4	10.0	48	4080	349	28.01
73	1.7	78.1	20.2	2.42	9.7	80.6	40.4	16.7	23.7	9.0	7.74	17.9	11.2	29.1	14.0	82	5380	440	31.46
74	1.8	80.1	18.1	3.49	16.1	108.7	49.5	22.1	27.4	2.8	7.41	8.9	3.5	12.4	1.2	54	3580	273	20.91
75	1.6	78.6	19.8	3.62	18.8	125.5	55.7	25.4	30.3	1.0	6.56	19.5	4.0	23.5	1.1	47	2000	260	19.61
76	2.6	74.3	23.1	2.28	9.7	78.3	38.1	15.6	22.5	.8	5.62	15.9	7.3	23.2	.8	55	2060	273	30.55
77	1.6	76.0	22.4	2.88	12.6	91.2	44.8	19.9	24.9	1.0	6.47	13.4	4.9	18.3	.6	59	3920	406	39.69
78	1.6	75.8	22.6	5.14	24.7	148.2	78.3	41.2	37.1	.9	6.68	23.3	9.0	32.3	2.0	53	6880	622	59.28
79	1.0	76.6	22.4	1.47	3.5	52.1	26.8	8.4	18.4	6.5	7.72	10.4	5.5	15.9	1.0	99	4450	348	33.60
80	.9	77.7	21.4	1.79	5.4	59.5	32.3	10.8	21.5	4.3	7.77	13.8	7.2	21.0	16.0	97	4700	302	23.27
81	1.4	74.7	23.9	2.71	11.5	86.1	40.9	18.1	22.8	.7	5.83	19.0	6.7	25.7	.8	69	2610	312	34.39
82	.7	85.0	14.3	7.79	52.6	337.7	121.2	98.3	22.9	.6	6.87	24.0	18.2	42.2	2.4	82	13260	1242	319.96
83	1.4	76.9	21.7	3.99	18.6	111.3	48.3	29.5	18.8	1.3	7.51	12.2	7.2	19.4	3.1	90	5210	482	31.49
84				11.87	79.5	482.9	160.5	135.9	24.6	1.7	6.55	28.7	11.4	40.1	1.8	241	12550	1349	131.64
85				7.33	57.2	266.2	111.6	79.6	32.0	.7	5.40	24.2	14.3	38.5	.9	75	3800	591	179.36
86	.1	75.9	24.0	4.99	30.4	171.5	70.2	46.1	24.1	.6	6.60	20.0	42.4	62.4	1.0	68	5570	1220	61.32
87	.9	80.8	18.3	2.78	12.5	87.0	41.7	22.0	19.7	7.2	7.62	8.3	6.2	14.5	1.0	79	4600	194	14.32
88	3.1	44.4	52.5	5.28	41.0	210.2	87.9	57.4	30.5	2.9	6.59	45.3	17.4	62.7	.8	134	4220	791	66.40
89				8.26	56.6	323.2	129.3	86.3	43.0	1.1	6.58	34.7	11.0	45.7	.5	165	9130	963	150.92
90				1.30	4.7	62.3	34.9	14.5	20.4	2.2	6.19	15.1	4.4	19.5	.6	85	2360	368	22.80
102				1.54	7.6	74.0	36.1	14.1	22.1	6.4	8.05	15.1	4.4	19.5	.6	46	5100	253	20.53
120				2.63	12.2	107.3	49.8	23.3	26.5	1.4	5.96	19.3	7.4	26.7	2.7	97	4380	418	33.72
121				8.96	73.0	647.8	185.6	157.6	28.0	1.7	6.67	26.0	22.4	48.4	7.0	150	10560	956	93.64
124				1.20	3.9	54.9	34.5	10.5	24.0	6.5	7.92	7.1	3.8	10.9	.9	64	4820	274	18.65
126				1.94	6.2	64.6	38.0	11.9	26.1	8.5	7.70	8.6	5.7	14.3	.6	78	5400	220	18.60
127	.2	75.0	24.8	2.15	5.7	63.2	37.6	13.8	23.8	.4	7.16	6.5	7.0	13.5	1.2	57	3210	375	17.00
129				3.20	13.4	93.7	49.8	22.9	27.0	5.7	7.78	11.9	8.2	20.1	1.5	79	6910	358	38.49
136				4.82	25.8	141.8	81.6	40.6	41.0	2.0	5.34	15.9	5.6	21.5	1.2	36	4990	291	79.80
137	1.7	70.1	28.2	.98	4.4	47.5	31.9	13.0	18.9	5.1	7.96	7.5	4.2	11.7	38.2	40	2940	156	14.91
154				9.58	74.2	281.6	127.8	101.6	26.2	1.1	4.70	162.0	23.5	185.5	2.1	78	5040	526	133.00
155				1.89	5.1	57.8	34.3	12.2	22.1	1.3	5.39	16.5	3.7	20.2	.8	43	1320	156	21.35
156				10.41	61.4	398.8	171.4	147.2	24.2	1.6	6.05	44.4	26.4	70.8	5.6	128	8720	1520	139.08
157				9.56	67.5	368.4	140.4	120.5	19.9	1.1	5.38	35.2	15.0	50.2	8.0	126	6840	942	123.88
159	1.1	75.0	24.0	1.83	4.3	58.0	36.6	13.7	22.9	3.1	7.25	7.4	3.4	10.8	.7	51	2980	411	21.40
163				9.94	65.6	369.5	174.9	150.0	24.9	3.4	4.00	53.7	10.6	64.3	5.7	307	2250	274	88.90
167				9.24	67.3	380.6	143.0	104.4	38.6	2.4	4.14	34.4	8.1	42.5	2.0	83	3290	231	142.12
168				1.97	4.6	60.3	36.7	11.5	25.2	.6	6.79	10.5	5.0	15.5	.8	56	2430	413	18.60
169				9.41	67.3	529.1	188.9	162.0	26.9	.9	5.00	39.2	16.6	55.8	3.0	85	1620	200	89.20
170				8.76	70.5	494.6	170.8	137.7	33.1	2.6	5.38	31.0	16.8	47.8	3.0	62	5240	674	36.42
172	.0	65.6	34.4	4.10	22.4	125.2	81.0	37.2	43.8	.6	5.61	21.1	6.3	27.4	.9	66	3500	426	72.96
175				10.12	62.6	941.6	205.0	171.1	33.9	1.8	6.04	48.4	23.4	71.8	11.0	416	8520	1260	68.32
176				10.86	69.1	594.9	191.6	158.7	32.9	.9	5.82	53.4	25.4	78.8	.8	38	3470	117	107.60
179				11.75	59.4	495.9	179.6	150.0	29.6	2.2	7.07	29.6	19.6	49.2	2.8	170	17360	796	171.00
180				2.42	22.5	101.2	37.5	22.4	15.1	1.4	7.08	8.5	4.5	13.0	1.3	46	3330	638	20.39
181				8.36	70.9	495.9	168.8	146.2	22.6	1.1	5.43	47.8	18.2	66.0	7.8	92	4620	486	56.56
183				11.42	57.4	475.9	188.6	144.1	44.5	1.4	6.05	37.6	35.0	72.6	4.0	194	11040	982	161.12
184				9.79	66.1	365.2	147.0	113.9	33.1	1.1	4.03	116.6	17.6	134.2	14.0	66	1250	120	91.00
185				9.11	66.1	375.3	155.7	128.0	27.7	1.4	5.64	27.6	14.6	42.2	3.0	116	6360	956	143.64

APPENDIX C1. (CONT.)

SAMPLE	SAND	SILT	CLAY	HYGMOIS	ORGMAT	WATABS	FLDCAP	WLTPT	AVWAT	CARB	PH	NH4	NO3	NTOT	P	K	CA	MG	CEC
186				2.58	14.9	94.1	48.7	19.7	29.0	4.5	7.68	12.6	3.7	16.3	1.2	46	4190	259	27.73
188				3.61	19.0	137.3	59.3	32.8	26.5	3.2	7.69	12.5	4.5	17.0	.6	42	5370	459	41.18
192				11.07	46.2	357.1	164.5	119.9	47.6	1.4	7.16	18.6	9.3	27.9	2.7	65	5050	681	96.52
193				4.84	26.0	159.9	77.4	39.1	38.3	5.5	7.47	15.0	5.3	20.3	1.5	128	7960	688	67.26
195	.8	84.0	15.2	1.37	3.0	49.2	29.5	7.7	21.8	10.7	7.65	7.4	3.1	10.5	1.8	82	4270	465	12.02
197				5.36	30.4	192.0	85.0	47.7	37.3	2.5	6.00	17.8	26.0	43.8	1.3	67	5290	713	65.74
200				1.55	6.7	66.2	33.7	14.9	18.8	7.0	7.92	11.8	4.3	16.1	3.1	50	3580	182	23.01
202				6.28	34.9	215.7	92.2	60.0	32.2	3.3	7.81	16.1	9.3	25.4	1.3	59	7540	1400	74.10
206				10 09	63.2	460.3	163.6	128.2	35.4	2.7	5.18	37.0	16.0	53.0	4.0	106	6260	750	70.76
207				9.15	63.0	379.6	174.0	117.0	56.9	2.7	5.46	21.6	12.8	34.4	2.1	50	6950	515	142.12
214				6.03	41.1	226.9	105.9	61.3	44.6	2.3	5.36	28.7	12.8	41.5	.7	31	4120	237	77 14
215				3.33	16.0	116.9	52.8	27.7	25.1	2.1	5.16	12.9	6.1	19.0	1.2	34	2400	144	41.16
218				12.23	64.0	462.4	192.5	139.0	53.6	1.9	6.27	33.6	15.2	48.8	.1	57	6870	357	121.80
223	.7	72.7	26.5	2.62	10.7	79.8	45.4	17.0	28.4	3.2	7.26	8.3	7.1	15.4	1.4	89	4880	359	21.70
225				1.91	7.0	67.0	41.8	11.9	29.9	5.2	7.72	12.2	8.0	20.2	.8	56	4490	490	15.90
229				2.94	13.5	84.1	49.1	22.8	26.3	2.4	5.79	14.7	4.4	19.1	1.6	61	2970	291	32.60
230				1.93	7.4	64.9	41.8	12.3	29.5	11.0	7.67	9.4	5.2	14.6	7.1	82	5710	398	17.70
233	1.3	78.7	20.0	1.66	4.9	55.1	36.7	10.1	26.7	6.9	7.66	19.4	4.8	24.2	3.1	96	4780	366	15.70
235	1.4	86.8	11.8	1.10	2.6	50.4	24.9	6.7	18.3	11.7	7.67	9.1	10.4	19.5	.1	102	4200	538	10.50
236				12.37	55.0	343.5	182.2	135.4	46.8	.7	6.40	26.7	9.1	35.8	2.0	131	4130	306	125.10
239				4.26	25.1	142.3	87.3	46.0	41.3	11.4	5.33	15.2	4.4	19.6	2.8	144	3530	562	34.60
241				1.73	6.8	73.0	29.5	13.7	15.8	1.6	7.85	7.8	11.9	19.7	.7	64	4920	301	16.80
242	1.0	84.4	14.6	1.45	3.4	61.1	23.5	9.5	14.0	13.6	8.02	8.0	9.8	17.8	.1	68	4520	364	13.40
243	1.6	73.4	25.0	1.49	2.0	49.1	27.2	9.6	17.7	1.8	7.86	6.5	4.7	11.2	.6	164	3420	514	13.80
244				1.42	2.7	50.2	28.6	10.5	18.1	1.2	7.18	6.1	4.5	10.6	.5	92	2250	381	15.60
246	.3	76.2	23.5	1.05	2.0	44.1	26.1	7.9	18.2	2.6	7.90	6.4	5.7	12.1	.2	60	2530	250	12.40
250				10.41	64.6	454.4	190.9	147.8	43.1	2.8	5.59	11.4	6.9	18.3	2.4	65	5100	131	116.20
251				12.15	63.6	550.3	199 3	151.3	48.0	1.0	5.81	13.2	24.0	37.2	2.9	70	5520	143	120.60
257				11.02	76.8	579.7	185.0	143.8	41.1	1.3	5.85	20.3	9.9	30.2	1.6	58	4110	173	73.00
258				13.43	75.6	487.8	222.1	152.0	70.2	1.7	6.33	9.8	6.2	16.0	1.7	94	7450	408	133.70
259	.1	62.4	37.5	2.66	5.8	75.1	32.0	18.7	13.2	7.2	4.29	7.3	7.8	15.1	21.5	206	790	222	21.50
260				12.70	69.4	397.2	170.4	148.2	22.2	1.0	4.63	23.9	5.4	29.3	46.3	312	4150	692	123.90
263				10.03	57.7	317.9	150.4	119.8	30.6	3.1	6.34	10.2	27.9	38.1	1.6	50	4630	517	85.00
264				2.08	3.1	54.5	35.1	11.8	23.4	12.4	7.90	7.5	5.2	12.7	1.1	94	5240	207	16.90
268				8.27	85.8	252.8	129.0	84.8	44.2	1.6	5.14	9.8	4.4	14.2	1.6	52	2260	241	72.80
269				2.48	6.5	70.0	42.3	15.0	27.3	1.1	6.72	7.7	7.6	15.3	1.2	60	3650	419	21.50

APPENDIX C2. ENVIRONMENTAL FACTORS FOR THE VASCULAR-ONLY DATA SET

SAMPLE	CMTY	DIST	DISINT	DSCORE	THAW	ASPECT	INCL	WATDEP	STMOIS	SLMOIS	TEMP	SNOW	WIND	AGE	STABLTY	CRYOTRB	BRSOIL	WATCOV	CARIBOU	MCRTN	GRDSQ	PTARM	BIRDS	INSECTS	OTHANML	TOTANML	M!CROTY	MICROHT
144	1	1	1	2	57	360	1	50	10	10	3	4	6	4	9	1	33	100	0	0	0	0	1	0	1	2	1	
158	10	1	1	2	14	270	2		6	7	3	4	7	6	8	1	0	0	0	0	0	0	0	0	0	0	2	15
160	10	1	1	1	19	112	5	0	6	7	3	4	7	7	8	2	0	0	0	0	0	0	0	0	0	0	2	20
161	10	1	1	2	15	90	2	0	5	7	3	4	7	5	9	8	0	0	0	0	0	0	0	0	0	0	9	20
162	12	1	1	1	16	90	2	0	5	7	3	4	7	7	9	8	1	0	2	0	0	0	0	0	0	2	2	15
164	10	1	1	2	16		0	0	6	7	3	4	7	6	9	3	0	0	2	0	0	0	0	0	0	2	2	10
165	12	1	1	2	15		0	0	5	6	3	4	7	6	8	4	2	0	1	3	0	0	0	0	1	5	2	15
166	18	1	1	2	15		0	0	4	6	3	4	7	6	9	2	1	0	3	0	0	0	0	0	0	3	7	10
171	5	1	1	2	28		0	6	9	10	3	4	7	6	10	1	10	100	0	0	0	0	0	0	0	0	1	
173	2	2	6	9	23		0	0	6	8	3	4	7	4	10	1	0	0	0	0	0	0	0	0	0	0	1	
174	22	2	6	9	25		0	0	6	7	3	4	7	4	10	1	0	0	0	0	0	0	0	0	0	0	1	4
177	8	1	1	2	25		0	0	6	8	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	1	10
178	3	1	1	2	34		0	13	9	10	3	4	7	6	10	1	0	100	0	0	0	0	0	1	0	1	1	
182	6	1	1	2	35		0	4	9	10	3	4	7	6	10	1	0	75	0	0	0	0	0	0	0	0	4	10
187	24	3	1	2			0		9	10	3	4	7	4	10	1	0	100	0	0	0	0	0	0	0	0	16	
189	33	3				180	20	0	2	3	3	4	7	4	9	1	5	0	0	0	0	0	0	0	0	0	11	20
190	34	3	4	7	58	0	2	0	5	6	3	4	7	4	9	3	2	0	0	0	0	0	0	0	0	0	14	10
191	31	3	5	8	48	0		20	9	10	3	4	7	4	10	1	25	90	0	0	0	0	0	0	0	0	13	15
194	33	3	6	9	38	270	5	0	5	6	3	4	7	4	8	1	20	0	0	0	0	0	0	0	0	0	15	5
196	25	3	5	8	50		0	35	9	10	3	4	7	4	10	1	40	100	0	0	0	0	0	0	0	0	13	
198	33	3	6	9	52	270	15	0	5	6	3	4	7	4	8	1	0	0	0	3	0	0	0	0	0	3	11	
199	33	3	6	9	42	180	5	0	6	7	3	4	7	4	9	1	0	0	0	0	0	0	0	0	0	0	14	
201	25	3	6	9			0	50	9	10	3	4	7	4	10	1	0	100	0	0	0	0	0	0	0	0	16	
203	5	1	1	2	47		0	4	9	10	3	4	7	6	10	1	0	90	0	0	0	0	0	0	0	0	1	10
204	7	1	1	2	45		0	0	6	8	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	5	4
205	10	1	1	2	25		0	0	6	7	3	4	7	6	10	1	0	0	2	0	0	0	0	0	0	2	2	20
208	18	1	1	2	27		0	0	5	7	3	4	7	5	10	4	0	0	2	0	0	1	0	0	0	3	9	8
209	5	1	1	2	42		0	5	9	10	3	4	7	6	10	1	0	90	0	0	0	0	0	0	0	0	1	
210	10	1	1	2	24		0	0	7	8	3	4	7	6	10	4	0	0	1	2	0	0	0	0	0	3	2	15
211	32	3	6	9	32	90	2	0	5	7	3	4	7	4	8	1	0	0	0	0	0	0	0	0	0	0	11	150
212	33	3	6	9	32	0	1	0	7	8	3	4	7	4	10	1	5	0	0	0	0	0	0	0	0	0	13	4
213	25	3	6	9	30		0	14	9	10	3	4	7	4	10	1	0	100	0	0	0	0	0	0	0	0	16	
216	35	3	4	7	24	0	1	0	5	6	3	4	7	4	8	1	0	0	1	0	0	0	0	0	0	0	12	10
217	18	1	1	2	23	180	2	0	5	6	3	4	7	6	8	1	0	0	0	0	0	0	0	0	0	0	2	15
219	30	3	5	8	28		0	0	6	8	3	4	7	4	10	1	0	0	0	0	0	0	0	0	0	0	14	5
220	8	1	1	2			0		7	8	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	1	10
221	25	3	5	8	47		0		8	9	3	4	7	4	10	1	0	5	0	0	0	0	0	0	0	0	14	8
222	19	2	5	10	55	0	20	0	5	5	3	3	7	3	6	1	2	0	0	0	3	2	0	0	0	5	10	10
224	11	1	3	5	54	90	20	0	5	6	3	6	7	5	6	5	0	0	0	0	0	0	0	0	0	0	10	10
226	22	2	7	12	75	45	10	0	5	6	3	5	7	3	4	1	85	0	0	0	0	0	0	0	0	0	10	2
227	22	2	7	12	65	45	20	0	5	6	3	5	7	3	4	1	20	0	0	0	0	0	0	0	0	0	10	5
228	22	2	7	12	60	45	20	0	5	6	3	5	7	3	4	1	80	0	0	0	0	0	0	0	0	0	10	5
231	22	2	7	12	63	270	40	0	4	5	3	5	6	3	2	1	85	0	0	0	0	0	0	0	0	0	10	5
232	22	2	7	12	72	270	15	0	4	5	3	5	6	3	4	1	15	0	0	0	0	2	0	0	0	2	10	7
234	13	2	7	12	50	270	25	0	5	6	3	5	7	3	8	1	0	0	0	0	0	0	0	0	0	0	10	20
237	34	3	3	6	35	0	2	0	5	6	3	4	7	4	9	1	0	0	0	0	0	0	0	0	0	0	12	2
238	2	2	6	9	35		0	2	8	9	3	4	7	4	10	1	0	95	0	0	0	0	0	0	0	0	1	
240	7	1	1	2			0		8	9	3	4	7	6	10	1	0	0	0	0	0	0	0	0	0	0	5	10
245	16	2	7	10	40		0		4	4	3	4	7	4	7	10	5	0	0	2	0	1	0	0	0	3	1	20
247	15	2	7	10	53		0		7	7	3	3	7	4	7	10	70	0	0	0	0	0	0	0	0	0	1	4
248	16	2	7	10	42		0		4	4	3	4	7	4	7	10	2	0	0	0	0	1	0	0	0	1	1	1

