To the Graduate Council:

I am submitting herewith a dissertation written by David Kent Smith, entitled "Floristic, Ecologic, and Phytogeographic Studies of the Bryophytes in the Tundra around Barrow, Alaska." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Botany.

Aaron J. Sharp, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

FLORISTIC, ECOLOGIC, AND PHYTOGEOGRAPHIC STUDIES OF THE BRYOPHYTES IN THE TUNDRA AROUND BARROW, ALASKA

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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title pg

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ABSTRACT

Floristic, ecologic, and phytogeographic studies of bryophytes were conducted in the tundra around Barrow, Alaska. The bryoflora was studied using both current and past collections from the area. The phytosociological structure of some bryophyte communities was investigated and described from a tundra tract selected for intensive study. Phytogeographic comparisons were made between the moss floras of Barrow and the Queen Elizabeth Islands.

Standard herbarium procedures for the collection, preservation, and documentation of bryophytes were used to survey the Barrow bryoflora. Community structure was analyzed using a restricted random field sample design which surveyed macrotopographic areas of low center polygon, high center polygon, and beachslope tundra. All bryophytes were recorded as present and cover was estimated using a cover-class scale. The bryophyte communities were delineated using an association analysis technique controlled by the test of Chi-square. Communities were compared using a Wisconsin-type ordination to determine if the bryophyte communities were distributed along certain environmental gradients.

A bryoflora consisting of 156 taxa was recognized

for Barrow. Representatives of high arctic, arctic-boreal, boreal, and cosmopolitan bryophyte elements were all found. Sixteen bryophyte communities were distinguished which were classified into three moisture series--hydric, mesic, and xeric. Several mesic communities were considered as transitional types. Ordination suggested that these communities were distributed, in addition to a primary moisture gradient, along nearly parallel gradients of macrotopography and soil acidity. A phytogeographical analysis of the Barrow and Queen Elizabeth Islands moss floras leads to the hypothesis that the Melville-Banks-Victoria Island group may prove to be the richest and most interesting concentration of bryophytes in the Nearctic.

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CHAPTER I

INTRODUCTION

During the summer of 1972 I was fortunate in being selected to participate in the I.B.P. (International Biological Program) U.S. Tundra Biome research effort located at Point Barrow, Alaska. A program was initiated that summer to study the tundra bryophytes especially as they relate to the total structure and functioning of the tundra ecosystem.

The immediate Biome objective was to describe the floristic and structural composition of the bryophytes in an area of moist meadow tundra. The effort was in cooperation with a number of other projects which collectively represented an intensive study designed to fashion a dynamic model of the Barrow tundra.

Shortly after the project began it became apparent that the description being prepared for the bryophytes was based upon an inadequately known bryoflora which was little understood. This situation prompted the present investigation.

Aims and Limitations

Two aspects of the bryophytes in the Barrow tundra

were investigated and the results are reported here. First was a need for as complete a record as possible of the bryophytes found in the Barrow tundra. With the completion of this portion of the investigation, the second phase was initiated, an ecological study designed to investigate and objectively classify bryophytic communities with regard to certain dominant micro-relief features in the Barrow landscape.

There are a number of advantages and disadvantages in using bryophytes for vegetational pattern analysis. Both are inherent in the small-size range of bryophytes as compared to larger more conspicuous vascular plants. Bryophytes occupy less space than vascular plants on an individual basis. Therefore, in the case of restricted species, their microenvironmental "niche" is well-defined, as opposed to species more or less unrestricted by habitat which show adaptations to a broad range of microenvironmental conditions. Nevertheless, bryophytes provide a natural system of related organisms at a high level of resolution for examining terrestrial vegetation. However, their small size also becomes a great liability in vegetational studies because identifications are often difficult, especially since specimens acquired during normal sampling often lack structures and features necessary for accurate identification. Also, the use of

bryophytes for the characterization of vegetation in most regions of the world would be a rather inane exercise.

In regions of middle and low latitudes it is often difficult to interpret the role of bryophytes with regard to total community structure and function. This is mostly due to the number of habitats occupied by mosses and liverworts and their relatively low contribution to biomass and cover in the community. For this reason many studies from temperate regions have been restricted to particular habitats where bryophytes occur on rocks, trees, and soils. Any study seeking to consider all habitats in a forest, for instance, would be a forbidding task.

In many ways high arctic tundra is structurally less complex than vegetation of boreal, temperate, and tropical zones. There exists an incomplete overstory of vascular plants consisting of sedges, grasses, forbs, shrubs and subshrubs but nowhere as dominating or stratified a canopy as found in forested ecosystems. Of the plants comprising the vascular canopy, many are small. Epiphytic bryophytes are virtually absent and occur only in the lower arctic zones. Instead, the bryophytes are monosynusial, mixed with lichens as a prominent often unbroken understory or not uncommonly

replaced by reduced herbs and colonial soil algae.

Bryoecological investigations conducted in the tundra biome are more relevant to large-scale interpretations of the vegetation since bryophytes are the dominant vegetational component of much of the tundra. A second advantage for using the tundra as a natural laboratory permits the application and testing of new methods in the study of bryocoenology, since tundra is the only biome where bryophyte diversity is both high and concentrated into a single synusial unit of the vegetation.

At Barrow the bryophyte component of the vegetation is often the dominant standing crop and covercrop in designated localities. Some communities of mixed vascular-bryophyte-lichen composition net the highest annual productivity in the bryophyte portion. Besides the proportional community relationships of the different plant forms which comprise the tundra, the bryophyte synusia has a greater importance in the Arctic than in other zonal ecosystems. This alone is the most marked advantage for studying the bryophytes at Barrow.

Among the disadvantages in using bryophytes for vegetation pattern analysis, certain species identifications and appropriate measures of community are the most limiting. Both of these were encountered in this study.

Problems in identification to species were numerous, mainly because no comprehensive regional flora exists for arctic bryophytes and little has been resolved concerning the known variation exhibited by arctic mosses and liverworts. As a result, the arctic bryoflora is poorly understood. This is a bit paradoxical since the flora itself is probably as well-known as any large region. The variation exhibited by etiolated, reduced, and morphologically odd forms of Arctic species is unmatched elsewhere.

Owing to their small size any effort to describe the bryophyte vegetation requires a slightly different approach than that used in macrovegetational descriptions. The study area must be definably small. This requires a carefully thought-out sample design if quantitative descriptions are desired. Bryophytes do not usually show a high degree of randomness in their distributions, but more often occur in swards, cushions, and mats of pure to slightly mixed species. Often the selection of an adequate sample size is more difficult since criteria, such as minimum area, are not necessarily a good measure of community dimension.

In measuring and describing plant communities, bryophytes are also quite difficult to report both accurately and meaningfully. Many of the preferred

methods for measuring macrovegetation such as total standing biomass, annual productivity, density, basal area, and foliar cover by species, are nearly impossible and usually impractical to use as measurements of bryophytic vegetation. Of the above, cover estimates based upon cover class scales have been useful, but the most often employed technique utilizes presence data and re-expression of it as frequency or constancy.

This study can only begin to probe the complexity of the bryophyte communities at Barrow but hopefully provides a necessary point of departure for future investigations and subsequent comparisons between Barrow bryophytes and those of other tundra areas. Perhaps insights gained here will ease the task of future studies allowing a more expeditious assessment of tundra bryophytes and therefore more complete knowledge of habitats, areas, and regions.

By no means should one consider that future bryological investigations would be unworthy at Barrow. This study should be considered a launching pad for additional studies designed to probe into floristic and ecological relationships in the Barrow bryoflora. Obvious areas still in need of study and not treated here involve taxonomy, physiology, autecology, and succession of bryophytes in tundra ecosystems.

Discussion of Selected Literature

A tremendous reservoir of bryological literature exists for subarctic and arctic regions of the world. Many of the more celebrated workers and their contributions have been ably discussed by Steere (1954a, 1971) in his reviews of arctic bryology. Therefore, it is unnecessary to recreate a chronicle of early bryological explorations and achievements in arctic regions. Most of the achievements have resulted from regional floristic treatments which out of necessity have touched upon the taxonomy, phytogeography, and descriptive ecology of arctic bryophytes. Of these three areas, bryoecology has been the least studied.

Within the Nearctic the high arctic North Slope of Alaska remained unknown bryologically until the last two decades. This area referred to by Hultén (1941) as the Arctic Coastal District of Alaska is an expansive area of coastal and continental tundra. The southern boundary of this district is marked by the mountainous divide of the Brooks Range and associated mountains. This broad drainage plain which extends north to the Beaufort Sea is bounded on the west at Cape Lisburn by the Chukchi Sea and extends east more than 600 miles to the delta region of the MacKenzie River of northwestern Canada.

Our knowledge of the bryophytes specifically from the Arctic Coastal District is due to the efforts of two highly regarded bryologists, William C. Steere and Herman Persson. As recently as 1951, Steere made his first visit to the North Slope of Alaska. Since then much of his work has focused on the interior foothill and montane provinces where he has found a number of interesting bryophytes (Steere, 1953a,b, 1956, 1958a,b,c, 1960; Steere and Schuster, 1960). The contributions of Persson (1962, 1963) are particularly valuable because his expertise with the European flora has recognized a number of species in the Alaskan Arctic which otherwise might have been misidentified.

Practically nothing has been reported in the literature which specifically enumerates the bryophytes known to occur in the Barrow vicinity. This is somewhat surprising since the establishment of the Arctic Research Laboratory (currently, Naval Arctic Research Laboratory) in 1947 has been the arm of support for other investigations on the North Slope of Alaska. Furthermore, besides Steere, other bryologists have visited and collected in the Barrow tundra. Their collections have not yet been reported in the literature.

Rastorfer (1972) presented the first species list for Barrow. Although his checklist merely sequenced the

earlier reports of Steere (1954b) and Persson (1962, 1963), it brought together for the first time a bryoflora consisting of 62 mosses and 10 hepatics. Subsequent to Rastorfer's list and in association with the U.S. Tundra Biome effort at Barrow, the University of Alaska Herbarium has provided a computer listing of all the bryophytes reported for Barrow and vicinity. Since this list is a compilation of published, communicated, and herbarium sources, it is considered preliminary to this study.

Besides the few cited papers concerning just Barrow, several reports from adjacent areas contain some pertinent floristic and ecologic information. These include discussions on the bryophytes found in the adjacent areas of the central Alaska-Yukon territories (cf. Persson, 1962; Persson and Gjaerevoll, 1957). Steere (1958d) reported on a collection of bryophytes from the MacKenzie River Delta. A small collection of bryophytes from Little Diomede Island in the Bering Strait was also reported by Steere (1938). The findings of Johnson, et al., (1966) in the report of the Cape Thompson Project have received little attention since they came into print. Although the vegetation descriptions do not rely heavily upon the bryophyte data, the list of approximately 100 species is phytogeographically important.

In the Canadian eastern Arctic where most nearctic bryology has been centered, several studies are particularly noteworthy. Our knowledge of the hepatic flora there is due to the fine pioneer work of Schuster (1951, 1959). Initially the mosses were admirably discussed by Steere (1948). Steere's early work on northern Ellesmere Island (Steere, 1959) has only recently been improved upon by Brassard (1971a,b). Numerous small papers have dealt with floras of other Canadian Arctic Islands. Reference to these may be found in the bibliographies of the above cited articles.

Studies of bryophytes which are aimed directly at their ecology are rather sparse in the literature dealing with the American Arctic. Brassard (1971a) has discussed 20 visually-grouped moss communities from northern Ellesmere Island. Holmen (1955) briefly described 21 bryophyte communities from Pearyland, Greenland. Recently, Rastorfer, et al., (1973) investigated the bryophytes of selected habitats at Prudhoe Bay, Alaska. They ordered a number of moss and hepatic species into a continuum using visually determined direct gradient analysis of the moisture-topography patterns. A similar analysis of the bryophyte vegetation in the Truelove Lowland, Devon Island (Pakarinen and Vitt, 1972) distinguished streamside, hydric meadow, and mesic meadow habitats. The most obvious

character of arctic-alpine bryophyte communities is that their structural organization appears closely associated with moisture gradients.

Much more descriptive ecology of bryophytes has appeared in foreign literature, especially from the Scandanavian countries of Europe. This is not surprising since these areas have a long history of western civilization and much of their terrain is arctic-alpine. The form which most European studies follow is best illustrated by three notable papers (Hesselbo, 1918; Gjaerevoll, 1950; Mårtensson, 1955, 1956).

In his monumental treatment of the bryophytes of Iceland, Hesselbo (1918) discussed all the species known at that time from the island. Discussions of communities were divided according to lowland and highland formations with an internal arrangement of communities along moisture gradients. Species were discussed as to their membership in groups forming different distributional categories: ubiquitous, meridional, boreal, and alpine. Also, species were mapped by their occurrence in altitudinal zones and geographical districts on the island. Measurements on the abundance of each species were made using a "frequency" scale.

Gjaerevoll's study of the snow-bed communities in Swedish Lappland (1950) was an endeavor similar to that of

Hesselbo, although he worked within a smaller area. Gjaerevoll was more quantitative by his use of a coverage scale to estimate the performance of various species within communities. Communities were ordered into several series corresponding to soil moisture and pH. These were then classified as communities rich in calciphiles or poor in calciphiles.

Mårtensson's work (1955, 1956) in the strict sense was not intended as an ecological treatise. His treatment, a comprehensive listing of the bryoflora of Tornetrask, Swedish Lappland, is a massive compilation of information from extant collections which incidentally contains a wealth of descriptive information.

Since the early 1950's a number of indirect (objective) methods for the study of vegetation have been developed and widely used by plant ecologists studying macrovegetation. Shimwell (1971) discusses the development of these techniques in three directions: (1) similarity measurements which can be presented as matrices, plexuses, or constellations, (2) ordination techniques which allow geometric comparisons, and (3) factor analysis where samples are located in an n-dimensional hyperspace. The latter two are generally considered multivariate techniques which allow simultaneous comparisons of more than two factors.

The use of multivariate techniques to investigate bryophyte vegetation has been rather limited so far (Watson, 1960; Proctor, 1967; Yarranton, 1967a,b,c; Beschel and Matveyeva, 1972; Bryant, et al., 1973). The study of Beschel and Matveyeva (1972) is particularly valuable to this study. They investigated tussocky tundra in Western Taimyr, Russia. Principal components analysis of vascular plant, bryophyte, and lichen cover indicated that the greatest amount of information about the vegetation was reflected in the patterns of distribution of the bryophytes.

The method used here for defining the bryophyte communities at Barrow is a hybrid technique which utilizes a system of objective classification originally described by Goodall (1953) and a comparison ordination technique of the Wisconsin School of phytosociology (Bray and Curtis, 1957). The use of these techniques together is apparently new to the study of bryophyte communities. The application of these techniques appears to have considerable value for the interpretation of the most obvious factors which affect bryophyte community organization.

CHAPTER II

THE BARROW REGION

Point Barrow (71° 23' N., 156° 30' W.) is the northernmost point on the Arctic Coastal Plain Province of Alaska (Figure 1). The Point is a gravel bar which extends about 4 miles northeast beyond the major portion of land. Eight miles southwest of the Point, along the mainland fronting the Chukchi Sea are the Eskimo settlements of Browerville and Barrow. Today approximately 2,500 Eskimos are permanently settled. About 2 miles north of the Browerville-Barrow villages is the Naval Arctic Research Laboratory. The tundra just south of the Laboratory is the location of the U.S. Tundra Biome intensive study site and the area most heavily studied in the present investigation.

Located approximately 500 miles north of the Arctic Circle, Barrow is well within the permafrost zone. The permafrost immediately inland from Barrow is among the thickest known. Leffingwell (1919) estimated the depth at 1,140 feet based upon determinations from the Schergin shaft in Yakutsk, Siberia, in 1828. Brown (1967) reported the permafrost thickness at greater than 300 meters. Other reports indicate the depth at between 1,300 and 1,330 feet

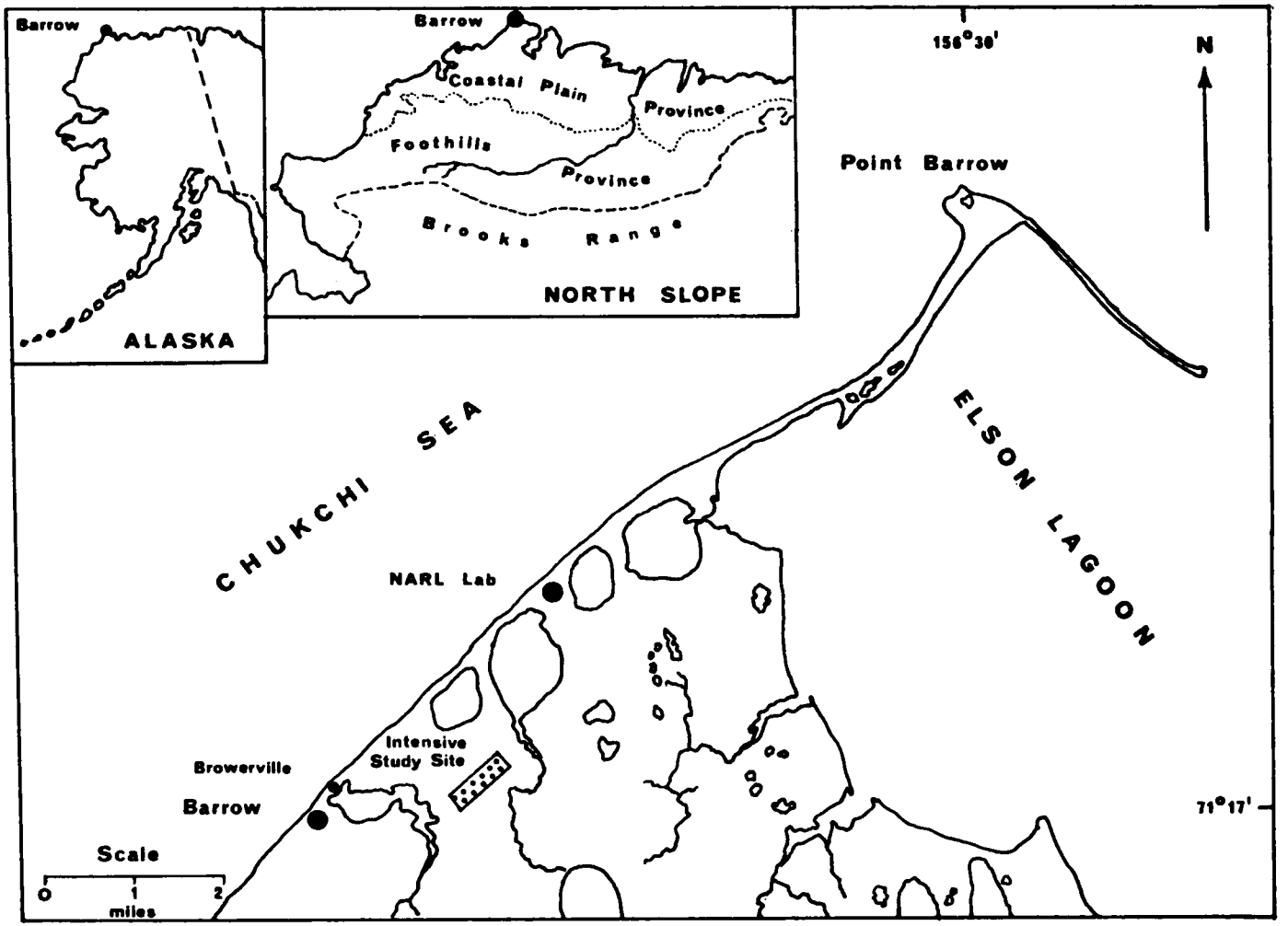


Figure 1. Map of Alaska, North Slope, and Barrow vicinity.

(McCarthy, 1952; Brewer, 1958; Price, 1972).

The Barrow landscape is one of the youngest on the Arctic Coastal Plain of Alaska. Indications are that it has emerged from the sea rather recently. Brown (1965) estimated the age at no older than 8,300 years based on carbon-dated peat deposits. Sediments from the current gravel spit were dated and found to be just over 1,000 years old. Those of the first inland ridge average 3,000 years old. According to Price (1972) the age of the exposed land could be greater than 10,000 years. His statement is based on calculations using simple conduction theory and normal ground-ice growth rates which were compared with the ice accumulation in the Barrow permafrost.

The Barrow peninsula is mantled by unconsolidated sediments of Pleistocene Age (Douglas and Tedrow, 1960). These sediments are included in the Gubic Formation which is composed of three lithologic units: Skull Cliff (oldest), Meade River (intermediate), and Barrow (youngest) (Brown, 1965). According to Brown (1967) the surface sediments are reworked marine, lacustrine, eolian, and alluvial deposits derived from parent materials of mid-late Pleistocene and Recent ages.

Climate

The Barrow climate is typical of the Arctic. It is

severe with long dark cold winters and short fully-illuminated cool summers. Frequently thick clouds and fog blanket the area, often unbroken for several days. Although the humidity is high most of the year the annual precipitation is rather low, falling mainly as snow. Persistent winds often laden with ice crystals blow across the tundra creating chill-factors and erosional forces hazardous to the plant life.

The seasonal range in temperature is less than the extremes found in more continental areas of similar latitude. The mean annual temperature based upon 32 years of records is -12.2° C (Brewer, 1958). Average normal daily temperatures for January are, maximum -23.0° C and minimum -30.6° C; for July, maximum 7.2° C and minimum 0.7° C (U.S. Weather Bureau averages, 1931-1960). Data available for 52 years indicate the lowest temperature recorded was -48.9° C and the highest was 25.6° C.

Only during the months of June, July, and August do the mean daily temperatures rise above freezing. Table I indicates that 1972 was a "typical" season with regard to temperature. An important feature of the daily minimum temperatures during the summer growing season is the number of frost-free days. Billings (1973) reported that the effective growing season at Barrow spans only

TABLE I

SELECTED WEATHER DATA MAY-SEPTEMBER, 1972, BARROW, ALASKA[a]

Month	Aver. °C Max.	Aver. °C Min.	Monthly Averages 1972	Monthly Averages 1931-1960	Wind Speed m.p.s.	Wind Direction Deg. from N.	Light Intensity Langleys/Day
May	-5.0	-10.6	-7.7	-7.8	3.5	90	483
June	2.2	-1.7	0.3	0.6	2.5[b]	60[b]	488
July	10.8	1.2	6.1	3.9	---	170	478
August	7.8	1.7	4.8	3.3	1.4	80	253
September	1.3	-2.2	-0.4	-0.6	1.6	60	128[b]

[a]Data obtained from U. S. Weather Bureau Monthly Summaries, 1972.

[b]Data based upon 5-year averages (1967-1971), not available for 1972.

71 days. In 1955 the number of frost-free days was 42 (Britton, 1966) which compares favorably with an average value, 43, for the years 1968-1972 (U.S. Weather Bureau Data). Table II reports these data monthly. It is important to note that the distribution of frost-free days is unpredictable for any year, and the extremes shown for 1968 and 1969 illustrate the rigorous nature of the climate. This unpredictable weather pattern is partly a manifestation of the lag in maximum and minimum temperatures behind the solstices in northern maritime environments (Britton, 1966).

The measurable precipitation at Barrow is low. Average annual accumulation is 108 mm (ca. 4+ inches) with a mean total snowfall of 739 mm (ca. 28+ inches). Black (1954) suggested that the standard methods for measuring precipitation are unreliable at Barrow since much of the moisture load is deposited with considerable wind. After measuring the average snowpack depth in winter and the degree of saturation of soils in summer, he concluded that the actual annual precipitation was more than twice the amount measured by the U.S. Weather Bureau.

Summer precipitation is probably more crucial to the success of plant life than the total annual moisture budget, since plants are active only during this period.

TABLE II

SELECTED 5-YEAR WEATHER DATA FOR JUNE-SEPTEMBER, 1968-1972, BARROW, ALASKA[a]

Month / Year		Number Days Min. Temp. > 0° C	Snowfall mm	Maximum Depth Snow Accumul. mm
June	1972	1	18	T[b]
	1971	10	5	127
	1970	7	T	51
	1969	17	15	76
	1968	2	20	102
July	1972	15	0	0
	1971	27	T	T
	1970	11	T	-
	1969	6	20	T
	1968	28	5	-
August	1972	22	5	T
	1971	6	61	51
	1970	12	T	T
	1969	1	188	76
	1968	27	8	T
September	1972	5	328	102
	1971	2	51	25
	1970	3	53	25
	1969	0	T	T
	1968	10	137	102

[a]Data obtained from U. S. Weather Bureau Monthly Summaries, 1968-1972.

[b]T = trace amounts.

Although the summer precipitation is low, Clebsch (1957) determined that it does exceed evapotranspirational losses.

Summer precipitation often falls as snow. Table II summarizes snowfall and accumulation data for 1968-1972. Like temperatures, periods of snowfall are unpredictable. Snow has been recorded during all months of the year. This can have a pronounced effect on the seasonal performance of plants when snow falls during July or August. The effects of interruptions in the normal growth cycle by unseasonal snow and ice storms have not been investigated at Barrow.

Wind probably represents the most destructive natural force to plant life at Barrow. During the cold winter months when the humidity is lowest, dessicating winds can destroy growth which has accumulated over many seasons. Areas of raised relief which are swept free of the insulating layer of snow can actually be denuded of vegetation by winds heavily laden with ice crystals.

Light is perhaps the most intriguing environmental factor in arctic regions. All areas north of latitudes 66° 30' experience at least one day per year when the sun neither rises nor sets. As one moves north into higher latitudes, the duration of such periods increases. At the latitude of Barrow (ca. 71° N) the sun sets permanently

in late November and does not reappear above the horizon until late January. Conversely, during the active growing season the sun never sets before late May nor before early August.

The effect of long days with continuous sunlight on the adaptations of arctic plants has been pondered and discussed many times. Billings (1973) commented that the low angle of the continuous summer sun is different in spectral quality and quantity than in equatorial regions. The reason for these changes is the greater thickness of the atmosphere which light travels through at the poles. The low angle of incident light and frequently clouded skies during the growing season potentially limit plant productivity. Savile (1971) however, has drawn to our attention the fact that even on cloudy days the light reaching the tundra is probably comparable to that reaching the forest floor in lower latitudes.

There is no doubt that conditions of light, temperature, and precipitation as snow create brief periods which are unfavorable for plant growth during the arctic summer. The adaptations of arctic plants to the cold environment have been discussed elsewhere (Porsild, 1951; Bliss, 1962; Savile, 1971). At Barrow unpredictable schedules of frost-free days, snowfall, and

compensation-point light certainly have had a combined influence on the adaptations of the plants found there.

Soils

The Barrow soils belong to a group known as Arctic soils. The Alaskan Arctic soils have been studied rather extensively. They have been classified into Lithosols (including Regosols), Arctic Brown, Tundra, and Bog soils (Tedrow, et al., 1958; Drew and Tedrow, 1962). Lithosols and Regosols are characteristic of young land surfaces that are resistant to soil formation. Arctic Brown is a moderately- to well-drained soil which has an active layer up to 4 feet deep. Tundra soils are considered intrazonal and occupy most of the Coastal Plain Province where drainage water is impeded but not impounded. Bog soils are found in areas of level or depressed relief and are usually inundated during the summer months.

Weathering of parent materials in the genesis of these soils apparently explains their fine texture (Hill and Tedrow, 1961). The role of moisture in their development has led to their interpretation as a drainage catena (Tedrow, et al., 1958; Douglas and Tedrow, 1960). Tedrow and Cantlon (1958) have elaborated on this viewpoint and contend that Arctic Brown, Tundra, and Bog soils are northern extensions or counterparts of podzol, humic

glei, and bog soils formed over permafrost.

Arctic Brown. This soil is considered the zonal soil of northern Alaska (Tedrow and Hill, 1955). It is a weak podzol and forms only on sites with adequate drainage. Less than 1 percent of the Arctic Alaskan land surface is mantled with Arctic Brown soil. On the Coastal Plain this soil develops only on the raised beachridges.

Arctic Brown has been studied at Barrow from areas on several beachridges. Drew, et al., (1958) studied a depth-of-thaw profile. They found that the soil thawed earlier and deeper than other Arctic soils. Re-freeze also occurred earlier than in other soils. This sequence was attributed to the low specific heat of the soil; a result of good drainage and low moisture plus poor surface insulation by the sparse cover of plants.

