36471

NAME OF AUTHOR *NOM DE L'AUTEUR* MARIANNE GOODRIDGE SEE

TITLE OF THESIS *TITRE DE LA THÈSE* ALPINE MACROLICHEN VEGETATION IN THE CANADIAN CORDILLERA OF ALBERTA AND THE YUKON

UNIVERSITY *UNIVERSITÉ* UNIVERSITY OF ALBERTA

DEGREE FOR WHICH THESIS WAS PRESENTED / *GRADE POUR LEQUEL CETTE THÈSE FUT PRÉSENTÉE* M. Sc

YEAR THIS DEGREE CONFERRED / *ANNÉE D'OBTENTION DE CE GRADE* 1978

NAME OF SUPERVISOR / *NOM DU DIRECTEUR DE THÈSE* Dr. L. C. Bliss

DATED / *DATÉ* 30 December 1977 SIGNED / *SIGNÉ* Marianne G. See

PERMANENT ADDRESS / *RÉSIDENCE FIXÉ*
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ALPINE MACROLICHEN VEGETATION IN THE CANADIAN CORDILLERA OF ALBERTA AND THE YUKON

by

MARIANNE GOODRIDGE SEE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

PLANT ECOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

SPRING, 1978

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Alpine Macrolichen Vegetation in the Canadian Cordillera of Alberta and the Yukon", submitted by Marianne Goodridge See in partial fulfilment of the requirements for the degree of Master of Science in Plant Ecology.

Lawrence C. Bliss
Supervisor

[illegible]

Lorene L. Kennedy

Date. December 21, 1977

I dedicate this thesis to my parents, David and Priscilla See, who first showed me "British Soldiers" (*Cladonia cristatella*) many years ago.

ABSTRACT

Alpine macrolichen vegetation was examined in west central Alberta and north central Yukon Territory in 1975 and 1976. Major objectives were to: (1) determine species richness (S), evenness (J), diversity (H') and cover; (2) examine habitat factors in relation to vegetation; (3) describe and compare communities; (4) evaluate community distribution; and (5) compare macrolichen and vascular plant communities. Study areas included Prospect Mountain and the Divide in the Mountain Park region, Alberta, and the Nahoni Range and Ogilvie Mountains in the Yukon. All areas were characterized by patterned ground, and comparable acidic and basic substrates were sampled in each region. In each of 42 stands (30 x 5m), macrolichen cover was estimated on different substrates within stratified random quadrats (10 x 40cm).

Macrolichen vegetation in the four study areas was most similar on an intraregional basis. In the northern (Yukon) region there was increased macrolichen cover, S, and H'. In contrast, J values were not significantly different between areas or regions, but varied with moisture regime. Lowest evenness occurred in mesic-wet sites and in dry species-poor stands while highest evenness was associated with well-vegetated upland sites.

Bray-Curtis and reciprocal averaging ordinations were used to elucidate relationships of vegetation to complex-gradients of moisture and substrate pH in each region.

Separate communities were delineated for vascular plants and macrolichens along these environmental gradients. The two types of plant communities exhibited partial correspondence in Alberta, and were closely correlated in the Yukon region. All macrolichen communities were comparable to vegetation reported in other studies, on a regional basis.

The relationships of environmental factors to individual macrolichen species were examined in each region with population response patterns. There were six ecological groups of species in each region which were associated with substrate pH. Comparisons between response patterns showed that the breadth of distribution for most species shifted on an interregional basis, corresponding partly to the predominance of dry, basic sites in the Alberta study areas. Macrolichen species generally showed a low degree of restriction to either acidic or basic sites but many were quantitatively more important on one substrate pH type than the other. Epiphytic species and those with broad ecological amplitude appeared to respond more to other microhabitat features such as substrate moisture than to substrate pH.

Similarly, distribution of communities corresponded to distribution of basic or acidic substrate, or to specific moisture regime. Thus, glaciation history is not a major factor responsible for present alpine macrolichen vegetation. Distribution elements in the macrolichen flora substantiate the fact that widespread dispersal has occurred in alpine areas of the Canadian Cordillera. Regional differences in

4.

macrolichen importance and species richness may reflect limited southward post-glacial dispersal, although it is suggested that climatic factors in the southern region may be limiting to northern populations.

The correspondence of macrolichens and vascular plant communities to environmental factors from regions in the present study are considered to be adequate for predicting vegetation within the uninvestigated, intermediate Cordilleran alpine areas.

ACKNOWLEDGEMENTS

I would like to express my sincere appreciation for continuing advice and support from my supervisor, Dr. L.C. Bliss. Contributions from committee members Dr. J.F. Addicott and Dr. L.L. Kennedy are also very much appreciated.

Several curators generously aided in lichen identifications, including M. Ostafichuk, Drs. C.D. Bird, I.M. Brodo, and A.C. Skorepa. Advice from Drs. I. Karnefelt, D.C. Lindsay, J.W. Sheard and H. Trass was also very helpful. Vascular plant identifications were verified by M. Dumais, W. Elisens, P. Mortimer, Dr. J.G. Packer and S. Wolf.

Exceptional assistance was provided by D. Maier and J. Roland in field work, and by R. Ellis and L. Kershaw in laboratory work. Data analysis was facilitated by advice from J. Campbell, T.D. Lee, W. Russell, Drs. R.A. Black, J.R. Busby, and B. Chernick.

Dr. G.E. Ball, R. Hobbs and Dr. D.H. Vitt contributed useful background information on northern biogeography. I would also like to thank the geologists who aided me: W. Kilby, Drs. L.A. Bayrock, R. Green, L.V. Hills, O.L. Hughes, D.K. Norris, and N.W. Rutter. Advice on soils was generously provided by T. Babb, Drs. G.M. Coen and W. Pettapiece.

The support of Drs. M.E. Hale and P.R. Gorham is much appreciated. Special equipment was made available by Drs. K.E. Denford, G.H. LaRoi and D.H. Vitt. Parks Canada staff kindly provided access into several areas of Jasper National

Park. I would also like to thank the Director of the University of Manitoba Field Station at Delta Marsh, Dr. J.M. Shay, for encouragement and the use of facilities.

Special thanks are due to the extensive advice of T.D. Lee and Dr. C.D. Bird throughout the study. The most significant contributions have been those of my husband, G.F. Tande, who provided continuing support and generously aided in all aspects of this research.

Financial support is gratefully acknowledged from Boreal Institute (1975, 1976), from NRC grants to L.C. Bliss (A4879) and to D.H. Vitt (A6390), and from graduate awards in the Department of Botany.

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INTRODUCTION

The emphasis of lichen ecology in North America was initially on the distribution and abundance of temperate forest epiphytes (Culberson 1955a, 1955b, Hale 1955, Beals 1965, Hale 1965); and terricolous species (Cooke 1955, Gorham 1957, Davis 1964, Looman 1964a, 1964b). Subsequent lichen vegetation studies have included saxicolous (Foote 1966, Yarranton 1967, Stottler 1976) and terricolous species (Fraser 1965, Lambert and Maycock 1968, Lechowicz and Adams 1974a, Wein and Speer 1975). Extensive literature has appeared on forest epiphytes due to the use of these lichens in air pollution studies. In contrast, vegetation studies of terricolous and saxicolous lichens are poorly represented, with few from high elevations and latitudes.

The distribution and abundance of terricolous lichen vegetation in alpine areas of North America presents a series of challenges to the ecologist. Many studies of alpine vascular plant vegetation are available, yet most of these include only conspicuous lichens or omit them due to taxonomic difficulties. As a result, alpine lichen vegetation is represented primarily by a limited number of floristic or qualitative vegetation studies. The situation is further compounded by poor access to many alpine regions, especially those in the northern Canadian Cordillera.

Alpine vascular plant communities have been described from the southern Canadian Rocky Mountains by Beder (1967), Bryant and Scheinberg (1970), Eady (1971), Trottier (1972), Broad (1973), and Kuchar (1973). Further north in Jasper National Park, alpine vegetation studies have been conducted by Hrapko (1970) and Kuchar (1975). These studies all have some qualitative or quantitative lichen data for the prominent species, but the degree of resolution is highly variable.

Few investigations of alpine vegetation have been carried out further north in the Cordillera: Ricker (1967) and Kojima (1973) have both described plant associations in the North Klondike River Valley in the Ogilvie Mountains, Yukon Territory. Neither study, however, includes comprehensive lichen vegetation data. An extensive amount of quantitative data has been obtained for lichens and vascular plants in mountains of the Yukon and Northwest Territories (Bird 1974a, 1974b), although vegetation analyses are lacking.

Alpine lichen vegetation is therefore only locally documented in the Canadian Cordillera, and is largely unknown in this mountain system as a whole. For these reasons, the present study was initiated to provide information on alpine lichen vegetation in west central Alberta and north central Yuko regions of the Cordillera. The objectives of this study were specifically to:

(1) determine trends and relationships in macrolichen species richness, evenness, diversity, and cover;

(2) examine the relationship of habitat factors (moisture,

substrate) with species, and with vegetation;

(3) describe and compare macrolichen communities;

(4) evaluate the effect of glaciation and substrate on vegetation distribution; and

(5) compare macrolichen and vascular plant communities.

It was deemed necessary to omit crustose lichens, or microlichens, from this project due partially to the difficulty or impossibility of field identifications. Therefore the major focus of the study is macrolichens, or the foliose and fruticose forms. This definition follows the use of the term by Lindsay (1975, 1976 pers. comm.).

The major reason for concentrating on macrolichens is that these lichens can become large enough to occupy considerable space in a habitat, which can then be measured as cover, or biomass (e.g. Wein and Speer 1975). They also are more comparable in size to vascular plants and are thus more likely to be affected by similar habitat factors than are microlichens. Macrolichen vegetation is emphasized in this study in recognition of the fact that the lack of previous detailed alpine studies is due partially to taxonomic difficulties. Looman (1964a) also has delineated lichen communities, and summarizes the rationale for this by stating:

> My treatment of the cryptogams as separate communities does, therefore, not imply recognition of these communities as independent entities; it merely recognizes the practical difficulties of identification.

The major benefit of the descriptions of macrolichen vegetation in the present study is the provision of a basis of comparison for further related investigations.

STUDY AREAS

Study areas were located in two major mountainous regions of west central Alberta and north central Yukon, Canada (Fig. 1). The Alberta areas are within the Nikanassin Range (52°50'N; 117°20'W) in the vicinity of the abandoned town of Mountain Park. The Yukon region includes an area in the Nahoni Range (65°36'N; 136°41'W) and another in the Ogilvie Mountains (64°18'N; 137°21'W). All areas have extensive alpine slopes on parent material of sedimentary origin.

Mountain Park Region, Alberta

Peaks of the Nikanassin Range rise to 2743 m at Prospect Mountain, and include Cheviot (2720 m) and Tripoli (2630 m) Mountains (Fig. 2). The study area is restricted to the eastern range slopes, extending south and east over the divide between the Cardinal and McLeod River systems. The Mountain Park region is presently designated as Reserved Crown Land, and is being reviewed for reclassification as a Permanent Ecological Reserve. Geology and floristics of the area have been initially described by Packer and Vitt (1974).

Access to the region is by the Grave Flats Road, south from Cadomin. An abandoned mining road extends west from the main road, along Prospect Creek and up onto the lower ridges (2042 m) of Prospect Mountain. The Grave Flats Road

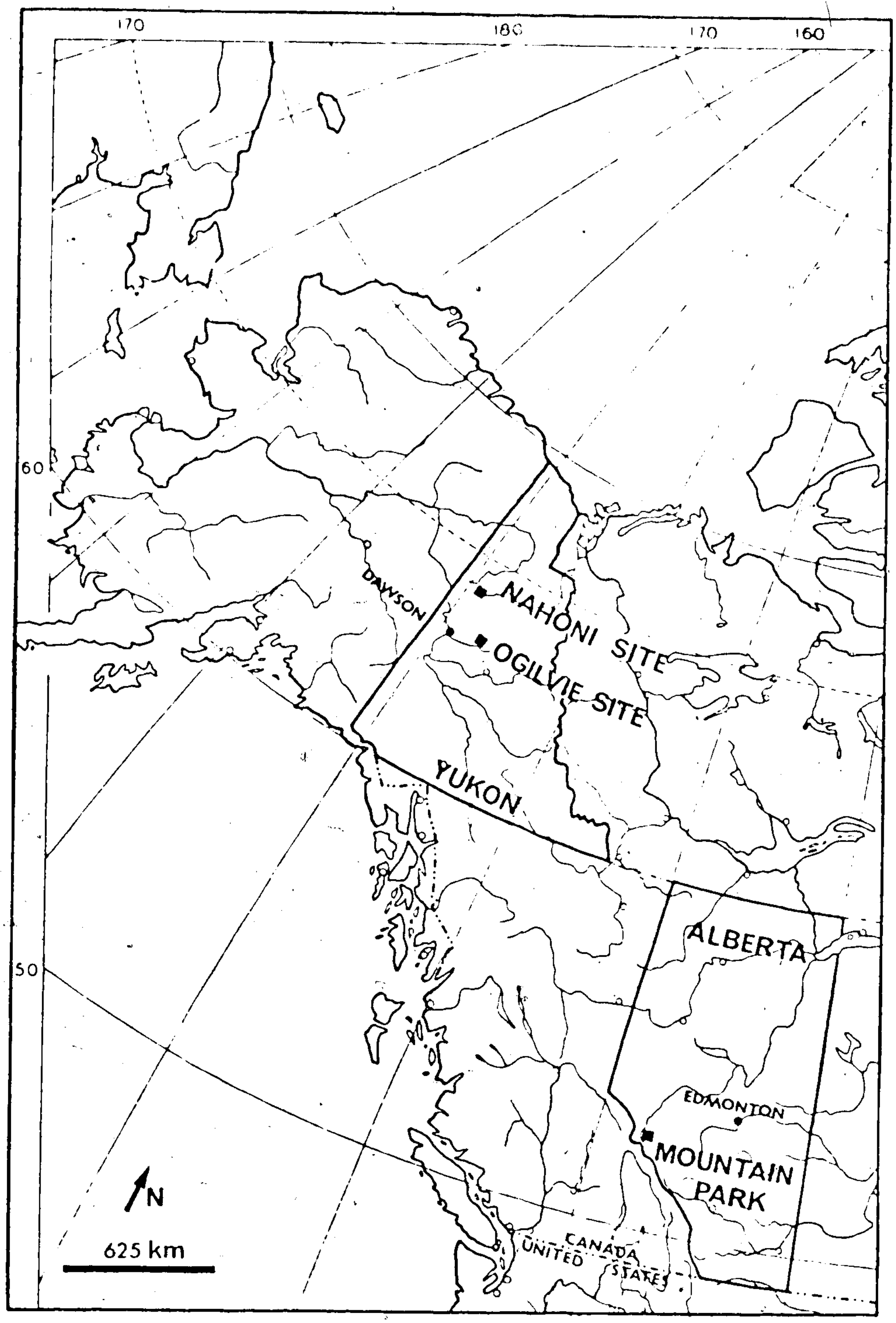

FIGURE 1. Location of Nahoni, Ogilvie, and Mountain Park sites in Yukon and Alberta regions, respectively.

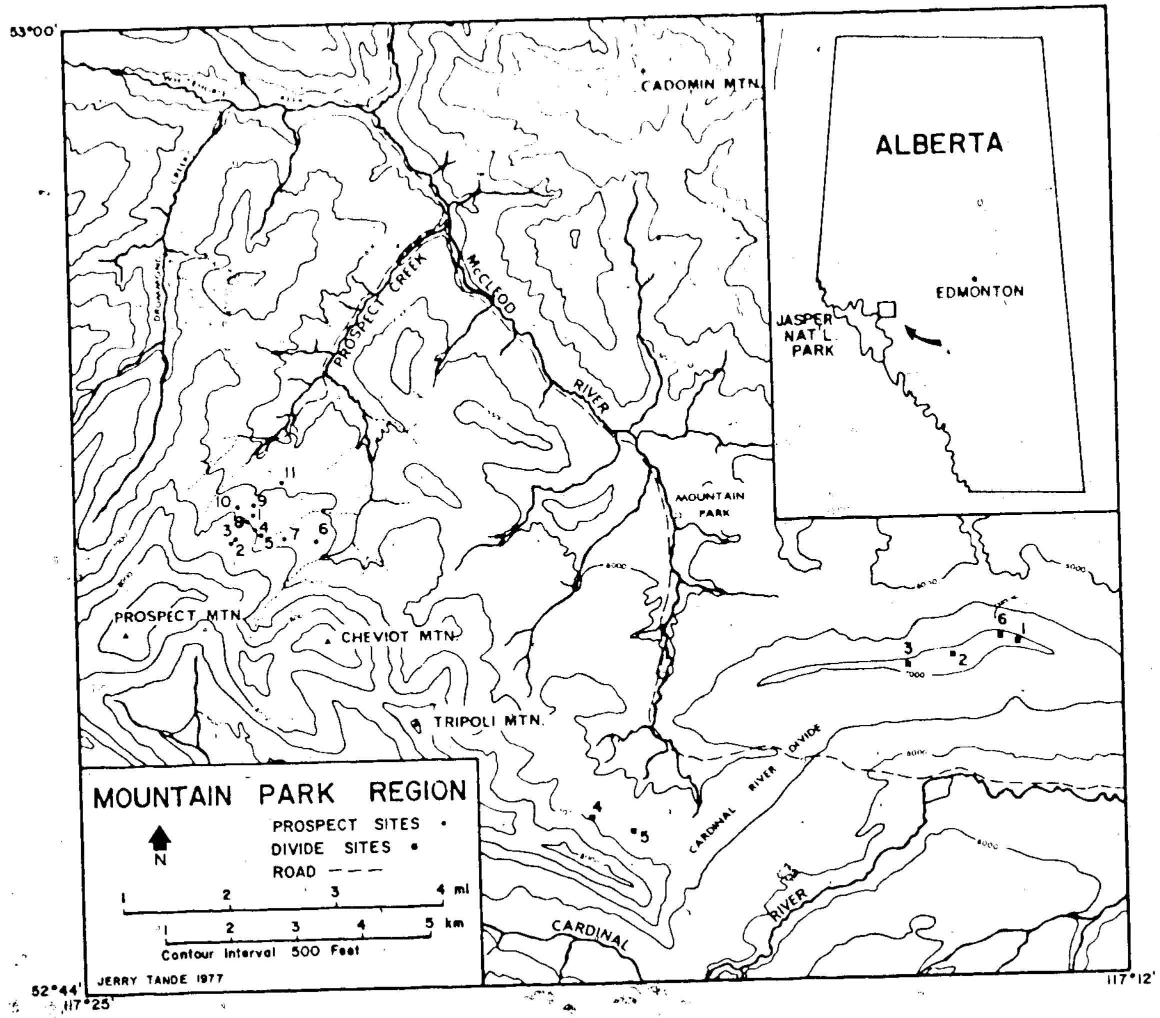

FIGURE 2. Location of stands on Prospect Mountain and the Cardinal River Divide in the Mountain Park region, Alberta.

continues southeast to the broad pass on the river divide at 1987 m. Known as the Divide, this ridge slopes north and east from the road and gradually reaches an elevation of 2149 m.

Sites at Prospect (Mountain) and the Divide (Fig. 2) represent the elevation range of alpine vegetation at these study areas.

Geology

Prospect Mountain

The Nikanassin Range marks the beginning of the Front Ranges of the Rocky Mountain Area in the Eastern Cordilleran System (Bostock 1970). The McConnell Fault separates the Front Ranges from the Foothills Area to the east (Mountjoy 1962, Stott 1963). Although this fault is situated above the west side of the Prospect Mountain study area, the Alberta sites are here considered within the Front Ranges due to the presence of the small Redcap Mountain group east of Prospect.

In the Prospect Mountain study area the bedrock is mainly composed of limestones, shales, sandstones and dolomite. The lower alpine and upper subalpine are underlain by Lower Cretaceous sandstone, shale and commercial coal beds of the Luscar Formation (Mellon 1966).

The Mountain Park Formation extends upslope on the southeast ridges of the study area adjoining the Luscar Formation. It is also of Lower Cretaceous origin and consists of shales and sandstones. The contact of the two formations is obscured by their similarity (Mountjoy 1962) and by colluvial materials derived largely from the steep Paleozoic peaks above the study area.

The Nikanassin Formation of Jurassic sandstones and shales is found above the Luscar Formation (Kryczka 1959). The top of this formation is separated from the uppermost Paleozoic rocks by the McConnell Fault. These highest formations include Devonian limestones, calcareous shales and dolomites (MacKay 1929).

Upper slopes within the study area are characterized by a major syncline and heavily faulted zones. Such complexes, in combination with mass wasting and periglacial processes have produced several different types of substrate and drainage patterns throughout the study area.

Drainage in the Prospect area is northeast towards Prospect Creek which subsequently flows into the McLeod River. The west side of Prospect is drained by the headwater streams of the Cardinal River.

Divide

The Cardinal-McLeod River Divide is composed of two distinct Upper Cretaceous marine shale and sandstone formations which are approximately separated by the Grave Flats Road. Cardium sandstone borders the Wapiabi shale along the road. Both are included in the Alberta Group, as is the Blackstone Formation (Stott 1963, 1966). Blackstone shale is found south of the others, where it borders the Devonian limestones and dolomites of Tripoli Mountain (MacKay 1929)...

The syncline core region on Prospect Mountain continues east onto the flat sandstone limb on the Divide. The Wapiabi shale south of the Grave Flats road represents the associated overturned sections (W. Kilby, pers. comm.).