APPENDIX C2. (CONT.)

SAMPLE	CMTY	DIST	DISINT	DSCORE	THAW	ASPECT	INCL	WATDEP	STMOIS	SLMOIS	TEMP	SNOW	WIND	AGE	STABLTY	CRYOTRB	BRSOIL	WATCOV	CARIBOU	MCRTN	GRDSQ	PTARM	BIRDS	INSECTS	OTHANML	TOTANML	MICROTY	MICROHT
249	16	2	7	12	48		0		4	4	7	4	7	3	7	10	80	0	0	0	0	0	0	0	0	0	1	5
252	14	1	4	6	17	0	20		4	5	3	4	7	5	8	1	0	0	0	0	2	1	0	0	0	3	5	10
253	15	2	7	12	38		0		5	6	3	4	7	3	7	10	70	0	0	0	0	0	0	0	0	0	1	1
254	16	2	7	10	39		0		5	5	3	4	7	4	7	10	75	0	0	2	0	0	0	0	0	2	1	7
255	20	1	4	6	43				3	4	3	4	7	5	8	1	0	0	0	0	0	2	3	0	0	5	5	5
256	20	1	5	8	40	225	5		4	4	3	4	7	4	6	2	10	0	0	0	3	0	0	0	0	5	10	15
261	14	2	4	7	22		0		4	4	3	4	7	4	10	1	2	0	0	0	2	0	2	0	0	4	10	10
262	14	1	4	7	27		0		3	4	3	4	7	4	10	1	0	0	0	0	0	0	2	0	0	2	10	10
265	29	3	3	6	26		0		5	6	3	4	7	4	10	1	0	0	0	0	0	0	0	0	0	0	14	15
266	30	3	3	6	28		0		6	6	3	4	7	4	10	1	0	0	0	0	0	0	0	0	0	0	14	15
267	25	3	6	9	30		0	2	9	9	3	4	7	4	10	1	0	30	0	1	0	0	0	0	0	1	1	

APPENDIX C3

ORDINAL SCALES*

scale	site moisture	soil moisture	summer air temperature	snow
1	Very dry, little or no moisture within 10 cm of surface. exposed to strong winds	Very dry. no apparent moisture, no clumping	Very cold sites. high altitude with north-facing slopes	Little or no snow cover in winter, ridge top sites
2	Very dry, little moisture near surface. somewhat less exposed sites	Very dry, some moisture but doesn't clump	Cold sites. high altitude with moderate solar exposure, north-facing coastal plain sites or flat sites extreme arctic coast	Little snow cover in winter, exposed slopes
3	Dry. some moisture near the surface, very exposed	Dry. clumps but then crumbles	Cold sites. moderate altitudes, flat coastal plain sites	Slopes usually snow covered in winter
4	Dry. some moisture near the surface, somewhat less exposed sites	Dry, clumps and stays in a ball	Cool sites. flat surface in Arctic Foothills	Slopes snow covered in winter, snowmelt by late May
5	Moist, top 10 cm continually moist to wet, moderately well-drained sites	Moist, binds, but can be taken apart	Moderate temperatures, south-facing slopes on Arctic Coastal Plain or high mountains	Shallow depressions, somewhat prolonged snow cover, melt by early June

ORDINAL SCALES (Continued)

scale	site moisture	soil moisture	summer air temperature	snow
6	Moist, top 10 cm near saturation, less well-drained sites	Moist, binds completely into gooey ball	Moderate temperatures, south-facing slope, Arctic Foothills	Snowpatches, snowmelt by late June or early July
7	Wet, continually saturated soil but no standing water	Wet, can squeeze some water out	Moderate temperatures, flat site at intermediate altitudes south of Brooks Range	Snowpatches, somewhat later snowmel by late July
8	Wet. usually with standing water early in summer	Wet, can squeeze lots of water out	Warm temperatures. flat site, lower altitudes south of Brooks Range	Snowpatches. later snowmelt, early August
9	Very wet, usually with standing water late in summer	Very wet, totally saturated	Warm, south-facing slopes at intermediate altitudes in interior Alaska	Snowpatches, very late snowmelt, late August
0	Very wet, deep standing water year round	Very wet, soil taken from underwater	Warmest south-facing slopes at lower altitudes in interior Alaska	Snowpatches, very late snowmelt, sometimes may have snow cover all yea

ORDINAL SCALES (Continued)

scale	surface Age	stability	cryoturbation	wind
1	Constant disturbance	Completely unstable, always moving (e.g., sand dunes)	0% of surface disturbed	Completely sheltered from the wind
2	Less than 1 year since severe disturbance	Annually unstable (e.g. avalanche slopes, river bars)	< 1%	Exposed to occasional very light (1-5 km/hr) winds
3	1-10 years	Periodically unstable (e.g., 50 year flood-plain)	1-2%	Very light winds common
4	10 to 100 years	Unstable, vegetation in patches, on slope	2-5%	Occasional light (5-10 km/hr winds
5	100 to 1000 years, last disturbance during late Holocene	Unstable, vegetation in patches, on flat	5-10%	Light winds common
6	1000 to 10 000 years last disturbance during early and mid-Holocene	Moderately stable, open vegetation, on slope	10-15%	Occasional moderate (20-30 km/hr) winds

ORDINAL SCALES (Continued)

scale	surface age	stability	cryoturbation	wind
7	Old surface, last disturbance during late Wisconsin (10.000 yrs. B.P.)	Moderately stable, open vegetation. on flat	15-25%	Moderate winds common
8	Old surface. last disturbance during early Wisconsin (30.000 - 70.000 yrs. B.P.)	Stable surface. completely vegetated. moderate slope	25-50%	Occasional strong winds (40-60 km/hr), winds otherwise light
9	Very old surface, last disturbance during pre-Wisconsin time	Stable surface. completely vegetated. slight slope	50-75%	Strong winds common. winds otherwise moderate
10	Very old unglaciated surface	Very stable surfaces. completely vegetated. flat	75-100%	Strong winds common. occasional very strong (> 60 km/hr) winds

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*These 8 scales are from Walker et al (1979). where they are given as modifications from Komarkova (1979).

ORDINAL SCALES (Continued)

scale	animal sign*	physical disturbance intensity
1	Small amount of sign	Undisturbed (for at least approximately 1000 years). Examples: upland surfaces unaffected by the thaw lake cycle. old drained lake basins.
2	Moderate amount of sign	Vegetation compressed but not killed; upper soil horizons essentially undisturbed. Examples: moderate foot traffic. single winter pass of a Rolligon.
3	Extensive sign	Vegetation compressed with some crushed or broken; upper soil horizons somewhat compressed. Examples: single summer pass of a Rolligon.
4		Vegetation crushed and broken with some destroyed; upper soil horizons compressed and/or somewhat churned. Examples: areas of Oumalik winter runway that were not bulldozed.
5		Much of vegetation destroyed and the remainder badly damaged; upper soil horizons strongly churned. Examples: multiple-pass vehicle trails.

ORDINAL SCALES (Continued)

scale	animal sign*	physical disturbance intensity
6		Vegetation completely destroyed; upper soil horizons completely disrupted so that new surface is mixture of organic material and mineral soil. Examples: mounds of bulldozed material, areas bulldozed and then smoothed.
7		All vegetation and organic matter removed leaving bare mineral soil. Examples: areas bulldozed down to mineral soil, frost boils, exposed mineral soil on eroding lake bluffs.

*Animal sign includes burrows, grazing, browsing, trampling, and feces.

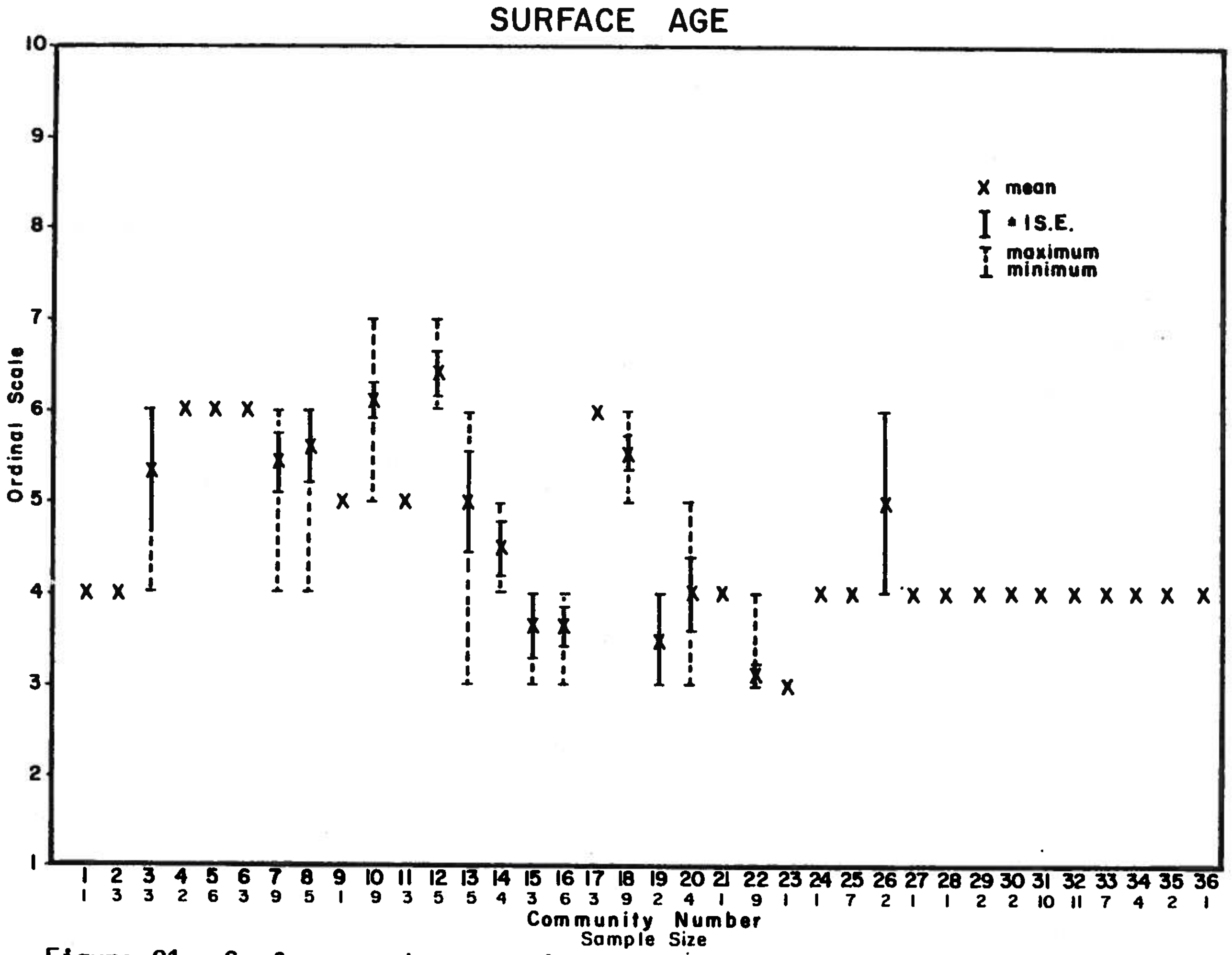

Figure C1. Surface age by community.

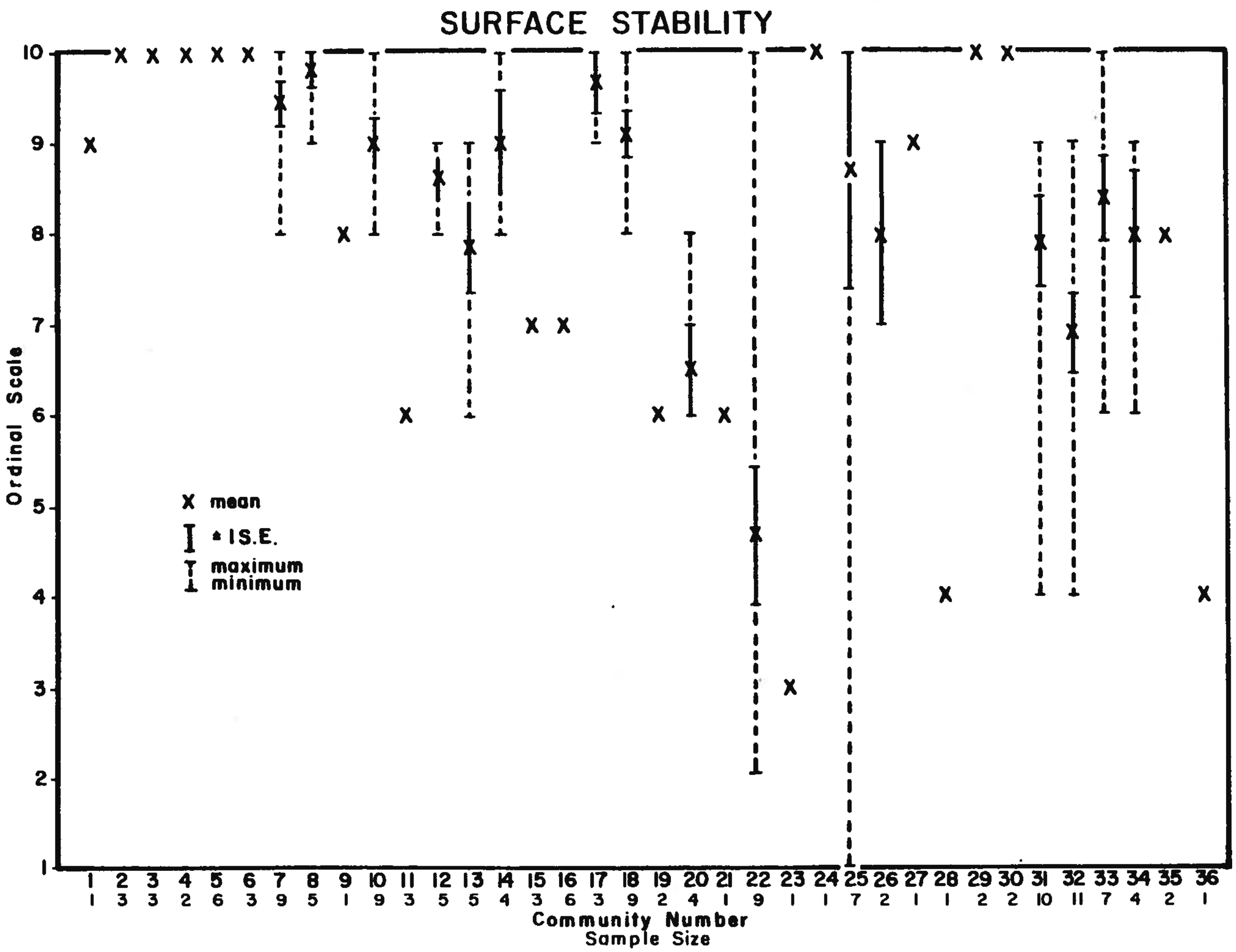

Figure C2. Surface stability by community.