Drew and Tedrow (1957) investigated the pedology of Arctic Brown soil at Barrow. In their study they described the chemical and physical structure of the soil. Besides a characteristic brown coloration in the upper horizon, organic matter averaged about 12 percent. Tedrow and Hill (1955) have found the organic fraction to be as high as 19 percent. There is a significant decrease in the amount of organic matter in the A_2 and A_3 horizons

where less than 1 percent occurs. Leaching effects produce low base saturation in the upper horizon creating distinctly acid conditions at the soil surface. In the lower horizons base saturation reaches almost 100 percent, resulting in a circumneutral pH reaction for the soil. The composition of the soil is 15 percent clay, 15 percent silt, and 70 percent very fine to coarse sand. Occasionally small pebble-sized rocks are present.

Tundra. This soil class includes Meadow Tundra soil and Upland Tundra soil. Both are developed in areas with gradual slopes through a pedologic process of low temperature gleization. Drew and Tedrow (1962) mentioned that Meadow Tundra soil is common on slopes of 8°-10° and produces a characteristic grey to grey-brown mottling in the upper horizon. Upland Tundra soil occurs on slopes greater than 10° where slightly better drainage permits a greater oxidation of the upper horizon. This results in darked colored soil. Both of these types have a similar active layer thaw-profile which extends to a maximum depth of 18 inches.

An investigation of Tundra soils at Barrow by Douglas and Tedrow (1960) resulted in a description of two dominant horizons; a fibrous organic surface layer up to 3 inches deep and a lower horizon of mineral soil with a

"blocky" structure. The pH values noted for this soil type ranged from mildly acid (pH=5.0) to slightly basic (pH=8.1).

Tedrow and Harries (1960) studied Tundra soils from both glaciated and non-glaciated areas. Minor constituent differences were found but generally all soils examined could be comfortably assigned to the Tundra soil class.

Bog. Bog soils are formed in areas of flat or depressed relief. Tedrow, et al., (1958) subdivided this genetic class into halfbogs which accumulate peat to 18 inches and bogs which accumulate peat greater than 18 inches. Bog soils are associated with marshland habitats. They thaw to shallower depths than other tundra soils and also show a lag in the refreezing schedule.

The distribution of soils at Barrow has been mapped by Drew (1957, cf. Brown, 1967). Trace amounts of Arctic Brown occur on uplifted beachridges. Most of the soil (75 percent) is of the Meadow Tundra type. Ten percent is boggy soil and 5 percent is Upland Tundra soil. According to Britton (1966) the soils of the wettest Barrow habitats are the halfbog variety.

Topography

The Barrow terrain has a number of topographic

features typical of the Arctic Coastal Plain. The area is dominated by numerous oriented lakes and extensive polygon fields. These latter areas of patterned ground can be classified as high center polygons, found on upland sites, or low center polygons, found on flat ground or the shallow concavities of drying lake basins. From aerial view one can easily discern the margins of old lakebeds often in superimposed series. These persistent markers on the landscape preserve the surface history of the area and indicate the unstable nature of the terrain.

The Barrow polygons have been known for many years from the lucid description of Leffingwell (1915). A recent survey of the Barrow tundra by Hussey and Michelson (1966) demonstrated that the polygonal ground patterns are the dominant microrelief feature of the area. The greater size of the low center polygons (30-200 feet) in contrast to the high center polygons (10-15 feet) is attributed to the multiple divisions of the land surface by secondary and tertiary ice wedges in the upland high polygon fields.

In 1952, Black studied the ice-wedge polygons at Barrow with regard to their origin and growth. He was able to confirm Leffingwell's contraction hypothesis. This hypothesis which is thoroughly discussed by

Lachenbruch (1966) and Price (1972) suggests that the expansion and contraction of the soil during freeze-thaw cycles in Spring and Fall causes cracking of the ground surface. These ground fissures then fill with water which promptly freezes at the level of the permafrost. Subsequent seasonal growth occurs as the ice fissures re-form and widen the ice wedge.

According to the classification of patterned ground by Washburn (1956), the Barrow polygons belong to the class of non-sorted polygons since there are virtually no rock fragments scattered on the soil surface. Washburn has concluded, following extensive study of many ground surface features in permafrost zones, that their origins are polygenetic. In the Barrow area, probably most of the cryopedologic processes are active although the least obvious is solifluction.

The oriented lakes on the Coastal Plain are also a prominent surface feature. They cover an area greater than 25,000 square miles and are confined to the province. In the northwest portion of Alaska, where Barrow is located, they become a dominant landscape feature (Black and Barksdale, 1949).

The creation, migration, and drainage of lakes and ponds in permafrost zones have been studied at Barrow and

elsewhere (Black and Barksdale, 1949; Hopkins, 1949; Carson and Hussey, 1960; Shacklette, 1961). The oriented lakes of northwestern Alaska have an average axis of 12 degrees west of north. They range in size from several tens of feet to over 9 miles in length with a lesser breadth. The overall form is ellipsoid. Depths range from 2 to 20 feet (Black and Barksdale, 1949).

The origin of these lakes has been rather speculative although Black and Barksdale (1949) suggested that wind and mass wasting were major factors. Carson and Hussey (1960) through a series of innovative experiments with dyes and floats studied the hydrodynamics of several lakes in the Barrow region. Their findings indicated that indeed, wind and permafrost melting were important in the development, migration, and emptying of the lake basins. The prevailing winds from the northeast and southwest are responsible for the orientation of the lakes. The constant wind direction creates longshore currents perpendicular to the wind vector. Currents reach a maximum velocity at the ends of the lakes where maximum erosion rates of those margins cause elongation.

Vegetation

The Barrow vegetation is physiognomically similar to other high arctic tundra communities. The plants are low

in stature, highly mixed, and distributed without apparent order across a discontinuous surface topography. This apparently randomized pattern has caused many arctic ecologists to challenge a Clementsian interpretation of arctic ecosystems. Griggs (1934) and Raup (1941) have pointed this out in discussions of the problems associated with the classification of tundra vegetation.

Several studies of vegetation in arctic Alaska have classified the macrovegetation according to physical structure (Hanson, 1953; Spetzman, 1959). Both of these investigators remarked on the hybrid influences of soil, frost action, drainage, and snow cover in the determination and regulation of community structure.

A series of studies carried out in the Seward Peninsula have investigated specifically the role of frost activity (congeliturbation) and soil instability in the distribution of some plant communities (Hanson, 1950; Sigafoos, 1951; Hopkins and Sigafoos, 1951; Sigafoos, 1952). In all cases the plants showed distributions rather consistently paralleling topographic sites and gradients. Few, however, mentioned the cryptogamic component of the vegetation in these areas.

Several studies which have specifically dealt with the vegetation in the Coastal Plain Province contain descriptions of some of the vascular plant communities

(Wiggins, 1951; Koranda, 1954; Clebsch, 1957; Spetzman, 1959). Of these, Clebsch (1957) and Wiggins (1951) conducted their studies in the Barrow vicinity and in both cases, the cryptogamic portion of the vegetation was neglected. Britton (1966) has provided the only discussion which integrates some information about the bryophytes into a discussion of the vegetation. His sole presentation is slightly misleading since the richness of the bryoflora there has escaped notice until now.

The flora of Barrow contains about 100 species of vascular plants. Until now, only 72 species of bryophytes were recorded for the area. No official listing of lichens is available, although a working list for the Tundra Biome contains around 60 species.

The distribution of vascular plant species at Barrow follows to some degree, the topographic variation. The coastal strand contains a number of species characteristic of that area: Mertensia maritima, Cochlearia officinalis, Saxifraga caespitosa, Elymus arenaria, and Puccinellia phryganodes, along with more common species widely distributed at Barrow (Britton, 1966).

The vascular plants found in areas of raised relief have been discussed by Koranda (1954, cf. Clebsch, 1957), Wiggins (1951), and Drew, et al., (1958). These are

areas where the deepest soil occurs (Arctic Brown) in the drier habitats. Common plants include: Vaccinium vitis-ideae, Cassiope tetragona, Arctagrostis latifolius, Poa arctica, Salix rotundifolia, Luzula confusa, Luzula nivalis, Potentilla hyparctica, Saxifraga spp., Stellaria spp., Carex aquatilis and an assortment of other species of occasional occurrences.

Most of the Barrow tundra is, however, neither beachstrand nor beachridge habitat. These other areas have not received the same degree of study as the more specialized habitats because they are monotonous in appearance by virtue of their vegetational uniformity. These areas are moist and wet meadow sites which are dominated by grasses and sedges. Species compositions often change by degree but total coverage is quite constant, approximately 100 percent. Species most abundant in the meadows are: Carex aquatilis, Dupontia fischeri, Eriophorum spp., Calamagrostis holmii, Arctagrostis latifolius, Saxifraga spp. and a host of other widely scattered and occasional wetland species. Occasional islands of willows and Petasites frigida occur in raised areas.

Across the tundra the vegetation is visually poorly differentiated on the basis of overall species composition. Certain indicator species with high fidelity

can be indicated for some habitats but for the most part the vegetation is too heterogeneous. In most cases the best way to differentiate between closely related habitats is to measure relative amounts of species. Still, instead of relying upon subtle compositional shifts in the vascular flora, a more natural choice for the description of the vegetation is the use of cryptogams. These more readily and precisely reflect the sudden changes in microhabitats within an area.

CHAPTER III

METHODS

Field Studies and Methods

The experience during the summer 1972 constituted the field portion of this study. Involved in this segment of research were extensive collections of bryophytes for floristic study, selection and sampling of an intensive study tract of tundra for phytosociological study, and a brief period of laboratory-oriented work during the summer when measurements on the relative soil moisture of the intensive study tract were made. Most of the field research was centered in the area of the I.B.P. Tundra Biome intensive study range. Occasional side-trips were also made to outlying areas of Barrow tundra and elsewhere on the arctic coastal plain of Alaska.

Field excursions away from the intensive study site were necessary to obtain good herbarium specimens and assure a more thorough census of the flora. Certain restricted habitats such as gravel beachstrands, beach bluffs, silted streambanks, low center and high center polygons, meadows, tundra pools, lake and lagoon margins, and naturally or man-made disturbance sites were distantly distributed localities.

General collecting from these habitats continued throughout the entire field season. This enabled me to observe the developmental sequence of many bryophytes, from their early season greening of post seasonal biomass to the growth and maturation of sporophytes. These observations were vital to the recognition of many species. These general collections aided by the sample core-quadrats taken from the intensive study site are the source of many of the new records reported for Barrow.

Two short-term studies were conducted at Prudhoe Bay and Meade River. Both were valuable in placing the Barrow tundra within a perspective relative to other high Alaskan tundra.

Prudhoe Bay is topographically much like Barrow. However, the bryoflora is substantially different between sites which in both areas have a similar topographic location. This difference is partially the result of the soil pH regimen. Barrow soil characteristically shows a weak to mild acid pH reaction, while Prudhoe Bay soil shows a circumneutral to basic pH reaction. Visual inspection of the bryophytes in both areas does not leave an obvious impression of well-segregated communities.

Meade River differs considerably from Barrow and Prudhoe Bay. The climate is more continental, topography

more rolling, and plant communities more distinct. The supposition that bryophytes are distributed along gradients related to topography and moisture is more clearly demonstrated in the Meade River tundra.

Selecting the intensive study site. The choice of a suitable sample site was a selection based upon compromise. Rather than attempt to spot-sample apparently similar habitats from areas of equivalent microrelief throughout the Barrow tundra, I decided that a more controlled sample design would possibly be more meaningful in describing and discussing bryophyte communities. At least for the bryophytes, I observed that distantly located sites which appeared similar, often showed marked differences in bryophyte composition. This suggested that environmental site differences like genetic origin of the substrate, age, and microclimate were visually undetectable.

To avoid a heterogeneous sample set, a small tract of tundra was chosen. It contained examples of the dominant microrelief features at Barrow but understandably not all moisture phases. The most important consideration was to keep the various topographic sites within the study tract as homogeneous as possible and thus permit later statements about the distribution of species and communities within the area.

Three topographic areas were grossly recognized in the intensive study tundra tract (Figure 2). These were, an area of low center polygons, an old beachslope, and an area of high center polygons. The three areas were contiguous along a transect 250 meters long, 10 meters wide, and oriented 55 degrees east of north into the prevailing wind. The relative position of the three topographic areas (sectors) followed a gradual habitat gradient from lowland to upland and from wet to dry.

This rather specific choice of location made it possible to minimize the effects of wind, a dominant climatic factor at Barrow. It was assumed that the closeness of the three sectors meant that there was insufficient distance between them to expect that community and species distributions could be other than site-factor related phenomena. Therefore, differences in community composition could be the result of site differences such as moisture, and soil pH.

Description of the intensive study site. The low polygon sector consisted of five low center polygons in various stages of development. Common to all were low, ponded centers which persisted throughout the summer in three of the polygons. In the three permanently ponded polygons, post series stands of Arctophila fulva were

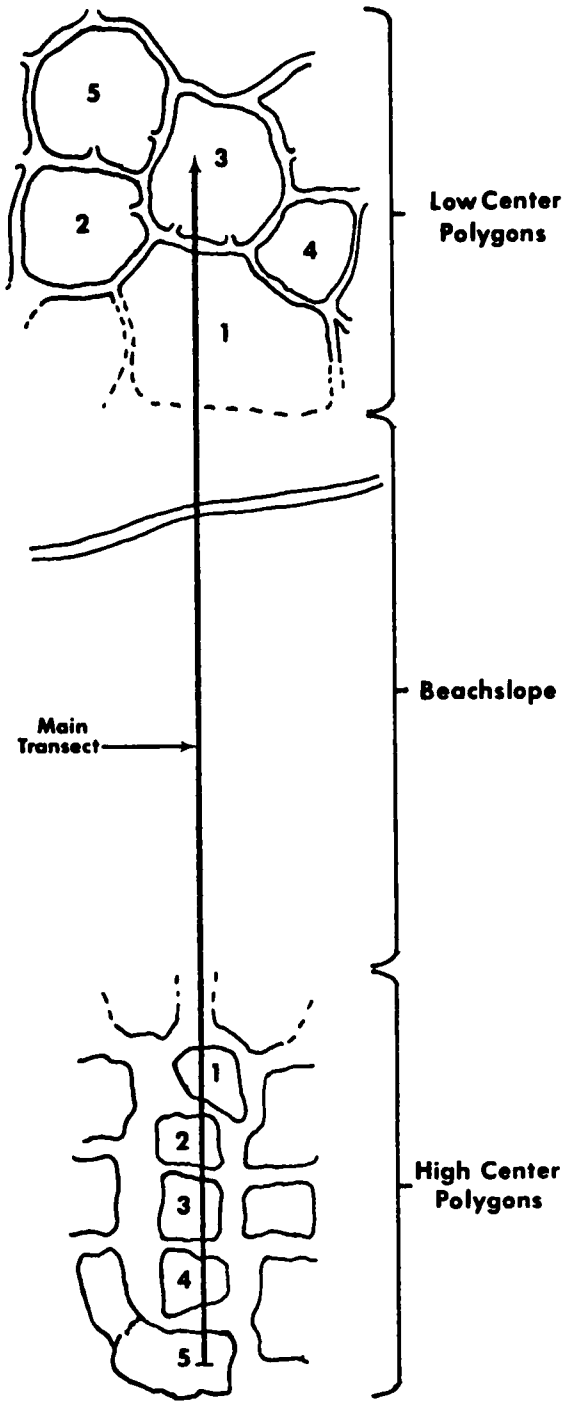


Figure 2. Three macrotopographic sectors of the intensive study site.

present. At the pond margins and in the centers of the two polygons not retaining water, the usual vegetation consisted of Eriophorum russeolum, E. scheuchzeri, Carex aquatilis, and Dupontia fischeri. Between the low center polygons, inter-polygonal troughs occurred over underlying ice wedges. Adjacent to the troughs, uplifted ridges formed a peripheral ring of high ground around each polygon center. Trough vegetation was similar to that found at the margins. The ridges and ridge slopes were the driest sites of the low polygon sector and naturally supported several additional species. Species such as Polygonum viviparum, Juncus biglumis, Pedicularis sudetica, and Saxifraga spp. were common here in addition to assorted ubiquitous grasses and sedges already mentioned. Salix rotundifolia occurred on the driest ridge-sites found at the intersecting corners of three or more polygons.

The beachslope had a natural division into a lower and upper section. This division was supported by changes in elevation, microtopography, and soil moisture. The lower beachslope section shared a number of characters of the low polygon sector, and the upper beachslope was similar to part of the high polygon sector.

Microtopographic variation was nearly absent in the lower beachslope where it graded into the low polygon

sector. Poa alpigena and Rumex arctica were found only in this section. Eriophorum angustifolium, Carex aquatilis, Alopecurus alpinus, and Luzula confusa were common. Saxifraga spp., Petasites frigidus, Stellaria laeta (sensu lat.), and Salix rotundifolia were also frequently present.

The upper portion of the beachslope was drier than the lower portion due to surface and subsurface drainage. The ground pattern of this section was rather unique, in the form of a reticulate network of small mounds and depressions. These small features were spaced between 30 and 50 cm from mound crest to crest and from one depression center to another. This alternating pattern of microrelief contained a rich assortment of differing habitats within an incredibly small area, often no more than 25 cm apart.

Carex aquatilis, Dupontia fischeri, Arctagrostis latifolius, and Poa arctica resided in the depression sites. Salix rotundifolia was clearly dominant on mounds. Scattered forbs considered collectively here as mesic species were: Papaver macounii, Pedicularis kaneii, Senecio atropurpureus, and Saxifraga punctata. Lichens in this section were more numerous than in other sectors.

The upper beachslope was connected to the high polygon sector through a transitional zone of broken and slumping high center polygons. The five high center

polygons of this sector were aligned along the transect axis. Interpolygonal troughs varied from 30 to 60 cm deep; and, of course, no interpolygonal ridges occurred because the entire central portion of the polygon was raised. These polygons were between 7 and 15 m in greatest diameter with slopes of 8°-37° depending on the aspect and degree of recent slope gradation. In general, the northeast-facing slopes were steepest, an apparent result of the constant exposure to prevailing winds.

The vascular flora was variable, reflecting the most extreme moisture conditions of any sector. Interpolygonal troughs were wet sites and contained ubiquitous sedges and grasses. Polygon slopes were mesic sites and supported a number of species such as: Petasites frigidus, Poa arctica, Potentilla arctica, Stellaria edwardsii, and some meadow grasses. The polygon tops were the driest sites and where vegetated by Arctagrostis latifolius, Luzula nivalis, Cassiope tetragona, Vaccinium vitis-idaea, and occasional vigorous individuals of Poa arctica. There was no vascular cover over much of the high polygon tops. Such "barren" areas resulted from heavy frost action and only supported bryophytes or lichens.

It is obvious from this description that topographic variation is more pronounced than vascular vegetational

composition. Table III is a list of the vascular plants which occurred in the intensive study site including information as to where they occurred. Without good quantitative data, vegetation descriptions based upon the vascular component would be quite similar for all three sectors. If the surface relief is considered a real image of differing habitats, then a measure of this variation might be expected to occur in the vegetation which grows only on the soil surface. Conversely, if the bryophytes are classifiable into communities which differ according to microhabitats, then a sample design must be devised to investigate that possibility.

Sampling techniques and strategies. Sample plot technique was used to assess both the vascular and non-vascular components of the vegetation. The location of the quadrat samples was restricted randomly to insure that all habitats in the three topographic sectors were sampled.

Two sizes of quadrats were selected for complete vegetation sampling. A circular core-quadrat with an area of 25 cm^2 was used to sample the bryophytes and served as a locus for the placement of a larger quadrat used to measure the associated vascular plants and common lichens. The larger quadrat, 20 x 20 cm, was centered over the smaller bryophyte quadrat.

TABLE III

THE DISTRIBUTION OF VASCULAR PLANT SPECIES
IN THE INTENSIVE STUDY SITE

Species	Low Polygon	Beach Slope	High Polygon
Alopecurus alpinus Sm.	-	X	-
Arctophila fulva (Trin.) Anderss.	X	-	-
Arctagrostis latifolia (R. Br.) Griseb.	-	X	X
Carex aquatilis Wahlenb.	X	X	X
Cardamine pratensis L.	X	-	X
Cassiope tetragona (L.) D. Don.	-	-	X
Cerastium beeringianum Cham & Schlecht.	-	X	-
Chrysosplenium tetrandrum (Lund.) Th. Fr.	X	X	-
Draba alpina L.	X	X	-
Dupontia fischeri R. Br.	X	X	X
Eriophorum angustifolium Honck.	X	X	X
Eriophorum russeolum Fr.	X	X	X
Eriophorum scheuchzeri Hoppe	X	-	-
Juncus biglumis L.	X	X	X
Luzula arctica Blytt	X	X	X
Luzula confusa Lindeb.	X	X	X
Papaver macounii Greene	-	X	-
Pedicularis kanei Durand	-	X	-
Pedicularis sudetica Willd.	X	-	-
Petasites frigidus (L.) Franch.	X	X	X
Poa alpigena (Fr.) Lindm.	-	X	-
Poa arctica R. Br.	X	X	X
Polygonum viviparum L.	X	X	-
Potentilla hyparctica Malte	-	X	X
Ranunculus nivalis L.	-	X	X
Ranunculus pallasii Schlecht.	X	-	-
Rumex arcticus Trautv.	-	X	-
Salix pulchra Cham.	X	X	-
Salix rotundifolia Trautv.	X	X	X
Saxifraga cernua L.	X	X	X
Saxifraga foliolosa R. Br.	X	X	X
Saxifraga hieracifolia Waldst. & Kit.	X	X	X
Saxifraga punctata L.	X	X	X
Senecio atropurpureus (Ledeb.) Fedtsch.	-	X	-
Stellaria edwardsii R. Br.	-	-	X
Stellaria laeta Richards.	X	X	X
Vaccinium vitis-idaea L.	-	-	X

The criteria used in choosing these two quadrat sizes were derived from preliminary studies of the same vegetation where quadrats ranging from 5 x 5 cm to 25 x 25 cm were tried. Data obtained from these early investigations indicated that no single quadrat was suitable for assessing all forms of the tundra vegetation. Therefore, the decision was made to employ two quadrats of different area which would accommodate the size differences among the plants.

The 25 cm^2 core-quadrat used for bryophyte sampling was chosen after a number of samples were surveyed for their floristic composition. Findings revealed that one could expect between five and twenty-five species of bryophytes within such a small area.

The high number of species present in such a small area suggested that the bryophyte synusia was an extremely heterogeneous assemblage of mosses and liverworts. In most instances, by increasing the area of the sample without exceeding the boundaries of the designated site, few additional species could be added. A few cases where the increase in sample area yielded a sizeable increase in species present were shown to be the result of indiscrete or mixed habitat sampling. Perhaps the greatest deterrent to enlarging the sample area was the needless expenditure of time necessary to carefully process each sample.

The vascular-lichen quadrat (20 x 20 cm) was found to be the most efficient size for assessing this component in contrast to the sample size used for the bryophytes. Larger areas were no longer representative of the vascular plants and lichens around the bryophyte sample, and smaller samples did not include enough information for adequate descriptions.

Certain data were recorded in the field as the sample quadrats were placed. These included presence for all vascular plants and common macrolichens, topographic position, aspect, relative cover by the vascular component, and the depth of the soil humus layer. After this procedure, the bryophyte core-quadrats were sampled destructively. Each sample was bagged separately, recorded as to location and returned to the laboratory for drying.

This treatment of the bryophyte samples was designed to preserve both the vegetal layer and the underlying soil to a depth of 4 cm. Instead of removing the bryophyte layer, it was left intact so that later study would have the benefit of an unaltered distributional pattern.

In addition to the vegetation samples 100 core-quadrats were taken to determine the relative moisture

conditions of the various habitats. All samples were taken over a 10-day period in late June and early July. Samples were taken to the same depth as the bryophyte cores, quickly transferred to air-tight tin canisters and transported back to the laboratory. There, fresh weights were recorded, and the specimens were placed in a drying oven at 105° C for 48 hours or until dry weight stabilized. This weight was then recorded, and the relative percent moisture was calculated using the formula:

$$\% \text{ moisture} = \frac{\text{fresh weight core} - \text{dry weight core}}{\text{dry weight core}} \times 100$$

Before, during, and after the collection of data from the intensive study tract, active collecting of bryophytes was conducted in and around the sample transect. This exercise was a necessary prelude to the later preparation of checklists from the core-quadrats since most of the bryophytes were sterile and/or less than optimal in vigor.

Sampling in the low center polygon sector. Six major stand types (microtopographic habitats) were designated in this transect sector. In this way the total number of samples was restricted to 250. The samples were distributed so that each stand type was sampled at least

twenty-five times. The following abbreviations refer to the six stand types: (LPc) Low polygon center, (LPm) Low polygon margin, (LPRs) Low polygon ridge slope, (LPRt) Low polygon ridge top, (LPTs) Low polygon trough slope, and (LPT) Low polygon trough.

The five low center polygons chosen as the sample area were located as shown in Figure 3. The sketch shows the labeling of the polygons and troughs used to classify the field samples. Transects drawn between the polygon centers and referred to by letters of the troughs they cross were part of the randomization scheme for the placement of the sample quadrats among the six stands. Figure 4 is a sketch of transect (c) which connects the centers of polygons 3 and 4.

Five pairs of quadrat samples were taken at each stand location. These five samples were located along a line perpendicular to the transect. Further insurance for randomness was accorded by placing the third quadrat (of the five per stand) directly over the transect. Quadrats 1,2,4, and 5 were then fixed at regular intervals, perpendicular, on each side of quadrat 3. The distance between adjacent quadrats was a measured 50 cm between core-quadrat centers.

This method of sampling was used throughout the low center polygon sector along all transects (a, b, c, d, e).

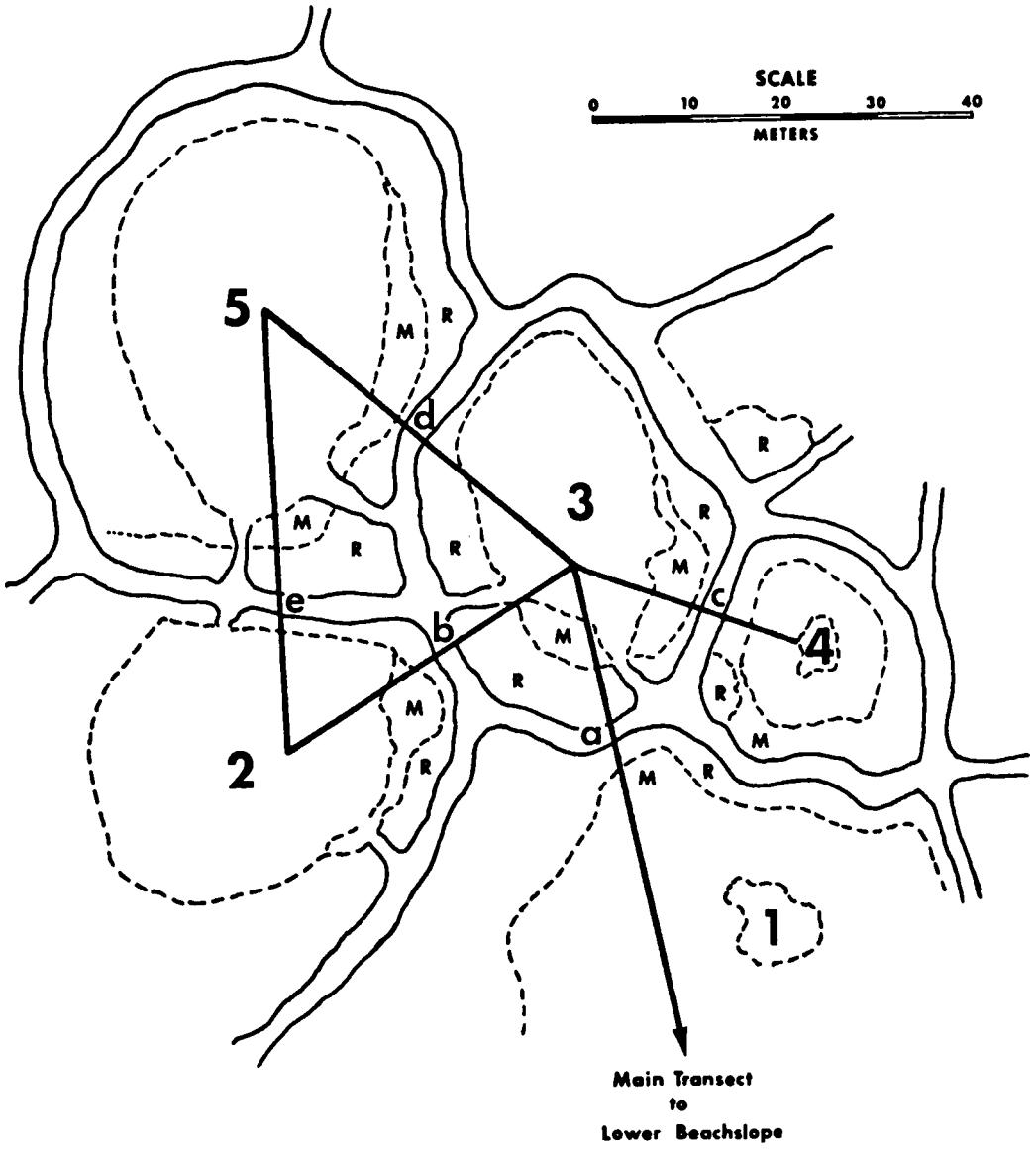


Figure 3. Sketch of sample area in low polygon sector. 1-5, low center polygons; a-e, interpolygonal troughs; M and R, margins and ridges.