Glacial History

The foothills and Front Ranges of the Rocky Mountains were glaciated in early Wisconsin time (>35,000 years B.P.). Erratics have been found throughout these areas at more than 2400 m (Bayrock and Reimchen 1975). During the Wisconsin, large regions of the foothills were not glaciated, or were only locally glaciated. To the north of the study area, early Wisconsin or Illinoian Cordilleran ice flowed northward in the Athabasca River Valley and coalesced with the main Laurentide ice outside the foothills (Roed 1968). Reeves (1973) postulates that this represents one of the few Cordilleran-Laurentide contacts in the otherwise ice-free corridor in the western plains of Alberta. He depicts this corridor as largely continuous into the unglaciated Yukon region during the early Wisconsin or late Illinoian (>55,000 years B.P.). The maximum ice fronts in classical Wisconsin times were less extensive, allowing an even wider corridor (Reeves 1973).

In late Wisconsin times, Laurentide and Cordilleran ice masses were in contact south of the study area in the Rocky Mountain House region (Boydell 1972). Recent geological evidence suggests that the major river valleys from the Athabasca to the Bow River were glaciated during the Wisconsin (L.V. Hills, pers. comm.). By 15,000 years B.P. southern Alberta and southwestern Saskatchewan were ice-free. Many mountain valleys were deglaciated by 10,500 years B.P. (Reeves 1973).

Bayrock (1969) indicates that the land from Montana into Alberta, Northwest Territories, northern Alaska and the Bering Strait was an available migration route to Asia during Nebraskan and Kansan times. He states that the first glaciation of the eastern Alberta region was in the early Wisconsin, possibly back into Illinoian time. Therefore, the Wisconsin is presumed to be the only time period in which the Laurentide and Cordilleran ice masses were in close proximity. The corridor between them is known to have been closed only in a few localities. In pre-Wisconsin times Cordilleran glacier ice extensively covered the foothills (Bayrock 1969). The existence or extent of contemporaneous Laurentide ice in Alberta is not known.

Patterned Ground

Prospect Mountain has steep rocky slopes with few signs of recent glacial activity. Level ridge-top areas are infrequently found. The slopes exhibit periglacial patterned ground features, indicating intensive frost action (Washburn 1973).

The most common patterned ground features are nonsorted stone stripes, which are separated by vegetation stripes. The relative size of vegetation versus stone stripes is quite variable, and appears to be a function of slope steepness and stability. Steeper slopes have small vegetated stripes, and these dwindle to small islands or spotted tundra (Bamberg and Major 1968) in the more unstable areas.

On wetter and gentler slopes the patterned features include steps and small gelifluction lobes. Relatively level areas support continuous vegetation or nonsorted stone circles.

Patterned ground features are characteristic of almost every Prospect stand, and the resulting micropatterns necessitated substrate stratification in the sampling design.

The Divide area is gently sloping with fewer patterned ground features than the slopes at Prospect Mountain. Nonsorted circles and stripes are most common. Frost shattering has formed a ridge-top sandstone fellfield in which patterned features were absent.

Soils

In Alberta, descriptive alpine soil studies have been carried out at Snow Creek Valley (Baptie 1968), Sunshine

(Knapik et al. 1973), and the Maligne Range (Hrapko 1970, Kuchar 1975). Both Jasper and Banff National Parks also have biophysical studies in progress which include alpine areas (I. Corns, pers. comm.).

Alpine soils in the Mountain Park region have developed from colluvial parent materials influenced by frost action. Permafrost may exist at this latitude in mountain soils above 1440 m (Brown 1967), although it has not been observed in the study areas. Soils on the Divide have not been described, and those on Prospect Mountain are currently under study (P. Mortimer, pers. comm.).

Climate

The climate of west central Alberta is Subarctic or Cold Snowy Forest (Dfc) in the Köppen classification system (Longley 1970, Root 1976). Powell and MacIver (1976) have analyzed weather records from this general region (Table 1). They have also summarized data for Grave Flats Lookout (52^o51'N; 117^o00'W at 2074m) which is the nearest comparable summer meteorological station to the study area (Table 1). This station and the study area are included in a High Elevation Mountain Area macroclimate designation which extends north and south of the Athabasca River (Powell and MacIver 1976).

Vegetation

Extensive alpine slopes are found on Prospect Mountain

TABLE 1. Meteorological summaries for west central Alberta and Grave Flats Lookout, Alberta, May-September 1969-1970 (Powell and MacIver 1976).

West-central Alberta

Rainfall mm		Highest mean daily temperature °C
July	100-130	10 (July)
June	70-110	
August	70-110	
May	70	
September	70	

Grave Flats Lookout

Total precipitation	Mean daily temperature
465	5.9
	Days above -2.2°
	121

between 1980 and 2134 m. The lower elevation represents the approximate limit of upright and krummholz tree growth, with some small patches of prostrate trees extending above on south-facing slopes.

Subalpine forests in this area are characterized by *Abies lasiocarpa* and *Picea engelmanii*. Tree limit is marked by a relatively sharp boundary of *A. lasiocarpa* on Prospect Mountain, with very little expression of ribbon forest. The forests below the upper subalpine areas are not extensive because a fire consumed most of the Prospect Valley vegetation in 1915 (G.F. Tande, pers. comm.). Revegetation has been slow, and is dominated by *Pinus contorta*.

Mesic and wet slopes in the lower alpine are characterized by shrub and herb meadows with *Aconitum delphinifolium*, *Castelleja miniata*, *Pedicularis bracteosa*, *Salix vestita*, *Trollius albiflorus*, and *Zygadenus elegans*. Other lower alpine slopes exhibit abundant growth of *Arctostaphylos rubra* and *Betula glandulosa*.

The dominant plant species on middle alpine slopes is *Dryas integrifolia*. Other frequent plants of lower cover are *Polygonum viviparum* and *Salix nivalis*. Conspicuous herbs include *Androsace chamaejasme*, *Erigeron grandiflorus*, *Hedysarum alpinum*, *H. mackenzii*, *Myosotis alpestris*, *Oxytropis campestris*, *O. podocarpa*, *Pedicularis lanata*, *Potentilla nivea*, *Saxifraga oppositifolia*, and *Silene acaulis*.

Upper alpine areas are very low in species richness. *Melandrium apetalum*, *Minuartia austromontana* and *Saxafraga oppositifolia* are found in the highest vegetated rocky slopes.

The snowbed habitat is very infrequent and is spatially restricted to small slope base areas. Characteristic species are *Cassiope tetragona*, *Phyllodoce glandulifera* and *Dryas octopetala*. Lichens are a minimal component of this vegetation.

The gentle slopes of the Divide area exhibit an extensive alpine meadow - subalpine forest mosaic, which grades into dry, low alpine slopes. Alpine vegetation forms a narrow band barely above the krummholz of *Abies lasiocarpa*. *Dryas integrifolia* is the dominant alpine species, occurring with *Polygonum viviparum* and *Salix nivalis*. Other important species include *Hedysarum alpinum*, *Kobresia bellardii*, *Pedicularis capitata*, *Potentilla diversifolia*, *Saxifraga tricuspidata*, *Solidago multiradiata*, *Stellaria monantha*, and *Zygadenus elegans*.

As on Prospect, late snowmelt areas are poorly represented. Species in such habitats include *Antennaria lanata*, *Cassiope tetragona*, *Dryas octopetala*, *Phyllodoce glandulifera*, and *Sibbaldia procumbens*.

Yukon

The northern study area is in the Nahoni Range, which consists of a low mountain series ranging in elevation from 900 to 1524 m. The study area includes the northern flanks of Brimston Mountain, and covers the elevation range of alpine vegetation on these slopes. Stands are also located on the slopes of unnamed ridges north of Brimston Mountain, with two sites in between the stand groups (Fig. 3).

The study area in the Ogilvie Mountains is located in a cirque 5 km northeast of One-eighty Lake, and north of Officer Creek. Elevation ranges from 1219 m near the lower of two tarns, to 2134 m on the highest peak. Steep rock faces and talus slopes characterize the upper 152 to 305 m of the mountains, in contrast to the gentle slopes of the Nahoni study area. Stands are located around the cirque in a region above wet meadows and below talus slopes (Fig. 4).

Both areas were reached by helicopter from Dawson, Y.T.

Geology

Nahoni Range

The Nahoni Range is part of the Porcupine Mountain Area, which is included by Bostock (1970) in the Eastern system of the Cordilleran Region. While detailed geological studies are presently unavailable for the Ogilvie River region, the stratigraphic succession for the smaller Brimston Mountain area has been determined on a preliminary

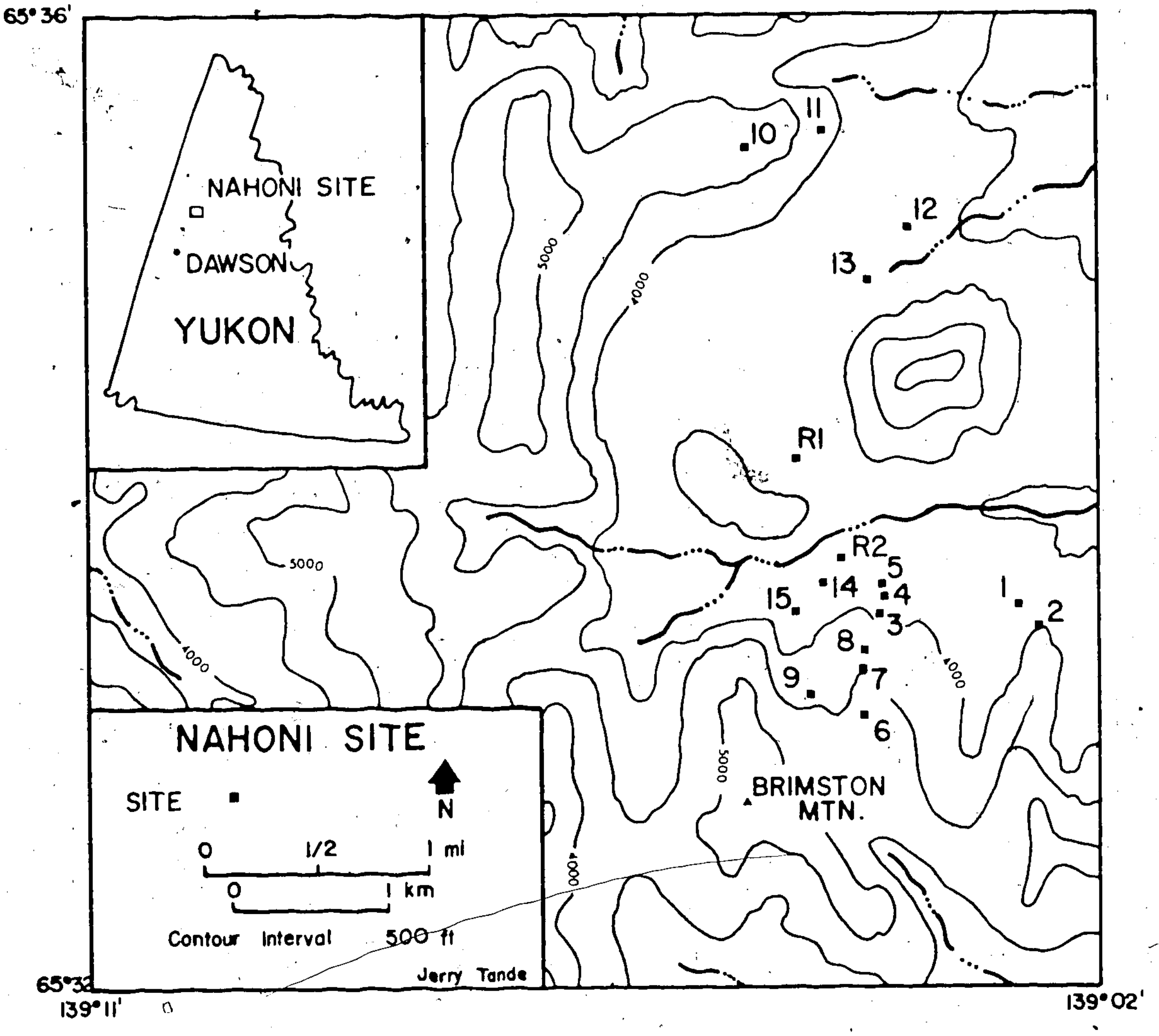

FIGURE 3. Location of stands in the Nahoni Range, Y.T.

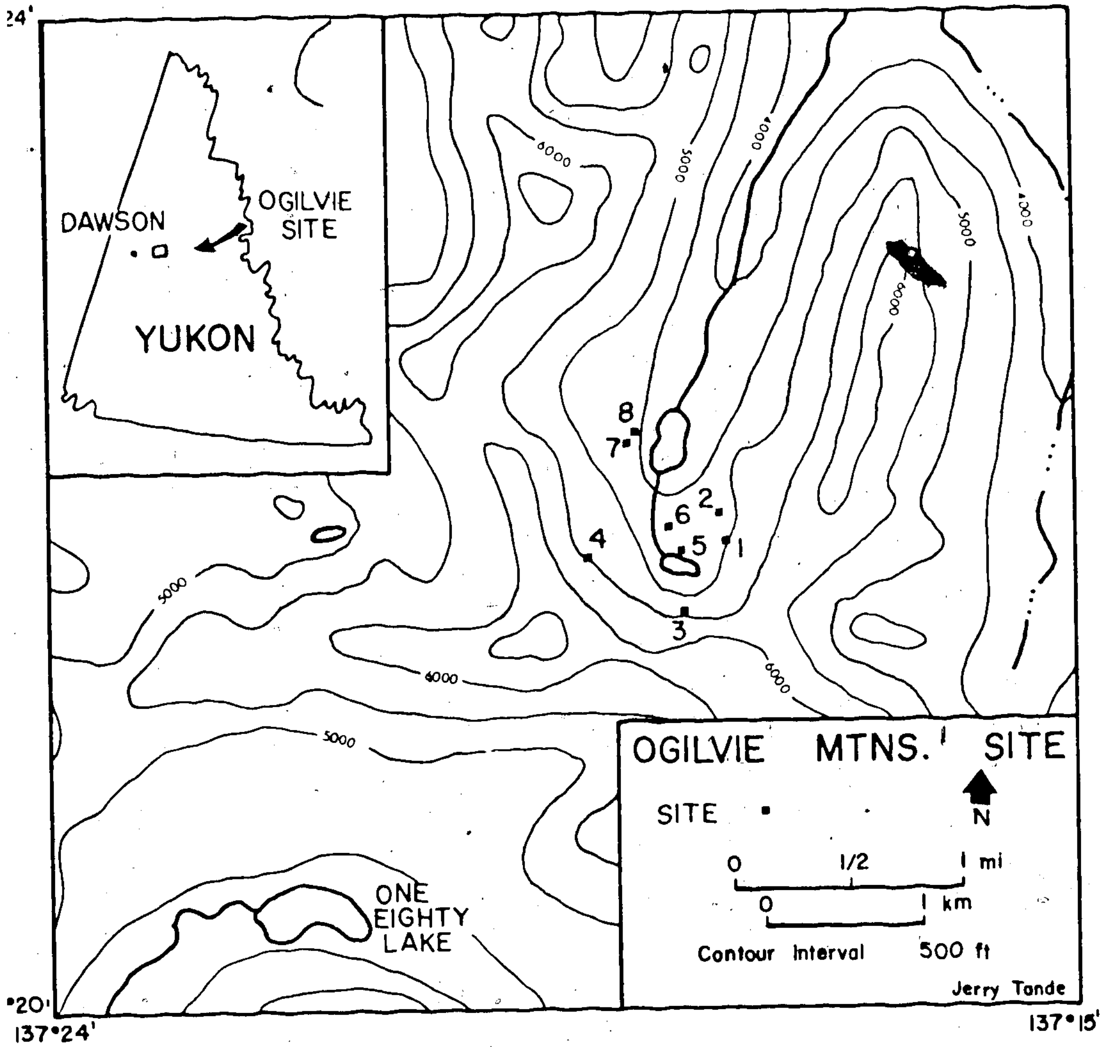

FIGURE 4. Location of stands in the Ogilvie Mountains, Y.T.

basis (D.K. Norris, pers. comm.).

The Hart River Formation occurs at lower elevations in the study area and consists of shale, limestone and dolomite with an unnamed shale at the base. Above this is the Ettrain Formation. It is a light grey, cliff-forming limestone which comprises the southern and eastern study area boundaries. Both formations are of Carboniferous age. The northern and western boundaries are light grey siliceous dolomite and limestone of Middle Devonian age. Such stratigraphic correlations are to be considered tentative until further studies are completed for this region.

Dendritic drainage patterns have developed in the Nahoni, and water from the study area flows east in streams which join a north-flowing tributary of the Whitestone River.

Ogilvie Mountains

The Ogilvie Mountains are part of the Northern Plateau and Mountain Area in the Interior Region of the Cordillera (Bostock 1970). The Ogilvies are separated from the Nahoni Range to the northwest by the broad valleys of the Ogilvie and Peel Rivers.

The geology of the cirque group including the study area has been documented by Green (1972). The rocks are Precambrian and Cambrian, and include: (1) gritty quartzite, sandstone, and quartz-pebble conglomerate; (2) black, maroon and green shales, and slates; (3) schistose quartzite, quartz chlorite schist, quartz-mica schist and phyllite; and (4) minor limestone and black chert. These outcrops characteristically form smooth ridges to about 2100 m, which are susceptible to frost action. The distinct mottled maroon and green shales are conspicuous from both air and ground.

Valley floors in the area are mapped as Quaternary age unconsolidated glacial and alluvial deposits (Green 1972).

The massif is drained by the Klondike River to the south via Officer and Davidson Creeks, and by the Middle Hart River to the north via Lake and Mouse Creeks. The study cirque drains north into a tributary of Lake Creek (Vernon and Hughes 1966).

Glacial History

Nahoni Range

The Nahoni study area lies within the unglaciated region of the Yukon (Bostock 1946). This large region exhibits very diverse terrain and is unified solely by the absence of glacial deposits (Hughes 1972).

Ogilvie Mountains

The glaciation sequence in the Yukon encompasses four advances of Cordilleran ice (Bostock 1966). These phases have been correlated with radiocarbon dates as follows: Nansen and Klaza in the early Pleistocene, more than 500,000 years B.P.; Reid in the early or pre-Wisconsin, 52,000 years B.P. or younger; and McConnell in the late

Wisconsin, 25,000-10,000 years B.P. (Rutter et al. 1976). Each subsequent advance was less extensive (Hughes 1972).

Ice advances in the Ogilvie Mountains have been documented by Vernon and Hughes (1966) and Ricker (1967), and have been correlated with Reid and McConnell ages (Hughes 1969, Hughes et al. 1972). During these periods, ice advanced in independent valley glacier systems, rather than in a continuous sheet of ice as occurred southward on the Yukon Plateau. Cordilleran ice sheet tongues extended northwestward along the Wind, Hart-Beaver and Middle Hart Valleys, and were joined by valley glacier ice from the eastern region of the Ogilvies (Hughes 1969).

The massif including the study area shows extensive glaciation of Reid age. South-facing cirques were not glaciated during the McConnell. However, the study area cirque and those on either side show evidence of recent glaciation (Hughes 1969, 1976 pers. comm.). Throughout the Ogilvie and Wernecke Mountains glaciation has been discontinuous, and markedly so in the last advance.

Rock glaciers were commonly formed in these mountains during Neoglaciation, 2,000-3,000 years B.P. (Vernon and Hughes 1966). Although none are present in the study cirque, several can be seen in the adjacent eastern valley and in the cirques across Lake Creek to the west (Vernon and Hughes 1966, Hughes 1969).

Patterned Ground

Patterned ground features are very common in both Yukon study areas. Sorted and nonsorted circles and stripes are found in the Nahoni area, with nonsorted stripes being most frequent in vegetated sites. Steps and gelifluction lobes are also evident and are better developed than in Alberta study areas. Hummocks are characteristic of many poorly drained sections of the Nahoni area.

Much of the Ogilvie cirque is not strongly patterned due to a predominance of wet meadows in the valley and extensive dry talus slopes above. In the intermediate zone slopes exhibit some sorted and unsorted stripes, and level areas have nonsorted circles and polygons. Whether ice is present in the depressions between nonsorted polygons is not known. Another feature in this area is a fellfield, patterned with sorted stone stripes.

Soils

No studies are known of soils from either Yukon area. Soils in the Nahoni Range have developed over bedrock from discontinuous felsenmeer with or without colluvium, or from extensive organic deposits (Hughes 1972). The better-drained Ogilvie area has fewer potential organic areas, and consists largely of glacial and alluvial materials over bedrock. Discontinuous permafrost is widespread in both areas (Brown 1967) although it was not investigated in the present study.

Climate

Few meteorological data exist for the Yukon study areas, therefore regional weather and climate must be ascertained from distant stations. Data from valley stations indicate that low annual precipitation and a wide temperature range characterize the region (Kendrew and Kerr 1955, Green 1972). Ricker (1967) tabulated meteorological data for Dawson (elev. 323.8 m) from 1901-1963, and elucidated trends of high relative summer precipitation and cold winter months. He designated this climate as Cold Snowy Forest (Dfc) due to winter dryness.

Meteorological records have been kept since 1966 at Mile 41 on the Dempster Highway (65°27'N; 138°13'W at 960 m) which are summarized in Table 2. Kojima (1973) also operated summer weather stations during 1972 and 1973 in the North Klondike River Valley along the Dempster Highway near Mile 41.

The highest station (1195 m) had a climate between Subarctic Tundra (ET) and Cold Snowy Forest (Dfc) in the Köppen system (Kojima 1973). The lowest station (740 m) was classified as Dfc, and the mean daily temperature difference between the two was 3.8°C. Virtually no frost-free period occurred in summer. Daily localized showers also characterized this area. The Nahoni Range lies north of Kojima's (1973) area, and may be in a region of Subarctic Tundra

TABLE 2. Meteorological summary for Mile 41, Dempster Highway Y.T. 1966-1973 (Kojima 1973).

Mean annual temperature °C	
	-8.9
Highest monthly mean temperature	
June	11.3
July	11.3
August	7.9
Total annual precipitation mm	
	428
Highest monthly mean precipitation	
August	60
July	47
February	39
June	38
October	38

rather than Cold Snowy Forest Climate (Ricker 1967).