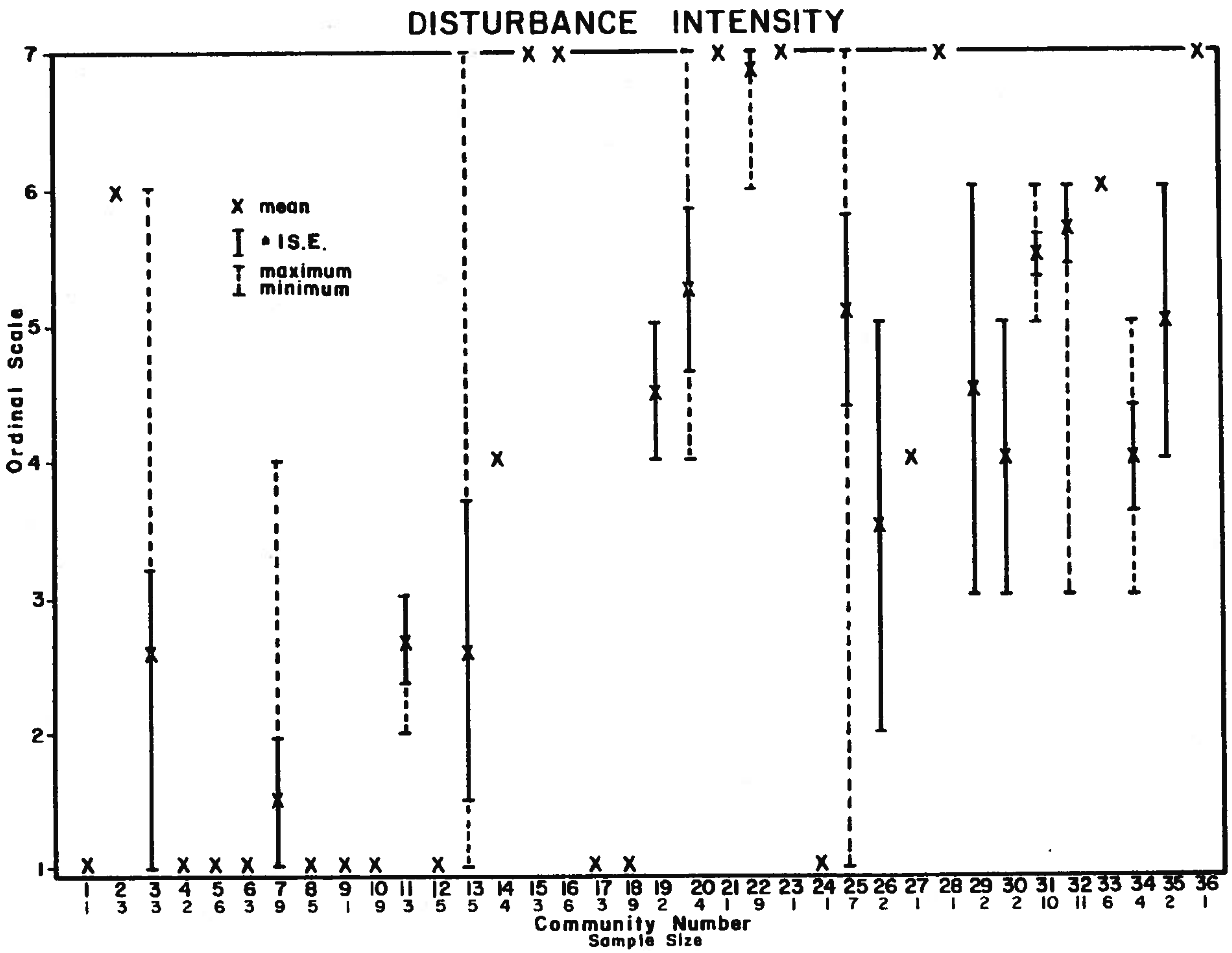

Figure C3. Disturbance intensity by community.

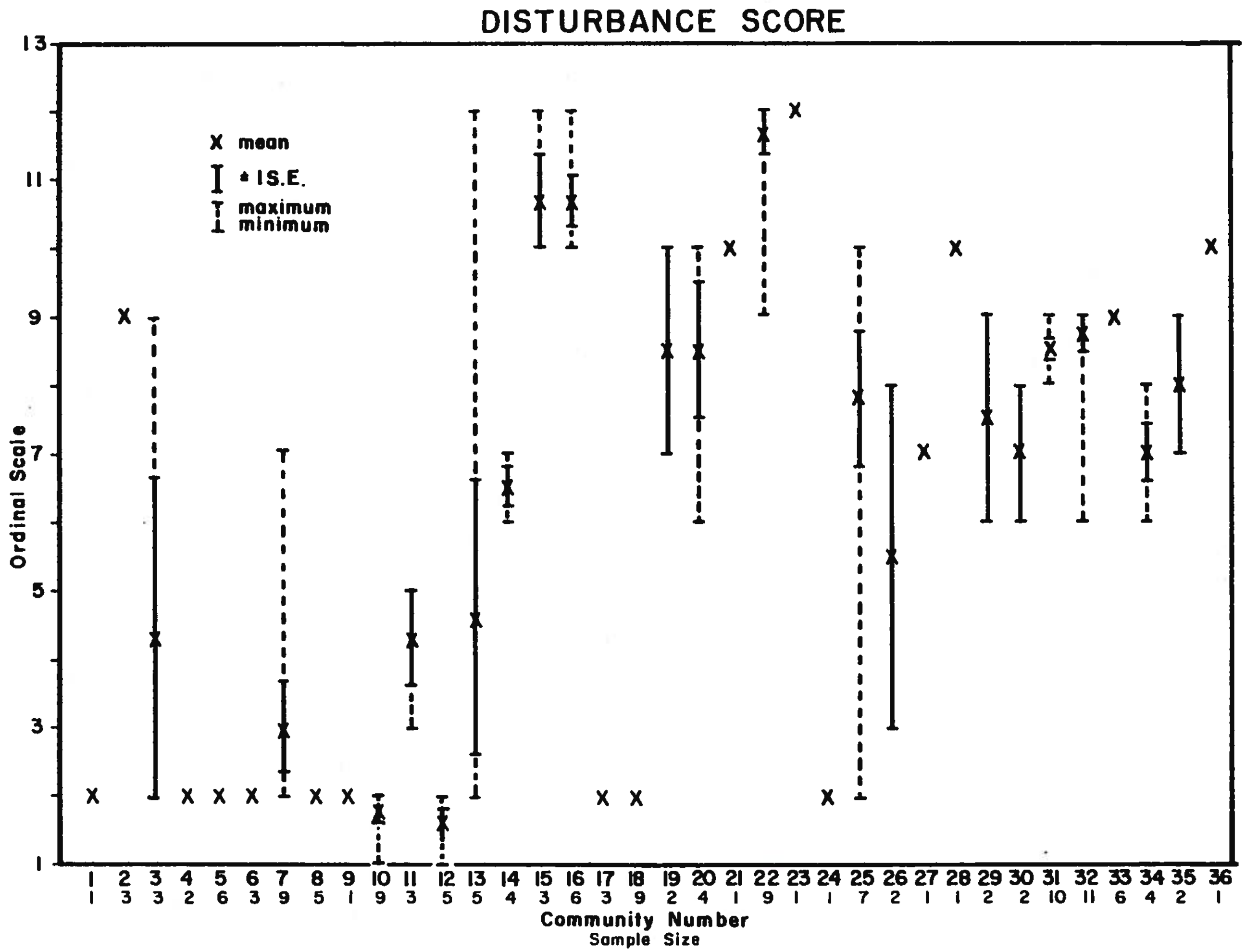

Figure C4. Disturbance score by community.

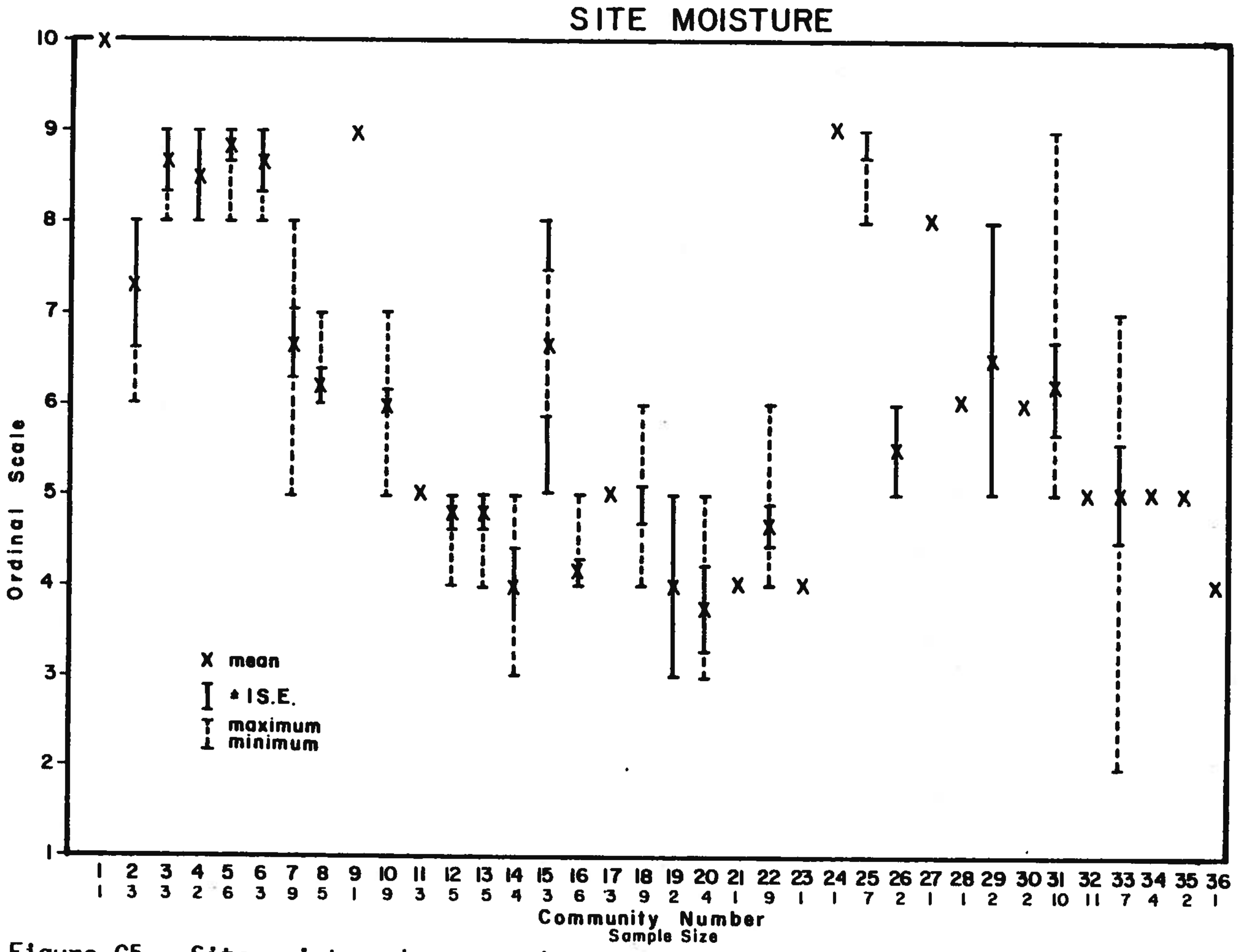

Figure C5. Site moisture by community.

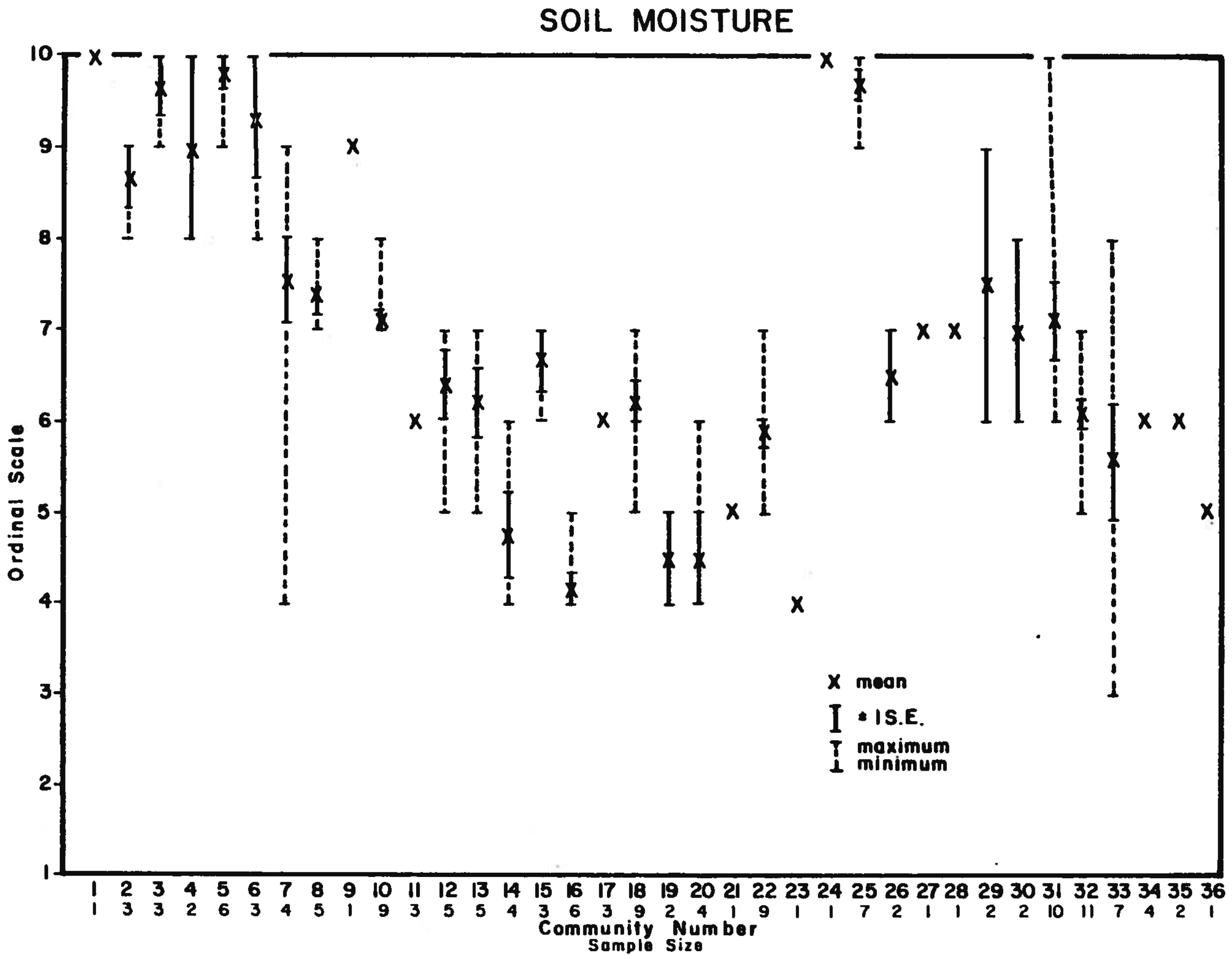

Figure C6. Soil moisture by community.