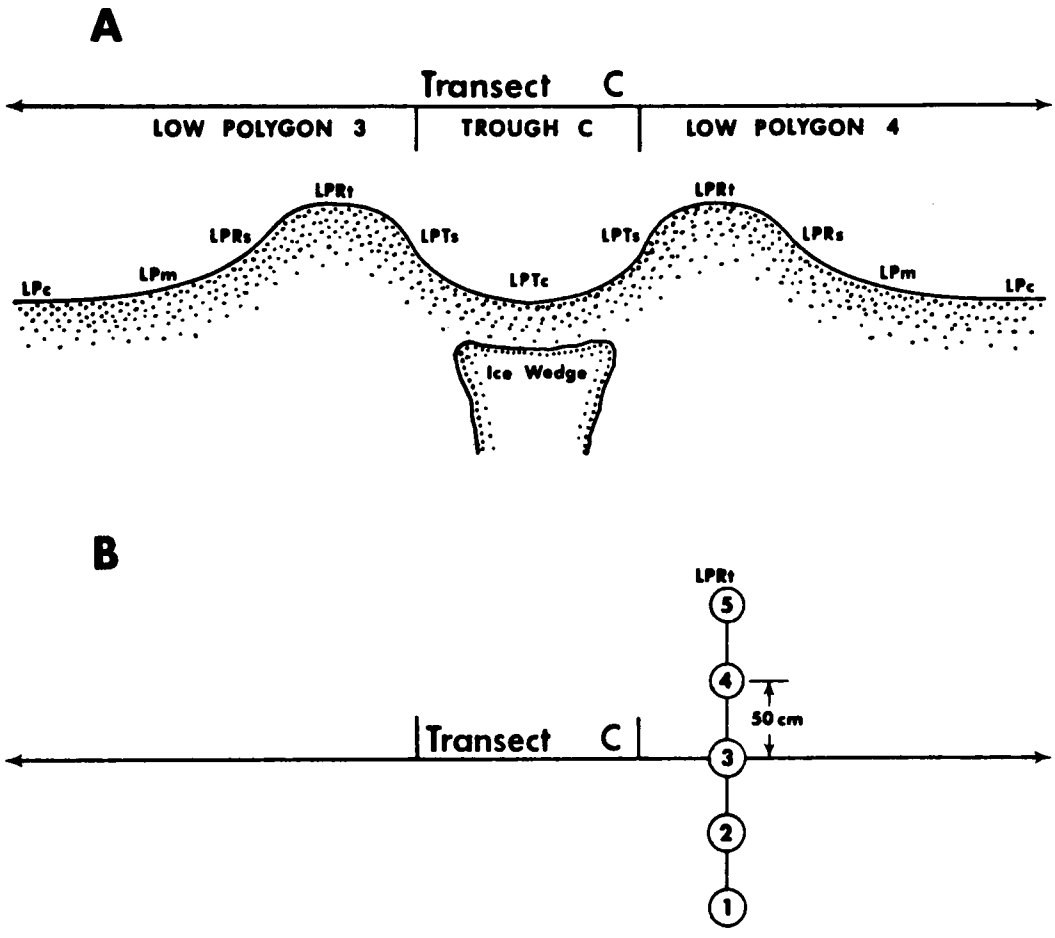


Figure 4. Sketch of transect (C) which connects low polygon centers 3 and 4.

A. Sectional view showing all habitats sampled. LPc - Low polygon center, LPm - Low polygon margin, LPRs - Low polygon ridge slope, LPRt - Low polygon ridge top, LPTs - Low polygon trough slope, LPTc - Low polygon trough C.

B. Top view showing the placement of 5 quadrats at LPRt in Low polygon 4.

The sample design yielded samples in the following proportions:

(LPc)	low polygon center	25
(LPm)	low polygon margin	45
(LPRs)	low polygon ridge slope. . . .	50
(LPRt)	low polygon ridge top.	50
(LPTs)	low polygon trough slope . . .	50
(LPT)	low polygon trough . . .	25
	Total. .	245

The loss of five samples from low polygon margins was the result of the habitat not being present in one of the polygons. At the time, it was judged unnecessary to sample five more from outside the study area since foreign samples would not have enriched the already large amount of data.

Sampling in the beachslope sector. The sampling procedure used in this sector along the transect was also a stratified randomized design set up to investigate the vegetational changes along a transect ascending the beachslope. As shown in Figure 5, the beachslope sector spanned about 90 m; its location approximately medial along the entire main transect. Because an old tracked vehicle scar crossed the lower end of the beachslope, sampling was omitted near that area.

A total of 140 paired quadrats were placed on the

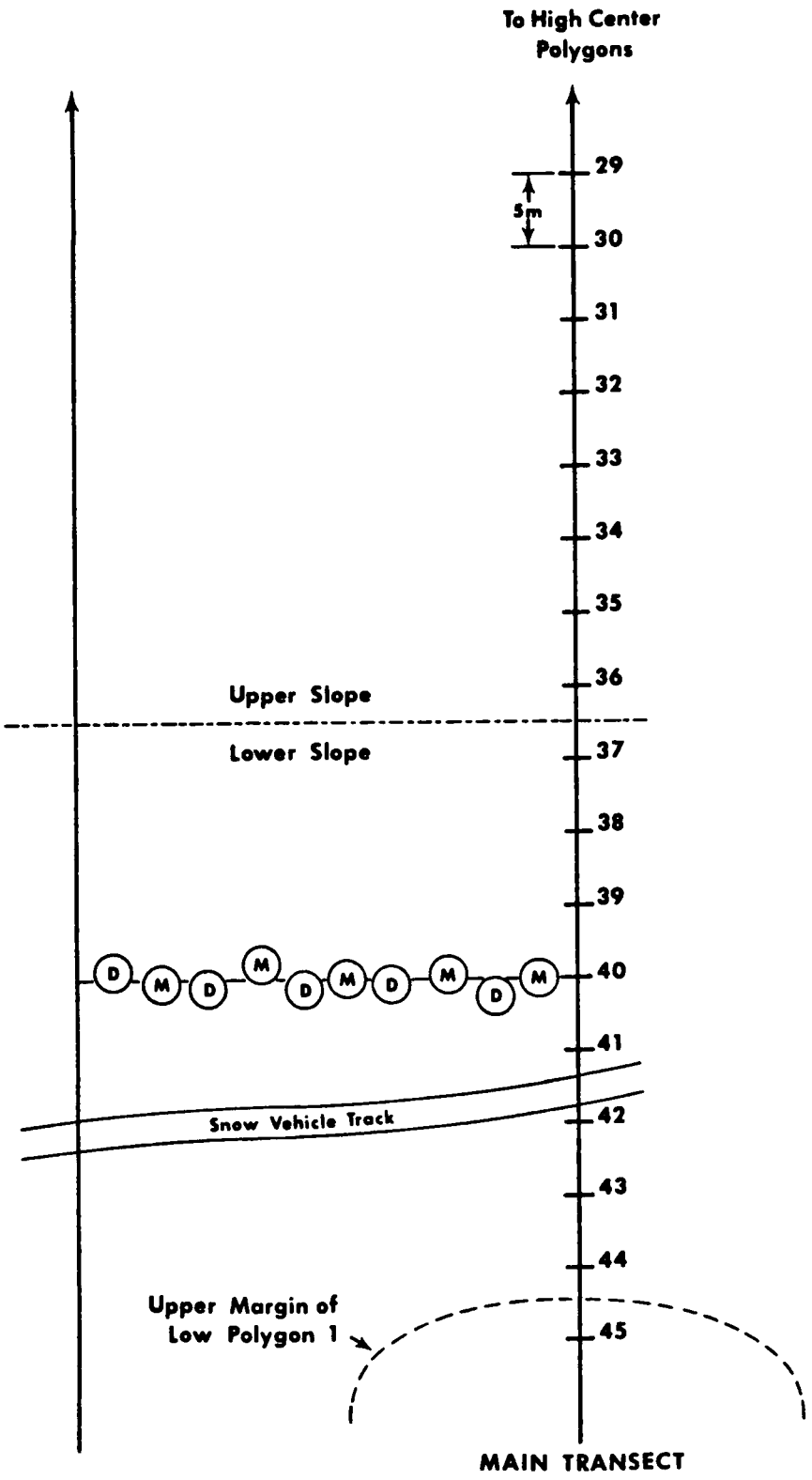


Figure 5. Sample design for beachslope sector. Transect 40-10 showing possible plot locations (M = mounds, D = depressions).

beachslope over 15 parallel sample transects which ran perpendicularly from the main transect. Each sample transect followed the natural contour of the slope. Each originated from a numbered stake and extended no more than 10 meters away from the main transect line. The main transect line connected all the stakes which were located at 5 meter intervals along the beachslope. Figure 5 also indicates the position of the sample transects and a schematic sample pattern for 10 quadrat pairs taken along transect 40-10.

In the randomization scheme used, quadrats were placed alternately along the sample transect in depressions and on mounds. The 10 samples per slope contour resulted in five samples from depressions and five from mounds. The distances between quadrats and from the main transect were recorded to indicate spatial relationships and ground patterns.

An arbitrary but perhaps real division of the beachslope into an upper and lower subsection distributed the samples in the following proportions:

lower slope depressions	30
lower slope mounds	30
upper slope depressions	40
upper slope mounds	40
Total	140

Sampling in the high center polygon sector. Sampling in this sector of the intensive-study site was similar to that used in the low center polygon sector. As Figure 6 shows, the five representative high center polygons in this sector were aligned along the main transect axis. This was a deliberate choice since the high polygons toward the back of the sample area received less direct wind-blasting and therefore might be expected to harbor slightly different bryophyte communities.

Eight stands were distinguished in the high polygon sector: (HPFb) frost boils on high polygon tops, (HPB) pure bryophyte communities on high polygon tops, (HPG) grass-sedge dominated communities on high polygon tops, (HPNs) high polygon NE-facing slopes, (HPSs) high polygon SW-facing slopes, (HPEs) high polygon SE-facing slopes, HPWs) high polygon NW-facing slopes, and (HPT) high polygon troughs. The troughs were sampled according to locations given in Figure 6. Troughs A, B, C represented shallow transverse troughs and D, E, F, G were deep troughs which also served as main drainage channels during the sheetwater runoff at spring snow-melt.

All eight stand types were collectively studied by sampling 200 quadrat pairs. These were distributed

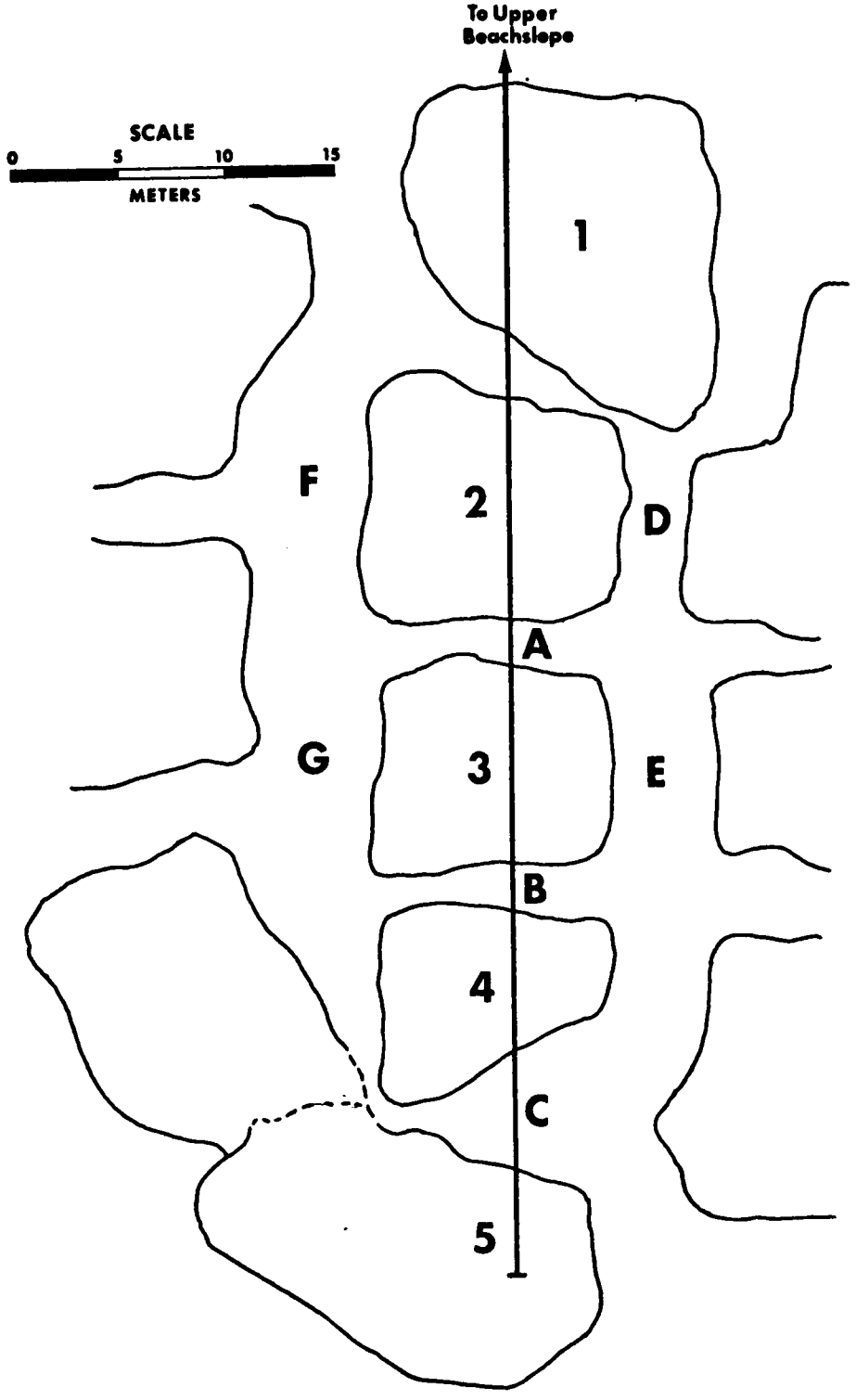


Figure 6. High center polygon sector. 1-5 high polygons, A-G interpolygonal troughs.

among the stands in the following proportions:

HPFb	15
HPB	25
HPG	25
HPNs	25
HPSs	25
HPEs	25
HPWs	25
HPT	35
Total	200

Specific quadrat locations were more arbitrarily selected in this sector because of the high number of stands. On the polygon tops quadrats were placed in different frostboils, bryophyte communities, and grass-sedge tussocks until the desired number of samples were obtained for each polygon.

Quadrat stations on the northeast- and southwest-facing slopes were located similar to the procedure outlined for the low polygon sector. Quadrat positions on the southeast- and northwest-facing polygon slopes were determined by placing the third quadrat over an imaginary point in the middle of the polygon slope which then fixed the remaining four quadrats on each side of quadrat 3. Sampling in the troughs was similar where after the third quadrat was positioned, the others became

fixed on either side of quadrat 3.

Laboratory Studies and Methods

Floristic and taxonomic laboratory studies at The University of Tennessee on the bryophyte flora of Barrow were complemented by a brief visit to the New York Botanical Garden Herbarium. Study of collections made by William C. Steere and housed at the New York Botanical Garden were most valuable. I was able to find a number of previously unreported species among his collections which are properly credited to Steere in Appendix B. Other reports of species previously unknown at Barrow are documented also in Appendix B. Vouchers are indicated by collection numbers representing core-quadrat samples, floristic collections, and in a few cases several overlooked literary reports. New reports resulting from my own field investigations are preserved as slides or collections in my personal herbarium, and at The University of Tennessee, Herbarium.

To name only a few literary resources which were helpful in the identification of the bryophytes, I call attention to the following manuals and floras: Grout (1928-1940), Frye and Clark (1937-1947), Schuster (1953, 1966, 1969), Arnell (1956), and Lawton (1971). Additionally, several papers dealing with the bryophytes from the Nearctic were valuable in alerting me to species

possibly to be found at Barrow (cf. Steere, 1954, 1971).

Core-quadrat analyses. Two kinds of measurements were taken from the core-quadrats in the laboratory. These were measurements of the upper 4 cm of soil and the bryophytes growing at the core surface. Each core was carefully divided into two fractions--a bryophyte and soil disc. The surface disc was saved for floristic study, and the soil disc was used to measure the hydrogen-ion activity (pH) and depth of humus accumulation at the surface.

During the pretreatment of the core-quadrat samples at Barrow the cores were dried at 70° C and bagged for shipment to The University of Tennessee. The procedure for determining the hydrogen-ion activity of the soil was, therefore, modified considering this fact.

The physical structure of the soil samples included a range of textures from peaty to highly mineralized material. To accommodate this broad compositional spectrum along with the method and duration of storage, and still obtain meaningful pH values, the following method was used.

The soil discs were ground with a mortar and pestle being careful not to pulverize the soil. The ground soil was transferred to two (one replicate sample)

40 ml plastic pill cups and hydrated with deionized distilled water to a sticky paste consistency. Often this required stirring and gradual addition of more fluid to the samples rich in organic matter. After the soil-water mixture reached saturation (sticky point), the paste was allowed to stand for 1 hour to reach equilibrium. The samples were then read using a Fisher Accumet pH Meter, Research Model 320 outfitted with a microprobe combination glass electrode. The pH values for each sample were recorded to one hundredth of a pH unit. All soil samples were processed in a continuous experiment within 12 months after their collection.

Soil dilutions can be an important consideration when making measurements of hydrogen-ion activity. Soil heavily laden with free hydrogen ions have been diluted as much as 1:40 (soil:water) without noticeable elevation in pH values (Kelley and Brown, 1921). Other investigators have found that more equal parts in the soil dilution yield more repeatable results (Salter and Morgan, 1923; Wilcox, 1936; Daubenmire, 1959; Peech, 1965). Chapman (1940) was of the opinion that the sticky-point paste soil dilution provided the best simulation of the hydrogen-ion activity present under field conditions.

Soluble salts in the soil have been shown to

decrease the pH values, an opposite effect of overdilution. This buffer effect can be remedied by using a 1N KCl wetting solution. Peech (1965) warns that pH determinations using this method often result in values between 1.5 and 2.0 pH units lower than those from water-wetted soils. An alternate method used by Schofield and Taylor (1955) employs a 0.01 M $CaCl_2$ wetting solution. This procedure seems to avoid the problems encountered with dilution, soluble salts, and claims to predict the actual hydrogen-ion activity of the soils in situ. Generally the pH values obtained from $CaCl_2$ dilutions are in the range of 0.5 pH units lower than those of 1:2 soil-water suspensions.

The choice of sticky-point pastes for the measurement of hydrogen-ion activity in this study was due to the variation in soil composition. The paste served as a suitable standard since no single soil-water dilution could be used to rehydrate all the soils. The paste avoided the problem of overdilution.

Pilot studies on the determination of the hydrogen-ion activity of Barrow soils showed that minor dilution differences did not affect the pH values. Measurements taken after a 1 hour equilibration period were also no different from measurements taken up to 24 hours after rewetting the soil.

Community measurements of bryophytes were taken from the surface discs of the core-quadrats. After the presence of each species was recorded, an estimate of cover for each species was made using a scale of coverage classes given in Table IV. A separate cover estimate was also made for the combined moss and hepatic components of the sample using the same cover class scale. Appropriate notes recorded the presence of sporophytes and any other peculiarities of the sample.

The use of presence, frequency, and cover are the measurements of importance for the separation and description of the bryophyte communities presented later.

Statistical Methods

Species presence lists for each sample were used in the classification of quadrat samples into community types. A commonly employed method utilizes the test of Chi-square for comparing the degree of association between two species. In this study Chi-square was used to determine if an association between numerous species pairs was significant due to some factor(s) other than chance random distribution.

Such a use of Chi-square must be controlled by selecting a critical value corresponding to a fixed level of significance (probability). In this study, the level

TABLE IV

COVER-ABUNDANCE SCALE USED TO MEASURE BRYOPHYTES

Class	Percent Cover	Abundance
0	less than 1%	Single large individuals, several diminutive individuals--no measurable cover.
1	1-5	Single-several large individuals, numerous diminutive individuals--minimal measurable coverage
2	6-15	Present-conspicuous, numerous large individuals, many small individuals.
3	16-35	Common, a major component.
4	36-65	Frequent, codominant or dominant.
5	66-85	Abundant, dominant.
6	86-100	Very abundant, dominant.

of significance chosen was $X^2=6.64$, which is a critical value at the 1 percent level of significance with a probability of .01. In testing for significant inter-specific associations the Chi-square was computed using the standard formula:

$$X^2 = \frac{(ad - bc)^2 n}{(a+b)\ (a+c)\ (c+d)\ (b+d)}$$

which may be found in most statistical texts. A brief discussion of the use of Chi-square is given by Cole (1949) and Goodall (1953). Pielou (1969) is more careful to point out the use and misuse of this test.

When a Chi-square value exceeds the critical value, the association between two species is considered significant. A Chi-square value less than the critical value or negative is considered a non-association or low association. In cases where the Chi-square value approaches the critical value, the calculation of Yate's corrected value (continuity correction for samples represented by low numbers of observations) produces a value somewhat lower (Fisher, 1954). If the Chi-square value is barely significant and the Yate's corrected value drops below significance, then the laborious task of calculating the exact probability is desirable.

The method used here, whereby the Chi-square value

was used to detect positive interspecific association, is thoroughly discussed by Goodall (1953). In his discussion on the objective classification of vegetation, he refers to non-random association between species as correlations. This term has a more restricted statistical definition and, therefore, the term association has been substituted in this study. Following the terminology of Williams and Lambert (1959), association will imply a statistically tested joint occurrence between any two species which exceeds chance at the chosen level of significance. Furthermore, the use of community in discussion hereafter is taken as a noncommittal circumscription of any plant assemblage regardless of ecological status.

CHAPTER IV

BARROW BRYOPHYTE COMMUNITIES

Delineation of Bryophyte Communities

Floristic, topographic, and soil pH data were transferred to keysort punchcards to facilitate the process of comparing core-quadrat samples. A single card was used to represent each sample which resulted in a masterdeck of 565 cards. This masterdeck was then used as the initial data set from which communities were split-out following the procedure of Goodall (1953).

I arbitrarily instituted several restrictions to Goodall's method, in my opinion, to expedite the operation of community delineation without creating a massive computational exercise and still maintain a high degree of confidence in resolving the bryophyte communities. Any species which did not attain a frequency of 20 percent in the original masterdeck (565) cards was excluded from all calculations of Chi-square at that level of community separation. However, since this 20 percent frequency minimum value was imposed at all levels of the community separation procedure, this restriction was not as rigid as one might first expect. As the masterdeck became reduced

through successive community delineations, the frequencies changed which both included and excluded different species at different levels in the analysis system.

The decision to restrict the calculation of Chi-square to only those species with a 20 percent or greater frequency was made because such a high number of species was found in the whole intensive study tract. If all possible species pair comparisons were made and tested by Chi-square among the 104 bryophyte taxa identified from the core-quadrats, the computational exercise alone for determining the first split of the masterdeck would have required 5,356 calculations. By restricting the number of species to be compared at any level of the analysis by choosing the 20 percent level for inclusion, reduced the number of comparisons necessary for choosing at which point to split the deck by greater than 90 percent.

A possible criticism is that by excluding the species with frequencies less than 20 percent from the tests on which are based the final communities (or groups), imposes a data restriction which omits some valuable information contained in the occurrence of infrequent species. I would point out that by using the divisive technique of Goodall, the separation of communities is based upon the most abundant species within the data set which show positive interspecific associations. Only if an

infrequent species, in this case one occurring less than 20 percent of the time, is also widely distributed will its presence in the overall vegetation remain an unimportant character of one or more plant communities. Rather, if a species is infrequent but restricted to a habitat due to some site factor(s), then as communities become extracted from the data set, that species will emerge as a prominent character of a particular community.

In the following discussion, the above will be clarified by retracing the steps involved with the separation of the first bryophyte community, Group A.

Masterdeck subdivisions. The following procedure is a description of the separation of Group A, one of twenty groups which were split out of the original data set of 565 cards. The flow diagram indicating the order of steps, and group separations for the entire data set is given at the end of this discussion.

All 565 cards containing the bryophyte presence data were combined into a masterdeck. Within the masterdeck 15 bryophytes had a frequency of 20 percent or greater. These may be considered the ubiquitous species of the intensive study site and are listed in Table V.

In the use of this technique one seeks to remove all heterogeneity within sample groups, thus basing

TABLE V

RELATIVE OCCURRENCE OF THE MOST FREQUENT BRYOPHYTES PRESENT IN 565 SAMPLES

Species	Presence	Frequency
Oncophorus wahlenbergii	229	41
Blepharostoma trichophyllum	224	40
Pohlia nutans	214	38
Drepanocladus revolvens	210	37
Pogonatum alpinum var. septentrionale	210	37
Calliergon sarmentosum	207	37
Dicranum elongatum	181	32
Cephaloziella arctica	177	31
Anastrophyllum minutum	175	31
Lophozia ventricosa	141	25
Tritomaria quinquedentata	140	25
Cephalozia pleniceps	135	24
Riccardia pinguis	126	22
Sphagnum spp.	120	21
Cinclidium subrotundum	112	20

community descriptions on group-sample homogeneity. Objectivity is maintained by testing the homogeneity of species group assemblages using Chi-square. Chi-square values which are significant indicate positive species-pair associations, and are therefore an indication of heterogeneity. Each instance of heterogeneity requires that the data set be split according to those species whose association is shown by the greatest value of Chi-square.

The total number of paired comparisons among the 15 most abundant species was 105. Of these, 67 showed positive interspecific association as measured by Cole's Index (Cole, 1949). The significance of these positive associations was tested using Chi-square. Fifty-six of the positive associations were significant at the 1 percent level (P=.01). Selected Chi-square values of extremely high significance were: Oncophorus wahlenbergii and Riccardia pinguis (X^2=166.83), Pohlia nutans and Dicranum elongatum (X^2=166.60), P. nutans and Anastrophyllum minutum (X^2=171.00), Anastrophyllum minutum and Dicranum elongatum (X^2=230.96), Anastrophyllum minutum and Lophozia ventricosa (X^2=194.47), Cephaloziella arctica and Riccardia pinguis (X^2=173.94), Dicranum elongatum and Lophozia ventricosa (X^2=205.64), and Riccardia pinguis and Cinclidium subrotundum (X^2=154.54).

These Chi-square values alone are ample proof that considerable heterogeneity existed among the data of the sample plots within the 565 card masterdeck. Accordingly, it was necessary to subdivide the masterdeck into two subdecks which could be retested to determine if heterogeneity was still present. Whenever the working deck was declared heterogeneous, the partitioning of it was based upon the most abundant species which showed significant interspecific association.