Vegetation

Nahoni Range

The Nahoni Range lies south of arctic treeline in the Yukon, and has sufficient elevation to be largely above alpine treeline. The vegetation is characterized by cushion plants, dwarf shrubs and low-growing sedges, grasses and herbs.

At lower elevations *Salix alaxensis* lines the major stream banks in the study valley. The flood plain meadows are rich in herbs such as *Epilobium latifolium* and *Lupinus arcticus*. *Betula glandulosa*, *Rubus chamaemorus* and various *Salix* species are also found along streams.

Dwarf shrubs are common on better drained slopes, including *Arctostaphylos rubra*, *Cassiope tetragona*, *Empetrum nigrum*, *Ledum palustre*, *Rhododendron lapponicum*, *Salix arctica*, *S. reticulata* and *Vaccinium vitis-idaea*.

Dryas octopetala is characteristically found with *Carex misandra* in upland sites. Many herbs are also conspicuous, such as *Arnica frigida*, *Astragalus umbellatus*, *Boykinia richardsonii*, *Minuartia arctica* , *M. elegans*, *Oxytropis maydelliana*, *O. nigricans* ssp *bryophi*[illegible] *Pedicularis lanata*, *Potentilla biflora* and *Tofieldia coccinea*.

Few species are found with *Dryas octopetala* on the uppermost slopes. These include *Carex misandra*, *Chrysanthemum integrifolium*, *Minuartia elegans* and *Cardamine purpurea*.

Snowbeds are dominated by Cassiope tetragona and Dryas octopetala with some Salix reticulata. Wetlands are common on poorly drained soils, and several areas of Eriophorum vaginatum occur in standing water. Sphagnum species are associated with most wetland sites, and dominate wet slopes with Betula glandulosa.

Ogilvie Mountains

The Ogilvie study area is in a massif which is above alpine treeline. Much of the valley consists of gently sloping meadows with moderately well drained to poorly drained soils. Many herbs are common, such as Aconitum delphinifolium, Anemone narcissiflora, Lagotis glauca, Myosotis alpestris, Parrya nudicaulis, Polygonum bistorta, Sedum rosea, and Valeriana capitata. The wettest meadow sites are dominated by the liverwort Paludella squarrosa, and various bryophyte species. Snowbeds are like those of Nahoni areas.

Drier uplands are dominated by Dryas octopetala, with Campanula lasiocarpa, Carex microchaeta, Hierochloe alpina, Luzula multiflora, Salix arctica, and Vaccinium vitis-idaea as important secondary species.

Dry acidic slopes are conspicuously characterized by the moss Rhacomitrium lanuginosum, with Hierochloe alpina, Vaccinium vitis-idaea and extensive lichen cover. Very few species are represented at the highest vegetated slopes, including Dryas octopetala and Saxifraga flagellaris.

METHODS

Vegetation Sampling

The method of vegetation sampling used in this study was designed for rapid data collection in areas where field equipment was limited by helicopter capacity. Other sampling techniques for terricolous alpine lichen communities are described in Bryant and Scheinberg (1970) and Bird (1974a, 1974b). General alpine sampling methods can be found in Mueller-Dombois and Ellenberg (1974) and Eddleman et al. (1964).

In each study area slopes were selected for stand location after an initial ground reconnaissance. Airphotos were useful in examining general study areas, but were too small scale for stand selection. Random stand selection was undesirable since vegetation on different patterned areas was to be examined. Therefore, criteria for stand selection were primarily subjective, without preconceived bias (Mueller-Dombois and Ellenberg 1974).

A stand size of 30 x 5 m (150 m^2) was utilized. Although related studies have used larger stands (Slack 1971, Lee 1976), environmental and plant community heterogeneity over short distances precluded a larger stand size. Each stand was required to exhibit certain internal characteristics as follows:

1. to represent the variety of combinations of aspect, slope and moisture attributes within alpine areas;

2. to include distinct vegetation assemblages if not represented above;

3. to be internally homogeneous for all attributes above, with no area of 2 m^2 conspicuously different;

4. to exhibit no visible disturbance (e.g. squirrels or man) greater than 1 m^2 in area.

The stand location procedure initially required a random point on a downslope line to locate a perpendicular line. From this second line another random point was taken to crudely locate the top corner of the stand. However, habitat diversity did not often permit objective choice in stand placement due to the homogeneity requirement (#3 above). Subjective evaluation of stand location was therefore considered adequate for rapid descriptive sampling in the heterogeneous alpine environment.

A stratified random sampling system was used within each 30 x 5 m stand (Mueller-Dombois and Ellenberg 1974). In each stand, six lines 5 m long were established at 5 m intervals. Along each line the number of substrate types were noted and representatives of each type were numbered. Numbers from a random table were used to select the locations for two 10 x 40 cm quadrats per substrate type, per line. In some stands the number of quadrats per substrate was one per line, to test the validity of the lower sampling intensity. Substrates were thus sampled equally rather than proportionally to facilitate direct data comparisons. The selected sample substrate was usually wider than 10 cm, therefore another random number was used to locate the midpoint of the 10 cm quadrat side along the 5 m tape.

Quadrat size was determined by establishing species-area curves (Mueller-Dombois and Ellenberg 1974) for a dry-mesic alpine area on Prospect Mountain. Stands characteristically had two substrates, stone stripes and vegetated stripes, and each was sampled with a total of either six or twelve quadrats. The latter arrangement is hypothetically depicted in Fig. 5.

Some snowbed and meadow communities were too small to sample within a 30 x 5 m stand, so a 15 x 5 m stand size was used. This stand contained three lines, and four quadrats per line with no recognized substrate heterogeneity. Wet-mesic communities were usually encountered at a slope base, and those sampled extended at least 15 m along the base. Therefore, the long stand axis was located perpendicular rather than parallel to the slope.

The 15 x 5 m stand was also used for sampling small polygons and circle areas. Stands with circles were partitioned into two substrates to include circle centres and borders. An additional border substrate was designated for polygons, and all substrate units for both patterned features were sampled with six quadrats.

Fellfield sampling was carried out in one stand each

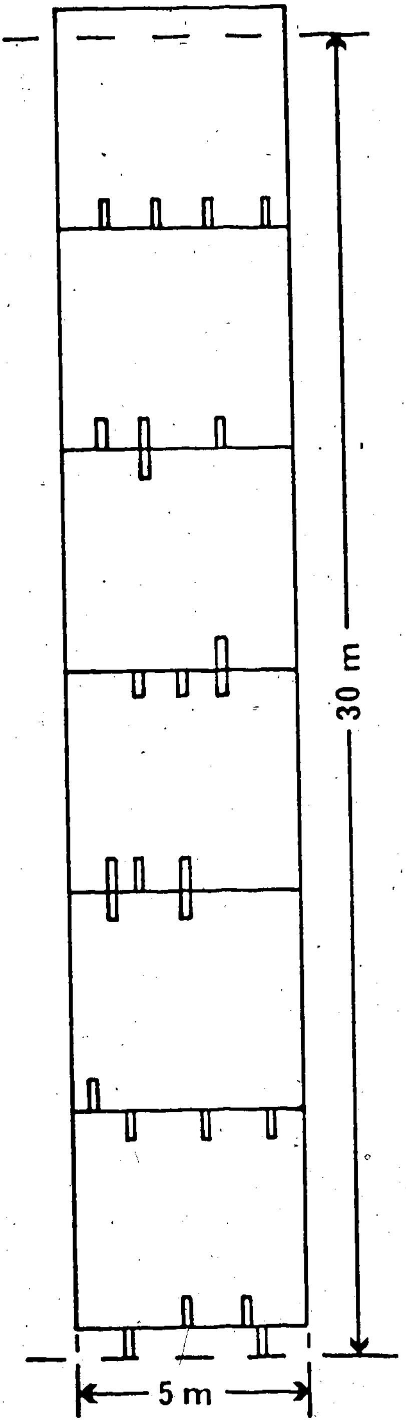

FIGURE 5. Representation of the 30x5m stand with quadrats randomly located on hypothetical substrates. Quadrat scale is approximate.

within the Divide and Ogilvie sites using twelve 10 x 10 cm quadrats centrally located on rocks. These quadrats were of maximum size for the rocks sampled, as larger ones would have eliminated 80% of the available rocks from sampling. Rock plots were located along the same stand lines as the terricolous lichen plots for the two stands. Other stands did not have rocks of sufficient sampling size.

Two Nahoni wetland sites were sampled using a 15 x 5 m stand. Species cover values were estimated for an entire stand or releve (Mueller-Dombois and Ellenberg 1974). These stands are designated R1 and R2 of the study area map (Fig. 3).

Data from the quadrats included a species list of all lichens, vascular plants and bryophytes; the estimated per-cent cover of these three groups separately; and combined cover as total vegetation. Cover of individual lichen and vascular plant species was also estimated as well as cover of rocks and bare soil. The cover estimation scale used was modified from that of Braun-Blanquet and of Daubenmire (Mueller-Dombois and Ellenberg 1974):

+ = present, less than 1%
1 = 1 - 5%
2 = 6 - 15%
3 = 16 - 30%
4 = 31 - 50%
5 = 51 - 75%
6 = 76 -100%.

Other attributes recorded were slope (degrees and aspect), elevation, position on slope, and conspicuous rock types. In each stand a list was compiled of plant species found which were not encountered in sampling. Characteristic stand features such as the dominant plant species and ground patterning were also noted. A minimum of six photographs per stand were taken from standardized viewpoints. Within the quadrats, evidence of disturbance and of lichen reproductive effort were recorded when present.

Voucher plant material was collected from the plots, and and from the surrounding areas. Nomenclature for vascular plants in Alberta follows Moss (1959), and Hulten (1968) and Porsild (1974) for additional Yukon species. Welsh (1967) and Wolf (1977) are used for Oxytropis and Minuartia, respectively. Bryophyte nomenclature follows Crum et al. (1973). A complete set of plant vouchers has been deposited in the herbarium of the University of Alberta (ALTA). Lichen specimens have also been deposited at the National Museum (CAN) and University of Calgary (UAC) herbaria.

Field work was carried out in Alberta during late June and mid-August 1975 and July 1976; the Yukon sites were sampled during July 1975.

Soils

A sample of surficial soil and rocks was taken centrally in each stand. Exposed soil was sampled rather than that underlying vegetation. These samples included the upper 4 cm of soil, since lichens were most likely to be in direct contact with this portion of the soil profile. Samples were screened through a 2 mm sieve, and dry color determined in daylight using a Munsell color chart.

Screened soils from 33 plots were analyzed for N, P, K, Na, pH, conductivity, free lime and sulfate, organic matter and texture by the Soils and Feed Testing Laboratory of Alberta Agriculture. The following methods were used:

(1) nitrogen (nitrate) extraction with water and $CuSO_4$-Ag_2SO_4 solution and determined by the Phenyldisulphonic Acid method;

(2) available phosphorus extraction with the modified Bray method of NH_4F-H_2SO_4 and determined by the combined nitric and vanadate molybdate colorimetric method;

(3) available potassium and sodium extracted with ammonium acetate and determined by flame photometry;

(4) pH and conductivity by a 1:2 soil-water extract with an electrode pH meter;

(5) free lime ($CaCO_3$) with 10% HCl;

(6) sulfate (SO_4) estimated from pH and conductivity using $BaCl_2$ to precipitate;

(7) aluminum and manganese extracted with $CaCl_2$ and read

directly on an atomic absorption spectrophotometer;
(8) organic matter and texture were estimated manually.

Lichen Identification

Lichen and moss specimens from each quadrat remained mixed in small paper collection bags until they were sorted and identified. This method of collection and storage traded field time for laboratory time, and also provided much better protection and padding for the lichen specimens. During the sorting, it was necessary to moisten and lightly press many of the macrolichen specimens to prevent further damage.

Several identification keys were necessary. The most useful keys for the study areas are by Imshaug (1957), Hale (1969) and Bird (1970), as well as those for the Great Slave Lake area (Thomson et al. 1969), Baffin Island (Hale 1954), and for the Alaskan Arctic Slope (Thomson, in press). Other sources for specific genera include <u>Alectoria</u> (Brodo and Hawksworth 1977), brown <u>Cetraria</u> (I. Karnefelt, pers. comm.), <u>Cladonia</u> (Ahti 1961, Thomson 1967, Bird and Marsh 1972), <u>Evernia</u> (Bird 1974c), <u>Hypogymnia</u> (Ohlsson 1973, Krog 1974), <u>Parmelia</u> (Bird and Marsh 1973a), <u>Peltigera</u> (Thomson 1950; M. Ostafichuk, pers. comm.), <u>Stereocaulon</u> (C.D. Bird, pers. comm), and <u>Umbilicaria</u> (Bird and Marsh 1973b).

Field identification was based upon morphological characters. Laboratory work permitted the use of chemical spot tests with standard reagents as follows:

P = paraphenylenediamene solution using Steiner's stable solution (Thomson 1967); also abbreviated PD.

K = 10-15% solution of potassium hydroxide crystals in water.

C = calcium hypochlorite powder in water; a stable substitute is sodium hypochlorite (commercial liquid bleach).

KC= an application of K followed immediately by an application of C.

I = 0.5 g iodine dissolved in 1.5 g potassium iodide with water (Duncan 1970), plus some alcohol or detergent to promote penetration.

CAT= chloramine-T powder mixed 5% in alcohol for each usage.

These reagents were applied to small thallus fragments using a micropipette, and the color reaction was noted (see Thomson (1967) for other chemical spot tests). The use of a longwave (3660 Å) ultraviolet lamp allowed sorting of species containing alectoronic, psoromic and squamatic acids. The low degree of chemical diversity in northern lichens did not warrant the use of thin-layer chromatography (TLC) as originally assumed.

Morphologically identical taxa with different chemistry were determined in the laboratory, and were designated by both species names (e.g. <u>Thamnolia subuliformis/vermicularis</u>). Where such taxa were allopatric, only one name is used.

Thin sections of apothecia were unnecessary for macrolichens encountered, with the exception of the genus Solorina. Since the majority of specimens were sterile, S. bispora, S. octospora, and S. saccata were placed under Solorina spp.

Extensive herbarium work at the Universities of Alberta and Calgary was required before and after fieldwork. Several lichenologists also verified my identifications (see Acknowledgements). Nomenclature follows Hale and Culberson (1970); the more recent treatments for genera listed above; and Brodo (1976), (Appendix A).

Vegetation Analyses

Introduction

The sampling program was designed to utilize cover values to indicate macrolichen species importance. In order to compare species assemblages and importance values on an intra- and interregional basis, indirect ordination was selected as the primary analysis technique.

In the indirect ordination procedure, the relationship of stands or samples are based upon vegetation similarity values (Bray and Curtis 1957). Indirect ordination may provide a more objective basis of interpretation than direct ordination when vegetation and environment relationships are unclear (Whittaker and Gauch 1973). Available environmental data can also be plotted on indirect ordinations to elucidate relationships. Strong correlations between environmental complex-gradients and vegetation will produce similar results when using either direct or indirect ordination techniques (Whittaker and Gauch 1973).

Indirect Bray-Curtis ordinations are also less susceptible to distortion under relatively high beta diversity when compared to the widely used principal components analysis, or PCA (Cottam et al. 1973). The latter technique has the advantage of objective definition of ordination axes, whereas Bray-Curtis ordination requires end point choices. Subjectivity of end point choice can be avoided by using the most dissimilar stands, as outlined by Bray and Curtis (1957, Mueller-Dombois and Ellenberg 1974). However, extremely dissimilar end stands may cause ecologically meaningless ordination clusters, necessitating a choice of alternative end stands (Cottam et al. 1973). Experimentation with different end stands is often advisable, and the final ordination is subjectively chosen as a result.

An objective technique for testing the validity of Bray-Curtis ordination is reciprocal averaging ordination or RA (Hill 1973, Gauch et al. 1977). This is an indirect, weighted-average ordination procedure which uses successive approximations to produce simultaneous species and stand ordinations. Reciprocal averaging is an eigenvector technique related to principal components analysis but it differs in the use of species ordinations to derive stand ordinations and vice versa. Species abundance in RA is also corrected so that two species with similar distributions in which one is rarer, have similar species scores (Hill 1973). The final order of stands and species is independent of the initial order, and is objectively derived (Gauch et al. 1977).

Advantages of RA include the accompanying species ordination (Hill 1973) and better stand ordination than PCA with high beta diversity (Gauch et al. 1977). Major floristic gradients are consistently arranged along the first axis, which can then be related to environmental factors (Gauch et al. 1977). Outlier stands are also readily detected in RA, which allows the elimination of such stands as end stand choices for other procedures such as Bray-Curtis ordination.

The combined use of reciprocal averaging and Bray-Curtis ordinations tends to minimize the disadvantages associated with each method alone, in addition to providing a species-stand table for use in community analyses.

Ordination

For analysis purposes, each substrate within a stand was recognized as a distinct sampling unit, or substrate unit, which contained an equivalent number of quadrats as all other units within the stand. For example, all stone stripe quadrats in a stand represented one substrate unit and all vegetation stripe quadrats were included in another.

Lichen and vascular plant species encountered in sampling were compiled and compared from all substrate units in the four study areas using Sørensen's (1948) coefficient of community as follows:

$$CC(j,k) = \frac{200(Sc)}{S_j + S_k}$$

where S_j and S_k are the total number of species in stands j and k; Sc is the total number of species common to both stands; and CC is coefficient of community. The initial use of CC elucidated floristically related groups which could then be analyzed quantitatively.

Cover values for all lichen and vascular plant species were tabulated using cover class midpoints as follows:

+ = 0 - 1	.5
1 = 1 - 5	3.5
2 = 6 - 15	10.5
3 = 16 - 30	23.0
4 = 31 - 50	40.5
5 = 51 - 75	63.0
6 = 76 - 100	88.0

In each substrate unit a mean species cover value was then calculated for each species, as well as the sum of the mean values of all species. Cover values for individual species were then transferred to IBM cards. Species were not included in the computer phases of analysis if they occurred in only one substrate unit with a total cover below .24%, as these represented very rare and infrequent species of uncertain ecological status.

All computer work was carried out at the University of Alberta Computer Centre on the IBM 360/67 computer. Analysis programs were obtained for the Cornell Ecology Programs

(CEP) assembled by Gauch (1973).

Initially a similarity matrix for macrolichens and vascular plants in each of the two study regions was calculated using the resemblance or distance matrix program (CEP #5). Separate matrices were obtained with coefficient of community (CC) and percentage similarity (PS) as follows:

$$PS(j,k) = \frac{200(w)}{P_j + P_k}$$

where P_j and P_k are the sums of quantitative values in stands j and k respectively; w is the sum of the lesser values for those species common to both j and k, and PS is percentage similarity (Bray and Curtis 1957).

The ~~most~~ dissimilar macrolichen substrate unit pairs were then chosen as end stands for a series of Bray-Curtis ordinations (CEP #4). End stand choice on the x-axis did not appear critical as similar results were obtained with several stand pairs. The final end stands were compared to those in reciprocal averaging ordination (CEP #20) of the same data set. Criteria for end stand selection on the y-axis are outlined in Mueller-Dombois and Ellenberg (1974).

All Bray-Curtis ordinations were based upon values for percent similarity. Unrelativized PS values are recommended for use with scaled cover values (Whittaker and Gauch 1973), and better stand separation occurred with these than with CC values. Reciprocal averaging ordinations were also constructed with PS for macrolichen and vascular plant data.

Plant Community Description

The species-stand tables from reciprocal averaging were modified to form differentiated tables (Mueller-Dombois and Ellenberg 1974, Whittaker 1975). These tables are organized to display groups of consant, rare, character- and differential-species within assemblages of similar stands. Constant species in this study are those which are found in more than 50% of all substrate units, with moderate to high cover values. Character-species and differential-species are restricted to certain stand groups and are used in this study to distinguish plant communities. Distributional centres define character-species, and distributional limits delineate differential-species (Whittaker 1975). High frequency values locate the species distribution in a stand group, within which the cover values may range from low to high. Rare species are low in both quantitative attributes, and are encountered in fewer than three substrate units per region with individual cover values below 1%.

The order of substrate units in all differentiated tables corresponds to the x-axis from reciprocal averaging ordination of macrolichen and vascular plant data. Similarity matrices of CC and PS values were inspected to determine which substrate units indicated dissimilarity between groups of internally similar substrate units. Character-species and differential-species were then established for these groups of substrate units.

The resulting species-stand groups on the differentiated tables were designated as communities. In each community, mean values of species cover and frequency were calculated from the included substrate units, and species were ranked in order of decreasing cover values. Two species with high cover and frequency were used to designate the communities, and three were used where distinction was otherwise unclear.

Diversity

The Shannon-Weaver (1949) index of diversity was calculated for all substrate units as follows:

$$H' = \sum_{i=1}^{S} p_i \ \ln p_i$$

where H' is diversity, p_i is the proportion of species i in the community of S species, and ln is the logarithm of base e. The components of this index, richness (S) and evenness (J) are also examined separately. Evenness was calculated as follows:

$$J = \frac{H'}{H'_{max}}$$

where H' is the Shannon-Weaver diversity index and H'_{max} = ln S (Pielou 1969).

Correlations between macrolichen cover, substrate pH, and diversity measures were tested with Spearman's Rank Correlation Coefficient (Sokal and Rohlf 1969). The T test for unequal variances (Sokal and Rohlf 1969) was used to detect differences within each of the above categories for different regions and areas.

RESULTS

Environmental Factors

In an effort to recognize the importance of plant-habitat interactions, the plant ecologist often uses environmental factors as indicators of plant species or community variability. Any given habitat factor relates to other interacting factors which can be collectively represented as complex-gradients (Whittaker 1975). The correlation of variability in communities and complex-gradients thus provides a first approximation of plant-habitat relationships.

Several environmental factors are assessed in the present study to detect such plant-habitat correlations for macrolichen species and species groups. Physical habitat factors are followed by vascular plant communities in order to establish an overall habitat context for interpretation of macrolichen data.