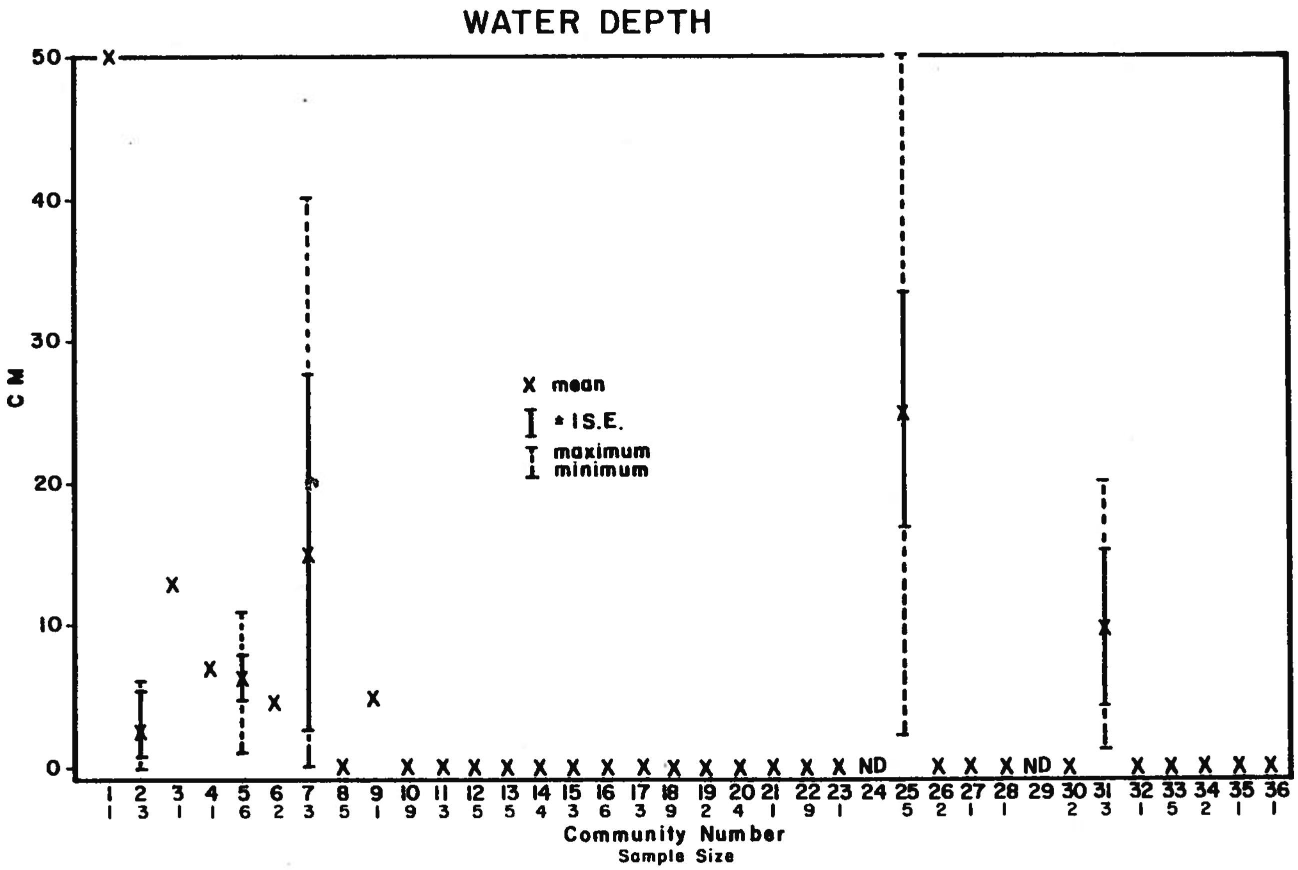

Figure C7. Water depth by community.

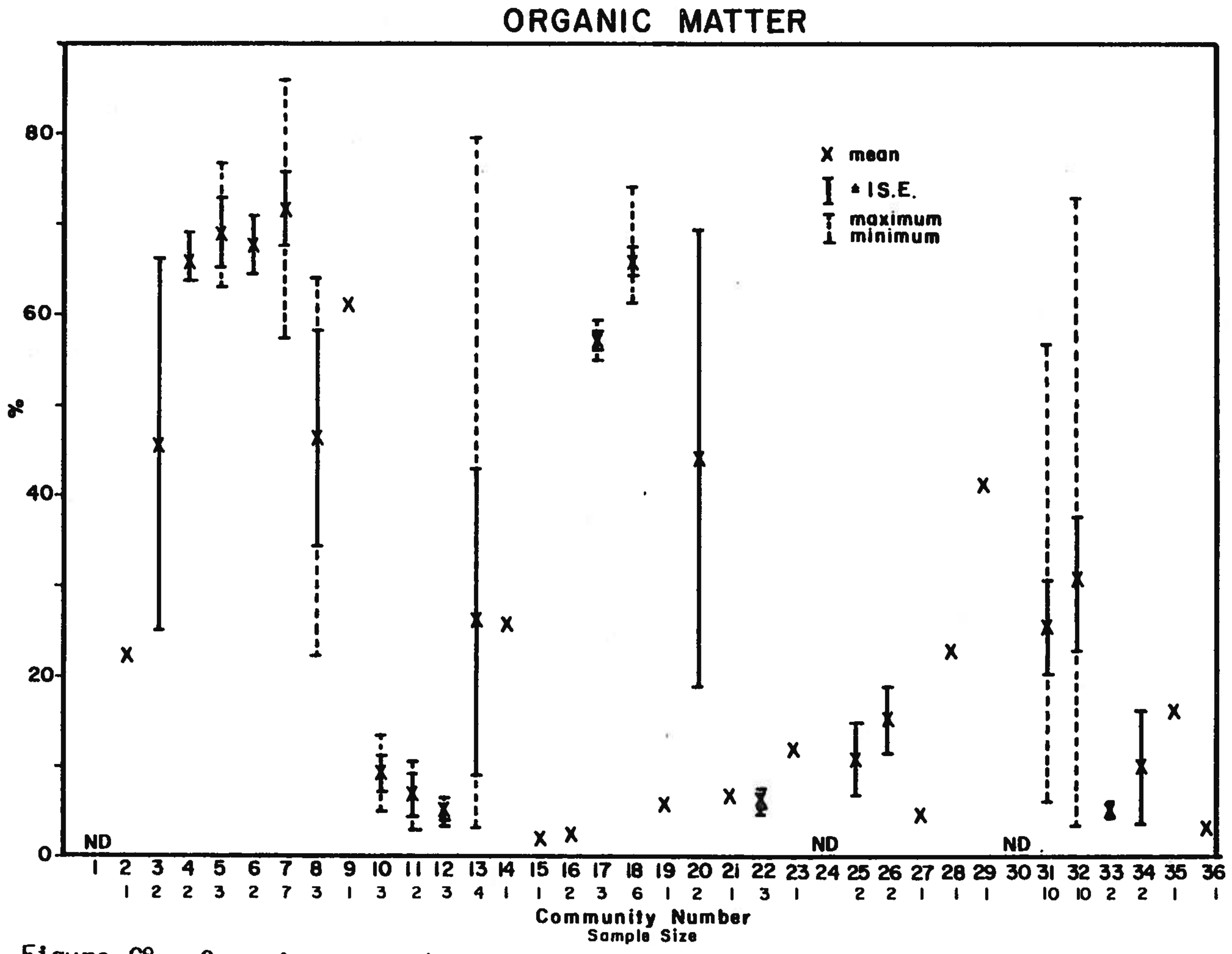

Figure C8. Organic matter by community.

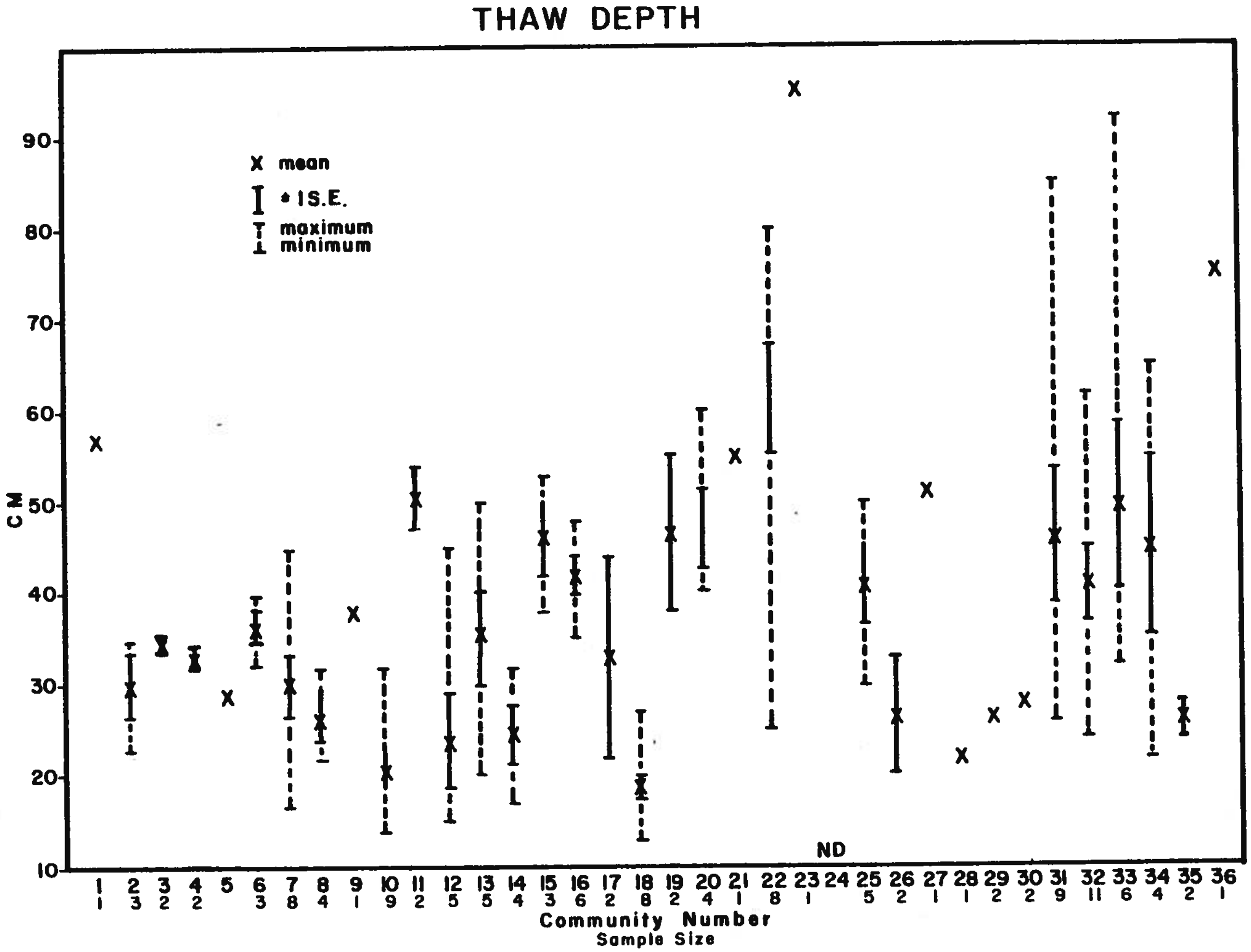
THAW DEPTH

Figure C9. Thaw depth by community.

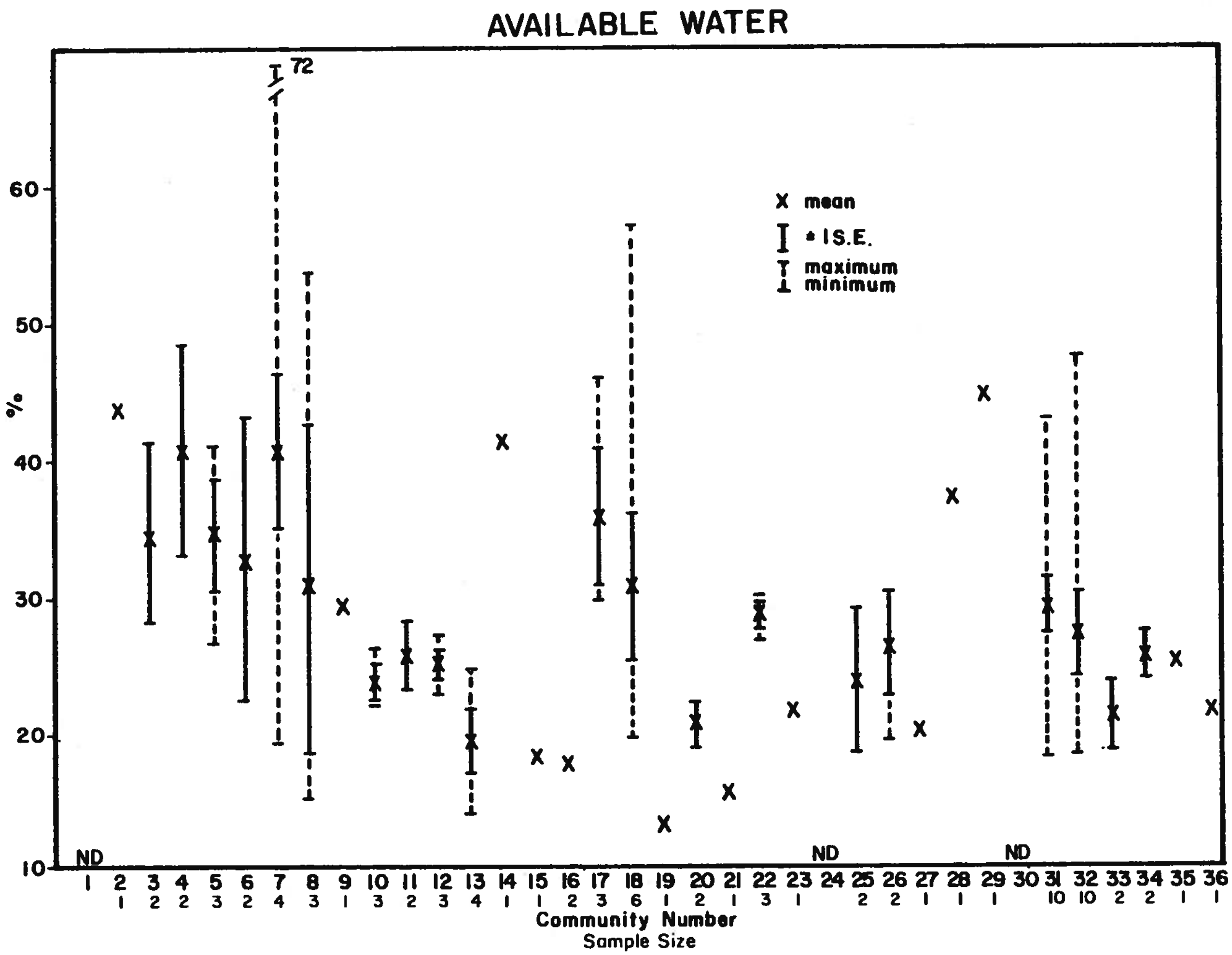

Figure C10. Available water by community.

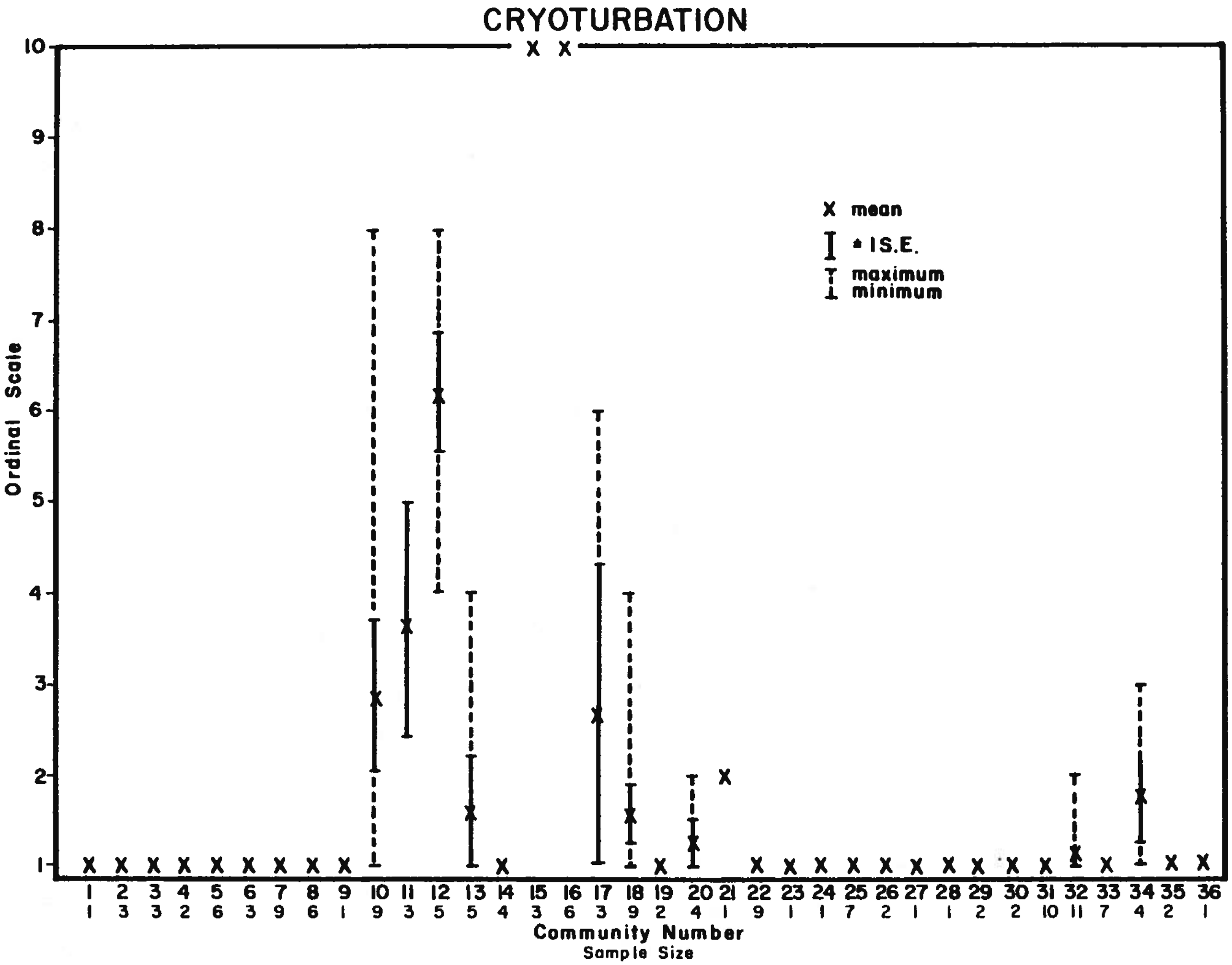

Figure C11. Cryoturbation by community.