The most abundant species in the masterdeck (working deck) was Oncophorus wahlenbergii with a presence of 229, or a frequency of 41 percent. Oncophorus wahlenbergii showed significant association with Pogonatum alpinum var. septentrionale (X^2=75.14), Calliergon sarmentosum (X^2=76.26), Blepharostoma trichophyllum (X^2=57.70), Drepanocladus revolvens (X^2=60.56), Cephaloziella arctica (X^2=163.73), Tritomaria quinquedentata (X^2=13.13), Cephalozia pleniceps (X^2=21.89), Sphagnum spp. (X^2=64.60), Cinclidium subrotundum (X^2=87.85), and Riccardia pinguis (X^2=167.83). The masterdeck was, therefore, split into two subdecks, a new working subdeck 229 defined by Oncophorus wahlenbergii with a frequency of 100 percent and a residual subdeck 336 which was set aside until later.

Within working subdeck 229, all species with a frequency of 20 percent or more were again tested for

possible significant positive associations using all species-pair combinations. Since Cephaloziella arctica was the most abundant species in subdeck 229, all possible associations with this species were tested first. Cephaloziella arctica was significantly associated with Calliergon sarmentosum (X^2=22.19), Drepanocladus revolvens (X^2=41.68), Riccardia pinguis (X^2=24.26), Cinclidium subrotundum (X^2=11.56), and Sphagnum spp. (X^2=14.14). Since this indicated further heterogeneity within subdeck 229, further subdivision of the working deck was necessary. Accordingly, the next subdivision was at the cleavage point marked by Cephaloziella arctica. This created a new working subdeck 141 and a residual subdeck 88. The residual subdeck was merged with the 336 residual of the first split. Subdeck 141 was defined at this point by Oncophorus wahlenbergii and Cephaloziella arctica both at 100 percent frequency.

The next step was to test for significant associations within working subdeck 141. Again, this began with the most abundant species other than those at 100 percent frequency within the subdeck. The most abundant was Drepanocladus revolvens which had a frequency of 73 percent. Significant associations were found in this subdeck between D. revolvens and Calliergon sarmentosum (X^2=10.16), Riccardia pinguis (X^2=9.38), and Cinclidium

subrotundum (X^2=9.38). This indication of further heterogeneity within subdeck 141 called for another subdivision. As before, subdeck partitioning was based upon the most abundant species showing significant association, thus subdeck 141 was divided at Drepanocladus revolvens. The new working subdeck was reduced to 103 data cards and the residual subdeck of 38 cards was merged with the other residual cards. The group defined to this point in the separation process contained Oncophorus wahlenbergii, Cephaloziella arctica, and Drepanocladus revolvens, all at 100 percent frequency.

Subdeck 103 still contained a number of significant associations between the species with frequencies of 20 percent or greater. The most abundant species, other than those at 100 percent frequency, was Calliergon sarmentosum with a frequency of 78 percent. It was significantly associated with Pogonatum alpinum var. septentrionale (X^2=19.37). This association was of some importance because it illustrated that a species which was present in a quantity less than 20 percent of the working subdeck at higher levels of species comparisons, emerged as a valid species for association comparisons at a lower level. The presence of P. alpinum var. septentrionale was not significantly reduced in the multiple divisions of the working deck at the higher level

splits, so that at this level, its presence was great enough to exceed the 20 percent frequency limit.

Subdeck 103 was redivided using Calliergon sarmentosum as a cleavage marker. This created a new working subdeck of 80 cards and a residual subdeck of 23 cards which was combined with the other residual subdecks. The new working subdeck 80 then defined by those species already noted at 100 percent frequency with the addition of Calliergon sarmentosum.

Subdeck 80 was next tested for significant associations. The most abundant species other than those at 100 percent frequency in this subdeck was Riccardia pinguis with a frequency of 76 percent. It showed no significant associations with any other species whose frequency was 20 percent or greater within subdeck 80. The next most abundant species, Pogonatum alpinum var. septentrionale with a frequency of 65 percent likewise showed no significant association with any other species. The third most abundant species, Odontoschisma macounii with a frequency of 61 percent showed a single significant association with Conostomum tetragonum (X^2=9.28).

Within subdeck 80 there were only 14 species which occurred with a frequency of 20 percent or greater. Therefore, 91 possible pair comparisons were tested using Chi-square. Since the level of chosen significance was

1 percent, then one out of one hundred Chi-square values from a single contingency of calculations could be accepted as a chance phenomenon. The Chi-square value of 9.28 for the Odontoschisma macounii-Conostomum tetragonum association was both singular and barely significant, therefore this association alone could not be accepted as certain proof of heterogeneity. Instead, the next most abundant species yet untested in subdeck 80 was checked for significant associations.

Blepharostoma trichophyllum was the fourth most abundant species with a frequency of 44 percent. A highly significant Chi-square value was calculated for the association between B. trichophyllum and Cephalozia pleniceps (X^2=36.29). Since this marked the second significant association among the contingency of 91 species-pair comparisons, there was no doubt as to the heterogeneity still present in subdeck 80. Although the Chi-square value was much higher for the association between B. trichophyllum and C. pleniceps than between Odontoschisma macounii and Conostomum tetragonum, the cleavage point for the subdivision of subdeck 80 was based upon O. macounii. This was the correct choice since O. macounii was the most abundant species in subdeck 80 which showed even a single significant association. The more abundant species Riccardia pinguis (frequency,

76 percent) and Pogonatum alpinum var. septentrionale (frequency, 61 percent) had shown no significant associations and could not be chosen as cleavage points.

The new working subdeck now contained 49 cards based upon a 100 percent frequency of Odontoschisma macounii plus the other species already present with a 100 percent frequency. The residual subdeck 31 was combined with the previous residuals.

Within subdeck 49 no significant associations appeared in the comparisons with the three most abundant species, Riccardia pinguis (frequency, 76 percent), Pogonatum alpinum var. septentrionale (frequency, 76 percent) and Cinclidium subrotundum (frequency, 55 percent). A highly significant association between the fourth most abundant species in subdeck 49, Blepharostoma trichophyllum with a frequency of 47 percent and Cephalozia pleniceps produced a Chi-square value of 17.31. Since the contingency of species-pair comparisons in subdeck 49, based upon a group of 11 species with frequencies equal or greater than 20 percent, was 55 total comparisons, this single significant Chi-square could be only marginally accepted as a non-chance occurrence. Since the probability of that Chi-square value is somewhat less than .001, and the number of total comparisons was only 55, this single significant association

was considered ample reason for further subdivision.

Blepharostoma trichophyllum became the final defining species for this group of 23 cards which now had the following species at 100 percent frequency: Oncophorus wahlengergii, Cephaloziella arctica, Drepanocladus revolvens, Calliergon sarmentosum, Odontoschisma macounii, and Blepharostoma trichophyllum. The residual subdeck of 26 cards was combined with the other residual subdecks. The residual subdeck now contained 542 cards.

Within subdeck 23 no significant associations occurred among species. This subdeck was finally homogeneous within. It was designated Group A, was defined by the six species of 100 percent frequency and was set aside.

The same procedure was followed for the extraction of Groups B-T from the residual masterdeck of 542 cards. The eventual result of the entire operation was a splitting-out from the original data set, 20 internally homogeneous groups tentatively representing distinct bryophyte communities. The entire operation is presented in the flow diagram of Figure 7. However, this was only the first of three steps which culminated in final descriptions of bryophyte communities.

The second step was to systematically recombine all

Figure 7. Flow diagram of masterdeck separation into homogeneous groups (communities) A-T.

Abbreviations--(Ana min) Anastrophyllum minutum, (Ble tri) Blepharostoma trichophyllum, (Cal sar) Calliergon sarmentosum, (Cep arc) Cephaloziella arctica, (Dic elo) Dicranum elongatum, (Dre rev) Drepanocladus revolvens, (Dre unc) Drepanocladus uncinatus, (Hyl spl) Hylocomium splendens var. obtusifolium, (Lop ven) Lophozia ventricosa, (Odo mac) Odontoschisma macounii, (Onc vir) Oncophorus virens, (Onc wah) Oncophorus wahlenbergii, (Pog sep) Pogonatum alpinum var. septentrionale, (Poh nut) Pohlia nutans, (Ric pin) Riccardia pinguis, (Sca pal) Scapania paludicola, (Tri qui) Tritomaria quinquedentata.

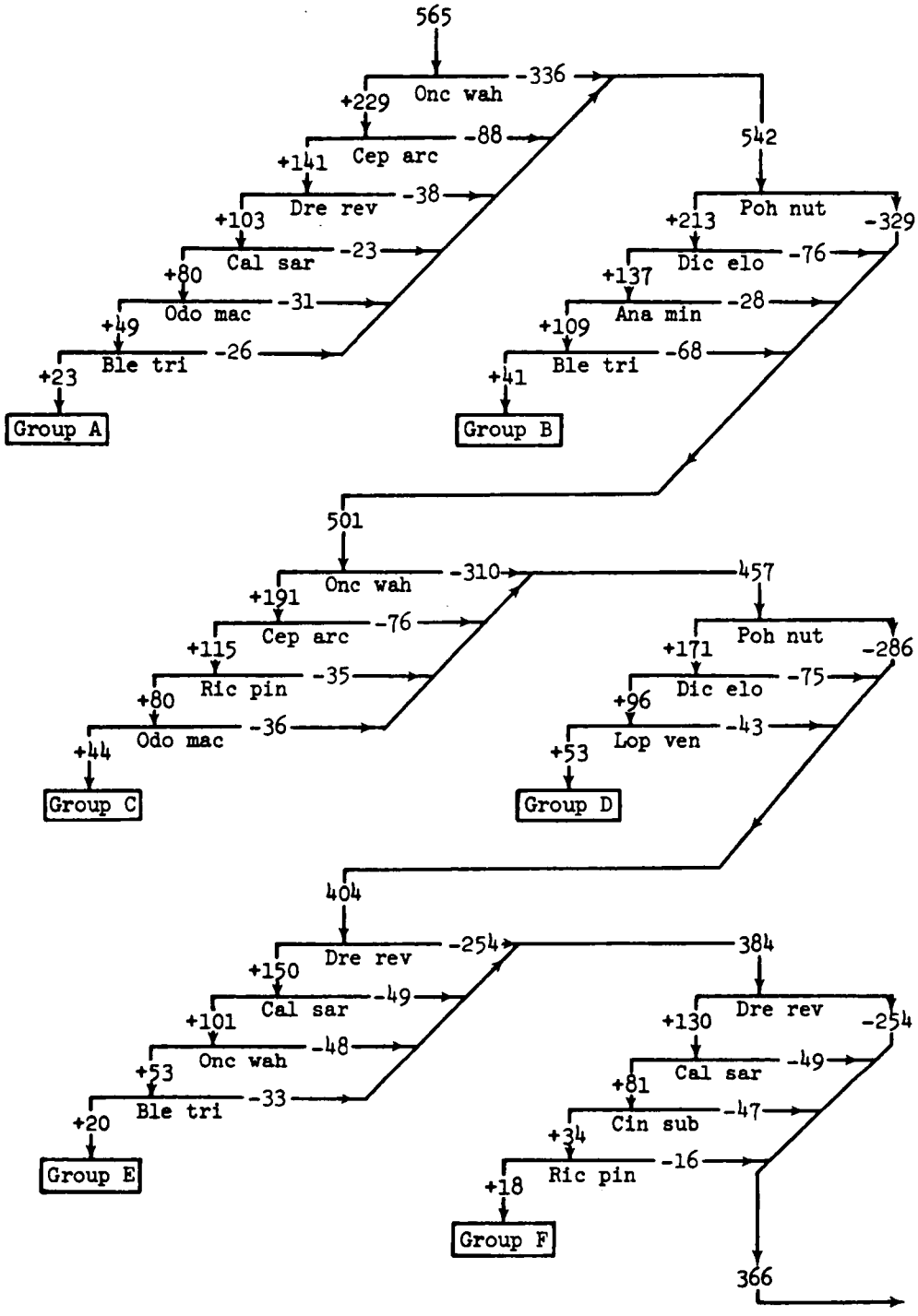

565
Onc wah
-336
+229
-88
Cep arc
+141
-38
Dre rev
+103
-23
Cal sar
+80
-31
Odo mac
+49
-26
Ble tri
+23
Group A
542
Poh nut
-329
+213
-76
Dic elo
+137
-28
Ana min
+109
-68
Ble tri
+41
Group B
501
Onc wah
-310
457
+191
-76
Cep arc
+115
-35
Ric pin
+80
-36
Odo mac
+44
Group C
Poh nut
-286
+171
-75
Dic elo
+96
-43
Lop ven
+53
Group D
404
Dre rev
-254
384
+150
-49
Cal sar
+101
-48
Onc wah
+53
-33
Ble tri
+20
Group E
Dre rev
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Cal sar
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-47
Cin sub
+34
-16
Ric pin
+18
Group F
366

Figure 7

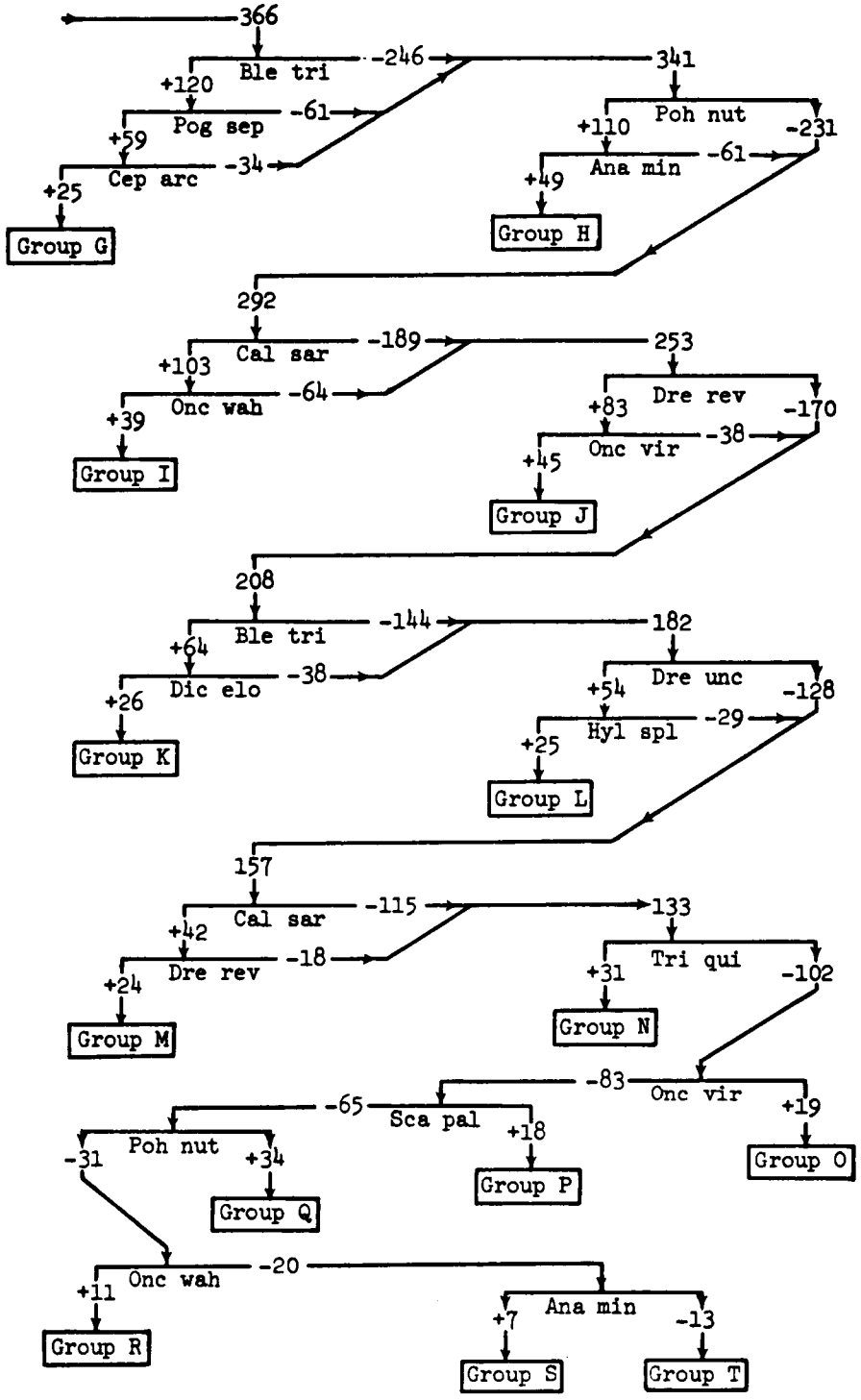


Figure 7 (continued)

groups by pairs and retest these group combinations using Chi-square to determine if heterogeneity was introduced within recombinant subdecks. If the recombinant subdecks showed no significant associations then they were assumed to be homogeneous within and the larger recombinant group was maintained. If significant associations reappeared after recombination, this re-creation of heterogeneous sample data affirmed the original evidence for keeping the groups separate.

The ultimate goal of this procedure was to reduce the number of groups and increase the size of any or all the groups through recombinations. By doing so, this utilizes the largest body of data for the community descriptions. This is a desirable characteristic of any method which results in the sufficient description of vegetation without creating an intolerably large number of only finely differing classes.

The recombination procedure required 190 group-pair comparisons among the 20 groups. Of the 190 group-pair comparisons only three emerged that showed a non-introduction of heterogeneity in the sample data. The three homogeneous recombinant groups were kept intact as groups A+E, H+S, and Q+T. A single marginal combination R+F showed several barely significant associations, but these did not exceed the number permissible as chance occurrences

and the recombination was rejected.

With the completion of the recombination procedure, the extraction of similar quadrat groups was essentially completed. However, during the compiling of species statistics for each group the recombinant group Q+T came into question. A re-evaluation of the Chi-square values for this recombination revealed that all values barely non-significant at the 1 percent level were significant at the 5 percent level. Furthermore, the recombinant group Q+T yielded the most abundant species, Pohlia nutans, as only present in 74 percent of the samples. Since Group T was the final residual subdeck of the groups extracted, I considered that it was an aggregate and artificial group composed of several samples from different communities which were not allocated during the separation of earlier derived groups. Thus, the recombinant group Q+T was also rejected.

Some decision was needed to reconcile the subdecks which were separated in the final portion of the extraction process. Groups N, O, P, Q, R, and T were the final groups extracted. Group S was successfully merged with H. Groups R and T were the last two groups of doubtful value and together comprised only 24 samples. They were considered together, residuals representing mixtures of samples which might have been allocated elsewhere in other groups.

An alternate interpretation could argue that they were representative of transitional sites on the tundra. However, I considered this interpretation as too artificial and prone toward neatly accommodating all the sample data.

From the 565 samples 16 communities were finally delineated, with only two being the result of recombination, A+E and H+S.

Ordination of Bryophyte Communities

The technique known as ordination was used to compare the 16 bryophyte communities which were defined by the objective divisive procedure described by Goodall (1953). Ordination techniques are not new to the study of vegetation, but they have had little application in the study of bryophyte communities.

Two early studies of importance by Hale (1955) and Culberson (1955) used indirect ordination of corticolous lichens and bryophytes in a continuum ordination of these communities, where the communities were ordered along a "climax" gradient of forest trees. More recently, Foote (1966) studied the saxicolous bryophyte-lichen communities in driftless Wisconsin using the comparative ordination technique of Bray and Curtis (1957). This technique is simplified as applied by Foote (1966) but

still permits a rather rapid dispersion of data within a n-dimensional hyperspace.

I have used the comparative ordination as presented by Foote (1966) to organize the communities already defined. The resulting patterns of dispersion are useful in supporting the inferences concerning groups of "closely related" communities.

Ordinarily, ordination can be applied directly to field-gathered data provided that data is retrieved from pre-determined sites of known homogeneity. Although the field-acquired data in this study was ordered at the time of sampling by defining presumably homogeneous habitats from the microrelief of the landscape, later analyses proved that in habitats of similar topography, several differing communities could be expected. This indicated extreme heterogeneity among the samples and required the use of some objective means to establish homogeneous clusteres of like floristic samples. Goodall's method (1953) served this purpose. The ordination of the clusters (groups) provides a tool for investigating the environmental gradients such as soil pH, moisture, and topography, as they relate to the distribution of the bryophyte communities.

Since ordination in the sense of Bray and Curtis (1957) allows one to compare any number of samples and

expresses the comparison by some scale of similarity, one must choose some measurement which standardizes the data, and then another which will compare those measurements. A number of community measurements have been proposed (Whittaker, 1967). In this study I have used the importance values for each species with a frequency of 20 percent or greater. These values are given in Appendix A (Tables X-XXV). In several instances, where a species occurred with less than a 20 percent frequency in a particular community, but was highly important in other communities, I included such species to permit finer comparisons between the communities.

For comparing any two communities I have used Kulczynski's community coefficient as expressed by Motyka, et al., (1950, in Bray and Curtis, 1957). This community coefficient:

$$C = \frac{2w}{a + b}$$

is a measure of the floristic similarity between any two plots, stands, communities, or other group designations. The coefficient C may vary from 0.00 to 1.00 representing the similarity of each pair comparison as totally dissimilar through a range to total similarity. The values (a) and (b) are the sums of the quantitative measures of the plants in each group being compared. The value (w) is

the sum of the lower values of the measures for those species which are common to both groups (a) and (b). The calculation of the community coefficient for each group-pair comparison allows the eventual compilation of a data matrix of coefficients which expresses the degree of similarity between all comparable groups.

The matrix of community coefficients comparing the 16 bryophyte communities is given in Table VI. These values were then used to station the communities in 3-dimensional space.

Axes construction and community location. The communities were ordinated along an (x), (y), and (z) axis in order to create the 3-dimensional model. The position of each community becomes relative to the two endpoints of each axis. Certain criteria are used to choose which communities are acceptable for endpoints, after which the remaining communities are aligned along the axis being constructed, relative to the two endpoints.

The (x) axis was the first construction. In order to determine which community should serve as the first endpoint, the community coefficients for each community in the matrix were summed. The community with the lowest sum was the community which was most dissimilar from the other communities. This was community P. The selection

TABLE VI

MATRIX OF KULCZYNSKI'S COMMUNITY COEFFICIENTS COMPARING COMMUNITIES

Bryophyte Communities	F-18	P-19	O-19	M-24	K-25	G-25	L-25	N-31	Q-34	I-39	B-41	AE-43	C-44	J-45	D-53	HS-56
F-18	---	.09	.08	.46	.19	.44	.09	.21	---	.64	.16	.67	.69	.16	.04	.06
P-19		---	.06	.05	---	.08	.19	.11	.06	.16	.04	.12	.12	.09	.04	.04
O-19			---	.04	.08	.09	.37	.16	---	.13	.08	.09	.08	.68	.02	.03
M-24				---	.03	.10	.02	---	---	.44	.04	.31	.34	.22	---	---
K-25					---	.48	.08	.31	.06	.24	.80	.33	.20	.03	.54	.37
G-25						---	.15	.30	.07	.41	.47	.68	.52	.07	.19	.21
L-25							---	.47	---	.17	.09	.14	.12	.48	.02	.02
N-31								---	.12	.28	.34	.29	.24	.17	.13	.16
Q-34									---	---	.22	---	---	---	.48	.56
I-39										---	.10	.66	.63	.19	.05	.07
B-41											---	.30	.20	.03	.73	.54
AE-43												---	.77	.13	.06	.09
C-44													---	.13	.06	.08
J-45														---	---	---
D-53															---	.75
HS-56																---

of the opposite endpoint was made by searching through only the coefficients which compared community P with the other communities. The community with the lowest coefficient relative to community P was the most dissimilar from community P and became the selection for the second endpoint. This was community K. The remaining communities were then located as points on the (x) axis relative to the similarities shared with both endpoints.

The (y) axis was constructed next. The same criteria for choosing endpoints were used except the communities which were eligible for selection were restricted to those lying within five points on either side of the midpoint of the (x) axis. Community Q located near the midpoint of the (x) axis had the lowest sum of community coefficients and became the first endpoint in the (y) axis construction. Community M was most dissimilar from community Q and became the selection for the second endpoint. The remaining community points were aligned along the (y) axis relative to the new endpoint communities.

The (z) axis was constructed using the same procedures using midpoint communities of the (y) axis. This resulted in the final axis construction with communities O and Q forming the endpoints.

Theoretically any number of axes can be constructed although beyond the third dimension the objects being ordinated fall into a n-dimensional hypervolume which is likely to be uninterpretable. By restricting the ordination to three dimensions one can then inspect the whole from the three planar projections of a cube and seek to discover previously obscured environmental gradients.

Axis interpretation. The information depicted by Figure 8 is not immediately apparent. By inspecting the planar views (xy), (yz), and (xz) repeating community clusters are visible. These ecological groups (sensu Whittaker, 1967) which appear in the ordination are similar to those alluded to in the classification and description of the communities in Chapter IV.

The fact that contours of environmental gradients fit best into the different 2-dimensional planes is an indication that some of the environmental gradients which influence the distribution of species and communities are somewhat intersecting rather than parallel. One might interpret such as a continuum of vegetation which is reflecting a plexus of environmental gradients. While the vegetation can be imagined as a linear continuum following the edaphic gradient of moisture and pH, such

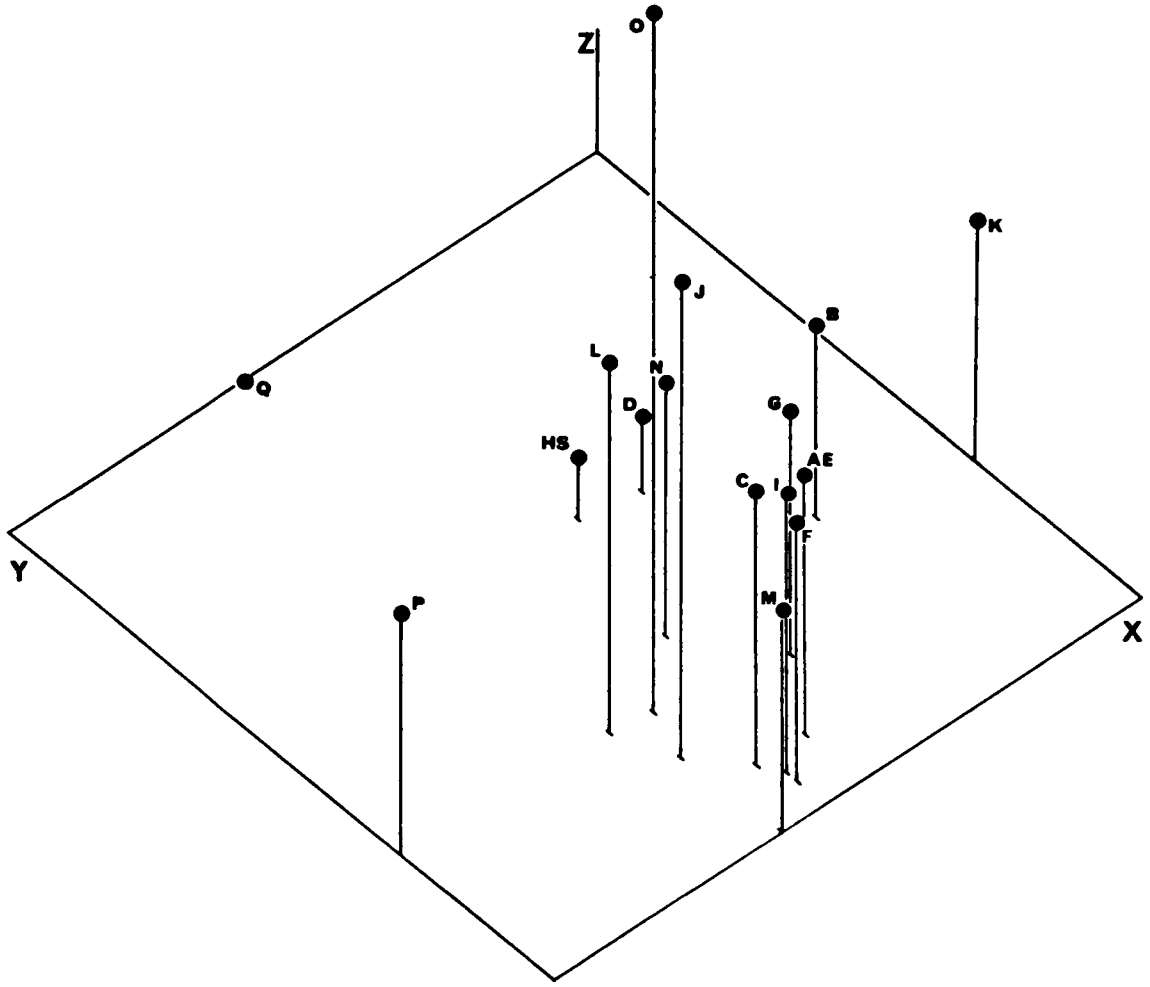


Figure 8. Three-dimensional ordination of bryophyte communities, A-Q, Barrow, Alaska.

an interpretation is a purely synthetic organization which is rarely met with as a linear sequence in the field. While all the points of a line which represent a vegetational continuum exist at Barrow, they are widely scattered.