Moisture Regime

Field measurements of soil or atmospheric moisture were precluded by limited sampling time. Therefore, soil moisture regime was estimated subjectively (Table 3) on the basis of field observations and relevant literature on plant habitats (Kershaw and Rouse 1971 , Rouse and Kershaw 1973, Larson and Kershaw 1975a). Moisture assessment also required consideration of topographic influences on snow accumulation and time of snowmelt (Table 3).

A significant microhabitat trend is evident in several

TABLE 3. Characteristics of stands and substrate units in Prospect (P), Divide (D), Nahoni (N) and Ogilvie (O) areas.

Stand	Substrate Units		M	S	T	Elev	Sl	A
P 1	P1	vegetation stripes	2	2	2	2121	26	NNW
	SP1	nonsorted stone stripes	1	2	2	2121	26	NNW
2	P2	spotted tundra vegetation	1	1	1	2210	22	E
	SP2	spotted tundra stripes	1	1	1	2210	22	E
3	P3	spotted tundra vegetation	1	1	1	2210	22	E
	SP3	spotted tundra stripes	1	1	1	2210	22	E
4	P4	vegetation stripes	3	2	2	2149	31	SE
	SP4	nonsorted stone stripes	1	2	2	2149	31	SE
5	P5	vegetation stripes	4	2	2	2137	34	ESE
	SP5	nonsorted stone stripes	1	2	2	2137	34	ESE
6	P6	meadow vegetation	4	3	3	2073	19	NW
	SP6	nonsorted stone stripes	2	3	3	2073	19	NW
7	P7	meadow vegetation	5	5	5	2042	19	NNW
8	P8	vegetation stripes	2	2	2	2134	24	NW
	SP8	nonsorted stone stripes	1	2	2	2134	24	NW
9	P9	vegetation stripes	4	4	4	2042	22	NNW
	SP9	nonsorted stone stripes	2	4	4	2042	22	NNW
10	P10	vegetation stripes	4	4	5	2100	26	N
	SP10	nonsorted stone stripes	2	4	5	2100	26	N
11	P11	vegetation stripes	4	3	3	1974	22	NW
	SP11	nonsorted stone stripes	1	3	3	1974	22	NW
11	21							
D 1	D1	vegetation stripes	5	5	5	2176	8	W
	SD1	sorted stone stripes	1	5	5	2176	8	W
2	D2	vegetation margins	4	3	3	2115	5	W
	SD2	nonsorted stone circles	1	2	3	2115	5	W
3	D3	fellfield vegetation	3	2	2	2134	16	S
4	D4	vegetation stripes	4	5	4	2134	8	NW
	SD4	nonsorted stone stripes	2	5	4	2134	8	NW
5	D5	vegetation stripes	3	2	2	2085	12	NW
	SD5	nonsorted stone stripes	1	2	2	2085	12	NW
6	D6	snowbed vegetation	6	6	5	2182	5	S
6	10							
N 1	N1	vegetation stripes	5	5	5	1119	18	W
	SN1	nonsorted stone circles	2	5	5	1119	18	W
2	N2	snowbed vegetation	6	6	6	1176	25	N
3	N3	vegetation stripes	4	3	2	1183	32	W
	SN3	nonsorted stone stripes	3	3	2	1183	32	W
4	N4	continuous vegetation	4	4	3	1158	22	WNW
5	N5	continuous vegetation	5	5	6	1128	12	NW
6	N6	vegetation stripes	1	2	2	1390	16	NW
	SN6	nonsorted stone stripes	1	2	2	1390	16	NW
7	N7	vegetation stripes	4	3	2	1349	29	NNW
	SN7	nonsorted stone stripes	1	3	2	1349	29	NNW
8	N8	vegetation stripes	2	2	2	1311	22	NNW
	SN8	nonsorted stone stripes	1	2	2	1311	22	NNW

TABLE 3. Continued.

Stand	Substrate Units		M	S	T	Elev.	Sl	A
N 9	N9	vegetation stripes	2	2	2	1289	29	W
	SN9	nonsorted stone stripes	1	2	2	1289	29	W
10	N10	vegetation nets	1	1	1	1402	5	SSW
	SN10	nonsorted stone circles	1	1	1	1402	5	SSW
11	N11	vegetation stripes	2	2	2	1256	15	E
	SN11	sorted stone stripes	1	2	2	1256	15	E
12	N12	vegetation nets	1	1	1	1167	5	S
	SN12	nonsorted stone circles	1	1	1	1167	5	S
13	N13	slate outcrop vegetation	1	3	2	1143	15	S
14	N14	snowbed vegetation	6	6	6	1082	8	N
15	N15	vegetation nets	2	2	2	1112	5	NW
	SN15	nonsorted stone circles	1	2	2	1112	5	NW
P1		shrub wetland	6	6	6	1067	16	NNE
P2		tussock wetland	6	6	6	1052	5	NW
17	27							
O 1	O1	vegetated outcrop	2	1	1	1521	22	SW
	SO1	nonsorted stone stripes	1	1	1	1521	22	SW
2	O2	fellfield vegetation	2	1	1	1463	22	SW
3	O3	vegetated outcrop	2	2	3	1615	23	N
4	O4	meadow vegetation	4	4	4	1676	30	E
5	O5v	frost crack vegetation	6	6	6	1417	0	S
	O5b	polygon border vegetation	5	6	6	1417	0	S
	O5c	polygon centre	4	6	5	1417	0	S
6	O6	snowbed vegetation	5	6	6	1420	12	N
7	O7	vegetated outcrop	2	2	2	1379	13	NE
8	O8	vegetated outcrop	5	5	4	1376	13	NE
8	11							

Categories

M = moisture: (1) dry; (2) dry-mesic; (3) mesic-dry; (4) mesic; (5) mesic-wet; (6) wet.

S = snow cover: (1) very light; (2) light; (3) light-moderate; (4) moderate; (5) moderate-heavy; (6) heavy.

T = snowmelt: (1) very early; (2) early; (3) early mid-season; (4) mid-season; (5) late mid-season; (6) late.

Elev = elevation in meters.

Sl = degrees slope.

A = aspect.

stands in which vegetated substrate units are much moister then corresponding stripe substrate units (Table 3). In most of these stands the snow estimates remain the same, which suggests that the drier microhabitat is a direct result of continued disturbance from frost action.

Soil

Quantitative data for soil characteristics are compiled in Table 4. Soil pH was the most variable factor assessed, ranging from 3.9 (Ogilvie) to 8.0 (Prospect). The pH values of acidic soils from the Ogilvie and Divide stands were significantly different ($P<.05$) from those of basic soils in Nahoni and Prospect stands (Table 5). Significant differences were not found between Ogilvie and Divide soils nor between Nahoni and Prospect soils. Therefore, within each region there were comparable acidic and basic substrates.

Values for nitrogen were generally low (Table 4) and may have been significantly altered by wetting and drying of many of the samples during prolonged wet field conditions. Phosphorus also was present in low amounts, while potassium values were moderate to high. The test for phosphorus may not actually indicate biologically available amounts, because this substance can be altered rapidly under field conditions (Brady 1974). Potassium is probably not limiting to growth except in the highly basic soils where calcium carbonate dominates the exchange complex. The

TABLE 4. Soil chemical characteristics for stands in Prospect (P), Divide (D), Nahoni (N) and Ogilvie (O) areas.

Stand		pH	C^1	Soil Nutrients ppm					T^2
				N	P	K	Al	Mn	
P	1	7.9	0.2	3.5	2.0	38.0	-	-	3
	2	8.0	0.3	2.5	2.0	59.0	-	-	1
	3	8.0	0.2	3.0	1.0	63.5	-	-	2
	4	8.0	0.3	4.5	1.0	48.5	-	-	2
	5	7.9	0.3	3.0	0.5	65.0	-	-	2
	6	7.0	0.1	0.5	10.0	113.0	-	-	3
	7	7.6	0.4	3.5	6.0	93.5	-	-	6
	8	7.9	0.2	4.0	0.5	57.0	-	-	2
	9	7.9	0.3	4.5	1.0	58.5	-	-	6
$\bar{X}$		7.8	0.3	3.2	2.7	66.2	-	-	-
D	1	5.7	0.2	1.5	12.5	117.5	-	-	6
	2	4.8	0.2	1.0	3.0	95.0	4.8	9.8	6
	3	5.4	0.1	1.0	4.0	74.5	2.0	4.4	2
	4	6.2	0.4	19.5	18.5	132.0	-	-	3
	5	7.3	0.4	7.5	2.5	107.0	-	-	6
$\bar{X}$		5.9	0.3	6.1	8.1	105.2	-	-	-
N	1	7.0	0.7	3.5	4.5	205.5	-	-	6
	3	7.2	0.6	13.0	2.5	155.0	-	-	6
	4	6.9	0.7	7.0	3.5	139.0	-	-	6
	5	4.9	0.6	0.5	5.0	288.5	-	-	6
	6	6.8	1.5	25.0	100+	120.5	-	-	6
	7	6.5	0.4	4.5	3.0	38.5	-	-	6
	8	7.1	0.5	6.5	3.5	86.5	-	-	6
	9	7.4	0.8	10.5	4.5	209.5	-	-	6
	10	7.5	0.5	12.5	0.0	44.0	-	-	6
	11	7.9	0.6	12.0	0.0	42.5	-	-	3
	14	6.0	0.5	0.5	8.0	85.0	-	-	6
	15	8.0	0.4	4.0	0.0	57.0	-	-	3
$\bar{X}$		6.9	0.6	8.3	11.2	122.6	-	-	-
O	1	3.9	1.8	50+	6.5	106.0	49.4	10.0	2
	3	5.5	0.9	20.5	14.5	132.5	2.2	8.4	6
	4	5.5	0.3	2.5	4.0	73.5	-	-	6
	5	5.1	0.1	2.5	0.5	60.0	2.6	9.2	3
	6	5.1	0.1	0.5	1.5	41.0	3.6	11.6	1
	8	4.2	0.1	0.5	0.5	41.0	56.4	10.2	2
$\bar{X}$		4.9	0.6	12.8	4.6	75.7	-	-	-

C^1 = conductivity (mmhos).

T^2 = texture: (1) very coarse; (2) coarse; (3) medium; (4) fine; (5) very fine; (6) organic, peaty.

TABLE 5. Substrate pH values compared for Prospect, Divide, Nahoni and Ogilvie areas using the Mann-Whitney U test (Sokal and Rohlf 1969).

Area	Number Samples	Sample Mean	P	D	N
Prospect	9	7.8	-		
Divide	5	5.9	**	-	
Nahoni	13	7.0	NS	*	-
Ogilvie	6	4.9	***	NS	***

* = P .05
** = P .01
*** = P .001
NS = no significant difference

values for nitrogen and phosphorus were similar to those found in other alpine areas (Hrapko 1970, Kuchar 1975) although potassium values in the present study were higher.

Values for aluminum and manganese were obtained only for soils with a pH value below 5.5. These nutrients become increasingly available to plants with decreasing pH, and can be toxic to some species at levels such as those in Ogilvie stands 1 and 8.

Sodium, organic matter and free lime (CaCO3) were estimated qualitatively. Sodium was low in all samples; likewise, conductivity values indicated very low amounts of salts. Free lime was only present where pH exceeded 7.6, and was then found in moderate quantities. Organic matter was rated as medium for Prospect and Ogilvie soils, and was high in Divide and Nahoni soils. These high values were also correlated to the texture categories (Table 4).

Vascular Plant Vegetation

Introduction

The vascular plant vegetation of the study areas was assessed in order to characterize the plant communities. The same quadrats and cover scale were used for estimating both lichen and vascular plant cover in order to maintain an efficient sampling procedure. The sampling intensity was therefore low for vascular plants (Mueller-Dombois and Ellenberg 1974) which resulted in an underrepresentation of species with low-moderate cover and (or) frequency.

Characteristic vascular plant species with relatively high cover and frequency values were thus emphasized in community designation and description.

Regional Results

A total of 159 species from 28 plant families were encountered in the alpine areas studied (Appendix B). These taxa were found in areas of measurable lichen abundance, which excluded most hydric sites an[illegible]ne meadows. Species data are therefore biased toward upland communities.

Vascular plant similarity values for the four study areas are compared in Table 6. The number of species used is low since these represent quantitatively sampled species. Areas within each major region are more closely related, regardless of local environmental factors. Also, vegetation in Prospect and Divide areas is more similar to that in Nahoni rather than that in Ogilvie areas.

Alberta

Vascular plant species in Prospect and Divide substrate units have been arranged into rare, constant, character- and differential-species groups (Table 7). Each of the four substrate unit groups is represented by species in the above categories.

The order of substrate units from left to right (Table 7) represents coincident complex-gradients of increasing moisture, and decreasing substrate pH. The first substrate

TABLE 6. Percent similarity va[illegible] for vascular plant vegetation in the four s[illegible] areas based upon Sørensen's coefficient of comm[illegible]

	Prospect	Divide	Nahoni
Ogilvie	15	18	45
Nahoni	28	21	
Divide	54		

Number of species tested	
Ogilvie	24
Nahoni	43
Divide	42
Prospect	44

Species total = 99

TABLE 7. Differentiated table for vascular plant vegetation from Prospect (P) and Divide (D) areas. Stand order and scaled abundance values (+ to 9) are derived from reciprocal averaging ordination.

	1	2	3	4	
	[illegible]	[illegible]	[illegible]	[illegible]	
CHARACTER AND DIFFERENTIAL SPECIES	+-+------	--------	----------	----	1 Carex petricosa
	+-+-+----	--------	----------	----	2 Oxytropis campestris
	-+++-----	--------	----------	----	3 Astragalus alpinus
	----++-+-	+-------	----------	----	4 Silene acaulis
	-----+-+-	--------	----------	----	5 Salix alaxensis
	----+--+-	+--+++-+	----------	----	6 Hedysarum mackenzii
	-----+---	+-----+-	-------+--	----	7 Pedicularis lanata
	---------	----+---	--+-------	----	8 Solidago multiradiata
	---------	----++--	+++-------	----	9 Festuca ovina[1]
	---------	--------	-+--+-----	----	10 Smelowskia calycina
	---------	--------	-+--+-----	----	11 Zygadenus elegans
	---------	----+---	----+-----	----	12 Aster alpinus
	---------	----++--	-----+----	----	13 Poa spp.
	---------	1------1	-2--------	----	14 Betula glandulosa
	---------	+------+	--------+-	----	15 Pyrola grandiflora
	-------+-	----++-+	--+--+-+-	----	16 Pedicularis capitata
	---------	----++--	--+--+-+-	----	17 Equisetum scirpoides
	---+--+++	--+-++--	-+---1---	----	18 Carex nardina
	---------	--------	-----1---	----	19 Carex misandra
	----+----	++------	--+--+-++	----	20 Kobresia bellardii
	---------	------+-	----+-+---	----	21 Minuartia sp.
	---------	------+-	++-----+-	--+-	22 Saxifraga tricuspidata
	---------	--------	---+-----+	--+-	23 Potentilla diversifolia
	---------	--------	--+-+--1-	---+	24 Dryas octopetala
	---------	----+---	++-+-1--2	--+-	25 Hedysarum alpinum
	---------	----+---	-+-+-1++2	--1+	26 Salix arctica
	---------	--------	----+--+-	-+2+	27 Artemisia norvegica
	---------	--------	----------	-+2-	28 Trisetum spicatum
	---------	-------+	----------	+--+	29 Festuca baffinensis
	---------	--------	+---------	---+	30 Minuartia rossii
	---------	--------	----------	---2	31 Cassiope tetragona
	---------	--------	----------	---2	32 Phyllodoce glandulifera
CONSTANT	-----++++	+-++++1+	++----+--	+---	33 Oxytropis podocarpa
	+++--++++	++++++-+	----------	+---	34 Saxifraga oppositifolia
	+-+----+-	++-+----	+++++--+-	--+-	35 Androsace chamaejasme
	++1+11+1+	1++1--++	--+-+-++-	+---	36 Carex rupestris
	+6797+75+	5+++6+58	+2++33++2	--+-	37 Dryas integrifolia
	---+++++-	+--+++1+	+++++++11	++++	38 Polygonum viviparum
	-------++	+--+++++	--+-++++-	++++	39 Salix nivalis
RARE	+--------	--------	----------	----	40 Potentilla fruticosa
	----+----	--------	----------	----	41 Lychnis apetala
	----+----	--------	----------	----	42 Antennaria alpina
	---------	+-------	----------	----	43 Tofieldia pusilla
	---------	+-------	----------	----	44 Arctostaphylos rubra
	---------	--------	-+--------	----	45 Erigeron humilis
	---------	--------	-+--------	----	46 Arnica alpina
	---------	--------	-+--------	----	47 Potentilla nivea
	---------	-----+--	----------	----	48 Stellaria monantha
	---------	--------	----+-----	----	49 Bromis inermis[2]
	---------	--------	----+-----	----	50 Campanula rotundifolia
	---------	--------	-------+-	----	51 Pedicularis flammea
	---------	--------	---------+	----	52 Pedicularis groenlandica
	---------	--------	---------+	----	53 Erigeron perigrinus
	---------	--------	----------	+---	54 Gentiana prostrata
	---------	--------	----------	-+--	55 Carex atrosquama
	---------	--------	----------	---+	56 Antennaria lanata
	---------	--------	----------	---+	57 Sibbaldia procumbens

[1] F. ovina var. brevifolia
[2] B. inermis var. pumpellianus

unit group includes the driest sites on Prospect Mountain, and the second group contains dry to dry-mesic habitats. Values of substrate pH correspondingly shift from 7.9-8.0 in group 1, to 7.3-8.0 in the second group.

The third substrate unit group consists primarily of Divide sites with a minor component from neutral-acidic and mesic sites from Prospect. Complex-gradients of moisture and pH overlap substantially in this group because the sandstone strata in acidic areas are better aligned for moisture retention (W. Kilby, pers. comm.).

Substrate units in the fourth group represent the most acidic and mesic-wet conditions in the Alberta study sites.

Four vascular plant communities have been recognized which correspond to the substrate unit groups on the differentiated table. These are: (1) *Dryas integrifolia - Carex rupestris*, (2) *Dryas integrifolia - Oxytropis podocarpa - Salix nivalis*, (3) *Dryas integrifolia - Hedysarum alpinum - Androsace chamaejasme*, and (4) *Salix nivalis - Artemisia norvegica*.

(1) *Dryas integrifolia - Carex rupestris*

Dryas integrifolia attains its highest mean cover value in this community, and is also the most dominant species (Table 8). *Carex rupestris* and *Saxifraga oppositifolia* are frequent but do not have particularly high cover values. Medium frequencies are found in *Oxytropis podocarpa* and *Carex nardina*.

TABLE 8. Vascular plant species in the *Dryas integrifolia - Carex rupestris* community (#1) in Alberta; mean cover, frequency (fre), and cover value range in 9 substrate units.

Species	Cover	Fre	Cover range
Dryas integrifolia	30.40	89	2.00-60.08
Carex rupestris	6.16	89	1.00-12.79
Carex nardina	1.30	44	.50- 6.25
Oxytropis campestris	1.04	33	1.27- 5.58
Saxifraga oppositifolia	.93	78	.50- 1.95
Hedysarum mackenzii	.60	11	5.37
Astragalus alpinus	.56	33	.50- 2.75
Oxytropis podocarpa	.52	44	.66- 2.43
Androsace chamaejasme	.32	22	.47- 2.41
Polygonum viviparum	.23	33	.37- 1.08
Potentilla fruticosa	.14	11	1.27
Kobresia bellardii	.12	11	1.12
Silene acaulis	.10	22	.25- .68
Salix nivalis	.10	22	.39- .50
Carex petricosa	.10	22	.36- .50
Pedicularis lanata	.07	11	.62
Salix alaxensis	.05	11	.43
Antennaria alpina	.03	11	.25

Two species groups in this community reflect differences in north and south aspect. Characteristic species in north-facing stands (P1, P8) include *Pedicularis lanata*, *P. capitata*, *Hedysarum mackenzii*, *Salix alaxensis*, *Silene acaulis* and *Oxytropis podocarpa*. South-facing stands (P2-P5) are represented by *Astragalus alpinus*, *Oxytropis campestris*, *Carex petricosa*, *Antennaria alpina*, *Lychnis apetala* and *Potentilla fruticosa*. Since the dominant species are consistent within this community, the substrate unit similarity values are not significantly affected by these species group.

(2) Dryas integrifolia - Oxytropis podocarpa - Salix nivalis

Communities 2 and 3 have a core group of character-species extending from *Kobresia bellardii* (#13) to *Solidago multiradiata* (#25) on the differentiated table (Table 7). North-facing stands include *Pedicularis lanata* and *Hedysarum mackenzii*, as in the first community.

The most frequent species in this community type are *Dryas integrifolia*, *Oxytropis podocarpa*, *Saxifraga oppositifolia*, *Polygonum viviparum* and *Salix nivalis* (Table 9). Mats of *D. integrifolia* are dominant, with all other species having relatively low cover values.

The greater species richness of this community compared to the first is attributed to the more mesic substrate conditions in representative substrate units. Most of these stands have minor topographic relief along stone

TABLE 9. Vascular plant species in the *Dryas integrifolia - Oxytropis podocarpa - Salix nivalis* community (#2) in Alberta; mean cover, frequency (fre), and cover value range in 8 substrate units.