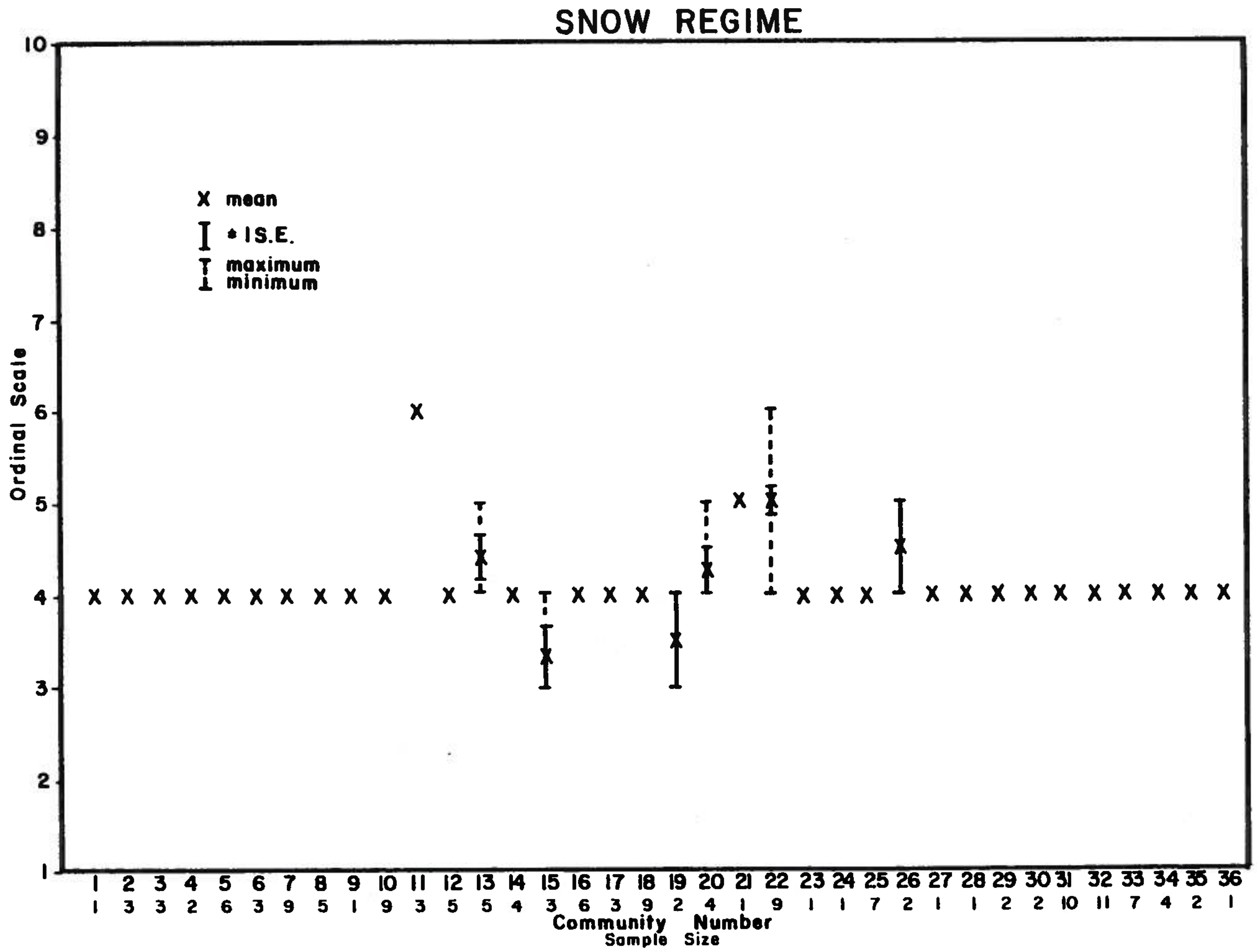

Figure C12. Snow regime by community.

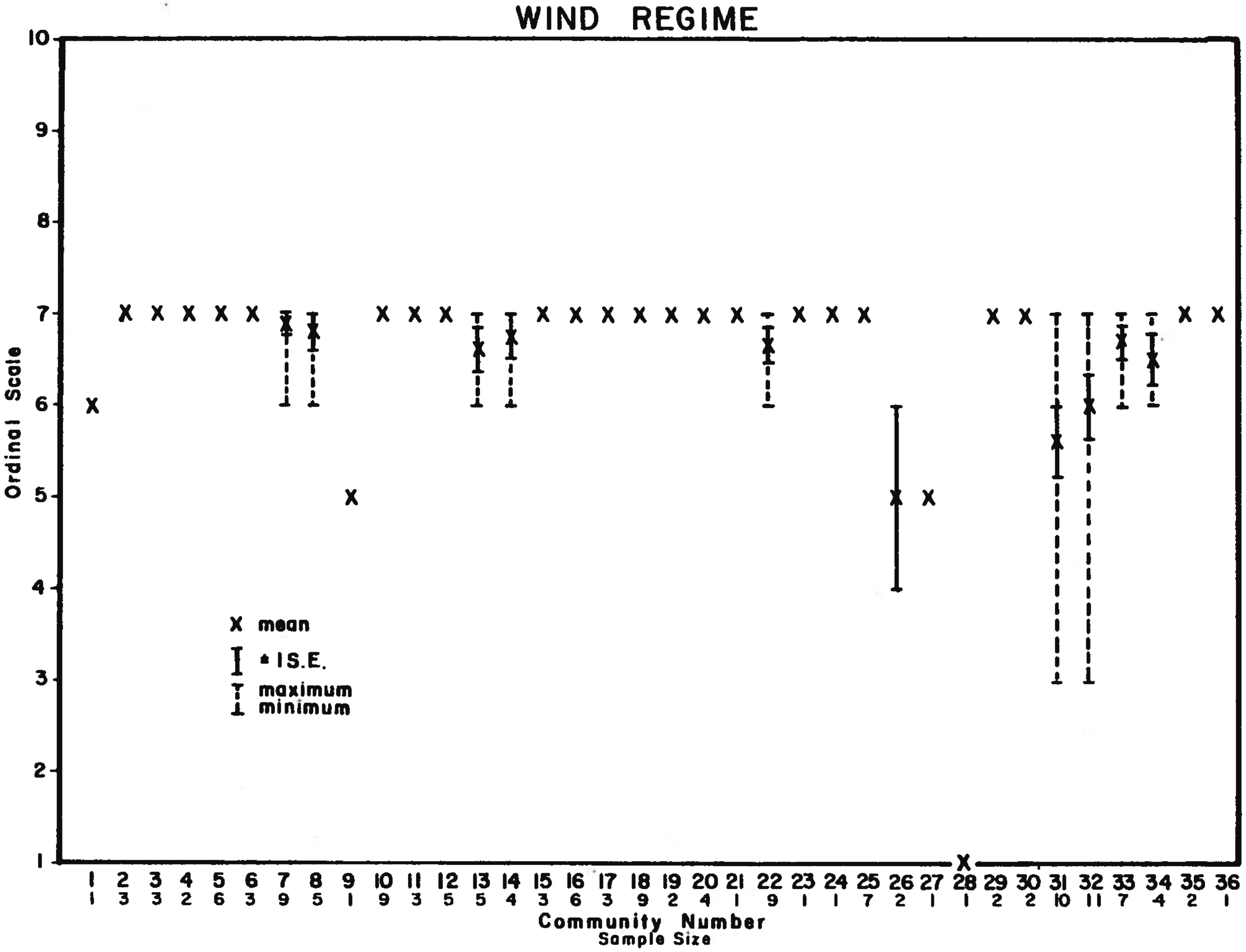

Figure C13. Wind regime by community.

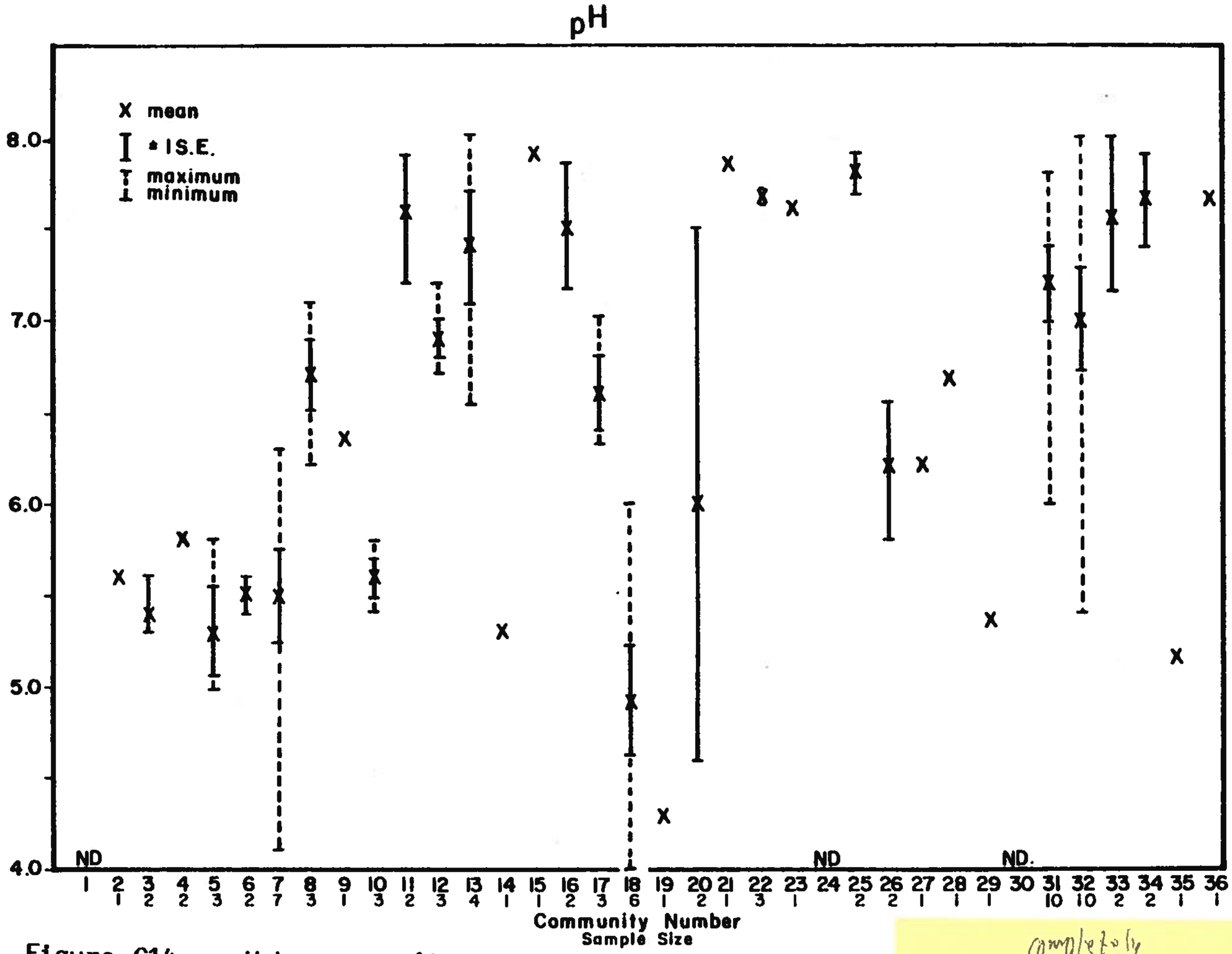

Figure C14. pH by community.

completely
mesic, disturbed
areas
6.8 -8.0

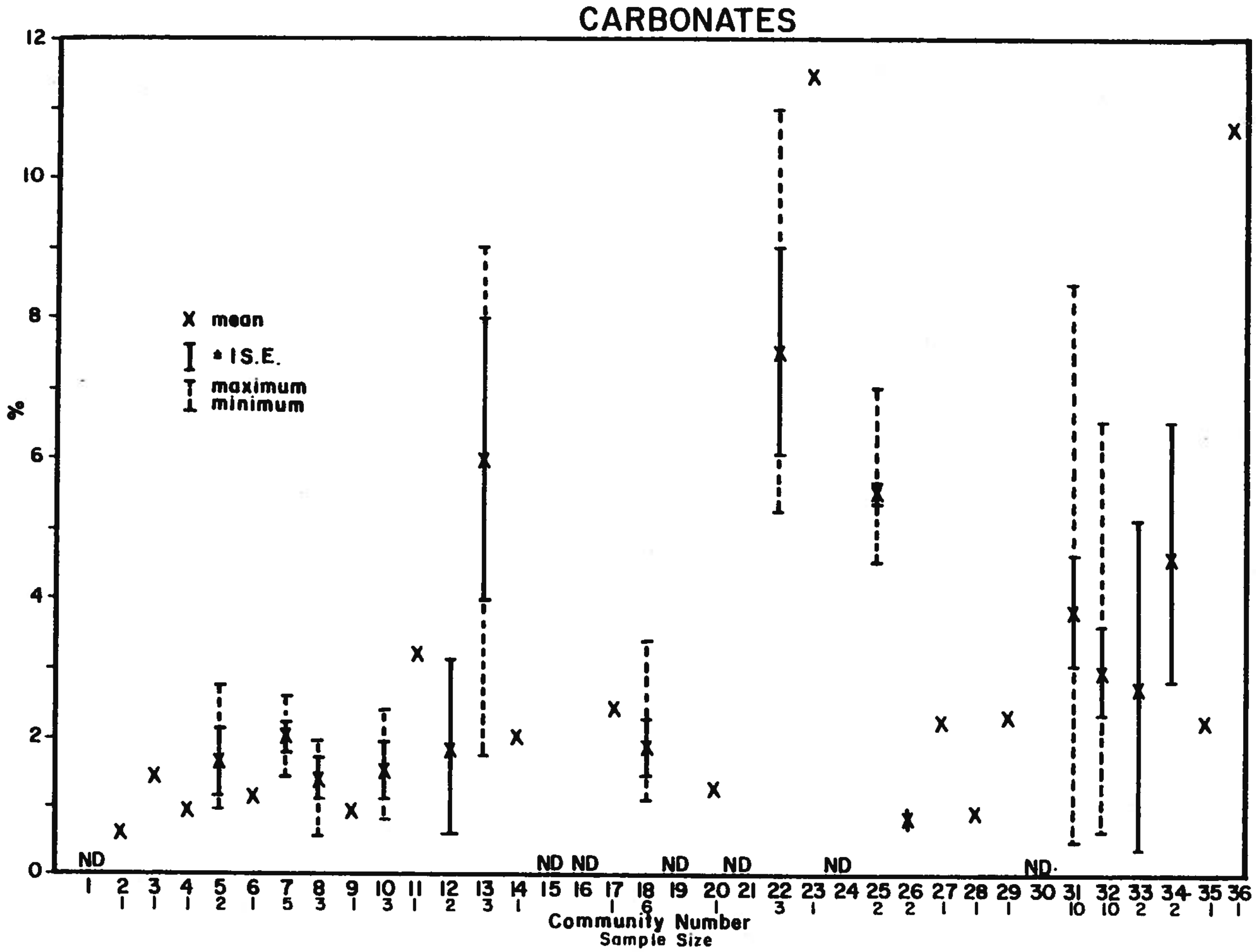

Figure C15. Carbonates by community.