Figure 9 is the ordination of the (x) and (y) axes. The communities are dispersed in what first appears to be a rather non-descript pattern. The most revealing underlying pattern which is shown by this ordination is a gradient relating to moisture. As one examines Figures 9, 10, and 11 the repeated occurrence of this moisture gradient becomes more apparent as discussed below.

Figure 10 is the ordination of the (x) and (z) axes. This projection gives the best continuous expression of the soil pH gradient. The moisture gradient is still present but is not represented in a linear series since the communities O, J, and L are mesic communities now held separate from the central cluster of communities which is a swarm of mesic and hydric communities. The xeric communities (Q, HS, D) remain conspicuously disjunct at the low end of the pH range.

Figure 11 is the ordination of the (y) and (z) axes. This projection is used to illustrate the segregation of communities according to macrotopography. Communities G, K,

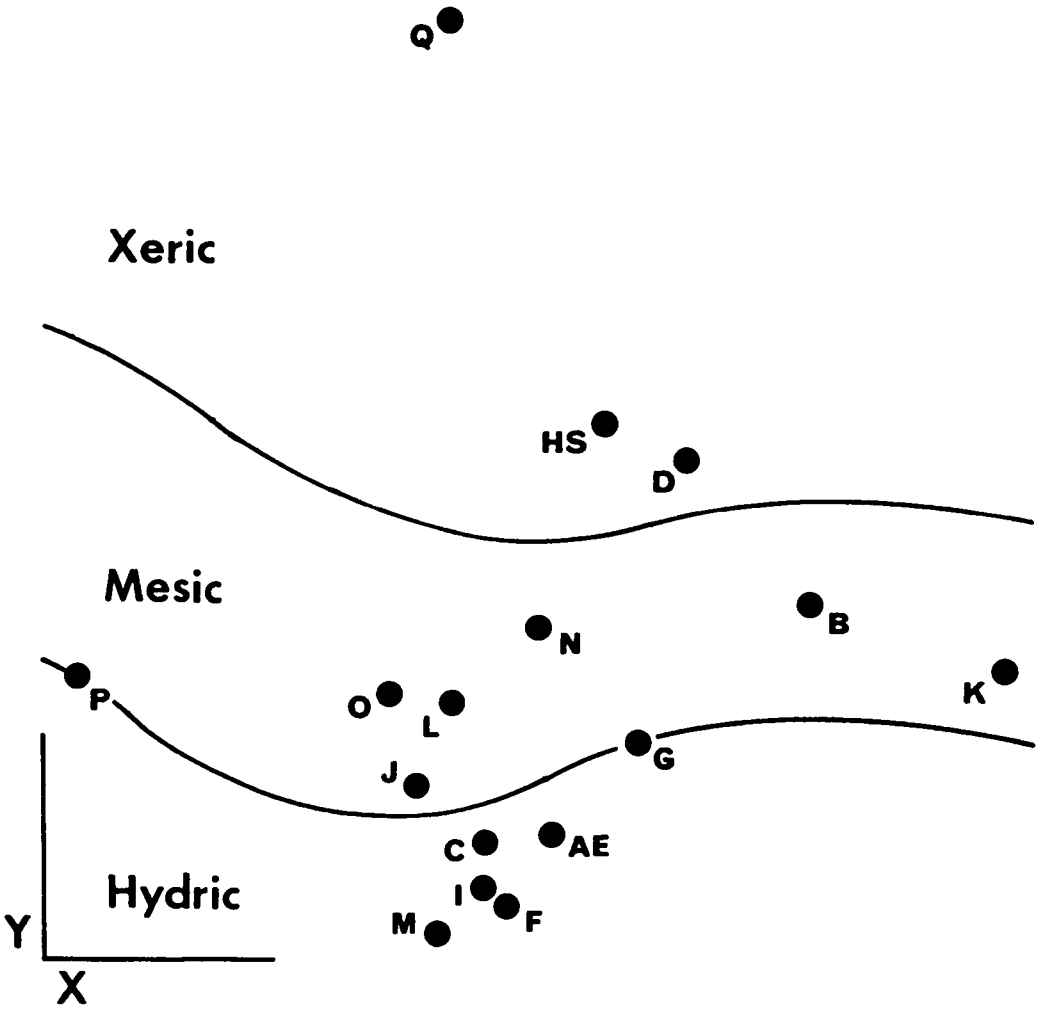


Figure 9. XY ordination showing contours which separate communities along a moisture gradient.

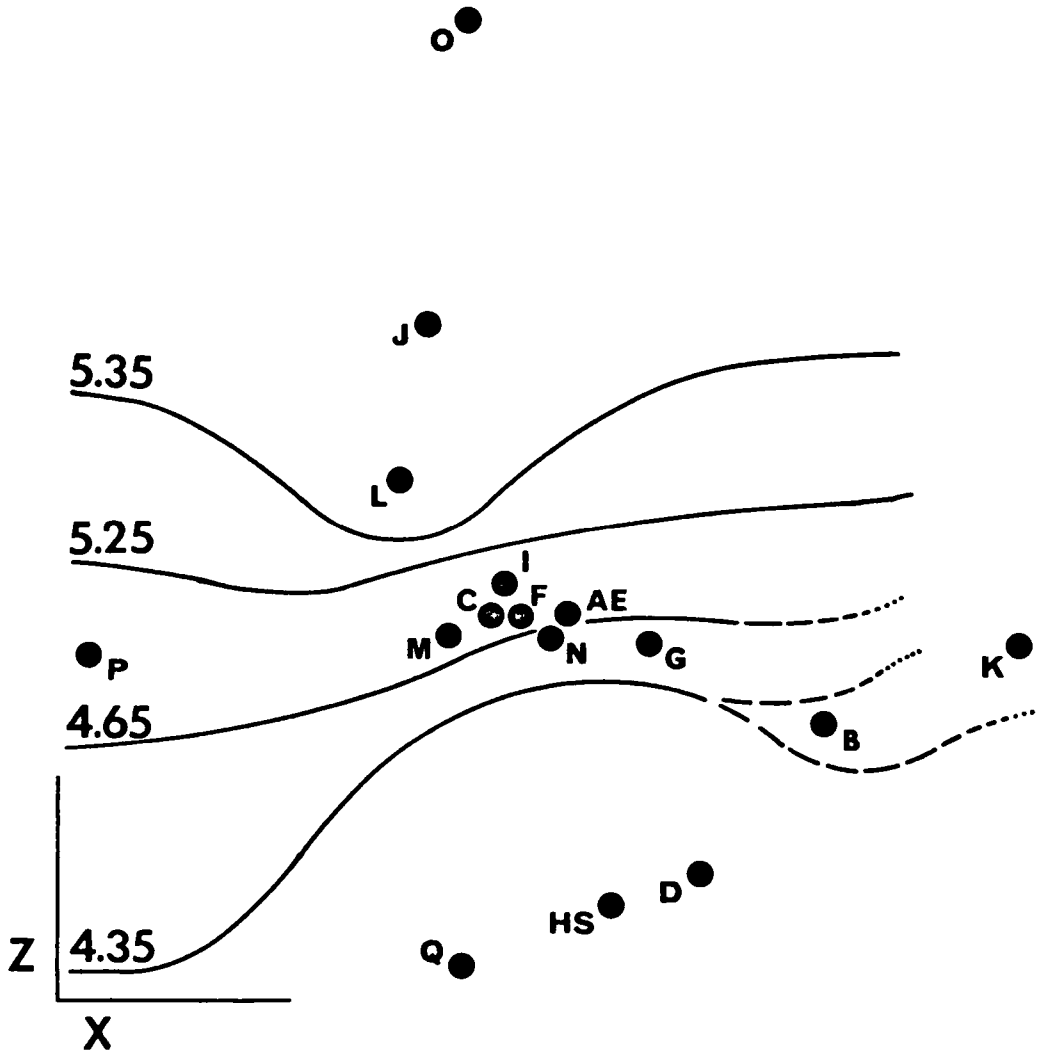


Figure 10. XZ ordination showing contours of soil pH which separate communities along a soil pH gradient.

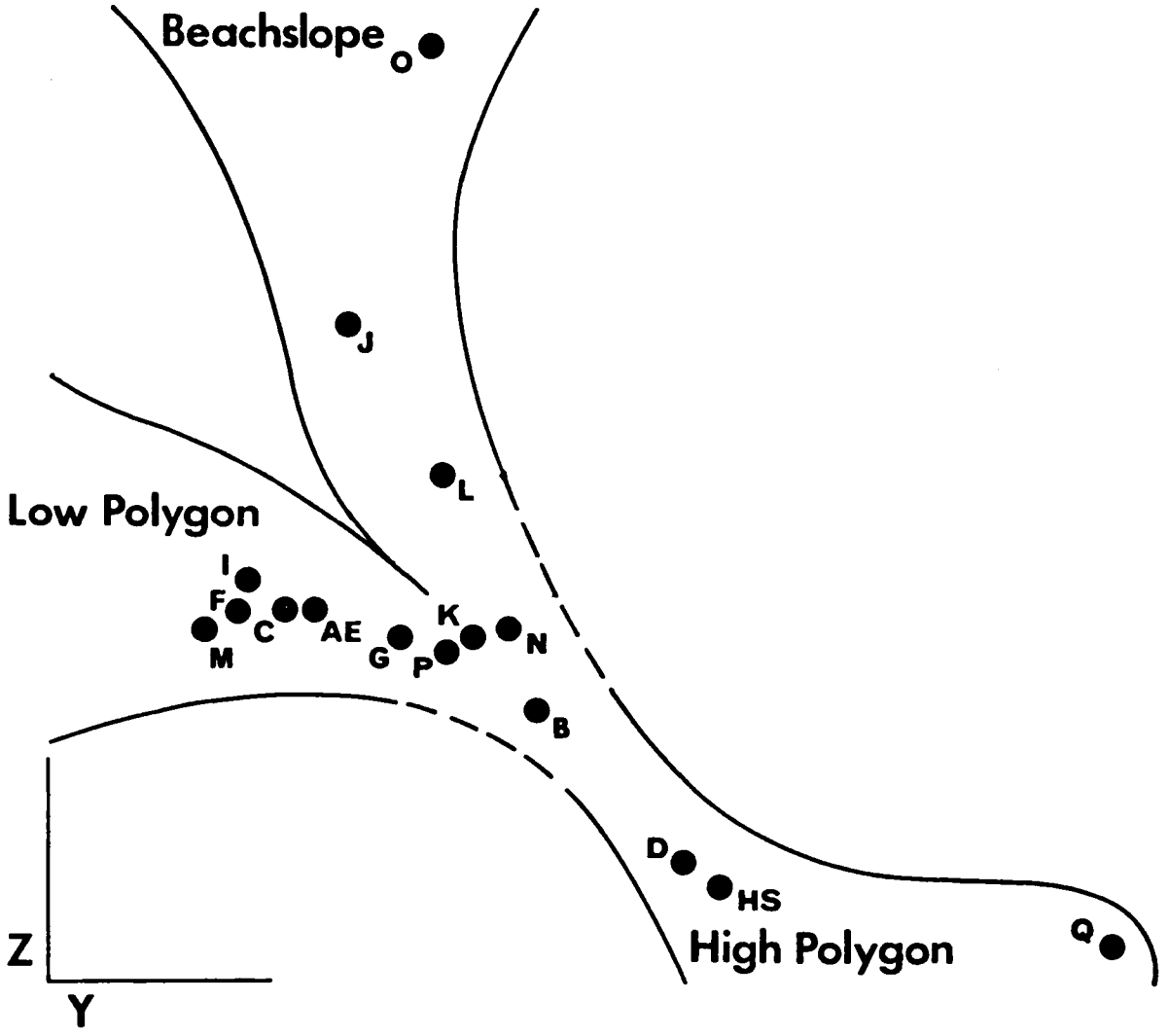


Figure 11. YZ ordination showing contours which separate communities according to macrotropography.

N, P and B are shown in positions transitional to all other communities which are characteristic of the three topographic sectors. The gradient of moisture is still present moving from left to right.

The ordination has revealed that at least the three environmental gradients of soil moisture, soil pH, and macrotopography are important for understanding the distributions of bryophyte communities at Barrow. The difficulties encountered when attempting to make visual assessments of the vegetation at Barrow are exemplified by the bryophyte communities. Their compositions are highly unpredictable. Certain community series can be delimited as most characteristic of sites which are wet, mesic, or dry, and within these three moisture classes the specific community composition will change markedly according to conditions of topography and exposure, soil pH, and degree of disturbance.

Description of Bryophyte Communities

The 16 bryophyte communities which were separated by the association analysis technique and compared by the ordination are described here. The descriptions are prepared from the data contained in Appendix A (Tables X through XXV). Species which occurred infrequently (less than 20 percent frequency), not formally treated in the

descriptions, are reported in Appendix A (Table XXVI).

The structure of each community was examined using four measurements of the contribution made by each species in the community. These measurements were frequency, average cover, dominance, and importance. Frequency is a percent measurement of the presence of any species among the sample plots assigned to each community. Average cover is a calculated value derived by converting the class-cover scale data to actual mean values of the class, then summing these actual cover values and dividing the sum by the number of sample plots per community. Dominance is simply the number of sample plots in a community in which a particular species occurred with an abundance as measured by cover, equal to or greater than 25 percent. Importance, denoted in Appendix A as "importance value" is a synthetic value derived by combining frequency and average cover.

An importance value can combine any number of measurements. For this reason it often becomes a preferred measure of species contribution in quantitative community descriptions. Importance values also have versatility in quantitative descriptions of vegetation as demonstrated here, since the importance values were used both in the ordination and descriptions.

An importance value was calculated for each species

which showed a frequency of 20 percent or greater. In a few exceptional cases, an importance value was calculated for species with a less than 20 percent frequency. These species were always present in greater quantities in the other communities and were included for comparative reasons if their presence was just one point less than the number necessary to give them a 20 percent frequency.

In order to calculate an importance value, each measurement to be combined must be scaled so that the synthetic value will not be biased by non-proportionalities among the combined measurements. The importance value used here was a combined frequency-average cover value. Since frequency is automatically based on a maximum value of 100, and this value was attained by at least one species per community by virtue of the association analysis technique, no adjustment of frequency values was required. However, since the Barrow bryophytes grow in such highly mixed stands, average cover measurements never have maximum values near 100 percent. If the frequency and average cover were combined directly, the importance value would weight frequency more than cover. To adjust (weight upward) the average cover values, the species which had the greatest average cover in each community was assumed to be 100. All other average cover values for the remaining species in the community were

then adjusted relative to the highest value. This procedure merely re-expresses common data as a percent of the maximum recorded value. Frequency and weighted average cover were then summed. This created a raw importance value for each species under consideration, and a maximum raw importance value of 200 since the maximum value for the two combined measurements was 100 each. For convenience, the raw importance values were then converted back to a base 100.

The advantage in using the importance values for community descriptions is that species with high frequency but low cover are reduced in importance within a community. Similarly, species with low frequency but with considerable cover when present, show up more importantly in the community species hierarchy.

The 16 bryophyte communities can be grouped rather naturally into hydric, mesic, and xeric series. This notion has been suggested by the ordination which indicates the communities are related along several gradients of moisture, soil pH, and macrotopography. Several communities appear transitional in nature and can be treated as such.

The following descriptions are based solely on the importance values for those species reported in Appendix A (Tables X through XXV). Dominant species are those with

importance values from 80-100, subdominant species from 40-80, and important associated species from 20-40. Discussions of site characteristics such as relative percent soil moisture, soil pH, and microtopographic position point out community differences not always as obvious after only floristic comparisons.

Xeric Bryophyte Communities

This community series was found in areas of raised relief. It is represented by three communities Q, HS, and D which follow, in this order, a moisture gradient from extreme dryness to dry. All three communities have similar soil pH ranges and are the most depauperate in floristic richness among the 16 bryophyte communities.

Bryophyte community Q. This community is dominated by Pohlia nutans and members of the family, Polytrichaceae. The collective occurrences of Pogonatum dentatum, Polytrichum piliferum var. hyperboreum, and Pogonatum alpinum formed a group which shared dominance with Pohlia nutans. Taken separately these species could be classed with Dicranum elongatum as important associated species.

This community was restricted to the high center polygon sector and almost exclusively to the polygon tops. Occasional sites were located on the high center polygon slopes. The usual site on polygon tops was frostboils,

grassy turfs, and pure bryophyte clumps. The pH of the soil surface had a mode-range of 3.75-4.35. Relative percent soil moisture was extremely low, ranging from 15 percent on the dry frostboil sites to 35 percent on purely bryophyte-dominated sites. The few sites located on the polygon slopes were not quite as xeric and appeared transitional to the next two communities which were also found in the high center polygon sector.

An important character of the xeric habitats is the low abundance of hepatic species, and only a slight reduction in the moss component when compared to the communities discussed hereafter. The depauperate hepatic flora (average cover, 5 percent) is a clear indication of the dessicating climatic conditions common to the high center polygon tops. The tiny liverwort Gymnomitrion coralloides occurred infrequently on these exposed sites, and to a lesser extent, Lophozia ventricosa and Orthocaulis binsteadii. Absent from this community were Massula opacifolia, Tritomaria quinquedentata, and Anastrophyllum minutum, all present in the next community of the high polygons where slightly more mesic conditions were found.

The abundance of mosses (average cover, 67 percent) is due principally to the presence of Polytrichaceous mosses. Members of this family are well-adapted to dry

habitats and their large size contributes heavily to the community cover in all habitats where they occur.

Bryophyte community HS. This community is dominated by Pohlia nutans and Anastrophyllum minutum. Subdominant species are Dicranum elongatum and Pogonatum dentatum. Important associated species are Polytrichum piliferum var. hyperboreum, Scapania mucronata, Cephalozia pleniceps, and Pohlia cruda.

Like community Q, this community was found in the high center polygon sector in all three habitats of the polygon tops, but more frequently on the slopes of the polygons. The pH of the soil had a mode-range of 3.85-4.45, slightly higher but probably of little significance. The relative percent soil moisture was similar to community Q for the sites on the polygon tops, but the greater frequency of this community on the polygon slopes indicates a general habitat shift towards greater moisture. Consistent with this interpretation was an average percent moisture on the slope sites of 70 percent.

The most marked difference between this community and community Q was the greater abundance of hepatics (average cover, 25 percent). The moss flora was little changed with an average cover of 63 percent. In addition to Gymnomitrion coralloides, Anthelia juratzkana was an

interesting addition to the hepatic flora of this community. A clear indication of the less rigorous climate associated with this community was the dominance of Anastrophyllum minutum and the common occurrence of Lophozia ventricosa, Orthocaulis binsteadii, Massula opacifolia, and Tritomaria quinquedentata.

Bryophyte community D. This community shows the greatest diversity of the three communities associated with the high polygon sector. It is dominated by Dicranum elongatum, Pohlia nutans, Lophozia ventricosa, and Anastrophyllum minutum. No subdominant species were recognized. The important associated species are Pogonatum dentatum, Orthocaulis binsteadii, Scapania mucronata, and Polytrichum piliferum var. hyperboreum.

Community D was found abundantly on the sloping sides of the high center polygons. Lesser occurrences were encountered on the high polygon tops, but in these sites the habitats were either the ground story of dense grassy clumps or luxuriant pure bryophyte turfs. Several sites in the low center polygon sector were allotted to this community type by the association analysis technique. These I included hesitantly. Their location on the interpolygonal ridge tops and the upper trough slopes places these samples closer to several communities of that topographic sector.

The pH mode-range was similar to that found in the previous two communities, 3.85-4.35. The relative percent soil moisture was higher, 106 percent, and was clearly reflected by the composition of the bryoflora. The average cover by mosses was unchanged, 63 percent, but the average cover by hepatics showed a significant increase to 55 percent.

Neither Gymnomitrion coralloides nor Anthelia juratzkana occurred in this community. Whereas the greatest floristic difference between this community and communities Q and HS was in the hepatic floras, an interesting comparison can be made using one species of the Polytrichaceae. Pogonatum alpinum was commonly encountered in both communities Q and HS. In community D this species was almost completely replaced by the var. septentrionale, a variety characteristic of moist habitats often associated with other meadow species.

The hepatic flora of this community is richer than in the other more xeric communities because moss-hepatic polsters often form on the high polygon slopes, where this microrelief adds diversity to habitats found in this community. These polsters form and develop to the greatest degree on the steeper slopes of the polygons and indicate a condition of unstabilized substrate either perturbated by wind action or cryoplanation. Processes

known to create bryophyte polsters elsewhere have been discussed rather recently (Price, 1969; Heusser, 1972; Marsh and Koerner, 1972). A good discussion of solifluction profiles by Hanson (1950) provides information for a similar mode of action in the formation of the polsters found at Barrow.

Mesic Bryophyte Communities

This community series was found in the beachslope sector of the intensive study tract. It consists of three closely related communities all characterized by a mesic environment with moderate drainage. The three communities J, O, and L are related in their bryofloristic composition, soil pH, and relative percent ground moisture. Differences are mainly proportional amounts of dominant and subdominant species which indicates microhabitat differences in relief and ground moisture. These communities are characteristic of the most calcareous habitats at Barrow.

Bryophyte community O. This community is narrowly defined by the single dominant, Distichium capillaceum. Subdominants are Oncophorus virens, Drepanocladus revolvens var. intermedius, Ditrichum flexicaule, and Tomenthypnum nitens. The choice to recognize the variety of D. revolvens here is contrary to the recent opinion of

Crum, et al., (1973); however, the differences between the variety and the species are demonstrable in this local area. D. revolvens from wet habitats of the low center polygon sector is separable from the var. intermedius of the beachslope sector according to Grout's (1928-1934) key. Important associated species are Scorpidium turgescens, Orthothecium chryseum, Bryum spp., Tortella tortuosa, Myurella julacea, Blepharostoma trichophyllum, Pogonatum alpinum var. septentrionale, and Calliergon sarmentosum.

Community O occurred in the middle of the beachslope but seemed to show a slight tendency toward growth on elevated soil-mound sites. The soil pH mode-range was 5.35-5.65. The relative percent soil moisture was exceedingly variable ranging from as low as 25 percent to as high as 275 percent depending on the site. Relative coverage values were 59 percent for mosses and a surprisingly low 3 percent for hepatics.

In this community several of the associated species were of interest. Both Tortella tortuosa and Tortella fragilis occurred in habitats included in this community. Scapania simmonsii, a distinctly arctic bryophyte, occurred with a 21 percent frequency although never in local abundance. This species although infrequently collected is apparently widespread in the north

circumpolar region (Steere, 1953b). The occurrence of Anthelia juratzkana in this community was not too surprising considering the calcareous nature of the substrate. Fissidens osmundoides was found only once, well concealed at the edge of a frost crack beneath a skirt of larger mosses.

Several conspicuous characters of this community and the two which are discussed next (communities L and J) are the low coverage values for the hepatics, the rarity of Polytrichaceous mosses, and the extremely high numbers of species which can be referred to as dominant, subdominant, and important associated species.

Bryophyte community J. This community is dominated by Drepanocladus revolvens, Distichium capillaceum, and Oncophorus virens. Subdominant species are Ditrichum flexicaule, Orthothecium chryseum, Tomenthypnum nitens, and Hylocomium splendens var. obtusifolium. Important associated species are: Scorpidium turgescens, Myurella julacea, Tortella tortuosa, Plagiomniom ellipticum, Ptilidium ciliare, Bryoerythrophyllum recurvirostrum, Bryum arcticum, Dicranum spp., Calliergon sarmentosum, Bryum spp., and Drepanocladus uncinatus.

This community is considered to be the richest on the beachslope and represents a mixed mesic bryophyte

community. It was found to occur primarily in the lower portion of the beachslope although not uncommonly in the depression sites in the middle to upper portions of the beachslope. The soil pH mode-range was 5.25-5.65 and the relative percent soil moisture averaged about 250 percent. Relative moss cover was 84 percent compared to a poor hepatic cover of 6 percent.

Like communities O and L, community J also had small amounts of Polytrichaceous mosses. The bryofloristic richness of the community is reflected in the occurrence of species such as: Dichodontium pellucidum, Fissidens arcticus, Fissidens osmundoides, Scapania simmonsii, Timmia austriaca, Bartramia ithyphylla, Lophozia alpestris, Myurella tenerrima, Orthocaulis kunzeanus, Rhizomnium andrewsianum, Tortella fragilis, and Tritomaria quinquedentata.

Bryophyte community L. This community is dominated by Hylocomium splendens var. obtusifolium, Drepanocladus uncinatus, Tomenthypnum nitens, and Ptilidium ciliare. Subdominant species are Plagiomnium ellipticum, Tritomaria quinquedentata, and Oncophorus virens. Important associated species are Aulacomnium turgidum, Ditrichum flexicaule, Distichium capillaceum, Bryum spp., Dicranum spp., Blepharostoma trichophyllum, Bryum pseudotriquetrum, and Oncophorus wahlenbergii.

This community was most abundant in the upper portion of the beachslope although it was found a few times in the lower beachslope. The floristic composition indicated the presence of moist depression sites of the upper beachslope. The soil pH mode-range was 5.35-5.65, and the relative percent soil moisture was similar to that of the other communities found exclusively on the beachslope, also located in moist habitats. Relative cover for the mosses was 77 percent, slightly higher than in community O, and for the hepatics, 14 percent, the highest value noted for the calcareous beachslope communities.

The bryoflora of this community was equally as diverse as that found in other beachslope communities. Besides those species noted as dominant and subdominant for communities J and O, three species imparting a distinctiveness to community L are Timmia austriaca, Mnium marginatum, and Rhizomnium andrewsianum.

Hydric Bryophyte Communities

Hydric bryophyte communities P, AE, C, F, I, and M are characteristic of the wettest habitats, either the moist troughs of the high polygon field, or the generally wet low-lying drained lake basins which are characteristically dissected into low center polygon fields. Within

the intensive study site, community P was restricted to the interpolygonal troughs of the high polygon sector, while all the other communities were characteristic of the low polygon sector and occasionally of isolated sites in the lower beachslope. Specific moisture data are lacking but an arrangement of these communities along environmental gradients is possible using floristic, soil pH, and coverage data.

Bryophyte community P. The single dominant species in this community is Scapania paludicola. Subdominant species are Drepanocladus uncinatus and Calliergon stramineum. Important associated species are Cephalo-ziella arctica, Drepanocladus exannulatus, and Campylium stellatum.

Additional common species found in this community are: Calliergon sarmentosum, Calliergon richardsonii, Oncophorus wahlenbergii, Plagiothecium denticulatum, Pogonatum alpinum var. septentrionale, Pseudobryum cinclidioides, and Ptilidium ciliare. I consider that taken together, the above species represent a rare community within the intensive study tract. However, this community is widespread at Barrow. I have noted that similar composition of bryophytes is characteristic of the large meadow sites elsewhere at Barrow, not specifically

sampled for community structure in this study.

This community was found only in the troughs of the high polygon sector and for this reason and its few dominant species, it is considered the best-defined community in this study. The soil conditions of the community were drier than in other communities of the hydric series. Relative percent soil moisture varied from 90 percent to 330 percent with an average value near 200 percent. The soil pH mode-range was 4.64-4.95, considerably higher than the other sites in the high polygon sector. In this community the relative cover by hepatics 39 percent nearly matched that for mosses, 45 percent.

Bryophyte community AE. This community is dominated by Oncophorus wahlenbergii and Cepahloziella arctica. Subdominant species are Blepharostoma trichophyllum, Drepanocladus revolvens, Cephalozia pleniceps, Calliergon sarmentosum, Cinclidium subrotundum, Pogonatum alpinum var. septentrionale, Odontoschisma macounii, Riccardia pinguis, and Sphagnum spp. Important associated species are Conostomum tetragonum, Bryum pseudotriquetrum, and Aulacomnium turgidum.