Species	Cover	Fre	Cover range
Dryas integrifolia	26.33	100	2.29-60.91
Carex rupestris	3.17	50	.50-10.04
Oxytropis podocarpa	2.89	88	.25-10.41
Betula glandulosa	2.45	25	9.08-10.50
Polygonum viviparum	1.97	75	.50- 9.50
Hedysarum mackenzii	1.45	50	.54- 7.25
Carex nardina	1.15	38	.68- 5.50
Saxifraga oppositifolia	.84	88	.25- 1.87
Hedysarum alpinum	.77	13	6.12
Salix nivalis	.63	75	.29- 1.40
Pedicularis capitata	.41	38	.58- 1.45
Kobresia bellardii	.37	25	.87- 2.08
Poa spp.	.36	25	1.12- 1.79
Androsace chamaejasme	.29	38	.50- .79
Festuca baffinensis	.28	13	2.25
Aster alpinus	.14	13	1.08
Saxifraga tricuspidata	.13	13	1.00
Minuartia sp.	.13	13	1.00
Arctostaphylos rubra	.11	13	.87
Pyrola grandiflora	.11	13	.37
Pedicularis lanata	.09	25	.25- .50
Equisetum scirpoides	.06	25	.25
Salix arctica	.06	13	.50
Festuca ovina var. brevifolia	.06	13	.50
Stellaria monantha	.05	13	.37
Silene acaulis	.03	13	.25
Tofieldia pusilla	.03	13	.25

and vegetation stripes which enhances mesic conditions.

(3) Dryas integrifolia - Hedysarum alpinum - Androsace chamaejasme

Dryas integrifolia is less dominant in this community and other species have correspondingly higher cover values (Table 10). Higher frequencies are found in Polygonum viviparum, Salix arctica, Androsace chamaejasme, Hedysarum alpinum, and S. nivalis. Of these, two herbs A. chamaejasme and H. alpinum characterize and distinguish this community type. Also H. alpinum is particularly important in the small subgroup of D1, D4 and D5.

Dryas octopetala is encountered in three Divide substrate units, presumably due to a preference for acidic or mesic conditions or a combination of these. This species is also found on Prospect, restricted to small patches with late snowmelt.

(4) Salix nivalis - Artemisia norvegica

Substrate units in the fourth community exhibit similar species composition and relative species importance to those in community 3, especially to the subgroup of D1, D4 and D5 (Table 7). The major difference is the reduction in frequency and cover of Dryas integrifolia, which otherwise dominates all the plant communities in this region.

The most distinct character-species is Artemisia norvegica (Table 11). Salix nivalis and Polygonum viviparum

TABLE 10. Vascular plant species in the *Dryas integrifolia - Hedysarum alpinum - Androsace chamaejasme* community (#3) in Alberta; mean cover, frequency (fre), and cover value range in 4 substrate units.

Species	Cover	Fre	Cover range
Dryas integrifolia	13.03	100	.50-26.66
Polygonum viviparum	4.67	89	.50-12.58
Salix arctica	3.72	67	.50-15.82
Hedysarum alpinum	3.57	56	.50-16.58
Salix nivalis	3.05	56	.50- 7.33
Betula glandulosa	1.84	11	16.58
Dryas octopetala	1.45	33	2.25-10.58
Carex rupestris	1.38	44	.58- 4.58
Oxytropis podocarpa	1.21	33	3.33- 4.00
Carex misandra	1.20	11	10.83
Carex nardina	1.17	22	1.00- 9.50
Androsace chamaejasme	.97	67	.50- 2.75
Kobresia bellardii	.86	33	.50- 6.08
Festuca ovina var. brevifolia	.73	33	.58- 4.00
Saxifraga tricuspidata	.67	33	1.00- 2.75
Pedicularis capitata	.54	33	1.00- 2.75
Artemisia norvegica	.48	22	.50- 3.83
Equisetum scirpoides	.39	33	.50- 1.00
Potentilla nivea	.25	11	2.25
Poa spp.	.19	11	1.75
Minuartia sp.	.17	22	.50- 1.00
Smelowskia calycina	.13	22	.58
Potentilla diversifolia	.12	22	.50- .58
Zygadenus elegans	.11	22	.50
Aster alpinus	.07	11	.66
Campanula rotundifolia	.06	11	.58
Pedicularis lanata	.06	11	.58
Arnica alpina	.06	11	.50
Bromus inermis var. pumpellianus	.06	11	.50
Erigeron humilis	.06	11	.50
Erigeron perigrinus	.06	11	.50
Minuartia rossii	.06	11	.50
Pedicularis flammea	.06	11	.50
Pedicularis groenlandica	.06	11	.50
Pyrola grandiflora	.06	11	.50
Solidago multiradiata	.06	11	.50

TABLE 11. Vascular plant species in the *Salix nivalis - Artemisia norvegica* community (=4) in Alberta; mean cover, frequency (fre), and cover value range in 4 substrate units.

Species	Cover	Fre	Cover range
Artemisia norvegica	6.13	75	.50-22.58
Phyllodoce glanduliflora	5.48	25	21.91
Cassiope tetragona	5.33	25	21.31
Trisetum spicatum	4.19	50	.50-16.25
Salix arctica	4.00	50	2.25-13.75
Polygonum viviparum	2.28	100	.87- 5.50
Salix nivalis	2.05	100	.50- 2.79
Carex rupestris	1.06	25	4.25
Dryas integrifolia	.88	25	3.50
Potentilla diversifolia	.69	25	2.75
Antennaria lanata	.57	25	2.29
Festuca baffinensis	.53	50	1.00 -1.12
Hedysarum alpinum	.44	25	1.75
Saxifraga tricuspidata	.44	25	1.75
Oxytropis podocarpa	.38	25	1.50
Androsace chamaejasme	.25	25	1.00
Gentiana prostrata	.15	25	.58
Carex atrosquama	.12	25	.50
Minuartia rossii	.07	25	.29
Sibbaldia procumbens	.07	25	.29
Dryas octopetala	.06	25	.25

exhibit 100% frequency, and can be considered as character-species for this community.

Trisetum spicatum is found as a differential-species in this community. Other species include Phyllodoce glanduliflora and Cassiope tetragona from a snowbed site. These were not intermixed; rather C. tetragona was at the base of the snowbank and P. glanduliflora extended out from the edge of the Cassiope mat. Two rare species also restricted to this stand are Sibbaldia procumbens and Antennaria lanata.

The inclusion of species-poor SP9 in this community is due largely to the absence of D. integrifolia. Otherwise, the presence of Carex rupestris, Saxifraga oppositifolia, and Oxytropis podocarpa suggest that its affinities are with the Dryas integrifolia - Carex rupestris community.

Yukon

The differentiated table for the Yukon vascular plant vegetation is divided into three substrate unit groups (Table 12). As in the corresponding Alberta data (Table 7), the high degree of species-stand overlap is probably due to the relative overrepresentation of common species.

Substrate unit group 1 consists of all Ogilvie sites except 03 and 04, with two additional mesic-wet Nahoni sites. Moisture regime is variable within this assemblage and substrate pH is acidic in all cases.

The second group represents more uniformly mesic-wet conditions and is predominantly located in Nahoni sites.

TABLE 12. Differentiated table for vascular plant vegetation from Nahoni (N) and Ogilvie (O) areas. Stand order, and scaled abundance values (+ to 9) are derived from reciprocal averaging ordination.

	[illegible]	[illegible]	[illegible]		
CHARACTER AND DIFFERENTIAL SPECIES	3++--------	---------	---------------	1	Hierochloe alpina
	-+-+-------	---------	---------------	2	Empetrum nigrum
	-53----6-2+	-3+1--+--	---------------	3	Cassiope tetragona
	2+3+1+++1++	+--------	---------------	4	Vaccinium vitis-idaea
	-123+12-1--	--+-+1+--	---------------	5	Carex microchaeta
	--+++++-+++	--++++-++	---------------	6	Salix arctica
	---++++-+--	---------	---------------	7	Campanula lasiocarpa
	---+--1+---	-----+---	---------------	8	Poa spp.
	-+--+---+--	-----+---	---------------	9	Luzula multiflora
	-------+---	----+----	---------------	10	Betula glandulosa
	--------+--	---------	---------------	11	Ledum palustre
	-------+---	---++--+-	--+------------	12	Pedicularis capitata
	-------+---+	---++2-++	---------------	13	Salix reticulata
	-------+-+-	---2+--++	----------+----	14	Rhododendron lapponicum
	-------+-+-	+--+----+-	---------------	15	Vaccinium uliginosum
	-----------	1---1----	---------------	16	Arctostaphylos rubra
	--------+--	--+--1---	---------------	17	Geum rossii
	---------+	--+------	---------------	18	Lycopodium selago
	-----------	----+--+-	---------------	19	Anemone parviflora
	-----------	----+---+	----+---------+--	20	Minuartia arctica
	-----------	-------+-	---+------+--+--	21	Myosotis alpestris
	-----------	-----+-+-	--------------+--	22	Cerastrium beeringianum
	----------+	---+--++-	-+----++-----+--	23	Silene acaulis
	---------+-	-+-----+-	--+---+---++++-	24	Oxytropis nigrescens[1]
	-----------	+------+-	---------------	25	Potentilla biflora
	-----------	-++------	++--------+--+--	26	Pedicularis lanata
	-----------	-+--+--+-	-++----+--++---	27	Tofieldia coccinea
	-----------	-+-+++++-+	-++-++++++-+++--	28	Astragalus umbellatus
	-----------	-+-+---+-	-----1--+------+	29	Carex scirpoidea
	-----+----	---------	---+---+--++---	30	Equisetum scirpoides
	-----------	--------+	++-------+-----	31	Oxytropis maydelliana
	-----------	---------	1----+-1-+-+---	32	Carex rupestris
	-----------	---------	---+-+-+-------	33	Lesquerella arctica
	-----------	---------	---+---+-------	34	Pedicularis sudetica
	-----------	---------	----------++---	35	Anemone narcissiflora
	-----------	---------	----+--+-------+	36	Chrysanthemum integrifolium
	-----------	---------	-------+------+	37	Minuartia elegans
CONSTANT	--2++-+2231	-64549771	19645623+7311++	38	Dryas octopetala
	-------+--	++-+--1--	--++1+-++12++++	39	Carex misandra
RARE	-+---------	---------	---------------	40	Lycopodium clavatum
	-+---------	---------	---------------	41	Vaccinium uliginosum[2]
	------+----	---------	---------------	42	Gentiana prostrata
	------+----	---------	---------------	43	Polygonum bistorta
	---------+-	---------	---------------	44	Arnica frigida
	-----------	----+----	---------------	45	Lupinus arcticus
	-----------	------+--	---------------	46	Eritrichium chamissonis
	-----------	-------+-	---------------	47	Polygonum viviparum
	-----------	---------	+--------------	48	Carex capillaris
	-----------	---------	--------------+	49	Castilleja hyperborea
	1	2	3		

[1] O. nigrescens ssp. bryophila
[2] v. uliginosum ssp. microphyllum

Stand N13 is included in this group, although its low similarity to other sites makes its location arbitrary in group 1 or 2. The remaining Nahoni substrate units exhibit high similarity to each other, with lower similarity to the two Ogilvie sites.

The largest assemblage of substrate units is found in group 3. These are dry Nahoni sites which include most of the stone stripe substrate units. This group represents the overlap in dry and basic ends of moisture and pH complex-gradients, respectively. Absence of dry Ogilvie substrate units suggests that substrate pH is the more critical factor correlated with species composition.

Substrate unit groups have been designated as the following communities: (1) *Vaccinium vitis-idaea - Dryas octopetala*, (2) *Dryas octopetala - Astragalus umbellatus - Salix arctica*, and (3) *Dryas octopetala - Carex misandra*.

Within these communities *D. octopetala* is the only consistently constant species, although *Carex misandra* is also frequent. Both species however have noticeable peaks in cover and frequency in communities 2 and 3.

(1) *Vaccinium vitis-idaea - Dryas octopetala*

The acidic condition of this community type is indicated by *Cassiope tetragona*, *Vaccinium vitis-idaea*, *V. uliginosum* and *Empetrum nigrum* (Table 13). *C. tetragona* is unevenly distributed and is important in the wettest sites of this group, whereas *V. vitis-idaea* is more evenly distribu-

TABLE 13. Vascular plant species in the Vaccinium vitis-idaea - Dryas octopetala community (#1) in the Yukon: mean cover, frequency (fre), and cover value range in 11 substrate units.

Species	Cover	Fre	Cover range
Cassiope tetragona	9.63	46	.50-39.66
Carex microchaeta	6.98	64	1.75-21.75
Dryas octopetala	6.66	73	1.18-15.33
Vaccinium vitis-idaea	5.90	100	.58-12.16
Hierochloe alpina	2.10	27	.50-19.25
Salix arctica	1.67	73	.50- 4.08
Poa spp.	1.33	27	.25-10.58
Empetrum nigrum	.83	18	3.83 -5.25
Luzula multiflora	.79	27	1.00- 6.08
Campanula lasiocarpa	.62	46	.50- 2.08
Vaccinium uliginosum	.47	18	1.12- 4.08
Carex misandra	.28	9	3.08
Ledum palustre	.16	9	1.75
Betula glandulosa	.16	9	1.75
Rhododendron lapponicum	.16	18	.25- 1.50
Lycopodium clavatum	.10	9	1.12
Salix reticulata	.09	18	.50
Equisetum scirpoides	.08	9	.91
Arnica frigida	.05	9	.50
Gentiana prostrata	.05	9	.50
Geum rossii	.05	9	.50
Lycopodium selago	.05	9	.50
Oxytropis nigrescens ssp. bryophila	.05	9	.50
Polygonum bistorta	.05	9	.50
Silene acaulis	.05	9	.50
Pedicularis capitata	.04	9	.41
Vaccinium uliginosum ssp. microphyllum	.02	9	.25

ted in all substrate units. Mesic substrate units are characterized by *Dryas octopetala*, *Carex microchaeta*, *Salix arctica* and *Luzula multiflora*. The driest habitat is that in 07, where *Hierochloe alpina* is of highest importance, followed by *V. vitis-idaea* and the moss *Rhacomitrium lanuginosum*.

Cover and frequency values of dwarf shrubs *Ledum palustre*, *Empetrum nigrum* and *Rhododendron lapponicum* are low, although *L. palustre* was encountered outside quadrats in two additional substrate units in this community. The larger shrub *Betula glandulosa* was restricted to one outcrop habitat on vegetation stripes.

Campanula lasiocarpa is the only herb which is frequently encountered, and it has characteristically low cover values. Other herb species were conspicuous but relatively insignificant components of this community.

(2) *Dryas octopetala - Astragalus umbellatus - Salix arctica*

Dryas octopetala attains its highest importance in this community (Table 14), excluding the dissimilar stand N13. Both *Astragalus umbellatus* and *Salix arctica* have secondary frequency values, but the former is more conspicuous and is also characteristic of Nahoni sites. *Salix arctica* is included in the community name because it is found in the two Ogilvie sites (03 and 04) which do not have *A. umbellatus*, and it also distinguishes this from the third community.

Three species groups can be delineated within this

TABLE 14. Vascular plant species in the *Dryas octopetala* - *Astragalus umbellatus* - *Salix arctica* community (#2) in the Yukon: mean cover, frequency (fre), and cover value range in 9 substrate units.

Species	Cover	Fre	Cover range
Dryas octopetala	30.34	89	8.33-57.17
Salix reticulata	4.07	56	.50-16.33
Cassiope tetragona	3.93	44	.50-20.08
Carex microchaeta	2.33	44	1.75- 9.91
Salix arctica	2.07	67	1.00- 5.58
Rhododendron lapponicum	1.92	44	.54-12.58
Arctostaphylos rubra	1.75	22	6.16- 9.58
Carex misandra	1.57	44	.50- 6.08
Astragalus umbellatus	1.25	67	.25- 2.75
Vaccinium uliginosum	.77	33	1.00- 4.00
Geum rossii	.73	22	.50- 6.08
Carex scirpoidea	.71	33	1.75- 2.37
Oxytropis nigrescens ssp. bryophila	.65	22	1.00- 4.87
Lupinus arcticus	.57	11	5.16
Betula glandulosa	.45	11	4.08
Oxytropis maydelliana	.43	11	3.91
Luzula multiflora	.39	11	3.50
Vaccinium vitis-idaea	.39	11	3.50
Silene acaulis	.31	33	.50- 1.83
Pedicularis capitata	.29	33	.50- 1.20
Carex capillaris	.22	11	2.00
Potentilla biflora	.21	22	.87- 1.00
Tofieldia coccinea	.20	33	.41- .87
Minuartia arctica	.13	22	.50- .66
Pedicularis lanata	.12	22	.50- .58
Cereastrium beeringianum	.10	22	.37- .50
Anemone parviflora	.09	22	.25- .54
Eritrichium chamissonis	.06	11	.50
Lycopodium selago	.06	11	.50
Poa spp.	.06	11	.50
Polygonum viviparum	.04	11	.33
Myosotis alpestris	.03	11	.25

community. On the differentiated table (Table 12) those species from Cassiope tetragona (#3) to Luzula multiflora (#9) are in both communities 1 and 2, and are character-species in the first community. Of these, L. multiflora is restricted to the Ogilvie area.

The second species group is from Betula glandulosa (#10) to Lycopodium selago (#13), and includes infrequent species from communities 1 and 2 which are character-species in the second community. In this group Pedicularis capitata, Rhododendron lapponicum, and Vaccinium uliginosum are found only in Nahoni stands. Arctostaphylos rubra is also in this group as a differential-species for the community. In contrast, Lycopodium selago occurs solely in Ogilvie stands. Geum rossii appears to be restricted to Ogilvie sites, but is also encountered infrequently in the Nahoni area. Geum glaciale is more restricted than G. rossii and is found only in Nahoni stand #7[illegible]

Species fro[illegible]uartia arctica (#20) to Carex scirpoidea (#29) are included in the third group which overlaps between communities 2 and 3. Anemone parviflora is restricted to Nahoni substrate units within community 2, whereas Potentilla biflora is also found once in community 3. The remaining species are primarily or exclusively found in the Nahoni sites in both communities.

(3) Dryas octopetala - Carex misandra

Dryas octopetala is the conspicuous dominant in this community, with character-species *Carex misandra* and *Astragalus umbellatus* (Table 15). *Oxytropis nigrescens* ssp. *bryophila* and differential-species *Carex rupestris* and *Equisetum scirpoides* are also important in this group.

The majority of species are herbs which replace the dwarf shrubs of the other two community types. *Rhododendron lapponicum* is abundant in only one site in comparison to its occurrence in 18 and 44% of the substrate units in communities 1 and 2, respectively. Characteristic herbs include *Pedicularis lanata*, *Silene acaulis* and *Tofieldia coccinea*.

This community represents dry Nahoni sites including all but one stone stripe substrate unit. Since the dry Ogilvie substrate units are very dissimilar to any in this group, correlation with a substrate pH complex-gradient may be important. Differences in regional plant distribution elements may also be involved.

Nahoni Wetland Stands

Species composition and relative importance values for two Nahoni wetland sites are tabulated separately (Table 16) as both were dissimilar to other sampled sites. Stand R1 and R2 represent a *Betula glandulosa - Rubus chamaemorus - Ledum palustre* community, and an *Eriophorum vaginatum* tussock stand, respectively.

Both stands exhibit well-developed hummocks, interspersed with water-saturated vegetation (R1) or with stan-

TABLE 15. Vascular plant species in the *Dryas octopetala* - *Carex misandra* community (#3) in the Yukon; mean cover, frequency (fre), and cover value range in 15 substrate units.

Species	Cover	Fre	Cover range
Dryas octopetala	20.24	100	2.79-36.33
Carex misandra	3.52	80	.50-11.17
Carex rupestris	1.95	33	.50-11.33
Oxytropis nigrescens ssp. bryophila	.93	40	.50- 4.50
Astragalus umbellatus	.93	67	.50- 4.91
Oxytropis maydelliana	.60	20	2.50- 4.00
Carex scirpoides	.58	20	1.00- 3.75
Silene acaulis	.54	27	.50- 3.83
Tofieldia coccinea	.37	33	.50- 2.75
Rhododendron lapponicum	.29	7	4.[illegible]
Equisetum scirpoides	.24	27	.50- .58
Pedicularis lanata	.16	27	.25- 1.00
Cerastrium beeringianum	.15	7	2.25
Anemone narcissiflora	.14	13	.58- 1.58
Myosotis alpestris	.14	20	.50- 1.00
Lesquerella arctica	.12	20	.58
Crysanthemum integrifolium	.10	20	.50
Minuartia elegans	.10	20	.50
Minuartia arctica	.08	13	.50- .66
Pedicularis sudetica	.08	13	.58
Pedicularis capitata	.04	7	.66
Castilleja hyperborea	.03	7	.50

TABLE 16. Cover class values for vascular plants in the Nahoni wetland stands R1 and R2.

	Cover class
R1	
Betula glandulosa	4
Rubus chamaemorus	3
Ledum palustre	3
Vaccinium vitis-idaea	2
R2	
Eriophorum vaginatum	4
Carex bigelowii & C. oederi	3
Salix reticulata	2
Ledum palustre	1
Rhododendron lapponicum	1
Vaccinium uliginosum	1
Vaccinium vitis-idaea	1
Dryas octopetala	1
Tofieldia coccinea	1
Betula glandulosa	1
Arctostaphylos rubra	1

Cover classes:
1 = 1 - 5%
2 = 6 - 15%
3 = 16 - 30%
4 = 31 - 50%

ding water (R2). Hummocks in R1 are 2-5 dm high, with the top portions 4 dm apart. Those in R2 are 2-3 dm high, and approximately 2-4 dm apart.

In R1 the first three species are restricted to occurrence on the upper hummock position, with Vaccinium vitis-idaea growing on the lower hummock areas. Mosses including Hylocomium splendens, Aulacomnium spp., and Sphagnum spp. formed a solid layer beneath the shrubs.

More vascular plant species are evident in R2 (Table 16), and only two are found in the lower hummock microhabitat. Salix reticulata and Tofieldia coccinea occurred on low as well as high hummock position, and no species were restricted to the lower area. Mosses on upper hummocks include Rhytidium rugosum, Dicranum sp., Aulacomnium spp., and Sphagnum spp. Lower hummocks were dominated by Tomenthypnum nitens, Aulacomnium spp. and Sphagnum spp.

Macrolichen Vegetation

Regional Results

Similarity values for macrolichen species in the four study areas indicate closest relationships between areas in each region (Table 17). Species composition from the Divide also appears similar to that in both Yukon areas, possibly due to a large proportion of constant species in Divide sites.