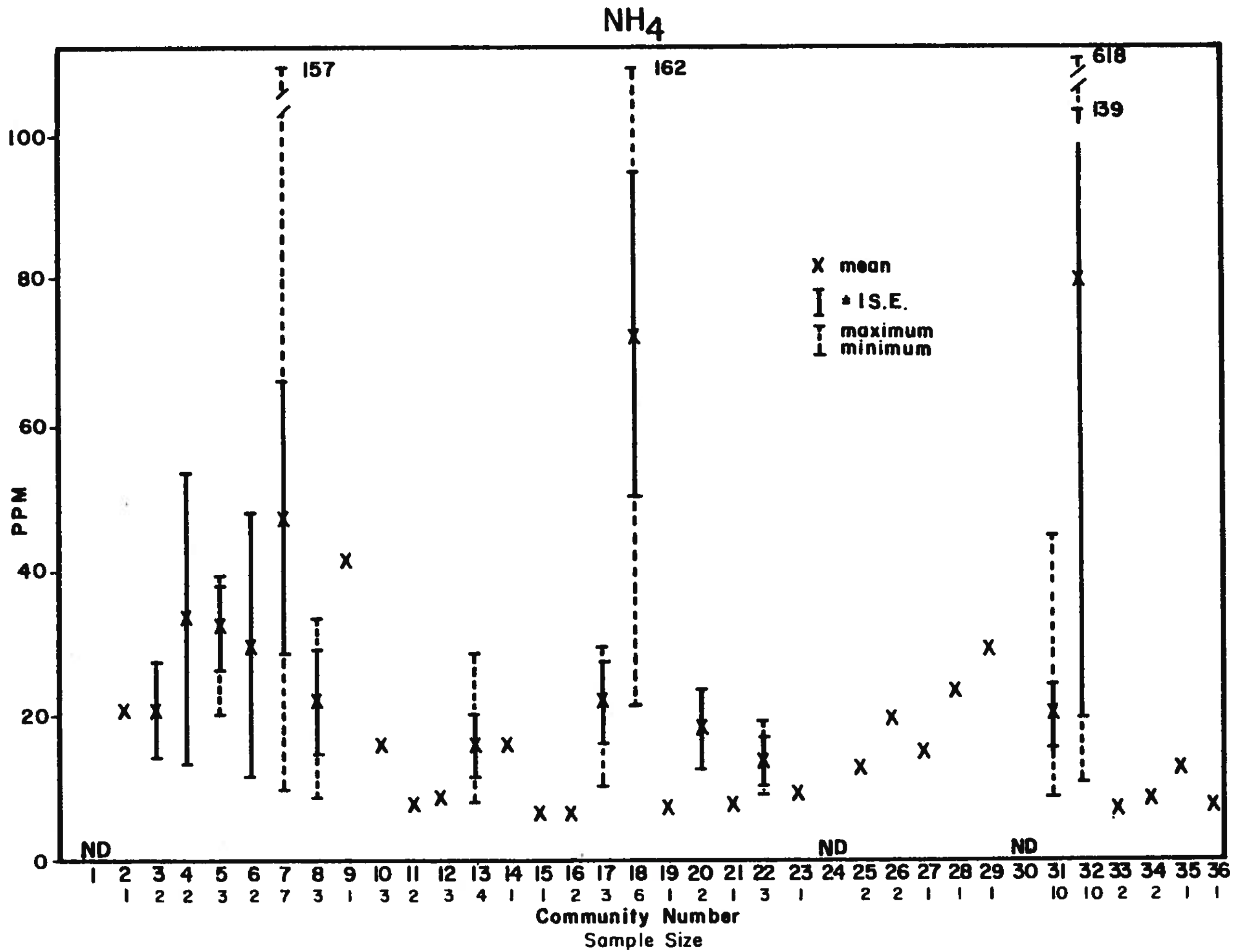

Figure C16. Ammonium by community.

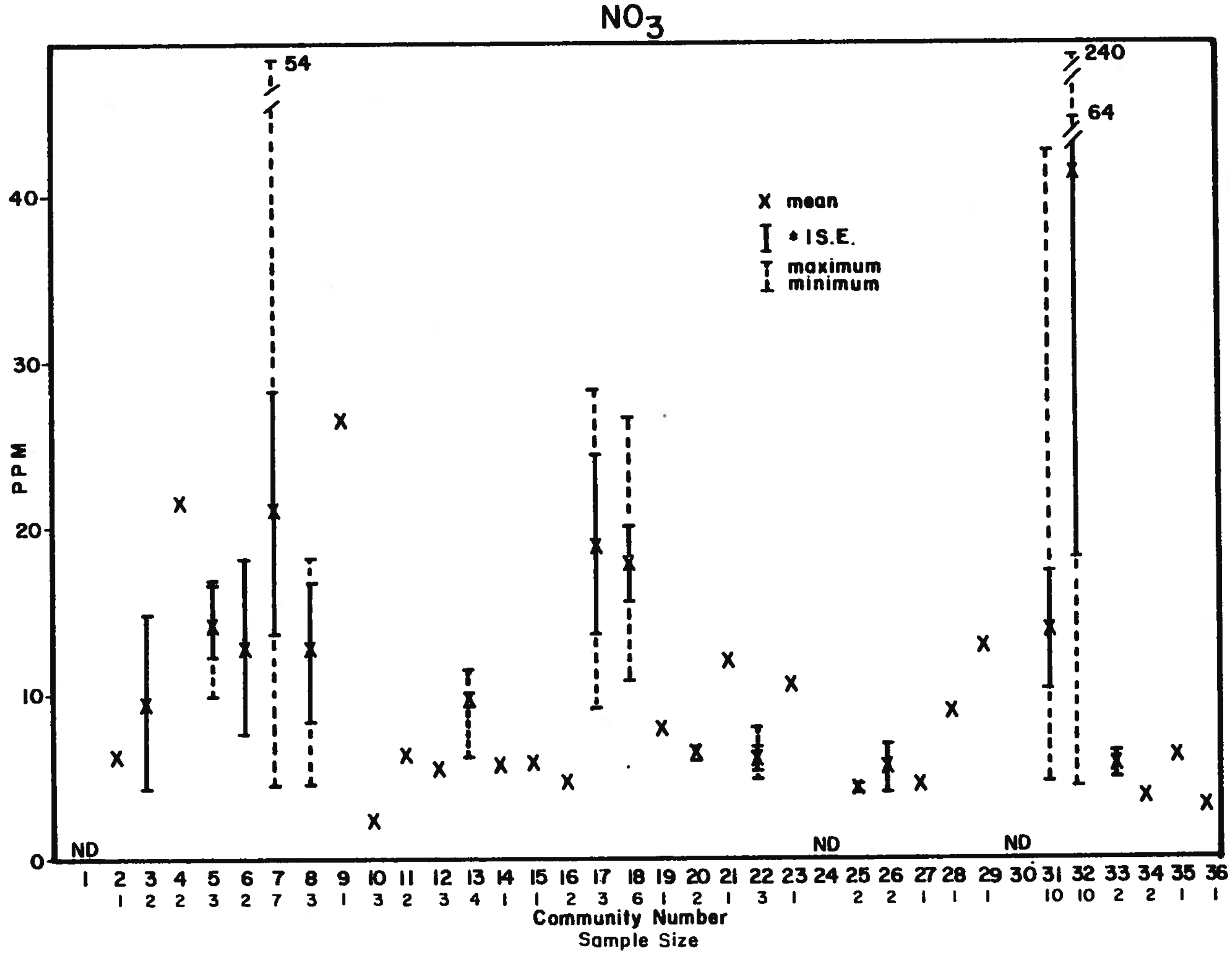

Figure C17. Nitrate by community.

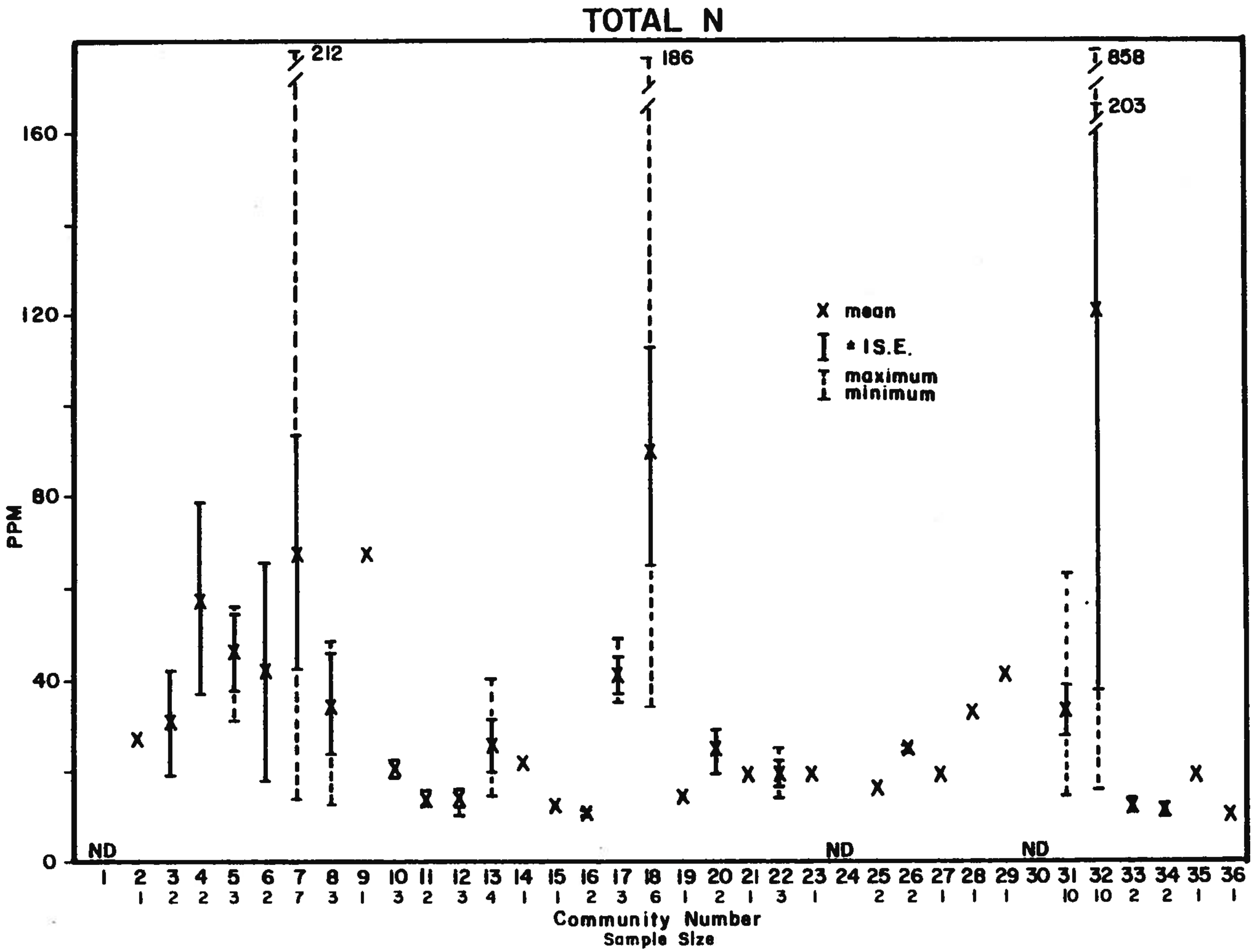

Figure C18. Total nitrogen by community.

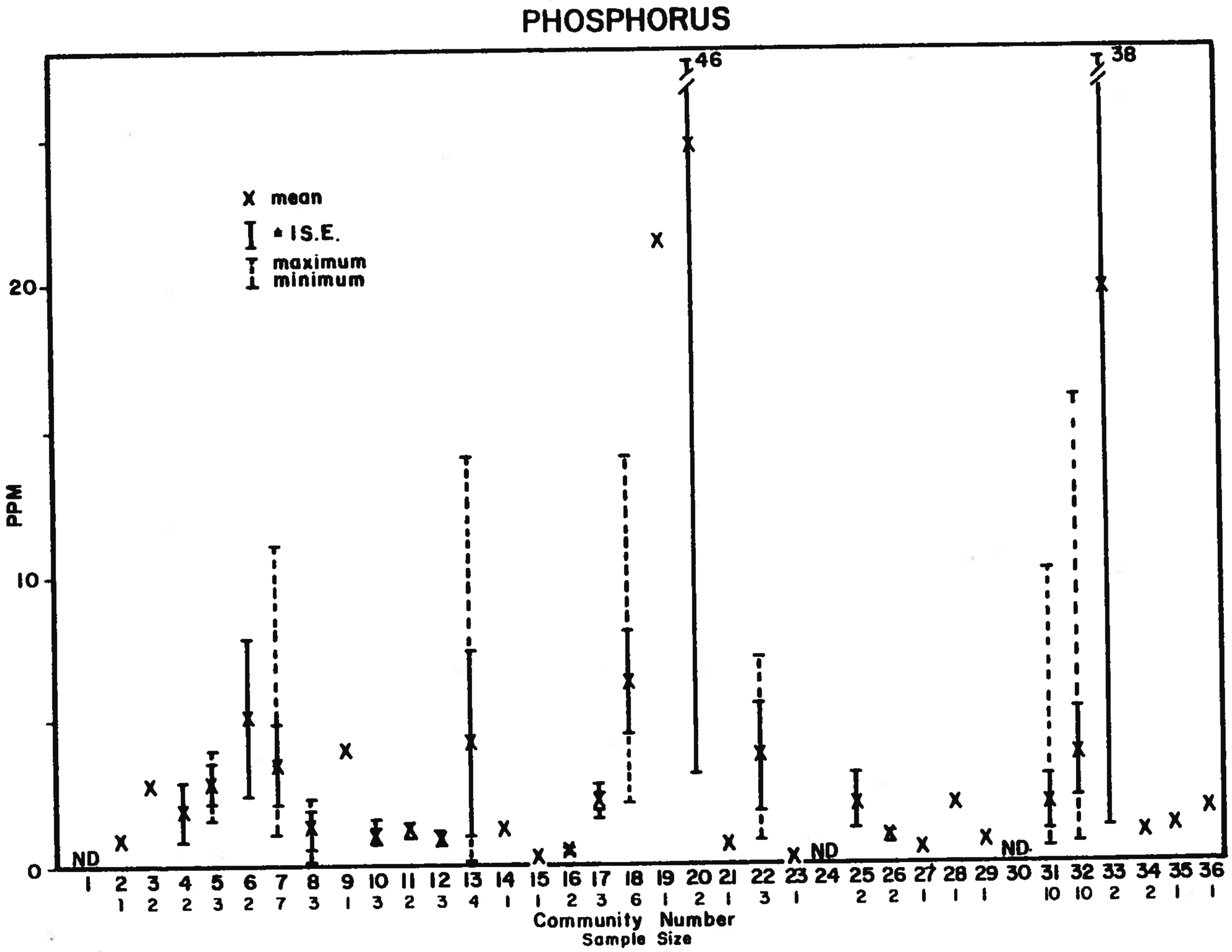

Figure C19. Phosphorus by community.

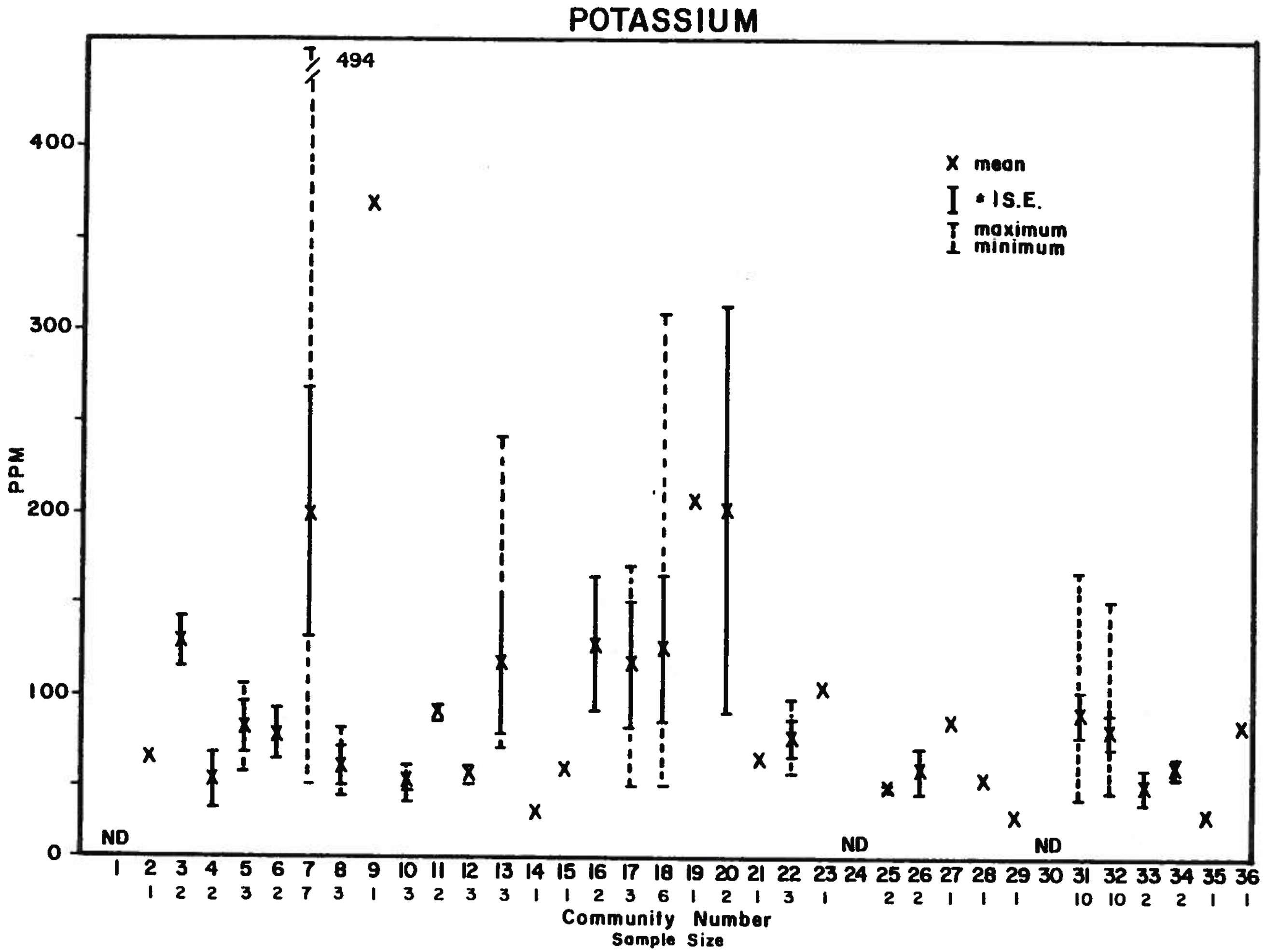

Figure C20. Potassium by community.