Relative percent soil moisture values around 400 percent indicate that this community occupied some of the

driest areas in the low center polygon sector. The soil pH mode-range was 4.65-5.05. This community was widely distributed in the low polygon sector on sites previously designated as polygon margins, interpolygonal trough slopes, polygon ridge tops, and polygon ridge slopes. In this community the hepatic cover of 67 percent exceeded the moss cover of 63 percent, a situation which made this community unique in the hydric series.

Besides the high number of subdominant species, the richness of this community is shown by the great moss-hepatic diversity among the species of lesser abundance. This community floristically is considered the richest in the low polygon sector.

Bryophyte community C. This community is dominated by Cephaloziella arctica and Oncophorus wahlenbergii. Subdominant species are Odontoschisma macounii, Riccardia pinguis, Drepanocladus revolvens, Pogonatum alpinum var. septentrionale, and Calliergon sarmentosum. Associated species of importance are Cephalozia pleniceps, Cinclidium subrotundum, Bryum cryophilum, Conostomum tetragonum, Cinclidium stygium, Sphagnum spp., Bryum pseudotriquetrum, Meesia longiseta, and Meesia uliginosa.

This community is almost identical to the preceding one and might be considered only a compositional variant, segregated from community AE only statistically. The

relative percent moisture is similar at about 400 percent and the soil pH mode-range is the same 4.65-5.05. This community was found on sites similar to those of community C, polygon ridge slopes, interpolygonal trough slopes, polygon margins, polygon ridge tops, and several outlying sites in the lower beachslope. The differences, therefore are minor, mostly relative amounts of species shared by both communities. Community AE is possibly a little wetter, but the greatest difference is a shift in the abundance of several species which are subdominant in community C and merely important associated species in community AE. Moss cover in community AE is 72 percent compared to a hepatic cover of 48 percent, a reflection of the shift in importance from subdominant to associated species.

Bryophyte community F. This community has the highest number of dominant species with Cephaloziella arctica, Calliergon sarmentosum, Drepanocladus revolvens, Cinclidium subrotundum, and Riccardia pinguis. Subdominant species are Oncophorus wahlenbergii, and Sphagnum spp. Important associated species are Calliergon richardsonii, Bryum cryophilum, Pogonatum alpinum var. septentrionale, and Bryum pseudotriquetrum.

The soil moisture conditions were slightly more saturated than the last two communities C and AE, with a

relative percent soil moisture near 500 percent. The soil pH mode-range was 4.85-5.05. This pH range is slightly narrower than the other communities already discussed for the low polygon sector. It is substantiated by the narrower range in sites where this community occurs: on interpolygonal trough slopes, interpolygonal troughs, and wet polygon margins. The average moss cover was 71 percent compared to average hepatic cover at 38 percent.

Bryophyte community I. This community is dominated by Oncophorus wahlenbergii with subdominants Calliergon sarmentosum and Drepanocladus revolvens. Important associated species are Pogonatum alpinum var. septentrionale, Bryum cryophilum, Sphagnum spp., Tritomaria quinquedentata, and Riccardia pinguis.

The relative percent soil moisture was similar to community F, around 500 percent. The soil pH was slightly higher, 4.85-5.25. Although this community was present in all three topographic sectors, it was restricted to decidedly wet habitats in all of them. It occurred on polygon margins, polygon slopes, polygon ridge tops, wet lower beachslope, and high polygon troughs. Moss cover averaged 74 percent while hepatic cover dropped to 27 percent.

Among the interesting species in this community, Oncophorus wahlenbergii a widespread and abundant species

in Barrow tundra, is singularly dominant only in this community where it is most often associated with either Drepanocladus revolvens or Calliergon sarmentosum. Together these make up the greatest portion of the cover. Several extremely interesting bryophytes which occurred in this community are Lepicolea fryei and Moerckia flotowiana.

Bryophyte community M. This community is dominated by Drepanocladus revolvens with the subdominants Calliergon sarmentosum and Drepanocladus exannulatus. Important associated species are Calliergon richarsonii, Cinclidium subrotundum, Sphagnum spp., and Scorpidium scorpioides.

This community is considered the most hydric of all communities with an average value for the relative percent soil moisture near 610 percent. The soil pH mode-range was 4.85-5.15. This community was restricted to a single microtopographic site-low polygon troughs. The average moss cover was 93 percent in contrast to the lowest hepatic cover anywhere in the intensive study tract, 1 percent. The community is characterized by hygrophilous mosses, particularly members of the ubiquitous wetland boreal family, Amblystegiaceae.

Transitional Bryophyte Communities

Four communities N, K, B, and G are considered

transitional to the other communities already described. Their transitional character is a reflection of intermediate conditions of soil moisture, soil pH, sites unrestricted by topography, and a floristic diversity which includes species from all other communities. As transitional types they are rather closely interrelated because all represent floristic-moisture phases of hepatic-moss turfs very similar to community D of the high center polygon sector. Certain affinities exist between each transitional type and communities already considered typical of the various topographic sectors. For instance, community G is topographically closest to the communities in the low center polygon sector but floristically diverse enough to be held separate from that hydric community series. Community N is floristically most like communities O, J, and L of the beachslope sector but topographically, this community is scattered across all sectors, and has a soil pH much lower than the calcareous beachslope communities. Of similar widespread occurrence are transitional communities K and B. Community B shows a closeness to the high polygon sector communities in soil pH only, and community K has no clear pH mode-range.

Bryophyte community G. This community is dominated by Cephaloziella arctica and Blepharostoma trichophyllum. Subdominants are Cephalozia pleniceps, Pogonatum alpinum var. septentrionale, Sphagnum spp., Conostomum tetragonum, Oncophorus wahlenbergii, and Dicranum angustum. Important associated species are Lophozia ventricosa, Tritomaria quinquedentata, Odontoschisma macounii, and Drepanocladus revolvens. Additionally interesting and peculiar species found in this community are Lepicolea fryei, Anthelia juratzkana, Massula opacifolia, Calliergidium pseudo-stramineum, Gymnocolea inflata, and Plagiothecium denticulatum.

Soil moisture conditions were, from all indications, most similar to those found in the drier portions of the low polygon sector. Relative percent soil moisture was about 300 percent. The soil pH mode-range was 4.55-5.05 another character of the low polygon sector. The average moss cover was 54 percent compared to a greater hepatic cover of 67 percent.

This community is close to the hydric series of the low polygon sector. The presence of Conostomum tetragonum, a species characteristic of the upper littoral zone of the low center polygon ponds, is in contrast with the species denoted as "interesting or peculiar." All of these coupled with rare occurrences of Ditrichum flexicaule,

Lophozia alpestris, Rhizomnium andrewsianum, Plagiomnium ellipticum, and Rhacomitrium lanuginosum, among others, illustrate the diversity in this community. Such diversity supports an interpretation of a transitional type.

Bryophyte community B. This community is dominated by Dicranum elongatum, Anastrophyllum minutum, Blepharostoma trichophyllum, and Lophozia ventricosa. Subdominant species are Pohlia nutans, and Pogonatum alpinum var. septentrionale. Important associated species are Tritomaria quinquedentata, Orthocaulis binsteadii, Cephalozia pleniceps, and Oncophorus wahlenbergii. Some of the occasional species which indicate a high diversity are Hylocomium splendens var. obtusifolium, Bartramia ithyphylla, Diplophyllum taxifolium, Drepanocladus revolvens, Plagiomnium ellipticum, and Riccardia pinguis.

Since this community was so widespread, occurring in nearly every topographic site sampled, it was impossible to cite a relative percent soil moisture value without specific data from each core sample. I would consider this community as one representing mesic habitats. The soil pH mode-range was 4.25-4.45, slightly acid, suggesting a close affinity to the communities of the high polygon sector. However, the average moss cover of 52 percent

which is much lower than the average hepatic cover of 72 percent, was a condition opposite to that found in the communities of that sector.

Bryophyte community K. This community is dominated by Blepharostoma trichophyllum and Dicranum elongatum. Subdominants are Lophozia ventricosa, Anastrophyllum minutum, Tritomaria quinquedentata, and Orthocaulis binsteadii. Important associated species are Oncophorus wahlenbergii, Pogonatum alpinum var. septentrionale, Cephalozia pleniceps, and Dicranum angustum. Other interesting species in this community are Massula opacifolia, Anthelia juratzkana, Gymnomitrion coralloides, Haplodon wormskjoldii, and Orthothecium chryseum.

This community and the next are considered the "most intermediate" types due to their great floristic diversity and lack of any pattern which would indicate a preference for any topographic sector. Community K had no trend whatsoever in soil pH or moisture. Moss cover was 40 percent compared to a much higher hepatic cover of 67 percent. Most interesting is the fact that this community contains the greatest abundance of members of the Lophoziaceae.

Bryophyte community N. This community is dominated solely by Tritomaria quinquedentata. The community has an

abundance of subdominants, Oncophorus wahlenbergii, Ptilidium ciliare, Plagiomnium ellipticum, Pohlia nutans, Pogonatum alpinum var. septentrionale, Blepharostoma trichophyllum, and Lophozia alpestris. All of these subdominants appear elsewhere as dominants in other communities which coupled with the fact that 69 species were found in this community type is rather certain evidence for considering it a transitional type.

The soil moisture of this community was indeterminable because no data were recorded for those samples. Like community K, it is a mesic community with no topographic affinities. The soil pH mode-range was 4.35-4.85, indicating a slight similarity to the communities of the low polygon sector. Moss cover at 48 percent was slightly higher than the hepatic cover at 40 percent. This then is the only transitional type where the mosses were more important in the community than the hepatics as measured by cover.

CHAPTER V

DISCUSSION

Floristic Considerations

Compared to many areas of the arctic north where something is known about the bryophytes, the report of the bryoflora made here indicates that the Barrow area is exceedingly rich and interesting. If one delimits the Barrow area as a coastal tundra strip running south of the Point 10 miles and inland 5 miles, then the report here of 156 taxa, 118 moss species with 6 varieties and 32 hepatic species, is quite remarkable (see Appendix B). These numbers certainly overshadow the number of vascular plants for the same region, given by Clebsch (1957) as about 100 species. Actually within the boundary set for this bryophyte flora one might not be able to find all the vascular plants of the larger Barrow vascular flora.

There are several reasons why the bryoflora of Barrow appears so rich. First, there are a number of taxonomic problems which undoubtedly have led to the report of several species which are probably not found at Barrow, or are ecotypic forms of a single species. Secondly, most of the American Arctic is not well known.

Northern Ellesmere Island is the only Nearctic region which I consider adequately known, principally through the fine efforts of Steere (1959), Schuster (1959), and Brassard (1971a,b).

I have chosen to use the information available for the Ellesmere region as a guide for assessing the completeness of the information now available concerning the Barrow flora. Brassard (1971a) reported 151 mosses compared to 143 vascular plants. Schuster (1959) reported 43 species of hepatics and 6 varieties. In Pearyland, Greenland, Holmen (1960) reported 134 mosses compared to 106 vascular plants. Because the hepatic flora of most regions is poorly known, comparisons between regions must be made using the moss floras and vascular floras.

On northern Ellesmere the number of vascular plants equals 95 percent of the mosses. On Pearyland the same ratio is 79 percent. At Barrow, assuming the vascular flora numbers 100 species, this ratio based on 118 moss species is 85 percent. This gives a rough indication that the Barrow moss flora is now adequately, although not completely, known. Reassessments of previously reported species and new discoveries of others will undoubtedly occur. I do not expect that the known

moss flora will ever equal that of northern Ellesmere Island.

The idea for a discrete bryophyte element composed of high arctic species is well-entrenched in the floristic literature (Herzog, 1926, 1932; Steere 1953b, 1965; Schuster, 1966, 1969; Holmen, 1960; Brassard, 1971a).

In 1953 Steere listed 66 mosses and 23 hepatics from arctic and subarctic zones with their known distributions from 16 regions. In 1965, Steere discussed specifically the high-arctic bryophyte element and included a list of 63 bryophytes which he assigned to that element. Brassard (1971a) suggested that six additional mosses should be added to the list of high arctic bryophytes. I would include in the list of hepatics, Massula opacifolia as the discussion by Schuster (1959) considers this, a high arctic derivative of the temperate-boreal Massula incisa.

The high-arctic bryophyte element is composed of a number of widely distributed moss species such as: Andreaea rupestris, Fissidens arcticus, Distichium hagenii, Tortella arctica, Desmatodon heimii var. arctica, Desmatodon leucostomus, Funaria arctica, Voitia hyperborea, Haplodon wormskjoldii, Bryum arcticum, Bryum cryophilum, Cyrtomnium hymenophylloides, Cyrtomnium

hymenophyllum, Cinclidium arcticum, Cinclidium latifolium, Rhizomnium andrewsianum, Aulacomnium acuminatum, Drepanocladus badius, Drepanocladus brevifolius, Campylium arcticum, Hygrohypnum polare, Psilopilum cavifolium, and Polytrichum piliferum var. hyperboreum. Several rare species with restricted distributions are: Arctoa andersonii, Barbula johansenii, Desmatodon ellesmerensis, Grimmia tenera, Pterigoneurum arcticum, Oligotrichum falcatum, and Lyellia aspera. A final group consists of a number of species which are of unknown distribution or known only regionally. Many are hepatics since they are the least studied to date. Included here are: Calycularia laxa, Lophozia pellucida, Lophozia hyparctica, Haplozia polaris, Lepicolea fryei, Hygrolejeunea alaskana, Scapania hyperborea, Scapania polaris, and Scapania spitzbergensis. Mosses include: Bryobrittonia pellucida, Ceratodon heterophyllus, Funaria polaris, Saelania glaucescens, Oreas martiana, Psilopilum laevigatum, Trichostomum cuspidatissimum, and Mielichhoferia macrocarpa.

There is little doubt that a high-arctic bryophyte element does exist. The basic problem involved with discussing the importance of this element in the bryoflora of any arctic region is that several of the member taxa are objects of debate within the concept of a species in

Bryology. Among the mosses, Steere (1965) notes the following species in the high arctic bryophyte element for which alternate interpretations of these taxa exist in the literature: Arctoa andersonii Wich. currently accepted as a northern variety of Arctoa fulvella (Dicks.) B.S.G. by Crum, et al., (1973); Andreaea obovata Thed. reduced to a "form" of Andreaea rupestris Hedw. by Crum, et al., (1973) and not recognized by Brassard (1971a) as a member of the high arctic element; Drepanocladus lycopodioides (Brid.) Warnst. considered a distinctly boreal species by Holmen (1960); Polytrichum hyperboreum R. Brown which has been known otherwise as a variety of P. piliferum Hedw.; Pottia obtusifolia (R. Brown) C. Muell. which has been called Pottia heimii (Hedw.) Fuern. var. obtusifolia (R. Brown) Hagen or the var. arctica Lindb. and is now listed by Crum, et al., (1973) as Desmatodon heimii (Hedw.) Mitt. var. arctica (Lindb.) Crum; Timmia comata Lindb. also known as a variety of T. norvegica Zett.; and Tortella arctica (Arnell) Crundw. and Nyholm which has been interpreted as a high arctic derivative of Tortella tortuosa (Hedw.) Limpr. and is thoroughly discussed by Crundwell and Nyholm (1963).

A similar list of hepatics could be presented particularly within the largely boreal-arctic macrogenus Lophozia. In this regard, Schuster (1969) treats and

newly describes a number of subspecies, varieties, and forms of Orthocaulis, Lophozia, and Tritomaria to accommodate the many ecotypes which regularly appear in arctic habitats.

I have tried to point out in the above discussion that the idea of a high arctic bryophyte floral element is not quite as coherent as some literature indicates. Undoubtedly a core element of truly "arctic" species does exist, but there is some question of how many species assigned to the element are northern extensions of boreal and occasionally temperate species which are responding to the cold environment by changes in their morphology. This is suggested by present and past subspecific taxa which have on occasion been considered part of the high arctic element. It is also somewhat disconcerting to find that a number of high arctic forms of bryophytes appear in literature with formal descriptions while others are recognized merely as cold regions stress variants.

The opinion I express here is one of the few rewards for studying the bryoflora of a region where well-developed individuals are an exceptional discovery. Too many of the bryophytes at Barrow are reduced, morphologically altered, and in highly crowded mixtures. Although these conditions are met with elsewhere in Tundra, the

examples in the Barrow bryoflora are more extreme. One of the most intriguing questions remaining is: why within the vegetation mosaic of poorly developed plants does one on occasion find specimens or small turfs of "normal" individuals?

The Barrow bryoflora. By inspecting the species list given in Appendix B (Table XXVII) one can see that the bryoflora is an interesting assemblage of species, representing floristic elements from both arctic and boreal zones.

Of 72 species which can be placed in the high arctic bryophyte element (Brassard, 1971a, plus Massula opacifolia) 26 occur at Barrow. These are: Bryum arctium, Bryum cryophilum, Bryum wrightii, Cephaloziella arctica, Ceratodon heterophyllus, Cinclidium arcticum, Cinclidium latifolium, Cyrtomnium hymenophyllum, Desmatodon heimii var. arctica, Desmatodon leucostoma, Distichium hagenii, Drepanocladus badius, Drepanocladus lycopodioides, Fissidens arcticus, Funaria arctica, Haplodon wormskjoldii, Lepicolea fryei, Massula opacifolia, Orthocaulis binsteadii, Orthocaulis quadriloba, Plagiochila arctica, Polytrichum piliferum var. hyperboreum, Psilopilum cavifolium, Rhizomnium andrewsianum, Scapania simmonsii, and Solenostoma pumilum ssp. polaris.

This represents a rich concentration of this floral element if one considers that the well-known bryofloras of northern Ellesmere and Pearyland, Greenland have 43 species and 29 species, respectively (Brassard, 1971a).

Bird (1969) and Bird and Hong (1969) have examined part of the bryoflora of west-central and southwestern Canada and discussed the geographic affinities of the bryoflora through a floristic element classification. A number of the Barrow bryophytes fall within the Pan North American, Arctic-Boreal, and Boreal Elements as presented by these authors.

The following Barrow bryophytes belong to the Pan North American Element. They are: Blepharostoma trichophyllum, Bryum pseudotriquetrum, Chiloscyphus pallescens, Desmatodon heimii, Aulacomnium palustre, Drepanocladus aduncus, Drepanocladus uncinatus, Leptobryum pyriforme, Lophozia ventricosa, Mnium marginatum, Plagiothecium denticulatum, Pohlia nutans, Ptilidium ciliare, Riccardia pinguis, Tortella tortuosa, and Tortula mucronifolia. These species are not restricted to the arctic, boreal, and temperate zones but occur over most of North America and are widespread elsewhere in the world.

The Arctic-Boreal Element as defined by Bird

(1969) comprises species which are distributed widely in the boreal belt but commonly have distributions which extend north well into the arctic zones. Barrow bryophytes which are members of this element are: Bryoerythrophyllum recurvirostrum, Bryum stenotrichum, Calliergon giganteum, Calliergon richardsonii, Campylium stellatum, Cephalozia pleniceps, Dicranum elongatum, Diplophyllum taxifolium, Distichium capillaceum, Distichium inclinatum, Ditrichum flexicaule, Encalypta vulgaris, Hylocomium splendens, Isopterygium pulchellum, Leiocolea heterocolpa, Lophozia alpestris, Meesia triquetra, Orthocaulis kunzeanus, Pohlia cruda, Polytrichum juniperinum, Polytrichum piliferum, Ptilidium ciliare, Scapania irrigua, Tomenthypnum nitens, Tortella fragilis, Tritomaria quinquedentata.

The Boreal Element contains species which are more or less restricted to this zone and naturally is not well-represented in the Barrow bryoflora. Most of the following species are however not uncommon at Barrow: Cirriphyllum cirrosum, Desmatodon obtusifolius, Encalypta ciliata, Encalypta rhaptocarpa, Moerckia flotowiana, Mylia anomala, and Myurella julacea.

Four species considered by Bird (1969) as Pan North American I have chosen to place in a separate group which for consistency should be called the "Ubiquitous

Element." Bryum argenteum, Ceratodon purpureus, Funaria hygrometrica, and Marchantia polymorpha are so widely distributed worldwide that I feel they should be recognized separately.

Only about one-half of the Barrow bryophytes are accounted in the previous listing. Steere (1948) provides capsulated distributional notes on the species he discussed for the Canadian Eastern Arctic. His information is not entirely complementary to the groupings of Bird (1969) or Bird and Hong (1969). However, most of the remaining species at Barrow fall into Steere's (1948) circumboreal and circumpolar distributional categories. Steere's circumboreal definition seems to include species of the Arctic-Boreal Element in Bird (1969). The hepatic flora too, seems to identify well with the general category of arctic-boreal distributed species.

Several species and groups of closely related species deserve special mention because they belong either to taxonomic complexes of unclear structure when encountered in arctic regions, or their mere presence at Barrow is unexpected. Some of these species are critical if one accepts entirely, the current concepts of the known high arctic bryophyte element.

Members of the Polytrichaceae which are abundant throughout the Arctic are particularly well-represented

at Barrow. A notably high number of subspecific taxa have been described under Polytrichum commune, Polytrichum juniperinum, and Pogonatum alpinum. Curiously, I have found at Barrow, plants which can be assigned to nearly every subspecific taxon of these species. I agree entirely with the opinion of Brassard (1971b) who in his discussion of Pogonatum alpinum comments on the intergradation among the various varieties of a remarkably distinct species. A possible interpretation of these moss species as indicated in the Barrow environment is that, the plasticity of the species are displayed within the relatively small area, because the plants are caught in a competitive "vise" between biotic and abiotic environmental forces.

Another widespread boreal-arctic genus, Dicranum, presents a taxonomic challenge in the Barrow area unmatched by all groups except perhaps members of the Bryaceae. At Barrow I have identified Dicranum angustum, D. elongatum, D. majus, D. muehlenbeckii, and D. spadiceum. I consider these determinations to represent a broad concept of arctic Dicrana as several additional species could be split from these collections. No sporulating species of Dicranum were found at Barrow, and in all cases plants were reduced and atypical. Both Dicranum scoparium and D. fuscescens have been recorded

from northern Ellesmere by Brassard (1971b) which indicates they extend into latitudes far north of Barrow. They are both recorded by Steere (1938) from Little Diomede Island in the Bering Strait, but were not found during the research effort at Cape Thompson (Johnson, et al., 1966). These I expect will eventually be found at Barrow. Dicranum majus was first documented at Barrow by Persson (1962). The species is very atypical never with pronounced serrations on the upper margin nor with toothed projections at the back of the costa as is usual for the species. Nyholm (1954) notes that this species is one of the most variable in the genus. Brassard (1971b) indicates that D. majus has been reported from northern Ellesmere, but he has not seen the material. It is unreported elsewhere in the Queen Elizabeth Islands (Brassard, 1971a). High arctic forms of Dicranum scoparium which have rudimentary projections on the back of the costa near the leaf-apex could easily be mistaken for Dicranum majus.

Of particular interest are the occurrences of the species: Aloina brevirostris, Dichodontium pellucidum, Cinclidium stygium, Meesia longiseta, Paludella squarrosa, Plagiothecium denticulatum, Plagiothecium piliferum, Mnium marginatum, Tortella tortuosa, and Tortella fragilis at Barrow. Also the lack of occurrence of several species

such as: Philonotis fontana, Stegonia latifolia, Barbula convoluta, Voitia hyperborea, Eurhynchium pulchellum, Hypnum cupressiforme, among others is somewhat perplexing since these are widespread in the Nearctic.

Steere (1950) mapped and discussed the distribution of Aloina brevirostris in North America noting the wide range of the species and dispelling the notion that it was restricted to the northern Rocky Mountains. In his review of its distribution Steere (1950) recorded at that time the northernmost Alaskan station near Wiseman on the south slope of the Brooks Range. Since then both Steere and I have found this species growing vigorously with sporophytes on silted streambanks in the Barrow area.

The occurrence of Dichodontium pellucidum I consider to be one of the most exciting discoveries at Barrow. This species occurs only sporadically in the Arctic (Steere, 1948), and Brassard (1971a) notes its occurrence only on Ellesmere and considers this species as part of the eastern segment of the Queen Elizabeth Island Bryoflora. It is apparently absent from the Pearyland moss flora, is reported from the Bow River Watershed, Alberta (Bird, 1973) and is widespread in Fennoscandia (Nyholm, 1954). In western North America this species is common (Lawton, 1971). Dichodontium

pellucidum is clearly a widely distributed boreal species which commonly extends into northern temperate and arctic regions. At Barrow the plants are extremely reduced, scarcely 5 mm high, and were found growing beneath the surface mat of larger bryophytes and lichens in an area of moderately drained tundra.

A number of the species more common at Barrow occur typically as reduced-growth forms. Plagiothecium denticulatum, P. piliferum, and Isopterygium pulchellum all occur as miniatures compared to plants from southern ranges. All are boreal species (Ireland, 1969) with Plagiothecium piliferum showing a center of distribution in the Pacific Northwest, Vancouver Island. Although Bird (1969) considers Plagiothecium denticulatum as pan-North American and Isopterygium pulchellum as arctic-boreal, Ireland (1969) reports only the latter from the North Slope of Alaska. All of these species grow within the bryophyte soil mat with only Plagiothecium piliferum an obvious part of the surface cover. Both Plagiothecium denticulatum and Isopterygium pulchellum are found entwined in the bryophyte mat at the soil-litter interface, an apparent habitat which affords some shelter at such high latitudes.

Meesia longiseta, Mnium marginatum, Tortella tortuosa, and Tortella fragilis are also present at

Barrow growing as highly reduced forms. High arctic forms of Tortella have been known for some time, most being referred to Tortella tortuosa. Crundwell and Nyholm (1963) revealed after study of many widely distributed collections from arctic stations, that the common arctic species Tortella arctica appears to differ in several characters from the boreal T. tortuosa. Several localities for T. arctica are reported for the Brooks Range and the northern foothills of Alaska by Crundwell and Nyholm (1963), but all collections from Barrow are comfortably referrable to T. tortuosa as a highly reduced form. Rare collections of T. fragilis were made in the intensive study tract. Their identity seems certain by the characteristic broken leaf-tips and the bistratose upper leaf-lamina.

Mnium marginatum was found only a few times as scattered shoots among more common species in calcicolous moss tundra. Strange occurrences such as this and Dichodontium pellucidum, I contend to have important but obscure meaning when discussing the Barrow bryoflora. These small plants scarcely 1 cm high were first identified as the more common Mnium orthorrhynchum, a member of the high arctic element. Recently Koponen (1972) devoted a special study to M. thomsonii Schimp. (=M. orthorrhynchum). A communication with this authority proved the Barrow

plants to be Mnium marginatum.

Paludella squarrosa is another interesting moss found at Barrow. This distinctive species was found only at the Point (Nuwuk) growing in wet mossy tundra of the gravel bar about 300 yards from Elson Lagoon. Warneke (1971) has mapped the distribution of this essentially circumboreal species. He indicates that this species is a subarctic postglacial relict in Europe, whose distribution is shrinking as a direct result of habitat destruction by man.

Meesia longiseta is a rare species in temperate North America (Grout, 1935). Nyholm (1958), however, reports it as scattered throughout the boreal belt. Neither Holmen (1960) nor Brassard (1971a) report this species for the eastern Nearctic. Rastorfer (1972) also makes no mention of this species as present on the North Slope. A single specimen collected and identified by W. C. Steere at the New York Botanical Garden from Cape Lisburn, Alaska, is a remarkable discovery. Barrow plants occur scattered in calcareous moss tundra, are extremely reduced and appear to grade into the common Meesia uliginosa. The genus is clearly divisible into the three species recognized by Crum, et al., (1973) in the low arctic-boreal range but can become somewhat confusing in the high arctic, especially when considering the

reduced forms of Meesia longiseta and Meesia uliginosa.

These discussions emphasize that an immense amount of interpretative thought is necessary to evaluate the bryoflora of any region in the Arctic. I have only discussed a few of the taxonomic and distributional problems associated with tundra bryofloras. Since the majority of the species are commonly distributed over a large range, often intercontinental, and extending across arctic-boreal life zones, it is no surprise that such plant distributions have been the subject of numerous other discussions. Considering the variations in growth-form, the cryptic habitats which many species occupy in marginal ranges, I consider much of the information which has been used to make floristic comparisons, ostensibly too final for the evidence. I offer in the next and final discussion a new phytogeographical analysis of the nearctic bryoflora.