As in the vascular plant data, the two regions appear floristically distinct. The only different trend between

TABLE 17. Percent similarity values for macrolichen vegetation in the four study areas based upon Sørensen's coefficient of community.

	Prospect	Divide	Nahoni
Ogilvie	32	53	69
Nahoni	39	60	
Divide	67		

Number of species tested

Ogilvie	42
Nahoni	46
Divide	34
Prospect	20

Species total = 63

vascular plant (Table 6) and macrolichen data is the lower macrolichen intra-region similarity for Alberta, versus the Yukon. This difference could imply that intra-regional differences such as substrate are more influential on vascular plants than on lichens in the Yukon, with the reverse for Alberta areas. While this may be the case, the data for vascular plants are less precise, and this difference may be caused by sampling error.

The intra-regional similarity of qualitative macrolichen data indicate that separate regional analyses are appropriate for quantitative data. Ordination results are presented first and are analyzed in relation to environmental factors. Differentiated tables are then used to establish macrolichen communities, as in the preceding section on vascular plants. An integration of macrolichen and vascular plant communities is then summarized for each region.

Alberta

Environmental Factors and Vegetation

The Bray-Curtis ordination of macrolichen vegetation from Prospect and Divide areas (Fig. 6) shows two distinct groups. Cluster A consists of stone stripe substrate units and vegetation substrate units of lower cover and species richness than in Cluster B.

Moisture regime and soil pH values were plotted on the ordination (Fig. 6) to aid interpretation of vegetation data. The dry-mesic boundary coincides with the division between

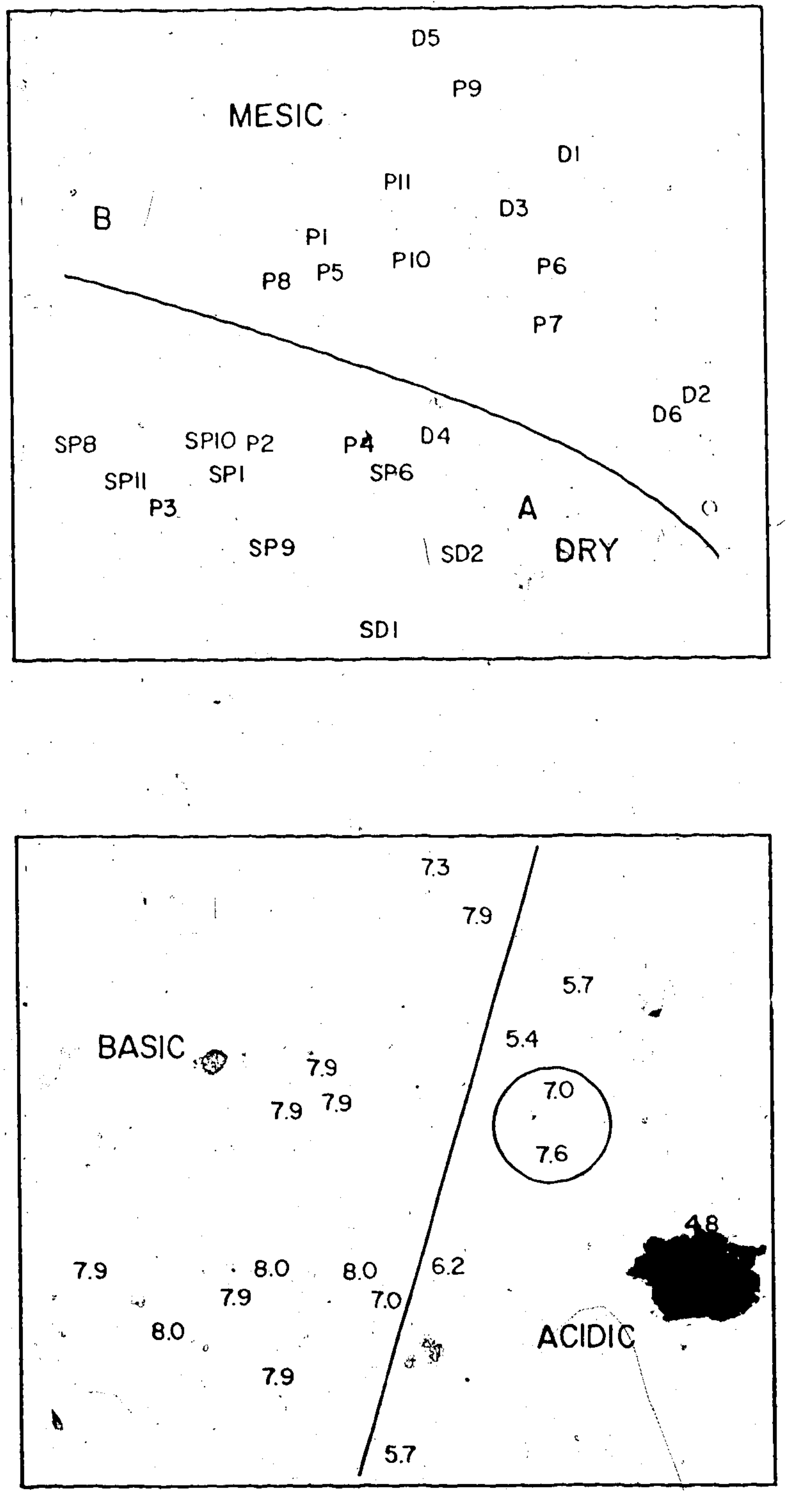

FIGURE 6. Moisture regime and substrate pH on the ordination of Alberta substrate units.

main ordination clusters since all stone stripes and three Prospect vegetation substrate units in cluster A are drier environments than those in cluster B. The exception to this is D4, which is most similar to mesic stands such as D1. Stand D4 was located centrally in relation to the end stands due to its dissimilarity to all of them.

Soil pH values (Fig. 6) include two groups which closely correspond to significant value differences (Table 5) and thus to substrate unit distinction between Prospect and Divide areas. However, Prospect substrate units P6 and P7 are in the Divide ordination area and D5 is in the Prospect area because these appear to represent overlapping portions of the pH complex-gradient in each area. Both P6 and P7 were on less basic substrates, and had higher similarity to end stand D2, than other Prospect stands. Substrate unit D5 was also on more basic soil than other Divide stands.

Integration of the soil and moisture groups with the ordination resulted in four ordination clusters (Fig. 7). Clusters 1(mesic) and 2(dry) include Divide substrate units, and clusters 3(dry) and 4(mesic) represent most Prospect substrate units.

Communities

The relationship of general species distributions to substrate units is displayed in a differentiated table (Table 18). The first substrate unit group (SP11-P9) represents Prospect ordination clusters 3 and 4 (Fig. 7).

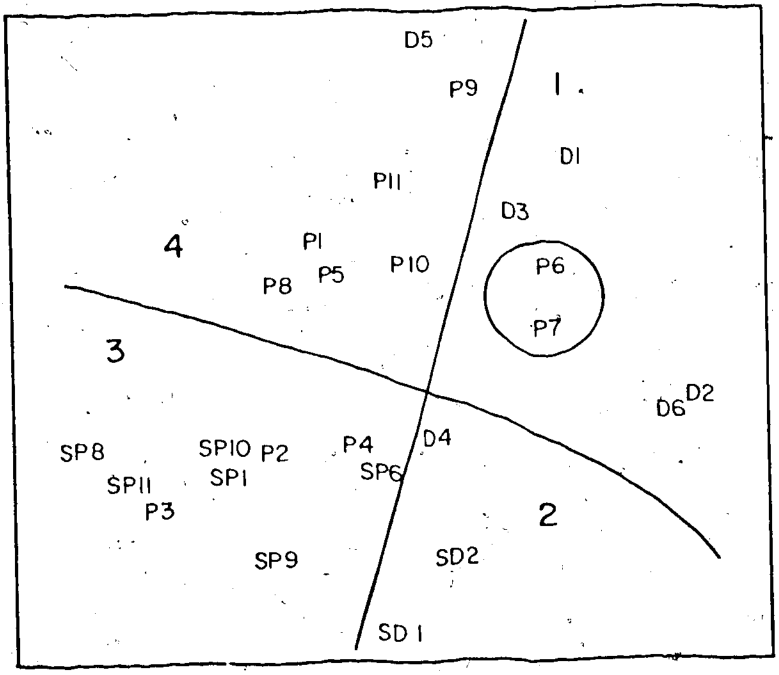

FIGURE 7. Integration of moisture regime and substrate pH on the ordination of Alberta substrate units: (1) mesic, acidic; (2) dry, acidic; (3) dry, basic; (4) mesic, basic.

TABLE 18. Differentiated table for macrolichen vegetation from Prospect (P) and Divide (D) areas. Stand order and scaled abundance values (+ to 9) are derived from reciprocal averaging ordination.

	SP11 SP3 SP1 P2 P11 P1 SP9 P8 P3 D5 P4 P5 P9	P7 P6 SD1 D2 SP6 D3 SP10 P10 SD2	D1 D6 D4		
CHARACTER AND DIFFERENTIAL SPECIES	+++-++++-+---	-------+-	---	1	Solorina spp.
	+++++1-1+++-+	-------+-	---	2	Dactylina ramulosa
	+21++1+21++1-	--++-1++-	+--	3	Cetraria tilesii
	----1+++----1	1------+-	-+-	4	Dactylina arctica
	---------+---	--+--+--[illegible]	---	5	Alectoria nigricans
	---------+---	--+6-2--+	211	6	Stereocaulon alpinum
	---------+---	+2-1+++3-	1+-	7	Peltigera rufescens
	-------------	-++1-+--+	+1-	8	Cladonia pyxidata
	-------------	-+---+++[illegible]	--+	9	Cladonia pocillum
	-------------	-++--+---	+--	10	Hypogymnia oroarctica
	-------------	-+--+----	+--	11	Leptogium saturninum
	-------------	-----3---	---	12	Parmelia taractica
	-------------	---+-----	++-	13	Cetraria islandica
	-------------	---------	1+-	14	Cladonia ecmocyna/gracilis
	-------------	---------	1+9	15	Peltigera aphthosa
CONSTANT	+++-1+++-1+++	1++---+2-	+--	16	Physconia muscigena
	+-++32+1-3251	+1+1-2-++	1--	17	Cetraria nivalis
	+-+-32+1-8--6	-1+--2---	3--	18	Alectoria ochroleuca
	+1++211276142	+211-4++-	2--	19	Thamnolia subuliformis
	++1133+3+6117	15+1+2+1+	7-+	20	Cetraria cucullata
	--+-1+++-2+-2	31+6+2-1+	2++	21	Cetraria ericetorum
	-++-+++1+-+2+	-++++2+++	+--	22	Cornicularia aculeata
RARE	----+--------	--+------	---	23	Alectoria chalybeiformis
	----+--------	-----+---	---	24	Cetraria laevigata
	-------------	---------	+--	25	Hypogymnia subobscura
	-------------	---------	+--	26	Psoroma hypnorum
	-------------	---------	-+-	27	Solorina crocea
	-------------	---------	-+-	28	Cladonia coccifera
	-------------	---------	-+-	29	Nephroma expallidum
	1	**2**	**3**		

Substrate units in the left side of group 1 (Table 18) are predominantly found in ordination cluster 3, corresponding to drier, basic environments. Most of the substrate units from P8-P9 are accordingly located in ordination cluster 4 in mesic and basic habitats.

The second and third substrate unit groups (Table 18) correspond to ordination clusters 1 and 2 from neutral-acidic habitats. Vegetation attributes of substrate units P7-D4 (Table 18) provide a slightly different and perhaps clearer division into two groups than that obtained using moisture regime (Fig. 7).

Vegetation groups on the differentiated table reflect moisture differences in abundance of species rather than in overall species richness. Major differences in species composition are correlated with substrate pH, which in turn reflects differences between the two areas sampled.

Substrate unit groups on the differentiated table have been designated as the following communities: (1) Cetraria cucullata - Thamnolia subuliformis - Cetraria tilesii, (2) Cetraria ericetorum - Cetraria cucullata - Peltigera rufescens, and (3) Peltigera aphthosa - Stereocaulon alpinum.

(1) Cetraria cucullata - Thamnolia subuliformis - Cetraria tilesii (Plates 1, 2)

Cetraria cucullata, C. tilesii and Thamnolia subuliformis are consistently common and frequent in substrate units

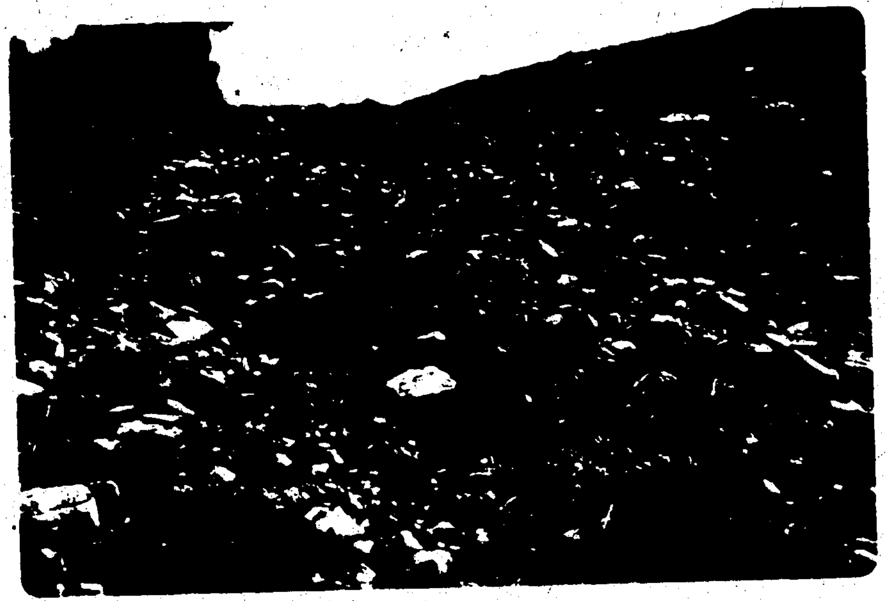

PLATE 1. Two views of the Cetraria cucullata - Thamnolia subuliformis - Cetraria tilesii community on Prospect Mountain.

PLATE 2. Two views of spotted tundra, in the *Cetraria cucullata* - *Thamnolia subuliformis* - *Cetraria tilesii* community on Prospect Mountain.

of this community type (Table 19). The fourth important species is *Alectoria ochroleuca*, which has high cover but is unevenly distributed. It is most often found growing on the sloping or riser portion of vegetation stripes which have step-like relief. Stripes of this type were more common on middle or lower slopes such as those in Prospect stands 1, 5, 9 and 11.

Frequent species include *Cetraria nivalis* and *Physconia muscicena* with moderate cover; and *Cornicularia aculeata*, *Cetraria ericetorum*, and *Dactylina ramulosa* with low cover. Both *C. tilesii* and *D. ramulosa* are particularly characteristic of dry, basic substrates but seldom attain high cover values in the Alberta study areas. Sterile, colonizing thalli of *Solorina* spp. are also frequent on mineral soil in stone stripe substrate units.

(2) *Cetraria ericetorum - Cetraria cucullata - Peltigera rufescens* (Plate 3)

Cetraria ericetorum and *C. cucullata* attain significant cover and frequency values in this community, as does the character-species *Peltigera rufescens* (Table 20). *Cornicularia aculeata* is frequently found with characteristically low cover, in comparison to *Cetraria nivalis* and *Thamnolia subuliformis* which have lower frequencies and higher cover. *Stereocaulon alpinum* and *Parmelia taractica* have noticeably clumped distributions in this community type. Approximately half the substrate units have scattered thalli of *Physco-*

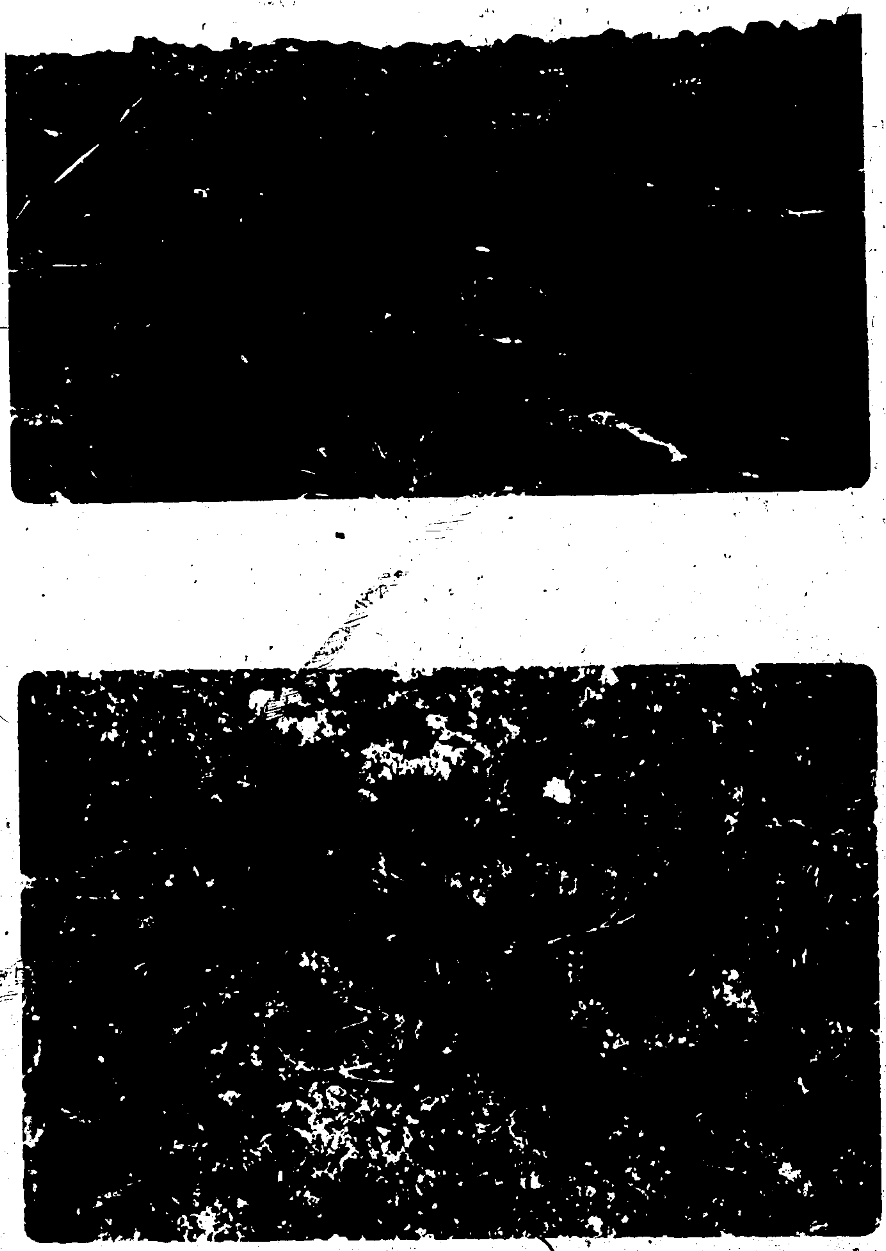

PLATE 3. Two views of the Cetraria ericetorum - C. cucullata - Peltigera rufescens community on Prospect Mountain.

[redacted]

TABLE 19. Macrolichen species in the *Cetraria cucullata - Thamnolia subuliformis - Cetraria tilesii community* (#1) in Alberta; mean cover, frequency (fre), and cover value range in 13 substrate units.

Species	Cover	Fre	Cover range
Cetraria cucullata	4.71	100	.45-14.66
Thamnolia subuliformis	3.92	100	.50-11.33
Alectoria ochroleuca	3.22	62	.33-15.08
Cetraria nivalis	2.88	85	.50-10.08
C. tilesii	2.08	92	.75- 4.08
Physconia muscigena	1.52	85	.33- 6.50
Cetraria ericetorum	1.18	62	.41- 4.25
Cornicularia aculeata	1.17	77	.31- 4.25
Dactylina ramulosa	.92	85	.37- 2.50
D. arctica	.63	38	.50- 2.79
Solorina spp.	.32	62	.41- 1.00
Alectoria nigricans	.08	8	1.00
A. chalybeiformis	.07	8	.87
Cetraria laevigata	.07	8	.87
Peltigera rufescens	.05	8	.58
Stereocaulon alpinum	.05	8	.58

TABLE 20. Macrolichen species in the Cetraria ericetorum - Cetraria cucullata - Peltigera rufescens community (#2) in Alberta; mean cover, frequency (fre), and cover value range in 9 substrate units.

Species	Cover	Fre	Cover range
Cetraria ericetorum	3.34	89	.50-12.08
C. cucullata	2.70	100	.50- 9.66
Thamnolia subuliformis	2.61	78	.66- 9.25
Stereocaulon alpinum	2.13	44	.58-13.00
Peltigera rufescens	1.91	78	.59- 5.70
Cetraria nivalis	1.32	78	.50- 5.00
Cornicularia aculeata	1.16	89	.50- 5.08
Physconia muscigena	1.05	55	.25- 4.41
Parmelia taractica	.84	11	7.55
Alectoria ochroleuca	.76	33	.58- 4.25
Cladonia pyxidata	.51	55	.25- 2.91
Cetraria tilesii	.46	55	.29- 2.50
Cladonia pocillum	.32	44	.37- 1.79
Dactylina arctica	.30	22	.50- 2.75
Hypogymnia oroarctica	[illegible]	33	.50- 1.00
Leptogium saturninum	.17	22	.50- 1.00
Alectoria nigricans	.13	22	.58
Dactylina ramulosa	.12	11	1.04
Solorina spp.	.11	11	.54
Alectoria chalybeiformis	.06	11	.50
Cetraria islandica	.04	11	.33
C. laevigata	.03	11	.25

nia muscigena, *Cladonia pyxidata*, *Cetraria tilesii* and *Cladonia pocillum*. *Alectoria ochroleuca* is much less important than in the first community, and is replaced partially by *A. nigricans* and *A. chalybeiformis* in mesic, acidic habitats.