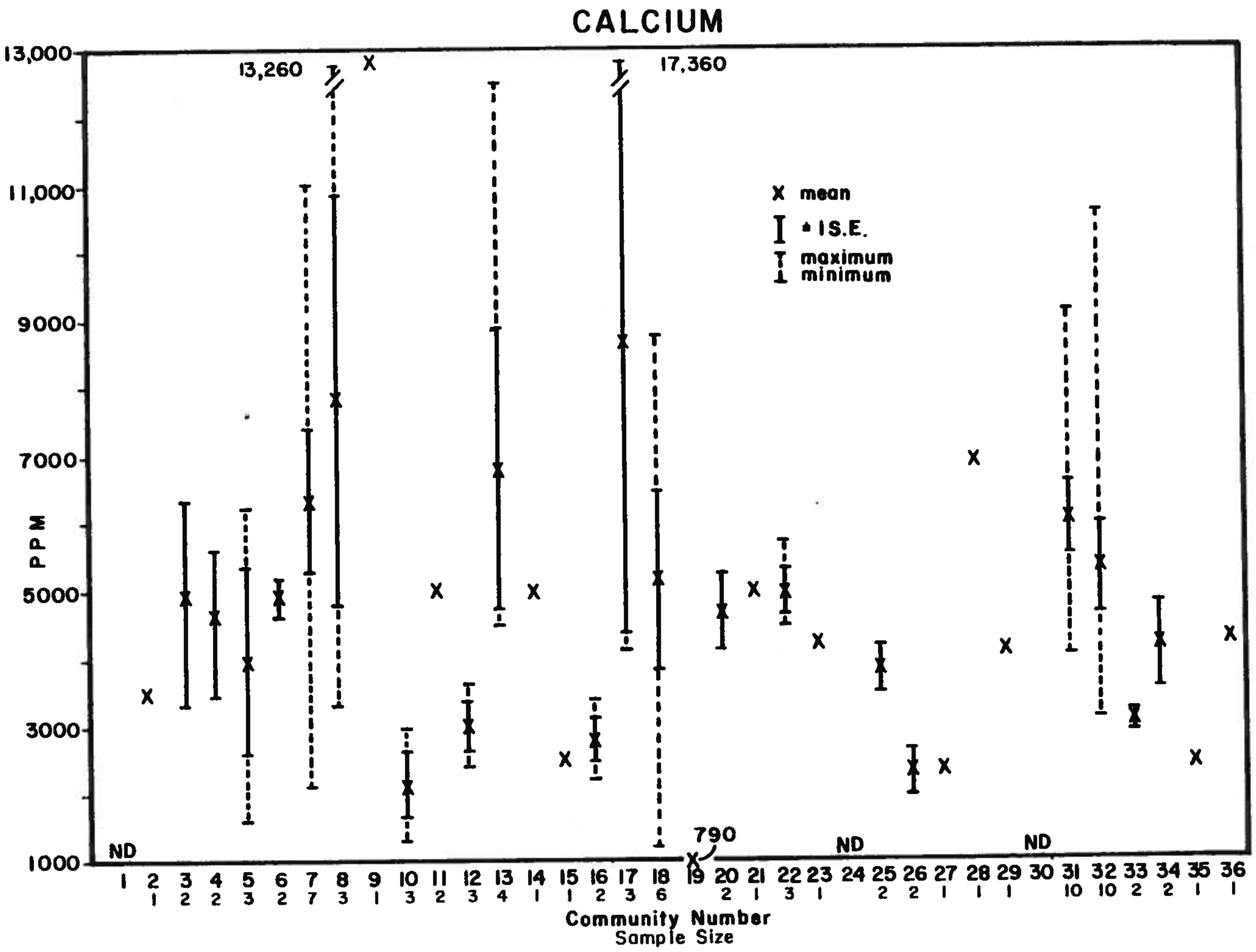

Figure C21. Calcium by community.

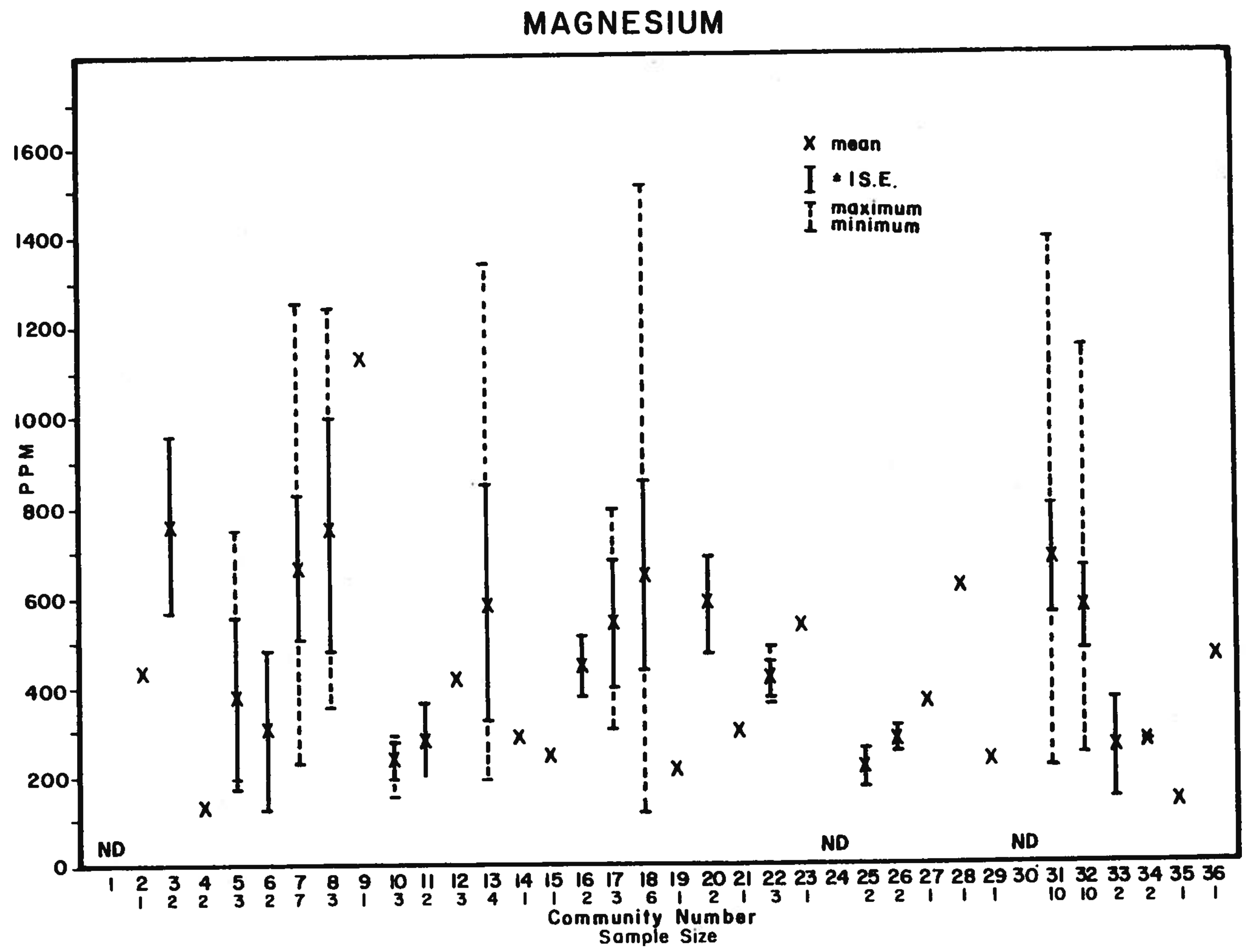

Figure C22. Magnesium by community.

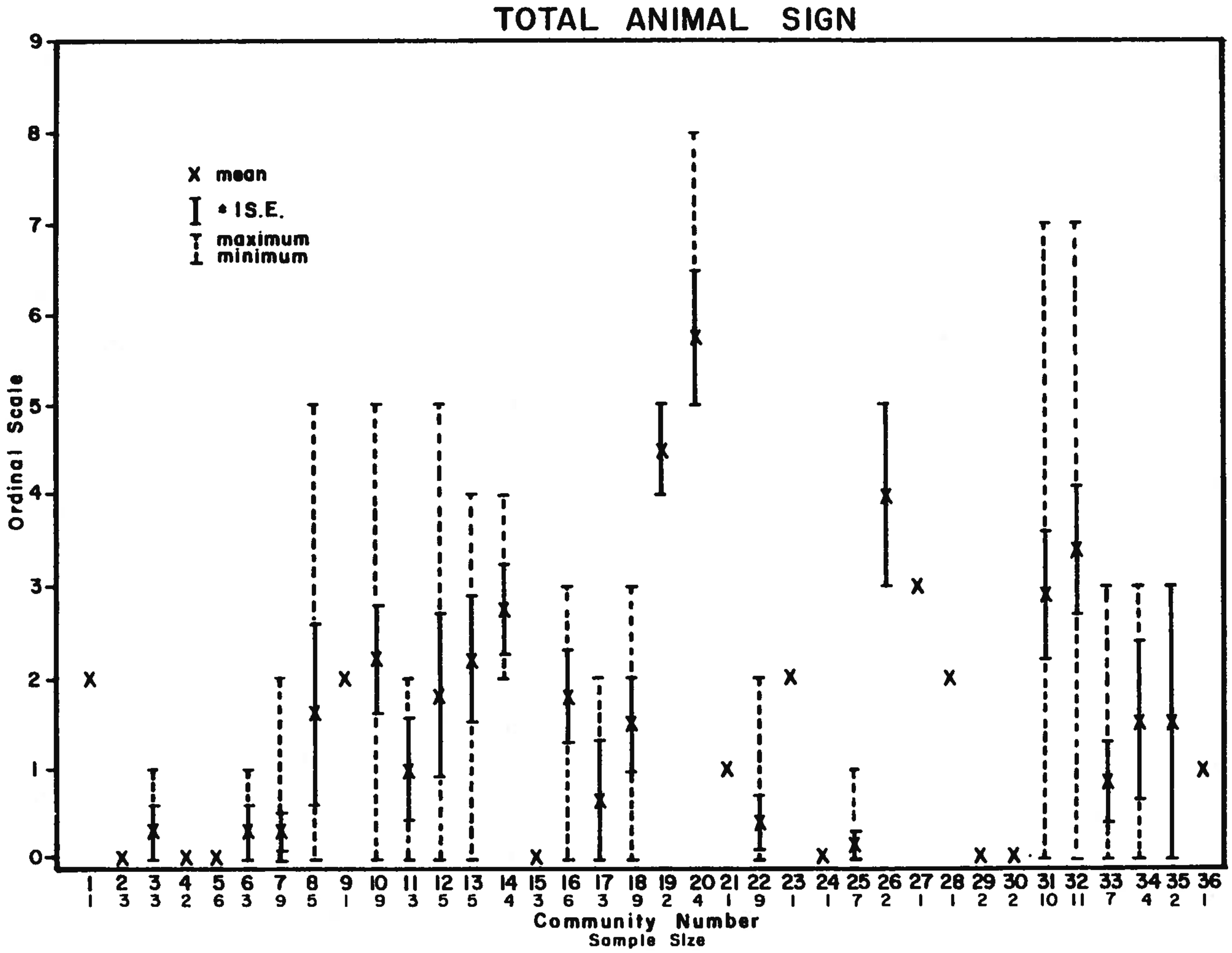

Figure C23. Total animal sign by community.

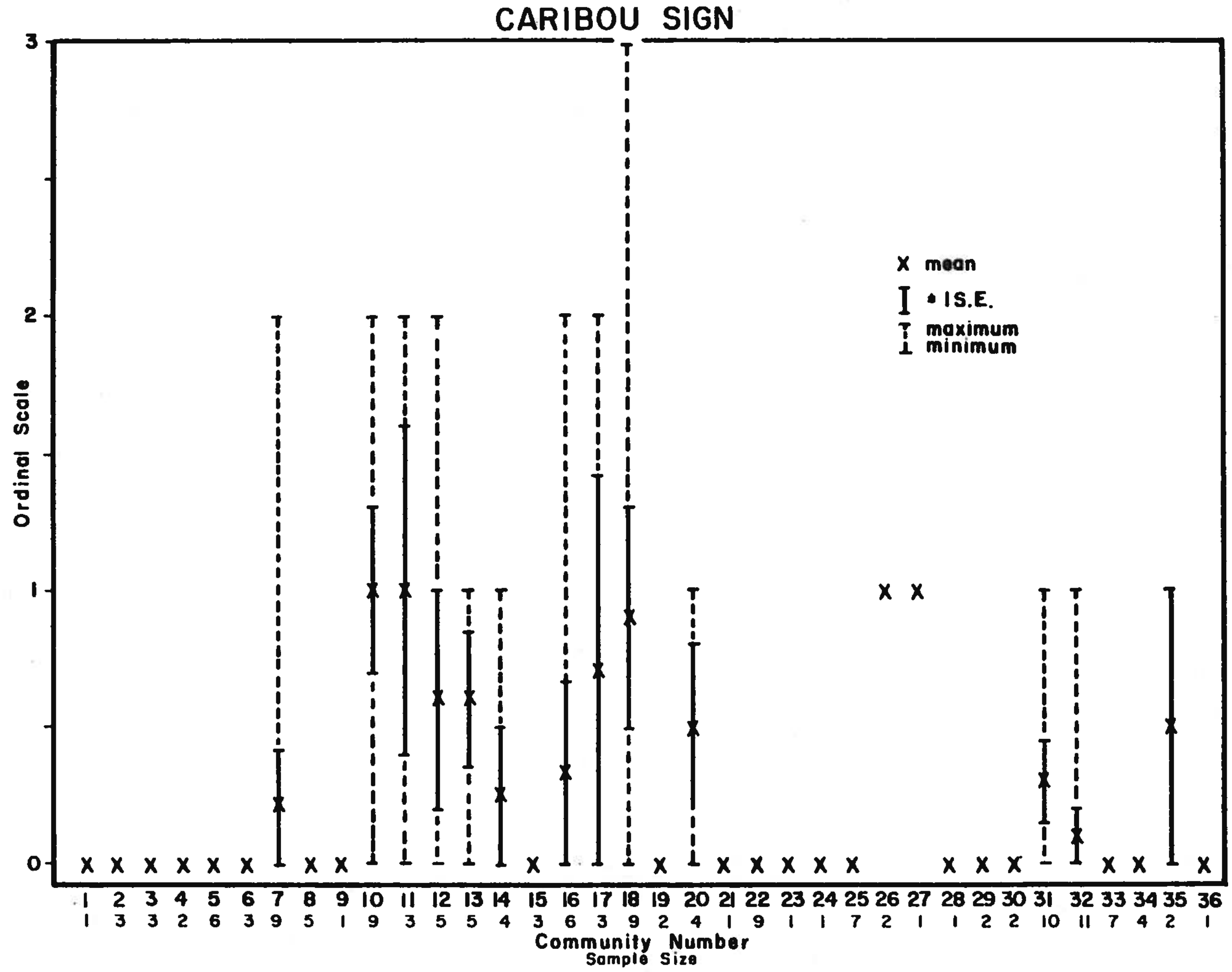

Figure C24. Caribou sign by community.