Phytogeographic Analysis

For this discussion I have drawn heavily on the data provided by Brassard (1971a) for the Queen Elizabeth Islands in the eastern Nearctic. Not only is this the most current and comprehensive study for this region, but also it provides a good contrast to the western Nearctic as represented by the Barrow bryoflora.

An unfortunate aspect of each region is the poorly studied condition of the hepatic portion of the flora. For this reason, the comparisons made concern only the moss floras.

As a stimulus for this discussion Brassard (1971a) indicated that the similarity between the moss floras of northern Ellesmere and Pearyland, Greenland, was less than might be expected since both regions are at similar latitudes (82-83° N.), have similar physiography, area, and are separated by less than 200 kilometers distance. He remarked that 30 percent of the mosses of northern Ellesmere were not present in Pearyland, and conversely 20 percent of the mosses of Pearyland were not present in northern Ellesmere. Brassard (1971a) does note that between the two areas one can compile a combined moss flora of 178 species of which 106 are found in both regions. I have constructed in Table VII a double matrix which directly expresses the similarities among the moss floras of the phytogeographic regions of the Queen Elizabeth Islands and Barrow.

The moss floras of northern, central, and southern Ellesmere are the most thoroughly known, judging from their respective numbers of species, 151, 138, 155. These three areas are on a single contiguous land mass so a comparison between their moss floras might be

TABLE VII

COMPARISONS AMONG THE BARROW AND QUEEN ELIZABETH ISLANDS MOSS FLORAS; NUMBERS OF SPECIES AND PERCENT OF THE COMBINED MOSS FLORAS[a]

Region (# Species)	Barrow	Melville	Prince Patrick	Bathurst	Devon	Axel Heiberg	S. Ellesmere	C. Ellesmere	N. Ellesmere	Ringnes
Barrow (118)	--	55	59	68	70	53	79	74	76	30
Melville (76)	40	--	58	67	63	45	71	67	72	33
Prince Patrick (96)	38	51	--	76	68	53	80	70	83	39
Bathurst (113)	42	55	57	--	77	51	94	90	93	34
Devon (118)	42	48	46	50	--	55	96	91	92	34
Axel Heiberg (79)	37	41	43	36	39	--	66	62	66	37
S. Ellesmere (155)	41	44	47	54	54	39	--	120	114	41
C. Ellesmere (138)	41	46	46	56	55	40	68	--	103	41
N. Ellesmere (151)	39	46	51	54	52	40	59	55	--	44
Ringnes (46)	22	37	38	27	26	42	26	29	29	--

[a]Upper right-hand matrix indicates the number of species shared by any two regions. The lower left-hand matrix is the percent of the total combined moss floras that is shared.

expected to reveal the greatest similarities.

Table VII indicates that the greatest percent similarity exists between the southern and central Ellesmere moss floras, at 68 percent. Northern and southern Ellesmere show a similarity of 59 percent, while central and northern Ellesmere show a similarity of 55 percent. A comparison between the northern Ellesmere and Pearyland moss floras indicates the similarity is 60 percent. It appears thus, that the similarity shown between northern Ellesmere and Pearyland is greater than might be assumed considering they are separated by 200 kilometers of water. A perusal of Table VII indicates further, that only in the case of the shared moss flora between southern and central Ellesmere (68 percent) does the percent similarity exceed that shown between Pearyland and northern Ellesmere.

The other percent similarities shown in Table VII have limited value as they stand alone. Certainly, only the Ellesmere regions can be considered fully prospected, where little change in the total flora will be made in the future. However, many of the other areas are not too well known and their known moss floras will undoubtedly increase in numbers of species following further exploration. Barrow, Axel Heiberg, and Ringnes have the lowest percent similarity values. Considering the distance

between Barrow and the other regions the values for Barrow may indicate significant floristic differences. The values for Ringnes more than likely reflect incomplete knowledge of that moss flora. Axel Heiberg shows little difference in percent similarities with other areas. It might be concluded that the sample from Axel Heiberg is incomplete and shows that ubiquitous species constitute the known portion of the moss flora there.

Table VIII re-expresses the data given in Table VII. The entire table is a single data set built from the number of species common to any two regions as expressed by a percent of the total moss flora in each region. For instance, in the comparison between Barrow and Melville, two values express the floristic similarity. The value 72 can be read at the row intersection of Barrow and Melville. This states that 72 percent of the Melville moss flora is present at Barrow. The value 47 can be read at the column intersection of Barrow and Melville. This states that 47 percent of the Barrow moss flora is present at Melville. The entire table states what percent of the moss flora of any single region is present in the moss flora of any other region.

Several trends are shown in Table VIII. First, the percent of the Melville moss flora (72) at Barrow is

TABLE VIII

COMPARISONS AMONG THE BARROW AND QUEEN ELIZABETH ISLANDS MOSS FLORAS; PERCENT OF THE MOSS FLORA OF ONE REGION FOUND IN OTHER REGIONS[a]

Region (# Species)	Barrow	Melville	Prince Patrick	Bathurst	Devon	Axel Heiberg	S. Ellesmere	C. Ellesmere	N. Ellesmere	Ringnes
Barrow (118)	--	72	61	60	60	62	51	53	50	65
Melville (76)	47	--	60	59	53	57	46	49	48	72
Prince Patrick (96)	50	76	--	67	58	62	52	51	55	85
Bathurst (113)	58	88	79	--	65	64	61	65	62	74
Devon (118)	59	83	71	68	--	70	62	66	61	74
Axel Heiberg (79)	45	59	55	46	47	--	42	45	44	80
S. Ellesmere (155)	67	93	83	83	81	84	--	87	75	89
C. Ellesmere (138)	63	88	73	80	77	78	77	--	68	89
N. Ellesmere (151)	64	95	85	82	78	84	74	75	--	96
Ringnes (46)	25	43	41	30	29	47	26	30	29	--

[a]The entire table is a single data set which indicates the percentage of each flora found in other regions. Data is derived from Table VII, page 136; see text pp. 138 - 140 for discussion.

conspicuously higher than for any other region. Melville is closer to Barrow than to the other areas, but not so much closer that one would expect it to show such a greater floristic similarity than either Prince Patrick or Bathurst.

All the values in the Ringnes column are exceedingly high. This is understandable since only 46 species are recorded for that region. Most of these species are part of the widespread, ubiquitous element found in the Arctic and naturally most are present in the other regions. Conversely, the values in the Ringnes row are low because the number of species in any other region also found at Ringnes are only a small portion of the total number for that region.

Naturally, the values for all three Ellesmere rows are high since these regions have many more species reported for each compared to the other regions.

The high numbers of species on Ellesmere have been combined with geological and zoological evidence to promote the notion that this region was partially ice-free during the Ice Age. This idea that a Quaternary refugium might have existed in the northern Ellesmere area also is discussed by Brassard (1971a).

Table IX presents two data matrices which as a final synthesis draws together in a standardized form the

TABLE IX

COMPARISONS AMONG THE BARROW AND QUEEN ELIZABETH ISLANDS MOSS FLORAS; AVERAGE PERCENT SIMILARITIES AND FLORAL SIMILARITY IMPORTANCE VALUES[a]

Region (# Species)	Barrow	Melville	Prince Patrick	Bathurst	Devon	Axel Heiberg	S. Ellesmere	C. Ellesmere	N. Ellesmere	Ringnes
Barrow (118)	--	60	56	59	60	54	59	58	57	45
Melville (76)	43	--	68	74	68	58	70	68	72	58
Prince Patrick (96)	36	60	--	73	64	58	68	62	70	63
Bathurst (113)	36	60	55	--	66	55	72	72	72	52
Devon (118)	36	52	44	43	--	58	72	72	70	52
Axel Heiberg (79)	37	53	48	39	41	--	63	62	64	64
S. Ellesmere (155)	30	43	39	41	40	38	--	82	75	58
C. Ellesmere (138)	32	46	38	45	43	40	47	--	72	60
N. Ellesmere (151)	30	46	43	42	39	39	39	38	--	62
Ringnes (46)	34	65	61	42	40	72	36	42	41	--
Totals	314	468	424	403	378	407	353	371	357	433

[a]Upper right-hand matrix is an average value of the two values comparing any two regions as shown in Table VIII, page 139. Lower left-hand matrix is a floral similarity value derived from the average percent similarity and the total number of species in the combined moss flora of any two regions (see pp. 140 , 143 for discussion).

floristic data presented in Tables VII and VIII. The upper right-hand matrix is an average similarity value derived directly from Table VIII, page 139. An example is, the Barrow-Melville value of 60, which is derived by averaging 47 and 72, the two values which express the percent of the Barrow moss flora at Melville, and the percent of the Melville moss flora at Barrow. The average value is a synthetic importance value which measures reciprocally the floral input of any two regions which are compared through the species they share in common.

At this point in the discussion, if we make an assumption that those regions which have the lowest numbers of species (e.g., Ringnes, Axel Heiberg, Melville, and Prince Patrick) are representing incompletely sampled floras, then we can go to the lower left portion of Table IX to see which regions show the greatest total similarity with all other regions.

In the lower left half of Table IX the resulting values are derived by dividing the average percent similarity from the upper half of the table by the total number of moss species in the combined moss flora of any two regions. For example, Barrow and Melville show an average percent similarity of 60. This value divided by 139, the total number of species found by combining

their floras, results in the value 43 which is a floral similarity importance value. This procedure is designed to adjust for the data among the regional comparisons, on the assumption that regions with low numbers of species in the moss floras reflect a condition of inadequate sampling. The most obvious effect of this procedure is that it tends to de-emphasize the importance of the Ellesmere floras with high numbers of species, and weighs the regions with fewer species more heavily.

Table IX, page 141, contains some extremely valuable information. First, the Barrow moss flora shows a trend toward lower affinity to all other regions than the other regions show among themselves. This observation is not too surprising since Barrow is far removed in distance from the Queen Elizabeth Islands.

The second and most interesting piece of information can be discovered by summing the similarity importance values for each region. Presumably, the region with the highest sum will share the greatest overall similarity with the other regions. Also, the region with the lowest sum, will reflect an overall dissimilarity with the other regions.

The lowest sum of the similarity importance values is Barrow which confirms the conclusion just made.

The region with the highest sum of the similarity importance values is Melville. I would direct the reader to the Melville column.

In nearly every comparison, Melville has the highest similarity importance value of all the comparisons of other regions. For example, among the Barrow comparisons, the Melville value 43 is considerably higher than those for other regions. This trend can be shown again in comparisons with Bathurst, Devon, and northern Ellesmere. In the comparisons with the other regions, the Melville value is in all cases the second highest similarity importance value.

Based upon this information, realizing that the floral information from most of the regions compared is incomplete, I am putting forth the hypothesis that the Melville area when fully prospected will be shown to contain one of the richest bryofloras in the Nearctic. I do not restrict my supposition entirely to the Melville phytogeographic region as defined by Brassard (1971a), but extend my thinking to include the Banks and Victoria Islands region.

There appears to me at this time no opposition to the idea that the Melville-Banks-Victoria Island group might well lie at the interface of three post-glacial floristic convergences. This conjecture incorporates the

belief of Brassard (1971a), that a high eastern arctic glacial refugium existed around northern Ellesmere during the Pleistocene. Steere (1965) has given similar evidence for a western arctic refugium on the North Slope of the Brooks Range, Alaska, which he refers to as the "Umiat Syndrome." The third floristic element could have moved north following the melting of the glaciers as an arm interjecting a strongly boreal element.

A final remark results from a recent article by Kuc (1973b) which lends support to my earlier supposition. Kuc (1973b) studied the altitudinal differentiation of the mosses at Purchase Bay, Melville Island and reported 98 species and 9 subspecific taxa. Kuc remarked on the unusually high number of species which he recorded from the small area (4 x 2.5 miles) he investigated. His floristic data amounts to, in total numbers, 22 more species than previously reported for Melville Island (Brassard, 1971a). However, more important is the report of 46 new species to the Island from this single study. These 46 species coupled with the 76 already reported by Brassard (1971a) brings the total Melville moss flora to 122 species.

Unfortunately, the species listed for the known moss floras of both Banks and Victoria Islands are

scattered through a large body of literature. Until these data are organized it will be difficult to assess the complete impact of the statements and conclusions made in my earlier discussion. However, Kuc (1973a) does lend additional supporting evidence for including Banks Island in the Melville-Banks-Victoria floristic group. He has found in the Masik River Valley of Banks Island, subfossil and extant bryofloras which indicate a unique past history and potentially a rich bryoflora elsewhere on the island.

As floristic data become more complete, particularly in the western Canadian Arctic, evidence should build toward resolving any questions raised against the interpretation I have given here.

CHAPTER VII

SUMMARY

Intensive investigations on the bryoflora of the Barrow region, Alaska, were initiated during field work conducted during the summer of 1972. Previous to this study only 72 bryophytes were reported in the literature from the Barrow area. No study on the bryophyte community structure in Barrow tundra has appeared previous to this investigation.

This bryofloristic study at Barrow consisted of general collections made throughout the Barrow area and the floristic information acquired during intensive study of bryophyte communities in selected habitats. The result was a total bryoflora of 156 taxa including 6 subspecific determinations. Also included in this list are several reports which were found while studying collections at the New York Botanical Garden.

The Barrow bryoflora is composed of species which can be identified as members of several phytogeographic elements. More than one-third of the species in the high-arctic bryophyte element are present at Barrow. An arctic-boreal element consisting of species which regularly extend from the boreal domain into the arctic

is strongly represented. A small group of species considered part of a boreal bryophyte element is also present at Barrow along with several ubiquitous or cosmopolitan species. A final list of considerable size includes species which are still unclassified as to their distributions.

A description of the vegetation from three selected areas of dominant topography was accomplished using the bryophytes as the primary character of the vegetation. Sample plot techniques were used to obtain floristic data from different microtopographic habitats within the area, to see if communities and habitats were discretely patterned. Gradients of topography, soil moisture, and soil pH were measured for their possible significance to the distribution of the communities and species investigated.

Field sampling was restricted to three topographic sectors: low center polygons, high center polygons, and an old beachslope connecting the two polygon fields. Among the three sectors, microtopographic habitats which were sampled were low center polygon centers, margins, slopes, ridges, interpolygonal slopes, and interpolygonal troughs; high center polygon tops including frostboils, grassy sods, and pure bryophyte turfs, NE-,SW-,SE-,NW-facing slopes, and troughs; and

beachslope mounds and depressions in lower and upper beachslope sections.

Floristic data on the bryophytes were recorded in the form of presence and an estimate of cover by species and class (moss and hepatic totals) was made using an average cover-class scale. This scale contained seven categories: 0= less than 1 percent, 1= 1-5 percent, 2= 6-15 percent, 3= 16-35 percent, 4= 36-65 percent, 5= 66-85 percent, and 6- 86-100 percent.

An association analysis technique proposed by Goodall (1953) was used to reduce the sample plot data into groups which were composed of homogeneous samples. The technique used tested interspecific associations using Chi-square. The chosen level of significance was 1 percent. Only those species which occurred 20 percent of the time or more were used in the species pair comparisons in order to reduce the number of calculations.

Sixteen bryophyte communities were partitioned from the sample data representing 565 plot samples. Soil moisture, pH, and topography were the primary gradients along which the bryophyte communities could be aligned. Of these, moisture was the dominant factor.

The bryophyte communities of the high polygon sector reflected the harsh environmental conditions of low percent soil moisture, pH and exposed upland

topography. Three communities, forming a xeric series, were distinguished. They were dominated by: Pohlia nutans, Polytrichum piliferum var. hyperboreum, Pogonatum alpinum, Pogonatum dentatum, Dicranum elongatum, Anastrophyllum minutum, Scapania mucronata, Cephalozia pleniceps, and Lophozia ventricosa.

The bryophyte communities of the beachslope sector represent a series in a mesic phase characterized by moderate drainage, circumneutral soil pH, and high diversity. Three communities were distinguished which were dominated by: Distichium capillaceum, Hylocomium splendens var. obtusifolium, Drepanocladus uncinatus, Tomenthypnum nitens, Ptilidium ciliare, Drepanocladus revolvens and var. intermedius, Oncophorus virens, Ditrichum flexicaule, Plagiomnium ellipticum, Tritomaria quinquedentata, and Orthothecium chryseum.

A hydric series of communities was distinguished which was found in the low center polygon sector. This group occupied sites of extremely wet soil which were mildly acid. Five closely related communities were dominated by: Oncophorus wahlenbergii, Cephaloziella arctica, Calliergon sarmentosum, Drepanocladus revolvens, Cinclidium subrotundum, Riccardia pinguis, Blepharostoma trichophyllum, Cephalozia pleniceps, Pogonatum alpinum var. septentrionale, Odontoschisma macounii, Bryum

cryophilum, Drepanocladus exannulatus, and Sphagnum spp. A single wetland community was found which occupied the trough sites of the high center polygon sector. This community was dominated by Scapania paludicola, Drepanocladus uncinatus, and Calliergon stramineum.

A final group of communities were distinguished which were interpreted as transitional. These communities were considered mesic but showed no definite trends in soil pH or topographic site. Dominant species among four transitional communities were: Cephaloziella arctica, Blepharostoma trichophyllum, Dicranum elongatum, Anastrophyllum minutum, Lophozia ventricosa, Tritomaria quinquedentata, Cephalozia pleniceps, Pogonatum alpinum var. septentrionale, Conostomum tetragonum, Oncophorus wahlenbergii, Dicranum angustum, Pohlia nutans, Orthocaulis binsteadii, Ptilidium ciliare, Plagiomnium ellipticum, Lophozia alpestris, and Sphagnum spp.

The bryophyte communities were ordinated using a synthetic importance value which combined the measures of frequency and average cover. Three dimensional ordination confirmed the interpretation of the communities as: hydric series, mesic series, and xeric series, with a transitional group of mesic communities.

The organization of the bryophyte communities into groups which ordinate along a primary moisture gradient

and a less obvious secondary gradient of soil pH is further complicated by microtopographic variation. It appears that these three variables are somewhat interdependent and that different degree combinations account for the numerous habitats which often occur in close proximity in the natural setting. Such an interpretation agrees with others who have expressed a similar opinion that tundra communities are without apparent order. Where communities are highly mixed with habitats often juxtaposed, transitional zones between sites are extremely narrow if present at all. For these situations, bryophytes are valuable in describing the vegetation because they represent the fine detail of the community structure.

A phytogeographical analysis of the Nearctic using the data of Brassard (1971a) from the Queen Elizabeth Islands in the Canadian Eastern Arctic and the data for Barrow derived in this study is most revealing. Floristic comparisons among Barrow and the nine regions of Brassard (1971a) indicates that the Melville-Banks-Victoria Island group may prove to contain one of the richest bryophyte floras in the Nearctic. Recent investigations by Kuc (1973a,b) on Banks and Melville Islands already lend convincing evidence to this hypothesis.

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APPENDIXES

APPENDIX A

TABLE X

BRYOPHYTE COMMUNITY A-E (43 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Oncophorus wahlenbergii	100	19.7	100	100	20
Cephaloziella arctica	79	16.6	84	82	16
Blepharostoma trichophyllum	100	6.2	31	66	4
Drepanocladus revolvens	100	4.0	20	61	2
Cephalozia pleniceps	65	10.0	51	58	10
Calliergon sarmentosum	100	2.0	10	55	-
Cinclidium subrotundum	72	6.6	34	53	4
Pogonatum alpinum var. septentrionale	79	4.6	23	51	2
Odontoschisma macounii	65	5.7	29	47	4
Riccardia pinguis	67	4.8	24	46	2
Sphagnum spp.	63	3.6	18	41	3
Conostomum tetragonum	40	5.7	29	34	4
Bryum pseudotriquetrum	42	0.6	3	22	-
Aulacomnium turgidum	35	1.0	5	20	-
Dicranum angustum	32	0.6	3	18	-
Tritomaria quinquedentata	21	3.1	16	18	4
Bryum cryophilum	23	2.0	10	16	2
Meesia longiseta	19	0.2	1	10	-

TABLE XI

BRYOPHYTE COMMUNITY B (41 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Dicranum elongatum	100	18.4	100	100	13
Anastrophyllum minutum	100	15.4	84	92	15
Blepharostoma trichophyllum	100	12.6	68	84	10
Lophozia ventricosa	78	14.6	79	78	13
Pohlia nutans	100	6.6	36	68	3
Pogonatum alpinum var. septentrionale	61	3.1	17	39	3
Tritomaria quinquedentata	32	3.9	21	26	2
Orthocaulis binsteadii	34	2.7	15	24	1
Cephalozia pleniceps	36	1.3	7	22	1
Oncophorus wahlenbergii	36	1.3	7	22	1
Aulacomnium turgidum	27	1.4	8	18	-
Sphagnum spp.	22	2.5	14	18	2
Scapania mucronata	27	1.0	5	16	-
Dicranum angustum	22	0.7	4	13	-

TABLE XII

BRYOPHYTE COMMUNITY C (44 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Cephaloziella arctica	100	19.0	100	100	19
Oncophorus wahlenbergii	100	15.6	82	91	13
Odontoschisma macounii	100	7.4	39	70	5
Riccardia pinguis	100	5.5	29	64	4
Drepanocladus revolvens	77	9.0	47	62	6
Pogonatum alpinum var. septentrionale	66	4.0	21	44	3
Calliergon sarmentosum	73	1.8	9	41	-
Cephalozia pleniceps	36	5.5	29	32	6
Cinclidium subrotundum	48	2.3	12	30	1
Bryum cryophilum	50	1.4	7	28	-
Conostomum tetragonum	36	3.7	19	28	3
Cinclidium stygium	30	5.0	26	28	4
Sphagnum spp.	39	1.4	7	23	1
Bryum pseudotriquetrum	39	1.0	5	22	-
Meesia longiseta	32	2.1	11	22	2
Meesia uliginosa	18	4.1	22	20	5
Blepharostoma trichophyllum	27	1.0	5	16	-
Calliergon richardsonii	23	1.2	6	14	1
Drepanocladus badius	18	1.8	9	14	2
Gymnocolea inflata	20	1.2	6	13	1
Aulacomnium turgidum	20	0.6	3	12	-
Tritomaria quinquedentata	18	0.3	2	10	-

TABLE XIII

BRYOPHYTE COMMUNITY D (53 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Dicranum elongatum	100	22.4	100	100	26
Pohlia nutans	100	16.0	71	86	24
Lophozia ventricosa	100	15.8	71	86	22
Anastrophyllum minutum	82	16.4	73	78	23
Pogonatum dentatum	40	8.2	37	38	8
Orthocaulis binsteadii	36	3.4	15	26	3
Scapania mucronata	38	0.7	3	21	-
Polytrichum hyperboreum	22	4.3	19	21	2
Cephalozia pleniceps	26	1.5	7	16	1
Pogonatum alpinum var. septentrionale	20	1.2	5	12	1
Tritomaria quinquedentata	18	1.3	6	12	1

TABLE XIV

BRYOPHYTE COMMUNITY F (18 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Cephaloziella arctica	72	22.9	100	100	8
Calliergon sarmentosum	100	16.3	71	99	7
Drepanocladus revolvens	100	14.3	62	94	6
Cinclidium subrotundum	100	11.9	52	88	5
Riccardia pinguis	100	9.6	42	82	2
Oncophorus wahlenbergii	78	9.8	43	70	3
Sphagnum spp.	72	1.4	6	45	-
Calliergon richardsonii	39	5.1	22	35	2
Bryum cryophilum	50	1.4	6	32	-
Pogonatum alpinum var. septentrionale	44	1.5	7	30	-
Bryum pseudotriquetrum	33	1.0	4	22	-
Cephalozia pleniceps	17	3.5	15	18	1
Meesia longiseta	22	0.3	1	13	-
Blepharostoma trichophyllum	17	0.8	3	12	-
Dicranum angustum	17	0.6	3	12	-

TABLE XV

BRYOPHYTE COMMUNITY G (25 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Cephaloziella arctica	100	18.3	100	100	8
Blepharostoma trichophyllum	100	11.6	63	82	7
Cephalozia pleniceps	64	14.3	78	71	7
Pogonatum alpinum var. septentrionale	100	4.2	23	62	2
Sphagnum spp.	52	9.9	54	53	5
Conostomum tetragonum	40	9.4	51	46	5
Oncophorus wahlenbergii	68	3.9	21	44	1
Dicranum angustum	64	2.5	14	39	1
Lophozia ventricosa	44	2.2	12	28	1
Tritomaria quinquedentata	40	2.2	12	26	1
Odontoschisma macounii	28	3.0	16	22	1
Drepanocladus revolvens	40	0.2	1	21	-
Aulacomnium turgidum	36	0.4	2	19	-
Anastrophyllum minutum	32	0.9	5	18	-
Pohlia nutans	20	2.8	15	18	1
Riccardia pinguis	28	1.1	6	17	-
Bryum pseudotriquetrum	24	1.2	6	15	1
Dicranum elongatum	24	1.0	5	14	-
Cinclidium subrotundum	24	0.6	3	14	-
Bryum spp.	20	1.1	6	13	-
Scapania mucronata	20	0.2	1	11	-

TABLE XVI

BRYOPHYTE COMMUNITY H-S (56 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Pohlia nutans	88	18.2	100	100	23
Anastrophyllum minutum	100	7.6	42	76	9
Dicranum elongatum	52	10.1	55	57	12
Pogonatum dentatum	36	5.8	32	36	4
Polytrichum hyperboreum	18	6.2	34	28	6
Scapania mucronata	38	1.0	5	23	-
Cephalozia pleniceps	30	2.0	11	22	2
Pohlia cruda	25	2.9	16	22	3
Pogonatum alpinum var. septentrionale	20	3.0	16	19	3
Dicranella grevilleana	20	2.2	12	17	2
Lophozia ventricosa	21	1.7	9	16	1
Massula opacifolia	21	1.3	7	15	1
Tritomaria quinquedentata	18	1.6	9	14	2

TABLE XVII

BRYOPHYTE COMMUNITY I (39 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Oncophorus wahlenbergii	100	19.8	100	100	12
Calliergon sarmentosum	100	5.8	29	64	2
Drepanocladus revolvens	54	14.0	71	62	8
Cephaloziella arctica	49	5.5	28	38	2
Pogonatum alpinum var. septentrionale	46	3.6	18	32	3
Bryum cryophilum	44	3.1	16	30	2
Sphagnum spp.	38	3.0	15	26	1
Tritomaria quinquedentata	26	3.7	19	22	3
Riccardia pinguis	33	1.8	9	21	1
Cinclidium subrotundum	31	1.0	5	18	-
Bryum spp.	31	0.6	3	17	-
Blepharostoma trichophyllum	26	1.3	6	16	1
Bryum pseudotriquetrum	28	0.5	2	15	-

TABLE XVIII

BRYOPHYTE COMMUNITY J (45 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Drepanocladus revolvens	100	9.0	89	100	4
Distichium capillaceum	80	10.1	100	95	7
Oncophorus virens	100	5.2	51	80	4
Ditrichum flexicaule	67	4.4	44	59	2
Orthothecium chryseum	69	3.8	38	57	3
Tomenthypnum nitens	62	4.5	44	56	4
Hylocomium splendens var. obtusifolium	67	2.4	24	48	-
Scorpidium turgescens	38	3.2	32	37	2
Myurella julacea	40	2.1	21	32	2
Tortella tortuosa	42	1.8	18	32	1
Plagiomnium ellipticum	22	3.4	34	30	4
Ptilidium ciliare	38	1.5	15	28	-
Bryoerythrophyllum recurvirostrum	33	1.6	16	26	2
Bryum arcticum	33	1.5	15	25	-
Dicranum spp.	33	1.6	16	26	1
Calliergon sarmentosum	38	0.8	8	24	-
Bryum spp.	36	0.6	6	22	-
Drepanocladus uncinatus	31	0.9	9	21	-
Blepharostoma trichophyllum	31	0.7	7	19	-