(3) *Peltigera aphthosa - Stereocaulon alpinum* (Plate 4)

The importance of differential-species *Peltigera aphthosa* and character-species *Stereocaulon alpinum* distinguishes this from other communities. *Cetraria cucullata* also attains high cover, but occurs with lower frequency (Table 21).

The three substrate units representing this community are all wet-mesic, acidic habitats with marked differences in species composition and abundance in comparison to either other community type. Wet or wet-mesic substrate units were small and infrequent in the Front Range study areas, so this community can only be characterized on a preliminary basis. Of the three substrate units, D1 appears to be transitional to the *Cetraria ericetorum - C. cucullata - Peltigera rufescens* community.

Rare species which also characterize this wet-mesic or snowbed community include *Psoroma hypnorum*, *Solorina crocea*, *Cladonia coccifera/metacorallifera* and *Nephroma expallidum* (Table 18). The brown *Cetraria* species *C. islandica* attains its highest importance in this community, while *C. ericetorum* is intermediate and *C. laevigata* is absent. Importance values for the six other constant species (Table 18) are due to occurrence in the transitional substrate unit D1.

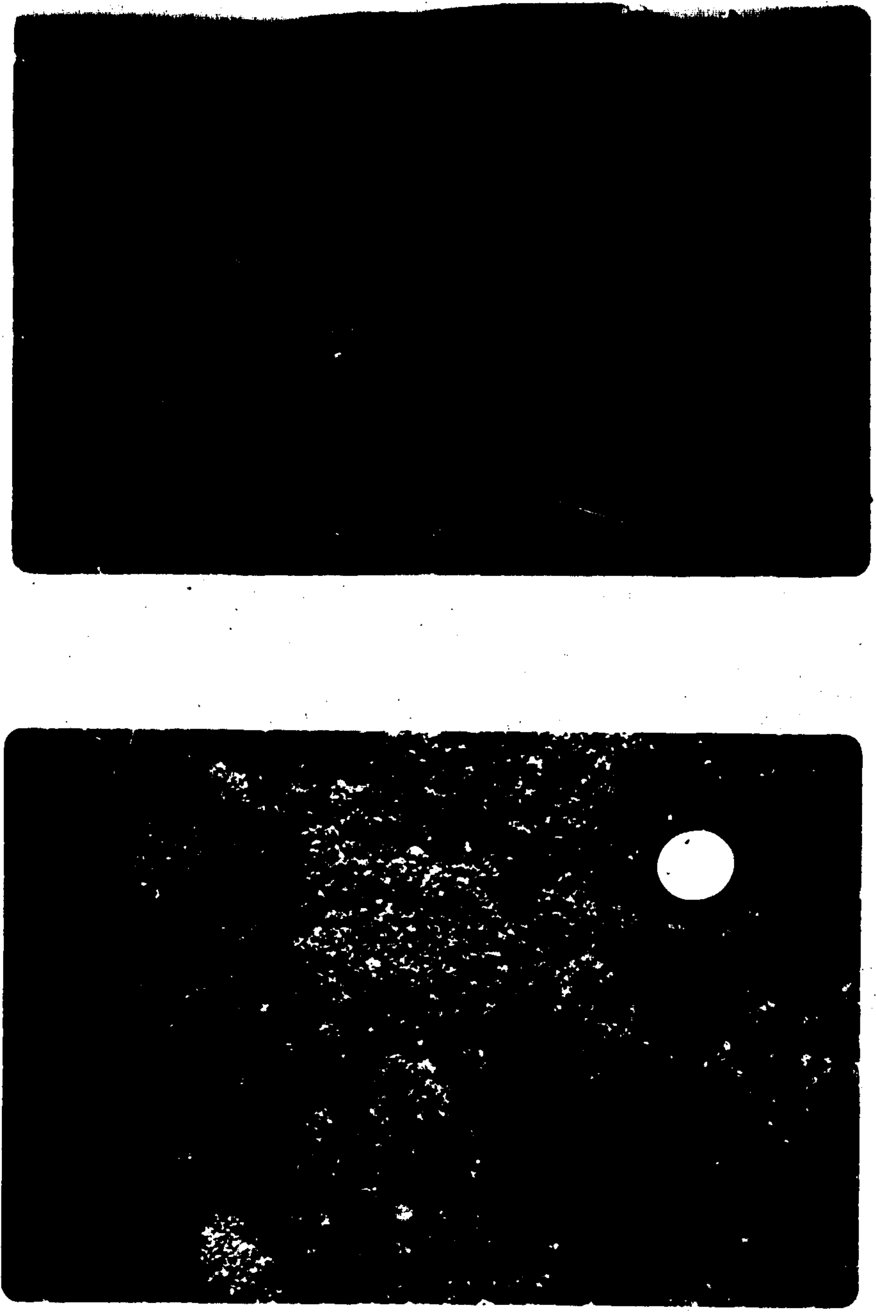

PLATE 4. Two views of the Peltigera aphthosa - Stereocaulon alpinum snowbed community on the Divide. Solorina crocea and Lepraria neglecta are also evident in the lower photo.

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TABLE 21. Macrolichen species in the _Peltigera aphthosa - Stereocaulon alpinum_ community (=3) in Alberta; mean cover, frequency (fre) and cover value range in 3 substrate units.

	Cover	Fre	Cover range
Peltigera aphthosa	7.14	100	.33-18.83
Cetraria cucullata	5.33	67	1.75-14.25
Stereocaulon alpinum	3.68	100	2.91- 4.50
Cetraria ericetorum	2.12	100	.50- 4.50
Alectoria ochroleuca	2.05	33	6.16
Thamnolia subuliformis	1.61	33	4.83
Peltigera rufescens	1.36	67	1.83- 2.85
Cladonia ecmocyna/gracilis	1.29	67	.37- 3.50
Cetraria nivalis	.94	37	2.83
Cladonia pyxidata	.78	33	2.33
C. pocillum	.61	33	1.83
Hypogymnia subobscura	.58	33	1.75
Cetraria islandica	.36	67	.50- .58
Nephroma expallidum	.29	33	.87
Cornicularia aculeata	.19	33	.58
Leptogium saturninum	.17	33	.50
Psoroma hypnorum	.17	33	.50
Cladonia coccifera	.12	33	.37
Solorina crocea	.10	33	.29
Cetraria tilesii	.08	33	.25
Dactylina arctica	.08	33	.25
Physconia muscigena	.08	33	.25

The main differential-species of snowbed stand D6 was *Lepraria neglecta*, a white crustose lichen. This species contributed 42% of the total lichen cover in D6. High crustose lichen cover was not encountered in other substrate units.

Yukon

Environmental Factors and Vegetation

Bray-Curtis ordination of macrolichen vegetation from Yukon areas shows two groups of substrate units (Fig. 8) which correspond to parallel Nahoni and Ogilvie coenoclines. Well-vegetated sites from both areas are at the lower left of the ordination (O5v, N2) grading to dry stone stripe substrate units at the upper right (SO1, SN10).

Moisture regime and soil pH values for the Yukon were plotted on the ordination (Fig. 8). Each area exhibited wet meadows or snowbeds; mesic slopes; dry ridge and stone stripe habitats. The moisture complex-gradient was therefore more clearly expressed in the Yukon than in Alberta (Fig. 6).

As in the Alberta data, significantly different soil pH groups (Table 5) corresponded to differences in areas, with O4 and N5 as exceptions (Fig. 8). The former was a meadow site with high similarity to Nahoni meadows, which seemed to override the substrate pH relationship. The N5 stand was on a Nahoni outcrop of very low pH where vegetation was more similar to Ogilvie substrate types than to

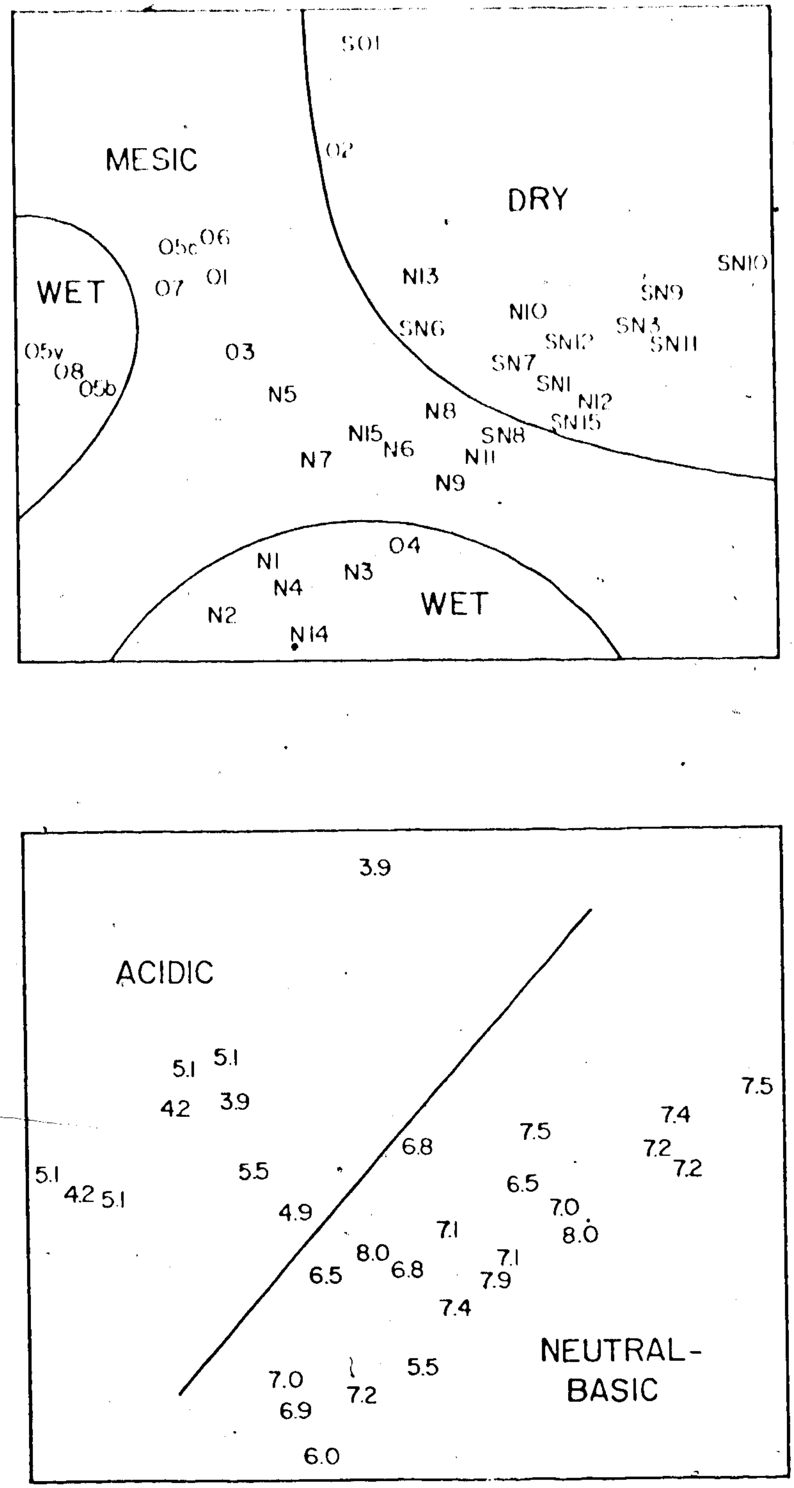


FIGURE 8. Moisture regime and substrate pH on the ordination of Yukon substrate units.

many in the Nahoni area. Stand placement in these two cases probably represent overlapping substrate complex gradients.

The slate outcrop at N13 is close to the regional division line and is intermediate in substrate pH. The vegetation data from this stand were extremely dissimilar to other sites, which resulted in the central position of this stand.

The synthesis of pH and moisture regimes (Fig. 9) shows the two parallel moisture gradients distinguished by substrate. Wet, mesic, and dry habitats are represented respectively within Nahoni clusters 1-3, and within Ogilvie clusters 4-6.

Communities

The vegetation in the Ogilvie area is qualitatively and quantitatively distinct from that in the Nahoni area. The first group of substrate units on the differentiated table (Table 22) is composed of all Ogilvie sites except O4. The order of substrate units in this group is highly similar to that along the x-axis from cluster 4-6 (Fig. 9), illustrating the comparability of the two ordination techniques used.

Correlation of a moisture complex-gradient with these substrate units is represented primarily by variability in species importance, and secondarily by species composition.

Substrate unit group 2 (Table 22) represents ordination cluster 1 (Fig. 9). The substrate unit N5 is of sufficient-

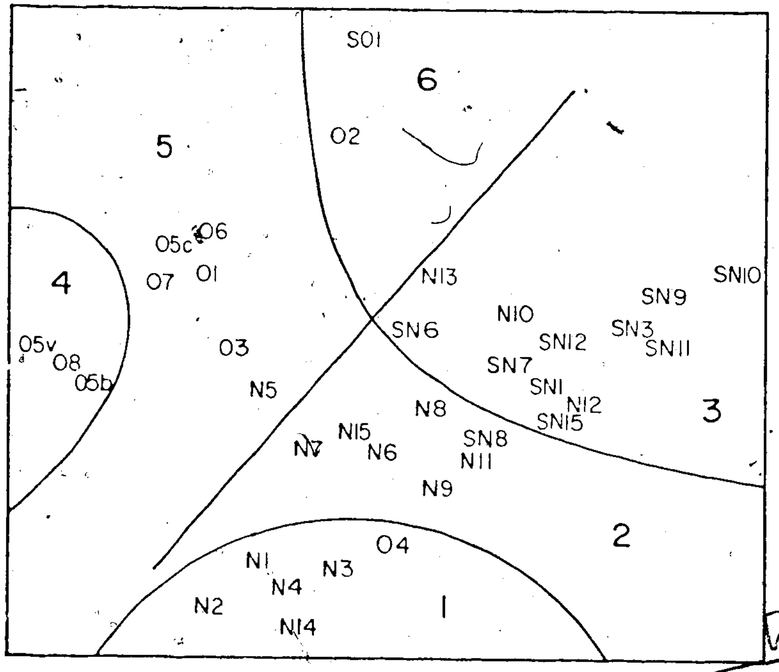


FIGURE 9. Integration of moisture regime and substrate pH on the ordination of Yukon substrate units: (1) wet, basic; (2) mesic, basic; (3) dry, basic; (4) wet, acidic; (5) mesic, acidic; (6) dry, acidic.

TABLE 22. Differentiated table for macrolichen vegetation from Nahoni (N) and Ogilvie (O) areas. Stand order and scaled abundance values (+ to 9) are derived from reciprocal averaging ordination.

	O5v O8 O7 O5b O5c O1 O6 O2 SO1 O3	N5 N1 N2 N7 O4 SN14 N4 N6 SN1	N15 N1 SN7 N4 N8 SN12 SN3 SN6 N12 SN15 N11 SN11 N13 SN5 SN9 SN10		
CHARACTER AND DIFFERENTIAL SPECIES	----+-+-+-	---------	----------------	1	Solorina crocea
	-+---+++--	---------	----------------	2	Cetraria nigricans
	+--1-+----	---------	----------------	3	Peltigera pulverulenta
	-+1-------	---------	----------------	4	Cladonia macrophylla
	1+-1++++--	---------	----------------	5	Cladonia crispata
	+1+11+++++	---------	----------------	6	Cladonia coccifera[1]
	1+11++1++2	+-+-++---	+---+-----------	7	Cladina rangiferina
	+2++1++++1	+-+-++++-	+-+-----++------	8	Cladonia ecmocyna[2]
	1354122+++	1-++++++-	++-++--++-------	9	Cladina arbuscula[3]
	1+-+----+-	--+------	+---------------	10	Cladonia uncialis
	33-+-+----	-11--1--+	----------------	11	Cetraria richardsonii
	+1++-+---4	-----+---	+-+-------------	12	Cladina stellaris
	-----+2-+-	3-----+--	+---------------	13	Sphaerophorus globosus
	+---++1---	+-+--++--	----------------	14	Peltigera aphthosa
	----------	-----++--	1---+-----------	15	Alectoria nitidula
	----------	+-+--11+-	32+11++12++++++-	16	Asahinea chrysantha
	----------	---+---1-	++112++2++3121+1	17	Cetraria tilesii
	----------	---------	+++++++-1++++-++	18	Parmelia separata
	----------	-------++	--++---+-+----++	19	Solorina spp.
	----------	--------+	2+-+-+---+--+---	20	Hypogymnia subobscura
	----------	---------	-----+--+-+++--+	21	Cornicularia aculeata
CONSTANT	3112114++3	23231122+	13121+++1+1-++--	22	Dactylina arctica
	++221+21+3	1++1-+21+	11+121+11+1-1++-	23	Cetraria nivalis
	12++2++++3	++122122-	12121++11+1+1+-+	24	Cetraria islandica
	+--++++++1	1+1222321	4312311252513++1	25	Thamnolia subuliformis[4]
	+---+1+++1	249117621	15+11+11+11+++++	26	Cetraria cucullata
	--+--++++3	++++-+11-	11+++++11+++1++-	27	Alectoria ochroleuca
	--++-+++-+	+++1121++	11+1+++1++1-+++-	28	Cetraria laevigata
	-+-++-++++	+--1---+-	--++1-++--1-1-++	29	Dactylina ramulosa
	-----+--+-	1-+--++1-	++++++-+1++-1++-	30	Cornicularia divergens
	+------+-+	-+-+--+++	-+++--++----+---	31	Cladonia pyxidata
	------+-+1	+-----++-	---+2-+++-+-++--	32	Alectoria nigricans
RARE	-++-------	----+----	----------------	33	Cladonia amaurocraea
	--+-------	---------	+---------------	34	Cetraria ericetorum
	-----+----	----+----	----------------	35	Psoroma hypnorum
	----+-----	+---+----	----------------	36	Peltigera malacea
	1	2	3		

[1] C. coccifera/metacorallifera
[2] C. ecmocyna/gracilis
[3] C. arbuscula/mitis
[4] T. subuliformis/vermicularis

ly low pH to be grouped in ordination cluster 5, yet has vegetation attributes which are transitional to wet and mesic Nahoni sites. The second group of substrate units (N1-N4) corresponds to the wet end of the Nahoni moisture complex-gradient.

The relationship of ordination clusters 1 and 4 is based upon character-species for both substrate unit groups 1 and 2. This group of eight species includes those from <u>Cladina rangiferina</u> (#6) to <u>Peltigera aphthosa</u> (#14) on the differentiated table. These species are found in wet to mesic sites in Ogilvie and Nahoni areas, with greater importance in the Ogilvie sites. In other words, moisture regime can override the correlation of pH and species composition. However, the lower quantitative Nahoni values for these species may be evidence of a less pronounced environmental factor such as pH, or a factor correlated with it.

Transitional substrate units N6, SN1, N15 and N3 are similar to substrate unit groups 2 and 3, but have slightly higher values within the group boundaries as delineated on Table 22. For instance, quantitative similarity values of N15 place it in group 3, whereas qualitative criteria would shift it into group 2.

The third substrate unit group consists of dry and mesic Nahoni sites. The mesic-dry sites are on the left two-thirds of group 3 with the driest on the right, again corresponding to general x-axis order (Fig. 9). Species composition of this group compared to the other two, relates closely to the substrate pH difference between areas. Such differences are enhanced by the interaction of the moisture complex-gradient.

Three lichen communities corresponding to the substrate unit groups are: (1) Cladina arbuscula/mitis - Cetraria nivalis - Cladonia coccifera/metacorallifera; (2) Cetraria cucullata - Dactylina arctica - Cetraria laevigata; and (3) Thamnolia subuliformis/vermicularis - Cetraria tilesii.

(1) Cladina arbuscula/mitis - Cetraria nivalis - Cladonia coccifera/metacorallifera (Plate 5)

Species of the Cladoniaceae account for 57% of the species richness in communities 1 and 2, with greater importance in the former. Cladina arbuscula and C. mitis combined have the highest quantitative values in this community (Table 23). These taxa are morphologically identical, and were conspicuously present with C. rangiferina in the majority of quadrats in each stand. The fourth reindeer lichen C. stellaris occurs with the others but is less widely distributed. Related Cladonia species which are abundant and frequent include C. coccifera/metacorallifera, C. ecmocyna/gracilis, C. crispata and C. uncialis.