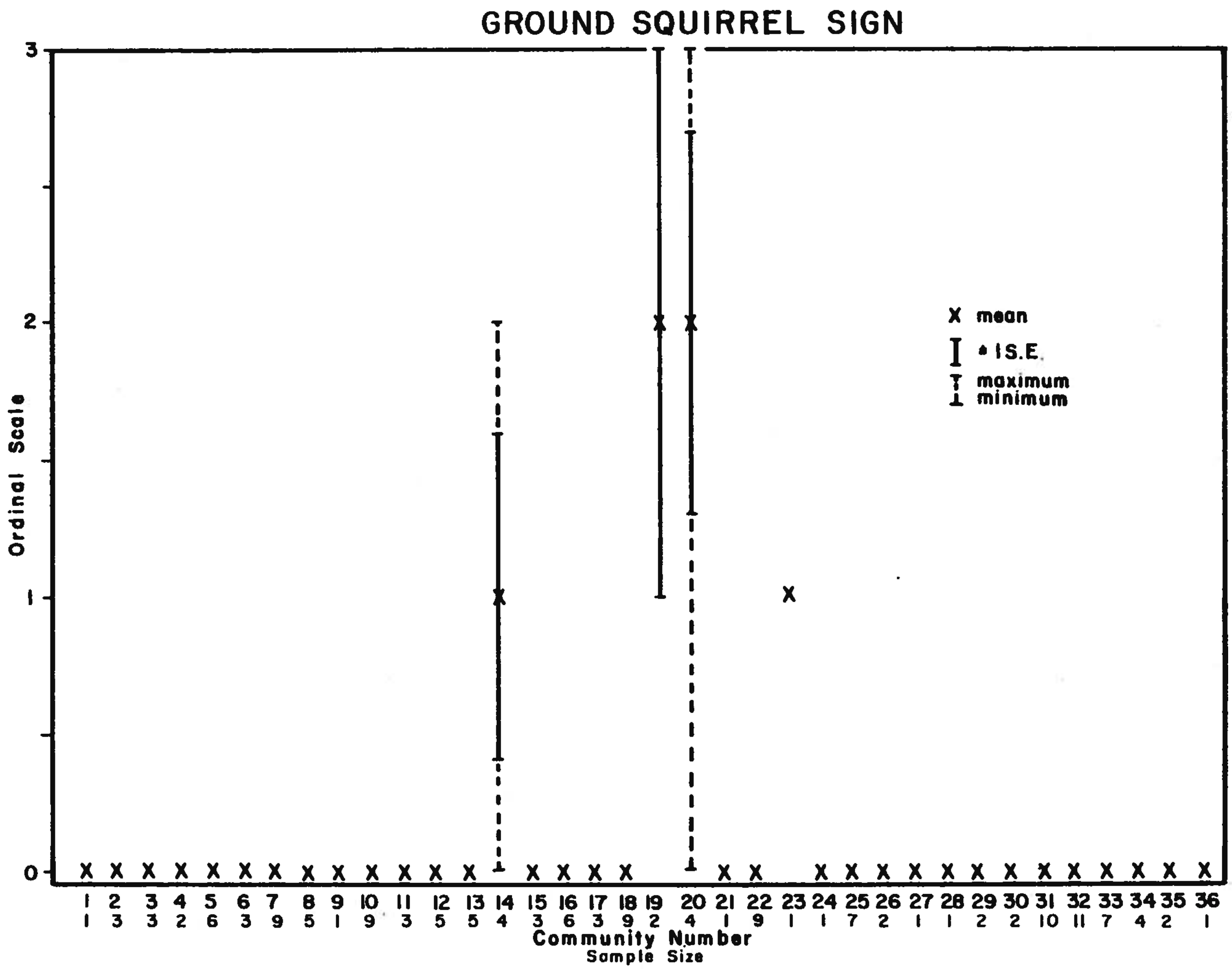

Figure C25. Ground squirrel sign by community.

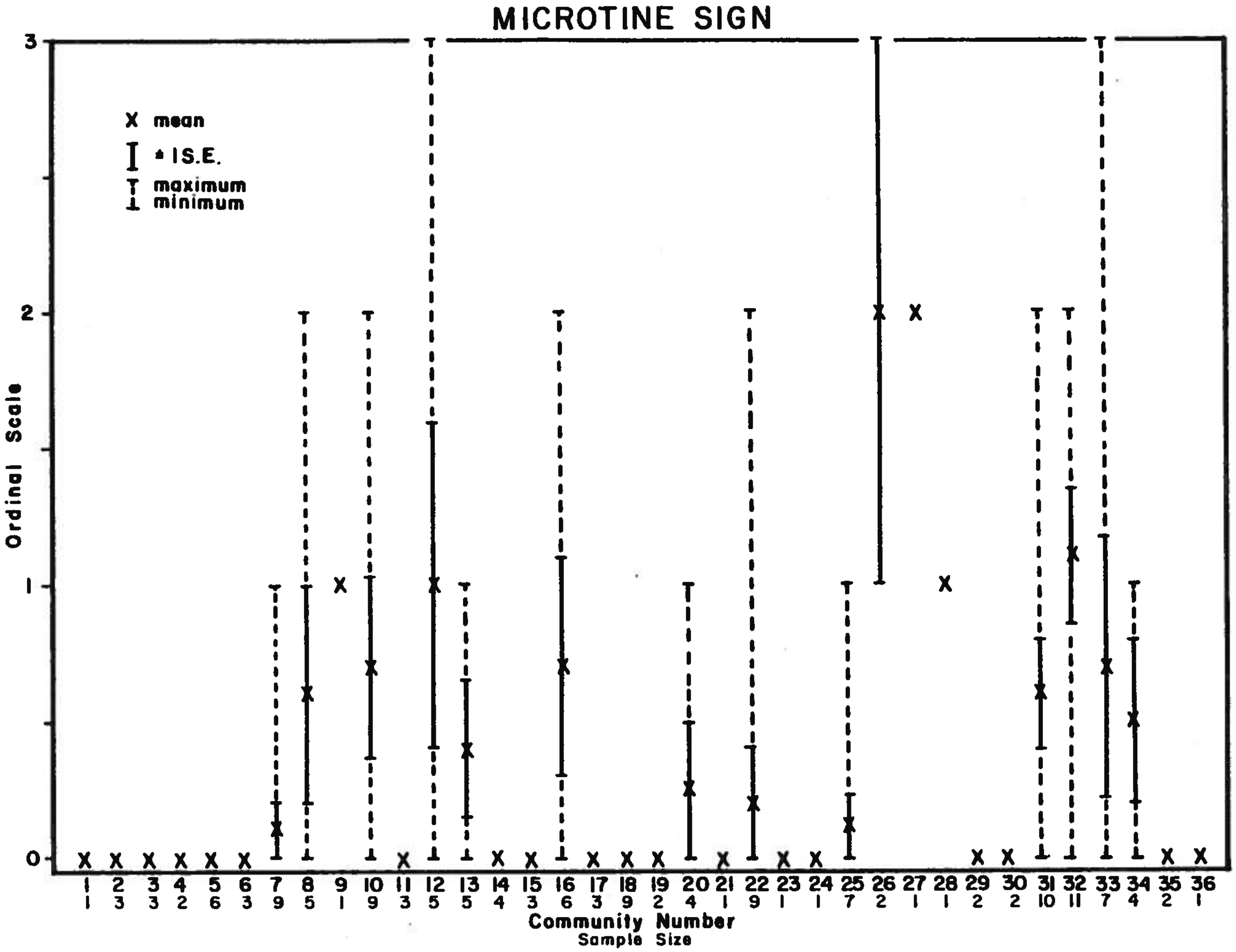

Figure C26. Microtine sign by community.

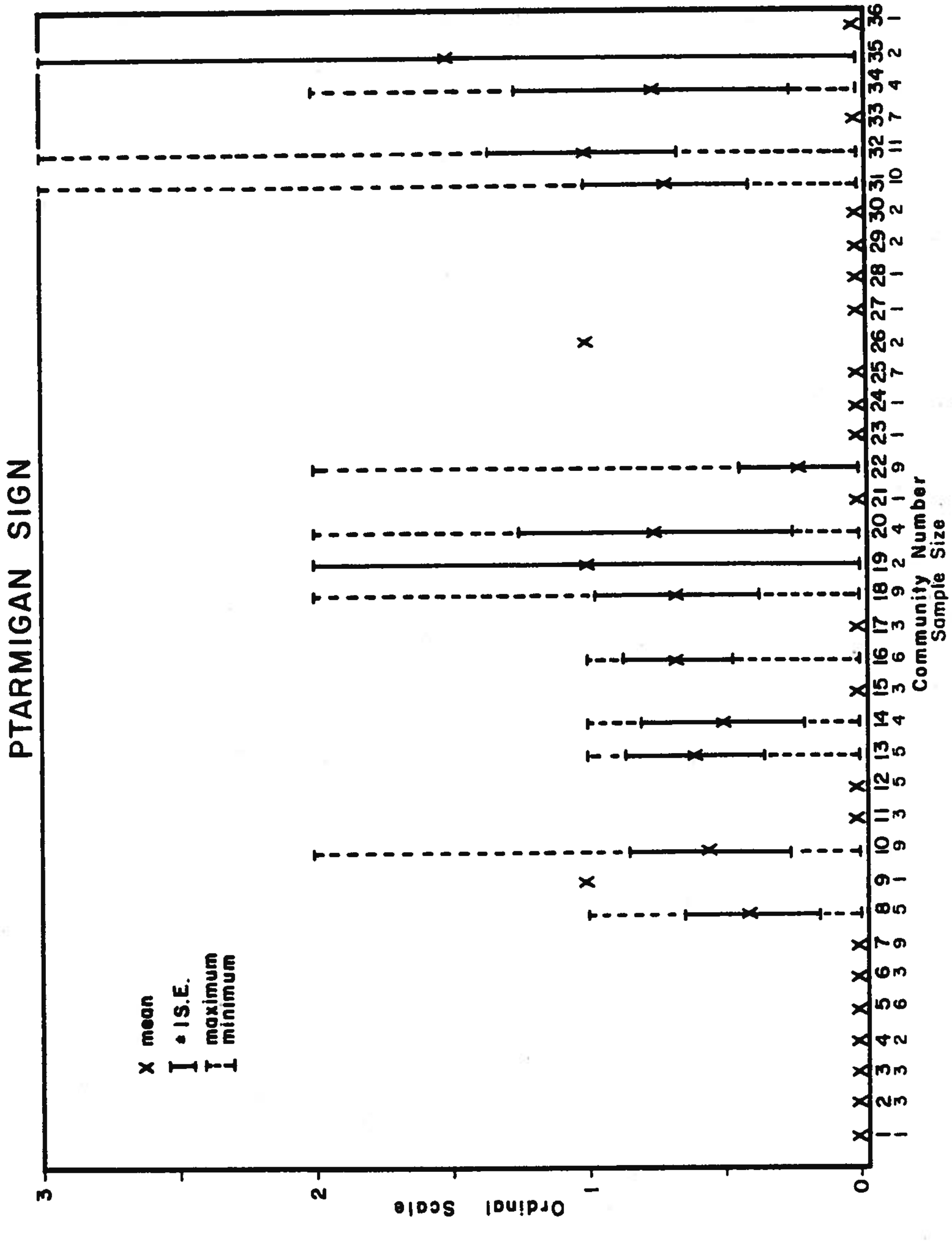

Figure C27. Ptarmigan sign by community.

APPENDIX D

DECORANA COMPUTATIONS

DECORANA is the FORTRAN program that does the computations of detrended correspondence analysis (DCA). DCA is explained from an intuitive approach in Chapter II, Hill and Gauch (1980), and Gauch (1982). The technical details are presented here, and were taken from Hill (1979b).

The first axis is calculated in the same way as in reciprocal averaging (Hill 1973, 1974). From Hill (1979b:3):

> Essentially, what is done is to take a set of species scores, then to define sample scores such that each sample score is the mean score of the species that occur in it, and finally to calculate new species scores so that the score of each species is the mean of the scores of the samples in which that species occurs. If this process, the two-way averaging iteration of reciprocal averaging, is repeated many times, then the scores will stabilize to a final solution which is independent of the initial scores and which has several desirable properties.

Mathematically, this is expressed (Hill 1979b:25):

> Let the data matrix be $A = [a_{ij}]$. Subscript i refers to rows (samples); subscript j refers to columns (species). The basic iteration of reciprocal averaging is to take a trial vector $y = [y_j]$, and to derive a new trial vector y' from it, according to the equations
>
> $$x_i = \sum_j a_{ij} y_j / a_{i.} \qquad (i = 1, \ldots, m)$$
>
> $$y'_j = \sum_i a_{ij} x_i / a_{.j} \qquad (j = 1, \ldots, n),$$
>
> where $a_{i.}$ and $a_{.j}$ are the row- and column-totals
>
> $$a_{i.} = \sum_j a_{ij} \; ; \; a_{.j} = \sum_i a_{ij} \quad \ldots .$$

> Repeated application of the basic iteration will lead eventually to the desired solution, but convergence is slow. At the expense of some rather complicted albegra ..., convergence has been speeded up. The essence of the algorithim ... is to represent the two-way averaging iteration approximately by a 4 x 4 symmetric tridiagonal matrix. The top eigenvector of the four-dimensional approximation is then sought, and used as a trial vector for the next ordination.

The primary difference of DCA from RA is the way in which the axes after the first are calculated. THe DCA technique eliminates the common quadratic relationship of the second axis to the first (Hill 1979b, Hill and Gauch 1980, Gauch 1982). From Hill (1979b:3):

> [In reciprocal averaging] [c]omponent axes subsequent to the first are derived by performing the identical iteration [as for the first axis], but at the end of each iteration taking out a regression on the first axis, so that the new scores are uncorrelated with those of the first axis. To obtain the third axis, we must demand also that the scores are uncorrelated with those of the second axis, etc.

Hill (1979b:26) continues:

> Unfortunately, ... this does not guaranteee that the subsequent axes are unrelated to the first axis. On the contrary, the second axis will often have a strong quadratic relation to it [arch effect].
>
> Detrended correspondence analysis uses a stronger form of detrending, that of taking out the mean in segments of the axis ....

Hill (1979b:3.5) describes the procedure:

1. Start with an arbitrary set of species scores.
2. Construct sample scores so that the score of each sample is the average of the scores of the species that occur in it. (With quantitative data the average is a weighted average, with weights proportional to the abundance of each species.)
3. Detrend the sample scores so that they have no systematic relation to the first axis. This is done by dividing the first axis into segments. Within each segment of the first axis the sample scores are readjusted to have zero

> mean ..., resulting in a detrended set of scores. To avoid edge effects, three separate detrendings are made, with different starting positions for the segments. The final sample scores are derived by averaging those obtained by each separate detrending.
>
> 4. Using the detrended samples scores, calculate new species scores in the usual way--i.e. as in reciprocal averaging--and return to stage 2.
>
> The iteration is continued until the scores stabilize. Finally, the samples scores are calculated by taking the mean species scores (as at stage 2 above), but this time not detrending.
>
> The iteration described above will converge to the second axis. To obtain the third axis, a similar detrending exercise must be applied with respect to the second axis, and so on for the higher axes.

After the axes are calculated, they are rescaled (Hill 1979b:5-6).

> In addition to the arch effect, reciprocal averaging has another fault, namely that the scaling of the axes does not have any clearly defined meaning. Indeed, ... it can scale an axis differently in different parts of the range of the axis. Typically, the ends of the axis are contracted, so that points separated by a given real difference are scaled by the ordination so as to be closer together if they lie at the ends of the axis than if they lie at the middle.
>
> In principle it would be desirable to have species appearing and disappearing at a steady rate along the axis. In practice there are several obstacles to achieving this aim directly, the most notable being that near the ends of the axis it is impossible to determine whether a species has really reached the end of its range, or whether its range has been truncated (either by incomplete sampling, or by a lack of suitable habitats in the world). A more attainable goal is that the species in each sample should on average have unit standard deviation. It is clear ... that the contraction of the scaling at the ends of the gradient is reflected in a reduced within-sample standard deviation. In other words, the standard deviation of the score of the species occurring in a sample is less at the ends of the gradient than in the middle.
>
> Clearly a better scaling can be achieved if those parts of the gradient where the standard deviation is low are expanded and those where it is high are contracted. The rescaling in

detrended correspondence analysis does just this. A local mean standard deviation is calculted at intervals along the gradient (heavily smoothed to avoid effects due to particular abnormal samples), and this is then used to rescale the species. In particular, if two species have scores x and x + dx on the original gradient (dx being a small quantity), and if the local mean standard deviation of samples with scores close to x is s(x), then after rescaling the species scores will be

$$r(x) \text{ and } r(x) = dx/s(x),$$

where r(x) is the rescaled value of x. In other words, the local scaling of the gradient has been multiplied by 1/s(x), with the intention of deriving a new scaling for which the within-sample standard deviation is approximtely unity at all points of the gradient.

It must be stressed that what has been done here is not entirely simple. The aim was to get a scaling of the samples for which there should be an even turnover of the species along the gradient. The way of achieving this was to rescale the species (not the samples) by expanding the local scaling in proportion to the reciprocal of the local mean-square deviation. The new sample scores are taken (as always in DECORANA) to be the mean scores of the species that occur in them.