TABLE XIX

BRYOPHYTE COMMUNITY K (26 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Blepharostoma trichophyllum	100	15.2	100	100	8
Dicranum elongatum	100	14.3	94	97	7
Lophozia ventricosa	76	8.2	54	65	4
Anastrophyllum minutum	64	7.9	52	58	4
Tritomaria quinquedentata	56	6.6	43	50	2
Orthocaulis binsteadii	56	4.4	29	42	1
Oncophorus wahlenbergii	36	5.9	39	38	1
Pogonatum alpinum var. septentrionale	48	1.8	12	30	1
Cephalozia pleniceps	40	1.5	10	25	1
Dicranum angustum	24	3.2	21	22	1
Sphagnum spp.	20	1.4	9	14	1
Aulacomnium turgidum	20	0.3	2	11	-

TABLE XX

BRYOPHYTE COMMUNITY L (25 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Hylocomium splendens var. obtusifolium	100	10.1	94	100	6
Drepanocladus uncinatus	100	8.0	74	90	5
Tomenthypnum nitens	64	10.8	100	84	4
Ptilidium ciliare	68	9.4	87	80	5
Plagiomnium ellipticum	40	7.9	73	58	4
Tritomaria quinquedentata	60	3.1	29	46	1
Oncophorus virens	44	4.6	42	44	2
Aulacomnium turgidum	56	1.1	10	34	-
Ditrichum flexicaule	48	1.3	12	31	1
Distichium capillaceum	40	1.6	15	28	-
Bryum spp.	40	0.7	6	24	-
Dicranum spp.	40	0.4	4	23	-
Blepharostoma trichophyllum	36	0.4	4	21	-
Bryum pseudotriquetrum	28	1.1	10	20	-
Oncophorus wahlenbergii	28	1.2	11	20	1
Rhizomnium andrewsianum	32	0.2	2	18	-
Myurella julacea	20	1.2	11	16	-
Calliergon sarmentosum	24	0.4	4	14	-

TABLE XXI

BRYOPHYTE COMMUNITY M (24 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Drepanocladus revolvens	100	42.6	100	100	. 17
Calliergon sarmentosum	100	8.3	19	60	4
Drepanocladus exannulatus	62	7.9	18	40	5
Calliergon richardsonii	54	5.5	13	34	2
Cinclidium subrotundum	50	0.8	2	26	-
Sphagnum spp.	38	0.6	1	20	-
Scorpidium scorpioides	21	7.7	18	20	3
Drepanocladus badius	21	5.6	13	17	3
Bryum cryophilum	25	0.3	1	13	-

TABLE XXII

BRYOPHYTE COMMUNITY N (31 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Tritomaria quinquedentata	100	7.5	100	100	5
Oncophorus wahlenbergii	48	6.2	83	66	5
Ptilidium ciliare	29	7.5	100	64	3
Plagiomnium ellipticum	26	6.4	85	56	4
Pohlia nutans	42	4.4	59	51	2
Pogonatum alpinum var. septentrionale	58	2.1	28	43	1
Blepharostoma trichophyllum	39	3.3	44	42	2
Lophozia alpestris	29	3.8	51	40	4
Bryum pseudotriquetrum	42	0.8	11	26	-
Tomenthypnum nitens	22	2.0	27	24	1
Plagiothecium denticulatum	19	1.7	23	21	2
Drepanocladus uncinatus	32	0.5	7	20	-
Ditrichum flexicaule	26	0.7	9	18	-
Aulacomnium turgidum	22	1.0	13	18	-
Dicranum spp.	26	0.4	5	16	-
Dicranum angustum	19	0.3	4	12	-

TABLE XXIII

BRYOPHYTE COMMUNITY O (19 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Distichium capillaceum	74	11.6	100	100	4
Oncophorus virens	100	2.4	21	70	-
Drepanocladus revolvens var. intermedius	79	4.5	39	68	1
Ditrichum flexicaule	84	2.4	21	60	-
Tomenthypnum nitens	63	3.1	27	57	1
Scorpidium turgescens	47	2.7	23	40	1
Orthothecium chryseum	47	2.6	22	40	1
Bryum spp.	53	1.0	9	36	-
Tortella tortuosa	47	0.8	7	31	-
Myurella julacea	37	1.6	14	29	1
Blepharostoma trichophyllum	42	0.4	3	26	-
Pogonatum alpinum var. septentrionale	26	1.6	14	23	-
Calliergon sarmentosum	32	0.5	4	21	-
Bryoerythrophyllum recurvirostrum	21	1.4	12	19	1
Hylocomium splendens var. obtusifolium	26	0.4	3	17	-
Ptilidium ciliare	26	0.3	2	16	-
Bryum arcticum	21	0.7	6	16	-
Scapania simmonsii	21	0.6	5	15	-

TABLE XXIV

BRYOPHYTE COMMUNITY P (18 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Scapania paludicola	100	30.2	100	100	9
Drepanocladus uncinatus	61	13.8	46	54	6
Calliergon stramineum	50	9.6	32	41	4
Cephaloziella arctica	44	5.7	19	32	2
Campylium stellatum	44	3.7	12	28	2
Drepanocladus exannulatus	33	2.8	9	21	1
Bryum pseudotriquetrum	28	2.7	9	18	1
Pohlia nutans	33	0.3	1	17	-
Calliergon sarmentosum	28	1.7	6	17	1
Bryum spp.	28	0.8	3	16	-

TABLE XXV

BRYOPHYTE COMMUNITY Q (34 SAMPLES)

Bryophyte Species	Frequency	Average Cover (%)	Weighted Cover (%)	Importance Value (I.V.)	Dominance and/or Subdominance
Pohlia nutans	100	25.2	100	100	16
Polytrichaceae	56	25.7	100	78	15
Pogonatum dentatum	30	12.5	50	40	6
Polytrichum hyperboreum	18	8.8	35	26	5
Dicranum elongatum	42	0.9	35	26	5
Pogonatum alpinum	18	6.9	27	22	3

TABLE XXVI

DISTRIBUTION OF BRYOPHYTE SPECIES WITH LESS THAN 20 PERCENT FREQUENCY AMONG BRYOPHYTE COMMUNITIES

Bryophyte Species	Bryophyte Communities															
	AE	C	B	D	F	G	HS	I	J	K	L	M	N	O	P	Q
Anastrophyllum minutum	2	4	-	-	-	-	-	5	2	-	4	-	10	5	-	-
Anthelia juratzkana	-	2	-	-	-	4	4	-	2	4	-	-	-	-	-	-
Aulacomnium palustre	2	-	2	-	-	-	-	2	-	-	-	-	6	-	6	-
Aulacomnium turgidum	-	-	-	4	6	-	4	18	9	-	-	-	-	10	6	-
Bartramia ithyphylla	-	-	10	-	-	-	5	5	18	-	12	-	6	-	-	3
Blepharostoma trichophyllum	-	-	-	4	-	-	12	-	-	-	-	8	-	-	-	6
Brachythecium turgidum	5	-	-	-	-	-	-	-	-	-	8	4	-	-	-	12
Bryoerythrophyllum recurvirostrum	-	-	-	-	-	-	-	-	-	-	12	-	3	-	-	-
Bryum spp.	14	7	7	-	-	-	4	-	-	12	-	8	-	-	-	3
Bryum arcticum	-	-	2	-	6	-	-	8	-	4	8	4	10	-	-	-
Bryum cryophilum	-	-	2	2	-	-	-	-	-	-	-	-	3	-	11	-
Bryum pseudotriquetrum	-	-	7	2	-	-	9	-	4	-	-	8	-	10	-	-
Calliergidium pseudostramineum	-	-	2	-	-	12	-	-	-	-	-	-	3	-	17	-
Calliergon richardsonii	9	-	-	-	-	4	-	10	-	-	-	-	-	-	-	6
Calliergon sarmentosum	-	-	10	2	-	12	-	-	-	-	-	-	13	-	-	-
Calliergon stramineum	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
Campylium stellatum	-	4	-	-	-	-	-	8	4	4	12	-	10	-	-	-
Cephalozia pleniceps	-	-	-	-	-	-	-	8	2	-	-	-	13	5	-	12
Cephaloziella arctica	-	-	17	6	-	-	9	-	-	12	-	8	13	-	-	3
Ceratodon purpureus	2	-	2	2	6	-	5	-	-	-	-	-	3	-	-	-
Cinclidium stygium	5	-	-	-	6	-	-	18	2	-	-	-	-	10	-	-
Cinclidium subrotundum	-	-	7	-	-	-	-	-	4	4	-	-	10	-	-	-

TABLE XXVI (continued)

Bryophyte Species	Bryophyte Communities															
	AE	C	B	D	F	G	HS	I	J	K	L	M	N	O	P	Q
Conostomum tetragonum	-	-	5	-	11	-	4	13	-	12	-	-	6	-	-	-
Dichodontium pellucidum	-	-	-	-	-	-	-	-	2	-	-	-	3	-	-	-
Dicranella crispa	-	2	-	-	-	-	-	-	-	4	-	-	-	-	-	-
Dicranella grevilleana	-	-	-	8	-	-	-	-	-	8	4	-	6	-	-	9
Dicranella subulata	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-
Dicranum spp.	-	-	2	-	-	-	5	13	-	-	-	-	-	16	6	3
Dicranum angustum	-	16	-	8	-	-	9	8	-	-	4	-	-	-	6	6
Dicranum elongatum	9	-	-	-	6	-	-	-	-	-	12	-	10	-	-	-
Diplophyllum taxifolium	-	-	7	2	-	-	-	-	2	-	-	-	10	-	-	-
Distichium capillaceum	2	-	-	-	-	-	2	15	-	-	-	8	10	-	-	-
Ditrichum flexicaule	7	9	5	4	6	8	2	10	-	4	-	-	-	-	-	-
Drepanocladus badius	2	-	-	-	-	-	-	13	-	-	-	-	-	-	-	-
Drepanocladus exannulatus	-	-	-	-	6	-	-	5	-	-	-	-	-	-	-	-
Drepanocladus revolvens	-	-	5	-	-	-	-	-	-	-	4	-	3	-	-	-
Drepanocladus revolvens var. intermedius	-	-	-	-	-	-	2	-	-	-	8	-	10	10	-	-
Drepanocladus uncinatus	2	2	5	2	-	4	4	15	-	8	-	8	-	-	-	3
Fissidens arcticus	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-
Fissidens osmundoides	-	2	-	-	-	-	-	-	7	-	-	-	-	5	-	-
Gymnocolea inflata	12	-	-	-	11	16	-	13	-	-	-	4	3	-	-	-
Gymnomitrion coralloides	-	-	-	-	-	-	7	-	-	4	-	-	-	-	-	9
Haplodon wormskjoldii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hylocomium splendens var. obtusifolium	-	2	7	2	-	4	5	13	-	8	-	4	13	-	-	-
Leiocolea heterocolpa	-	4	2	-	-	-	-	-	2	-	12	-	3	-	-	-
Lepicolea fryei	-	-	-	-	-	4	-	2	-	-	-	-	3	-	-	-
Lophozia alpestris	7	9	2	4	6	12	5	18	13	16	8	-	-	5	6	3

TABLE XXVI (continued)

Bryophyte Species	Bryophyte Communities															
	AE	C	B	D	F	G	HS	I	J	K	L	M	N	O	P	Q
Lophozia ventricosa	2	-	-	-	-	-	-	-	9	-	-	-	10	-	-	6
Massula opacifolia	9	-	17	8	-	12	-	-	-	12	-	-	3	-	-	-
Meesia longiseta	-	-	-	-	-	-	-	15	-	-	-	-	-	-	-	-
Meesia triquetra	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Meesia uliginosa	2	-	-	-	6	-	-	13	-	-	-	-	3	-	-	-
Mnium marginatum	-	-	-	-	-	-	2	-	-	-	16	-	-	-	-	-
Moerchia flotowiana	-	4	2	-	-	-	-	2	-	-	-	-	-	-	-	-
Mylia anomala	-	2	2	-	-	-	-	-	7	4	-	-	-	10	-	-
Myurella julacea	5	16	-	-	-	-	-	18	-	-	-	12	10	-	-	-
Myurella tenerrima	-	-	-	-	-	-	-	-	11	-	-	-	-	5	-	-
Odontoschisma elongata	12	7	-	-	6	-	-	5	-	-	-	-	-	-	-	-
Odontoschisma macounii	-	-	2	-	6	-	-	15	4	-	-	-	13	16	-	-
Oncophorus virens	-	-	2	-	-	-	2	5	-	4	-	-	13	-	-	-
Oncophorus wahlenbergii	-	-	-	6	-	-	5	-	7	-	-	-	-	5	11	-
Orthocaulis binsteadii	2	-	-	-	-	8	12	-	-	-	8	-	10	-	-	3
Orthocaulis kunzeanus	-	-	-	-	-	-	-	-	11	-	4	-	3	10	-	-
Orthocaulis quadriloba	2	-	5	4	-	-	-	-	2	-	8	4	-	10	-	-
Orthothecium chryseum	-	-	-	2	-	-	2	5	-	4	16	8	13	-	-	3
Plagiomnium ellipticum	-	-	5	-	-	8	2	8	-	8	-	4	-	5	6	-
Plagiothecium denticulatum	7	-	5	-	-	8	2	5	-	-	16	8	-	-	6	6
Plagiothecium piliferum	-	-	-	-	-	-	2	-	-	-	-	-	16	-	6	3
Pogonatum alpinum	-	-	2	6	-	-	12	-	2	-	4	-	10	-	6	-
Pogonatum alpinum var. septentrionale	-	-	-	-	-	-	-	-	13	-	8	-	-	-	17	3
Pogonatum dentatum	-	-	17	-	-	4	-	2	-	-	-	-	-	-	-	-
Pohlia bulbifera	-	-	5	2	-	-	2	-	-	4	-	-	-	-	-	-
Pohlia cruda	2	-	5	8	-	4	-	-	2	8	8	-	3	-	-	6

TABLE XXVI (continued)

Bryophyte Species	Bryophyte Communities															
	AE	C	B	D	F	G	HS	I	J	K	L	M	N	O	P	Q
Pohlia nutans	7	2	-	-	6	-	-	8	2	4	4	-	-	-	-	-
Pohlia proligera	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Polytrichum commune var. maximoviczii	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	3
Polytrichum var. nigrescens	2	14	-	-	6	-	-	5	2	-	-	4	-	-	-	3
Polytrichum var. yukonense	-	2	-	10	-	-	2	-	-	-	-	-	-	-	-	3
Polytrichum juniperinum	5	-	7	-	-	8	2	2	9	12	8	-	3	-	-	-
Polytrichum piliferum	-	-	7	12	-	-	2	-	-	8	4	-	-	-	-	-
Polytrichum piliferum var. hyperboreum	-	-	-	-	-	-	-	2	-	4	-	-	-	-	-	-
Polytrichum strictum	2	-	5	-	-	4	2	-	-	-	4	-	3	-	-	-
Pseudobryum cinclidioides	2	-	2	-	6	-	-	-	-	-	-	-	-	-	11	-
Psilopilum cavifolium	-	-	-	2	-	-	9	-	-	-	-	-	-	-	-	-
Ptilidium ciliare	-	2	2	2	-	8	2	2	-	8	-	-	-	-	17	-
Rhacomitrium lanuginosum	-	-	-	-	-	4	2	-	2	4	8	-	3	5	-	-
Rhizomnium andrewsianum	12	7	12	4	-	12	2	13	18	8	-	-	16	-	-	-
Riccardia pinguis	-	-	5	-	-	-	-	-	-	-	-	-	6	10	-	-
Scapania irrigua	5	7	5	6	11	12	4	10	2	8	4	-	3	5	11	-
Scapania mucronata	2	-	-	-	-	-	-	8	9	4	8	-	13	5	-	9
Scapania paludicola	-	-	-	-	-	-	-	8	-	-	-	-	13	-	-	-
Scapania simmonsii	-	-	-	-	-	-	-	2	9	-	-	-	-	-	-	-
Scorpidium scorpioides	-	9	-	-	-	-	-	2	-	-	-	-	3	10	-	-
Scorpidium turgescens	-	-	-	-	-	-	-	5	-	-	12	4	-	-	-	-
Solenostoma pumilum ssp. polaris	-	2	2	-	-	-	-	-	4	-	4	-	3	5	-	-
Sphagnum spp.	-	-	-	6	-	-	2	-	-	-	-	-	6	-	-	3

TABLE XXVI (continued)

Bryophyte Species	Bryophyte Communities															
	AE	C	B	D	F	G	HS	I	J	K	L	M	N	O	P	Q
Timmia austriaca	-	-	-	-	-	-	-	-	2	-	4	-	3	-	-	-
Timmia norvegica	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-
Tomenthypnum nitens	-	2	2	-	-	-	2	5	-	-	-	8	-	-	-	-
Tortella fragilis	-	-	-	-	-	-	-	2	11	-	-	-	-	10	-	-
Tortella tortuosa	-	-	-	-	-	-	-	8	-	-	12	4	13	-	-	-
Tritomaria quinquedentata	-	-	-	-	6	-	-	-	16	-	-	4	-	-	-	-

APPENDIX B

TABLE XXVII

BRYOPHYTE SPECIES LIST, POINT BARROW, ALASKA[a]

Bryophytes
Musci
*Aloina brevirostris (Hook. & Grev.) Kindb.--Smith #2708
Aulacomnium palustre (Hedw.) Schwaegr.
Aulacomnium turgidum (Wahlenb.) Schwaegr.
Bartramia ithyphylla Brid.
Brachythecium nelsonii Grout
Brachythecium turgidum (C. J. Hartm.) Kindb.
Bryoerythrophyllum recurvirostrum (Hedw.) Chen
Bryum arcticum (R. Br.) B.S.G.
Bryum argenteum Hedw.
Bryum calophyllum R. Br.
*Bryum cryophilum Mart.--Smith #2324
Bryum nitidulum Lindb.
Bryum pallens (Brid.) Sw. ex Roehl.
*Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer & Scherb.--Smith #2325
Bryum salinum Hag. ex Limpr.
Bryum stenotrichum C. Muell. as B. inclinatum (Brid.) Br. & Sch.
*Bryum wrightii Sull. & Lesq.--Smith LPr 3c-5
*Calliergidium pseudostramineum (C. Muell.) Grout--Smith #HPTD 1-3
Calliergon giganteum (Schimp.) Kindb.
*Calliergon orbicularicordatum(Ren. & Card.) Broth.--Karczmarz (1971)
*Calliergon richardsonii (Mitt.) Kindb. ex Warnst.--(NY) Steere #15174
Calliergon sarmentosum (Wahlenb.) Kindb.
*Calliergon stramineum (Brid.) Kindb.--(NY) Steere #15223
Campylium stellatum (Hedw.) C. Jens.
Ceratodon heterophyllus Kindb. ex Macoun
Ceratodon purpureus (Hedw.) Brid.
Cinclidium arcticum (B.S.G.) Schimp.
*Cinclidium latifolium Lindb.--Smith #2254
*Cinclidium stygium Sw.--Smith LPm 2b-1
*Cinclidium subrotundum Lindb.--Smith LPr 3d-2

TABLE XXVII (continued)

Bryophytes
Cirriphyllum cirrosum (Schwaegr. ex Schultes) Grout
Conostomum tetragonum (Hedw.) Lindb.
*Cyrtomnium hymenophyllum (B.S.G.) Holmen--Webster #72-0421
Cynodontium alpestre (Wahlenb.) Milde
Desmatodon heimii (Hedw.) Mitt. var. arctica (Lindb.) Crum
Desmatodon leucostoma (R. Br.) Berggr.--(NY) Steere #16352
Desmatodon obtusifolius (Schwaegr.) Schimp.--(NY) Steere #15095
*Dichodontium pellucidum (Hedw.) Schimp.--Smith #33-7
Dicranella cerviculata (Hedw.) Schimp.
Dicranella crispa (Hedw.) Schimp.
*Dicranella grevilleana (Brid.) Schimp.--Smith #2307
*Dicranella subulata (Hedw.) Schimp.--(NY) Steere #15070
Dicranum angustum Lindb.
Dicranum elongatum Schleich. ex Schwaegr.
Dicranum majus Sm.
*Dicranum muehlenbeckii B.S.G.--Smith #35-1
*Dicranum spadiceum Zett.--(NY) Steere #15084a
Distichium capillaceum (Hedw.) B.S.G.
Distichium hagenii Ryan ex Philib.
Distichium inclinatum (Hedw.) B.S.G.
Ditrichum flexicaule (Schwaegr.) Hampe
Drepanocladus aduncus (Hedw.) Warnst.
*Drepanocladus badius (C. J. Hartm.) Roth--(NY) Steere #15141
Drepanocladus exannulatus (B.S.G.) Warnst.
*Drepanocladus lycopodioides (Brid.) Warnst.--Steere #15182
Drepanocladus revolvens (Sw.) Warnst.
*Drepanocladus var. intermedius (Lindb.) R. Wils.--Smith #37-3H
*Drepanocladus uncinatus (Hedw.) Warnst.--Smith #2055
Encalypta alpina Sm.
*Encalypta ciliata Hedw.--(NY) Steere #19027
Encalypta procera Bruch
Encalypta rhaptocarpa Schwaegr.
*Fissidens arcticus Bryhn--Smith #35-7H
*Fissidens osmundoides Hedw.--Smith #34-2c
*Funaria arctica (Berggr.) Kindb.--Smith #2100
*Funaria hygrometrica Hedw.--Smith #2155
Haplodon wormskjoldii (Hornem.) R. Br.
*Hypnum bambergeri Schimp.--(NY) Steere #20015
Hylocomium splendens (Hedw.) B.S.G. var. obtusifolium (Beh.) Paris
Isopterygium pulchellum (Hedw.) Jaegr. & Sauerb.
Leptobryum pyriforme (Hedw.) Wils.
*Meesia longiseta Hedw.--Smith #LPm 2b-5
*Meesia triquetra (Richt.) Angstr.--(NY) Steere #20297

TABLE XXVII (continued)

Bryophytes
*Meesia uliginosa Hedw.--Smith #72-12
*Mnium marginatum (With.) Brid. ex P.-Beauv.--Smith #2460
Myurella julacea (Schwaegr.) B.S.G.
*Myurella tenerrima (Brid.) Lindb.--(NY) Steere #19055
Oncophorus virens (Hedw.) Brid.
*Oncophorus wahlenbergii Brid.--(NY) Steere #15052
Orthothecium chryseum (Schwaegr. ex Schultes) B.S.G.
*Orthothecium strictum Lor.--(NY) Steere & Crum #20003
*Paludella squarrosa (Hedw.) Brid.--Webster #72-0024
*Plagiomnium ellipticum (Brid.) Kop.--Smith #2486
Plagiomnium rugicum (Laur.) Kop.
Plagiothecium denticulatum (Hedw.) B.S.G.
*Plagiothecium piliferum (Sw. ex C. J. Hartm.) B.S.G.--Smith #2004
*Pogonatum alpinum (Hedw.) Roehl.--Smith #2026 var. septentrionale (Brid.) Brid.
Pogonatum dentatum (Brid.) Brid.
*Pohlia annotina (Hedw.) Lindb.--(NY) Steere #15113
*Pohlia bulbifera (Warnst.) Warnst.--Smith #29-1H
Pohlia cruda (Hedw.) Lindb.
Pohlia nutans (Hedw.) Lindb.
*Pohlia proligera (Kindb. ex Limpr.) Lindb. ex Arnell--(NY) Steere #16357
*Polytrichum commune Hedw. var. maximoviczii Lindb.--Smith #HPEs 3-1
*Polytrichum var. nigrescens Warnst.--Smith #LPm 5d-1
*Polytrichum var. yukonense (Card. & Ther.) Frye--Smith #2349
*Polytrichum juniperinum Hedw.--Smith #2006
*Polytrichum piliferum Hedw.--Smith #2412
*Polytrichum var. hyperboreum (R. Br.) C. Muell.--Smith #2348
*Polytrichum strictum Brid.--Smith #2415
*Pseudobryum cinclidioides (Hueb.) Kop.--Smith #2037
Psilopilum cavifolium (Wils.) Hag.
*Rhacomitrium heterostichum Hedw.--Smith #2044
*Rhacomitrium lanuginosum (Hedw.) Brid.--(NY) Steere #19074
Rhizomnium andrewsianum (Steere) Kop.
*Scorpidium scorpioides (Hedw.) Limpr.--Smith #Lpm 1a-1
Scorpidium turgescens (T. Jens.) Loeske
*Sphagnum capillaceum (Weiss) Schrank--(N&) Steere #15800
*Sphagnum var. tenellum (Schimp.) Andr., (=S. rubellum) Smith #2375
*Sphagnum cuspidatum Ehr. ex Hoffm.--Smith #LPT e-1
*Sphagnum fimbriatum Wils. ex J. Hook--(NY) Sharp #A-5843
Sphagnum girgensohnii Russ.
Sphagnum squarrosum Crome
Splachnum vasculosum Hedw.

TABLE XXVII (continued)

Bryophytes
Tetraplodon mnioides (Hedw.) B.S.G.
*Timmia austriaca Hedw.--(NY) Steere #15188
*Timmia norvegica Zett.--(NY) Steere & Crum #20008
Tortula mucronifolia Schwaegr.
Tortula ruralis (Hedw.) Gaertn., Meyer & Sauerb.
*Tomenthypnum nitens (Hedw.) Loeske--Smith #32-1H
*Tortella fragilis (Drumm.) Limpr.--Smith #34-1H
*Tortella tortuosa (Hedw.) Limpr.--(NY) Steere #15185
Trichodon cylindricus (Hedw.) Schimp.
Hepaticae
Anastrophyllum minutum (Schreb.) Schust.--Persson (1963)
*Anthelia juratzkana (Limpr.) Trev.--Smith #36-7
*Blepharostoma trichophyllum (L.) Dum.--Smith #2476
*Cephalozia pleniceps (Aust.) Lindb.--Smith #2307
Cephalozia bicuspidata (L.) Dum.--Persson (1963)
Cephaloziella arctica Bryhn & Douin
Chiloscyphus pallescens (Ehrh.) Dum.
Diplophyllum taxifolium (Wahlenb.) Dum.--Persson (1963)
*Gymnocolea inflata (Huds.) Dum.--Smith #LPm 2b-2
*Gymnomitrion coralloides Nees--Smith #LPm 2b-2
*Leiocolea heterocolpa (Thed.) M. A. Howe--Smith #32-9
*Lepicolea fryei Persson--Smith #LPm 3b-5
*Lophozia alpestris (Schleich.) Evans--Smith #HPTF 2-m
Lophozia ventricosa (Dicks.) Dum.
Marchantia polymorpha L.
*Massula opacifloia Culm.--Smith #2025
*Moerchia flotowiana (Nees) Schiffn.--Smith #2029
*Mylia anomala (Hook.) S. Gray--Smith #38-3H
*Odontoschisma elongata (Lindb.) Evans--Smith #LPs 3b-4
*Odontoschisma macounii (Aust.) Und.--Smith #LPr 3d-2
*Orthocaulis binsteadii (Kaal.) Evans--Smith #LPr 1a-4
*Orthocaulis kunzeana (Hueb.) Evans--Smith #43-7
Orthocaulis quadriloba (Lindb.) Evans
Plagiochila arctica Bryhn & Kaal.
*Ptilidium ciliare (Web.) Hampe--Smith #2436
*Riccardia pinguis (L.) Gray--Smith #LPm 1a-1
Scapania irrigua (Nees) Dum.
Scapania mucronata Buch
Scapania paludicola Loeske & K. Muell.

TABLE XXVII (continued)

Bryophytes
*Scapania simmonsii Bryhn & Kaal.--Smith #38-1
*Solenostoma pumilum (With.) K. Muell. ssp. polaris (Berggr.) Schust.--Smith #LPm 2b-5
Tritomaria quinquedentata (Huds.) Buch

*These species are new reports for the Barrow area.

[a]All species listed here and not cited may be found in Persson (1962, 1963), Steere (1954b), and Rastorfer (1972).

VITA

David Kent Smith was born in Oakland, California on October 19, 1946. He is the third of five children of Gerould Hammond Smith and Mary Elizabeth Smith. He completed both his primary and secondary school education in 1964 when he was graduated from Santa Ana Senior High School, Santa Ana, California.

He was admitted to Humboldt State College, Arcata, California where he received his B.A. degree in Biology in 1969. The following year he was graduated from the same institution with a M.A. degree in Biology.

In 1970, he entered the Department of Botany at The University of Tennessee, Knoxville, Tennessee to pursue study toward the Doctor of Philosophy degree in Botany. He expects to receive his Ph.D. degree at commencement, August, 1974, attended by his wife, Mary.