Seven differential-species are found in this community including C. coccifera/metacorallifera, C. crispata, Peltigera pulverulenta, Cladonia macrophylla, Solorina crocea, and Cetraria nigricans. Of these, C. nigricans and Cladonia

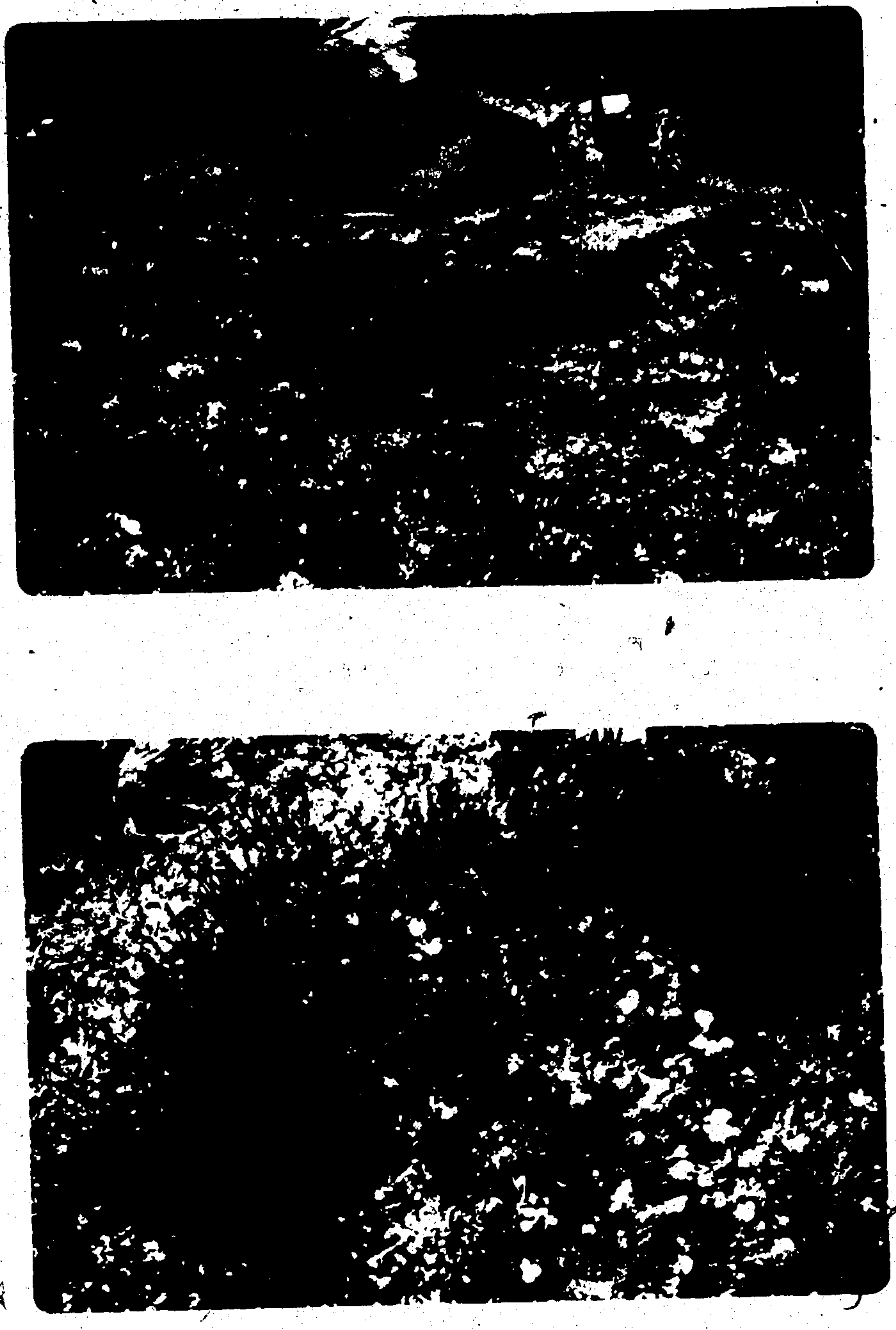


PLATE 5. Two views of the Cladina arbuscula/mitis - Cetraria nivalis - Cladonia coccifera/metacorallifera community in the Ogilvie Mountains. Cladina stellaris is conspicuous in the lower photo.

[redacted]

TABLE 23. Macrolichen species in the Cladina arbuscula/mitis-Cetraria nivalis - Cladonia coccifera/metacorallifera community (#1) in the Yukon; mean cover, frequency (fre), and cover value range in 10 substrate units.

Species	Cover	Fre	Cover range
Cladina arbuscula/mitis	6.04	100	1.08-14.[illegible]8
Cetraria nivalis	4.93	100	.78-11.33
Dactylina arctica	4.40	100	.50- 9.25
Cetraria islandica	4.01	100	1.58-11.33
Cladina rangiferina	3.25	100	1.08- 7.58
Cetraria richardsonii	2.29	40	.50-10.00
Cladina stellaris	2.15	60	.25-14.25
Alectoria ochroleuca	2.01	60	.50-11.33
Cladonia coccifera/metacorallifera	1.93	100	.50- 4.25
C. ecmocyna/gracilis	1.90	100	.25- 6.12
C. crispata	1.32	70	.25- 4.91
Dactylina ramulosa	1.26	70	.25- 3.25
Cetraria cucullata	1.06	70	.50- 3.25
Thamnolia subuliformis/vermicularis	1.15	80	.50- 3.75
Sphaerophorus globosus	.98	30	.50- 7.50
Cladonia uncialis	.83	40	.75- 4.41
Peltigera pulverulenta	.74	30	.58- 4.83
Cetraria laevigata	.62	60	.50- 1.83
Peltigera aphthosa	.59	40	.50- 3.83
Cladonia macrophylla	.54	30	.25- 4.66
Alectoria nigricans	.49	30	.50- 3.83
Solorina crocea	.44	30	.50- 2.25
Cetraria nigricans	.38	40	.25- 2.00
Cladonia amaurocraea	.38	20	1.25- 2.58
C. pyxidata	.22	30	.58- 1.12
Cornicularia divergens	.16	20	.50- 1.08
Cetraria ericetorum	.11	10	1.08
Peltigera malacea	.05	10	.50
Psoroma hypnorum	.05	10	.50

coccifera/metacorallifera were otherwise encountered only in Nahoni stand N13.

In the genus *Cetraria*, *C. nivalis* and *C. islandica* are more important quantitatively than *C. laevigata* or *C. nigricans*, and *C. ericetorum* is relatively rare. *Cetraria cucullata* has intermediate importance values to *C. islandica* and *C. laevigata*. In wet depressions *C. richardsonii* is important, and is less evenly distributed within a stand than the other abundant congeners.

Only three regionally constant species *Cornicularia divergens*, *Cladonia pyxidata* and *Alectoria nigricans* are important in this community. This may be related to the increased numbers and abundance of differential- and character-species, compared to the other communities (Table 22).

Both *Solorina crocea* and *Sphaerophorus globosus* are restricted to mineral soil in late snowmelt sites. In wet vegetated sites large thalli of *Dactylina arctica* are frequent, with high cover. *Cladonia ecmocyna/gracilis* and *C. crispata* are also found in this habitat, where they are interwoven with vascular plant vegetation.

Driest sites in this community type are on exposed acidic outcrops dominated by the moss *Rhacomitrium lanuginosum*, *Cladina* spp., *Cetraria nivalis* and *Alectoria ochroleuca*. The marked co-occurrence of these pale species suggests a relationship between plant color, and energy and water relations in these sites.

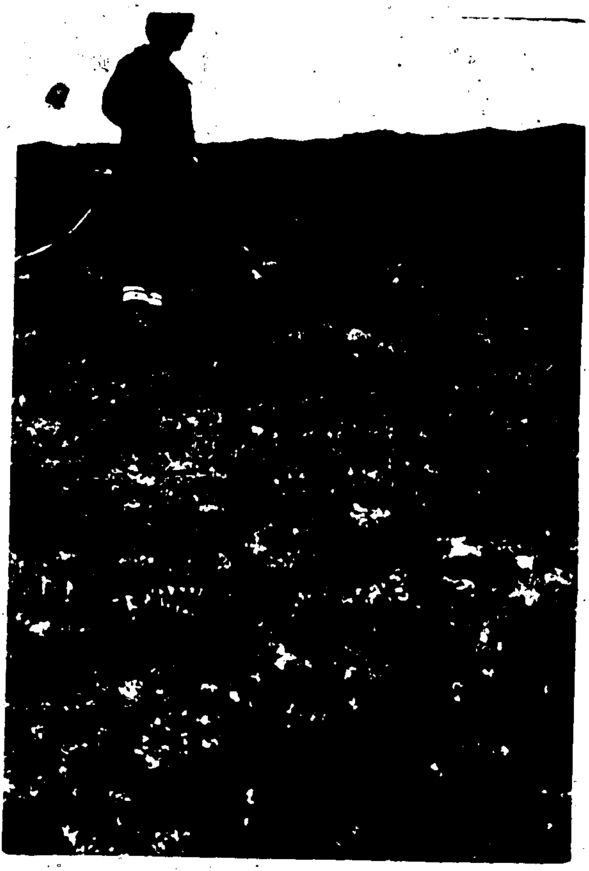
The basidiolichen Coriscium viride was found in one stand (O2) in Dryas octopetala vegetation. It is the only northern representative of this small and poorly understood group of lichenizing fungi. In its vegetative state it greatly resembles sterile Cladonia species, and because of this is probably more common in northern regions than collection records imply.

(2) Cetraria cucullata - Dactylina arctica - Cetraria laevigata (Plate 6)

Cetraria species such as C. cucullata, C. islandica, and C. laevigata occur with increased importance in this community, compared to community 1. Conversely, most of the Cladonia species are present with lower relative importance values to those in the first community. Within the first 15 species listed in Table 24, only Cladina arbuscula/mitis represents this lichen group.

Nahoni snowbeds, mesic depressions and slopes are represented in this type. The first nine species (Table 24) are all abundant and robust in mesic to wet habitats. Sphaerophorus globosus is also found on wet mineral soil as in the first community. Stereocaulon alpinum is present in mesic sites, although it is rare and quantitatively minor. The absence of Solorina crocea may be due to other habitat factors such as pH.

Upland species are also found in this community, including Cornicularia divergens, Asahinea chrysantha, and the



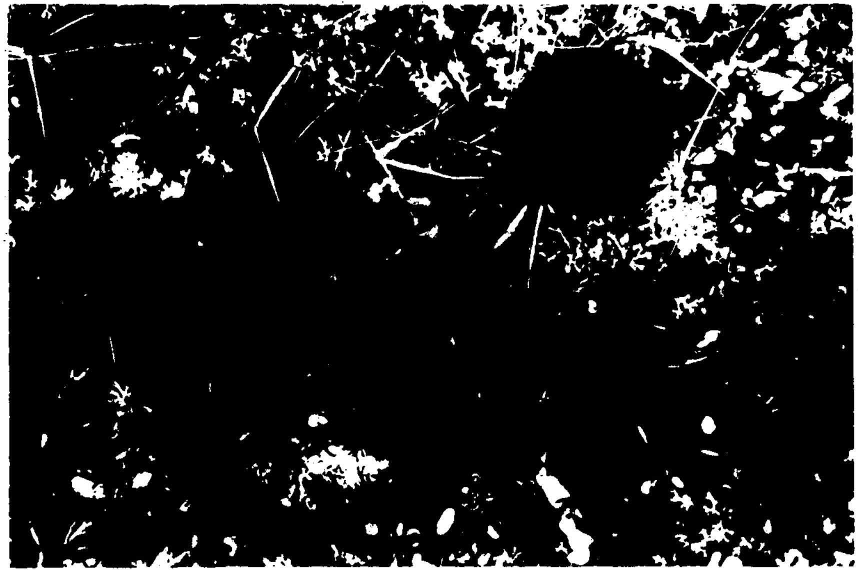


PLATE 6. Two views of the *Cetraria cucullata* - *Dactylina arctica* - *Cetraria laevigata* community in the Nahoni Range. *Cetraria richardsonii* is conspicuous in the lower photo.

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TABLE 24. Macrolichen species in the Cetraria cucullata - Dactylina arctica - Cetraria laevigata community (#2) in the Yukon; mean cover, frequency (fre), and cover value range in 9 substrate units.

Species	Cover	Fre	Cover Range
Cetraria cucullata	12.17	100	3.25-29.04
Thamnolia subuliformis/vermicularis	5.33	100	2.41- 8.78
Dactylina arctica	5.19	100	1.50-11.33
Cetraria islandica	4.25	89	2.00- 7.50
C. laevigata	3.20	100	.58- 6.70
C. nivalis	2.58	89	1.00- 6.12
Alectoria ochroleuca	1.47	78	.50- 5.50
Cladina arbuscula/mitis	1.46	78	.58- 3.75
Cetraria richardsonii	1.43	44	.50- 5.25
Cornicularia divergens	1.32	55	.25- 5.41
Asahinea chrysantha	1.29	55	.29- 4.25
Sphaerophorus globosus	1.13	22	.29- 9.91
Dactylina ramulosa	.79	33	.58- 3.41
Cetraria tilesii	.50	22	.66- 3.83
Cladonia ecmocyna/gracilis	.47	67	.25- 1.41
Cladina rangiferina	.46	44	.25- 2.08
Cladonia pyxidata	.44	55	.33- 2.00
Peltigera aphthosa	.41	44	.29- 1.37
Alectoria nigricans	.36	33	.50- 2.16
A. nitidula	.13	22	.25- .95
Solorina spp.	.13	22	.50- .66
Peltigera malacea	.11	22	.50
Cladonia amaurocraea	.06	11	.58
Hypogymnia subobscura	.06	11	.58
Psoroma hypnorum	.06	11	.58
Cladonia uncialis	.03	11	.25
Cladina stellaris	.03	11	.25

less important species *Dactylina ramulosa*, *Cetraria tilesii*, *Cladonia pyxidata*, *Alectoria nigricans* and *A. nitidula*.

(3) *Thamnolia subuliformis/vermicularis - Cetraria tilesii*

Species of mesic to dry habitats are most important in this community (Plate 7). The drier sites are characterized by greater importance of *Thamnolia subuliformis/vermicularis*, *Cetraria tilesii*, *Asahinea chrysantha*, *Alectoria ochroleuca*, *A. nigricans*, *Cornicularia aculeata*, *C. divergens*, *Parmelia separata* and *Dactylina ramulosa* (Table 25).

Species with mesic associations include *Cetraria cucullata*, *C. islandica*, *C. laevigata*, *C. nivalis* and *Dactylina arctica*. Representatives of the Cladoniaceae are relatively minor in this community type.

Nahoni Slate Outcrop Stand

This and two other stands are discussed separately due to low similarity values with stands in the three designated communities. The slate outcrop stand (N13) is most similar to N15, but is dissimilar to communities 2 and 3 which are both related to N15.

The distinctiveness of this stand is due largely to the dominance of *Stereocaulon alpinum*, which was rarely found in other stands. Vegetation data for this stand are otherwise characterized by high species richness with low cover for most species (Table 26).

Some species such as *Cetraria nigricans* and *Cladonia coccifera/metacorallifera* are found exclusively in Ogilvie

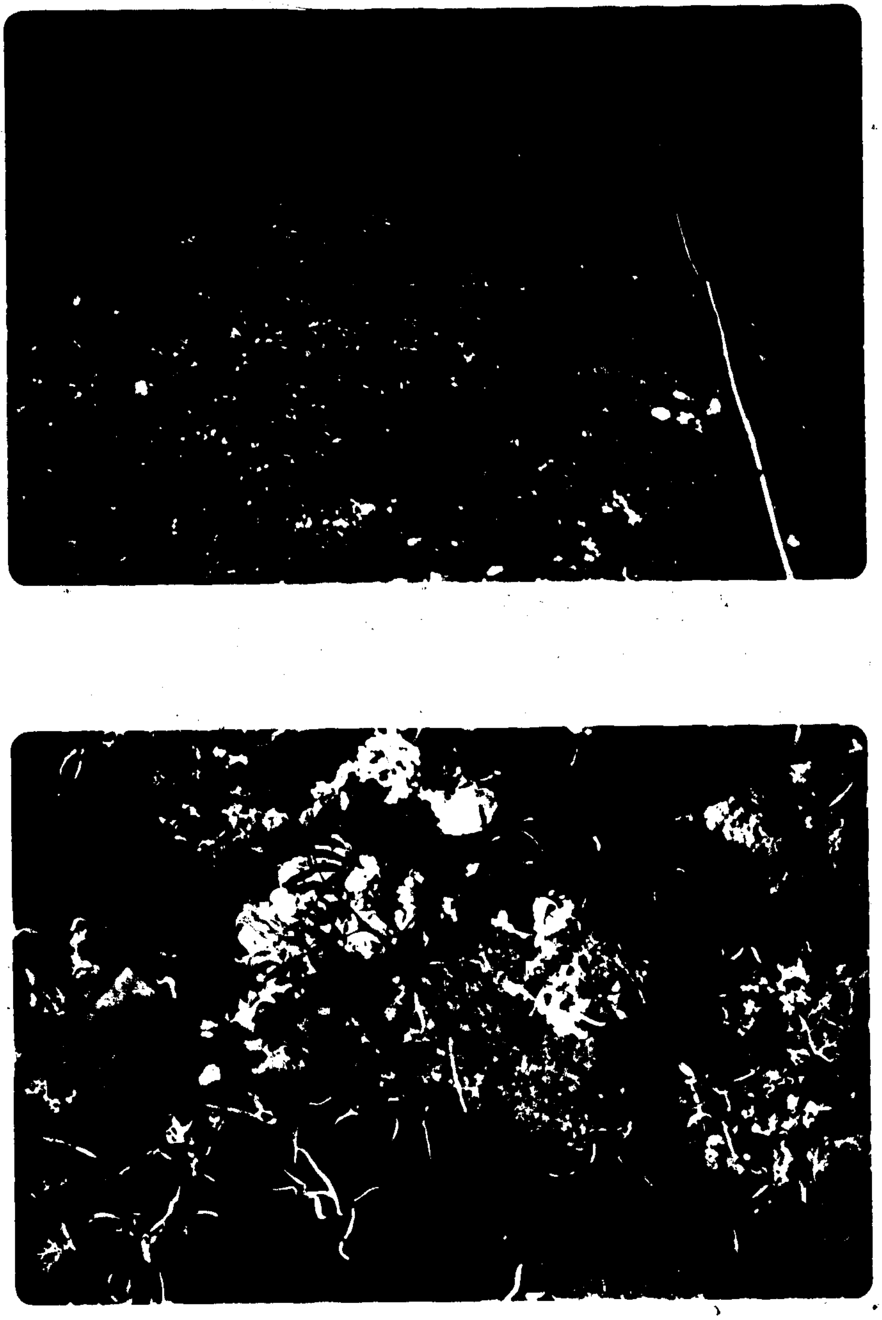


PLATE 7. Two views of the Thamnolia subuliformis/vermicularis'-Cetraria tilesii community in the Nahoni Range. Asahinea chrysantha and Cetraria laevigata are conspicuous in the lower photo.

[redacted]

TABLE 25. Macrolichen species in the *Thamnolia subuliformis/vermicularis* - *Cetraria tilesii* community (#3) in the Yukon; mean cover, frequency (fre), and cover value range in 16 substrate units.

Species	Cover	Fre	Cover range
Thamnolia subuliformis/vermicularis	7.49	100	2.41-14.66
Cetraria tilesii	4.13	100	1.50- 9.25
C. cucullata	3.51	100	1.08-15.00
Asahinea chrysantha	3.27	94	.50- 8.83
Cetraria islandica	3.27	94	.50- 8.00
C. nivalis	2.89	88	.58- 6.75
Dactylina arctica	2.83	81	.50- 8.83
Cetraria laevigata	2.43	88	1.00- 5.00
Alectoria ochroleuca	2.13	94	.50- 5.50
Cornicularia divergens	1.52	81	.50- 5.50
Parmelia separata	1.17	88	.50- 3.25
Dactylina ramulosa	1.02	56	.50- 4.00
Hypogymnia subobscura	.69	36	.58- 6.75
Alectoria nigricans	.68	50	.25- 5.83
Cornicularia aculeata	.57	36	.58- 2.75
Cladina arbuscula/mitis	.29	36	.50- 1.08
Cladonia ecmocyna/gracilis	.25	25	.58- 2.08
Alectoria nitidula	.24	12	.58- 3.25
Cladonia pyxidata	.22	36	.25- 1.00
Solorina spp.	.22	36	.50- .66
Cladina stellaris	.15	12	.50- 1.83
Sphaerophorus globosus	.11	6	1.75
Cladina rangiferina	.08	12	.66
Cetraria ericetorum	.03	6	.50
Cladonia uncialis	.03	6	.50

TABLE 26. Cover class values for macrolichen species in the Mahoni slate outcrop stand SHB.

Species	Cover class
Stereocaulon alpinum	2
Thamnolia subuliformis/vermicularis	2
Cetraria nivalis	2
Sphaerophorus globosus	1
Cornicularia divergens	1
Alectoria nigricans	1
Hypogymnia physodes	1
Cladonia ecmocyna/gracilis	1
Parmelia separata	1
Alectoria pubescens	1
Cetraria nigricans	1
Cetraria cucullata	1
Hypogymnia subobscura	1
Alectoria nitidula	1
A. ochroleuca	1
Asahinea chrysantha	1
Cladina rangiferina	1
Cetraria ericetorum	+
Cladina arbuscula/mitis	+
Cladonia uncialis	+
Asahinea scholanderi	+
Dactylina ramulosa	+
Cladonia coccifera/metacorallifera	+
Cornicularia aculeata	+
Cladonia amaurocraea	+
C. macrophyllodes	+

Cover classes:
+ = less than 1%
1 = 1 - 5%
2 = 6 - 15%

sites except for occurrence in this stand. *Asahinea scholanderi* is encountered only in this outcrop vegetation.

Reasons for the distinct combination of species composition and relative importance values cannot be readily determined from these data. Perhaps the small slate fragments afford a unique combination of dry acidic substrate characteristics in a region of predominantly basic habitats.

Nahoni Wetland Stands

These hydric sites were sampled differently than other stands (see Methods) to provide general information on the far end of the moisture complex-gradient. Stand R1 is a *Betula glandulosa* - *Rubus chaemaemorus* - *Ledum palustre* streamside community, and stand R2 is dominated by *Eriophorum vaginatum* with *Carex biglowii* and *C. oederi*. The terrain is underlain by permafrost, and vegetated hummocks are interspersed with wet areas or standing water. Both stands are dissimilar to the three described macrolichen communities.

In R1 the important macrolichen species on upper hummocks include *Peltigera aphthosa* and *Cetraria cucullata*, with *Cladonia chlorophaea*, *Dactylina arctica* and *Cladina rangiferina* (Table 27). Major species of lower hummocks are *Cladina arbuscula*, *Dactylina arctica* and *Nephroma arcticum*. The last species is only found in very wet sites.

The upper portion of *Eriophorum vaginatum* tussocks has high cover of *Cetraria cucullata* and *Cladonia amaurocraea*. Lower tussock habitats are dominated by *Cladina arbuscula*

TABLE 27. Cover class values for macrolichen species in the Nahoni wetland stands R1 and R2.

R1	Cover class
Cetraria cucullata	2
Peltigera aphthosa	2
Dactylina arctica	2
Cladina arbuscula	2
Nephroma arcticum	2
Cladonia amaurocraea	1
Cladina rangiferina	1
Peltigera canina	1
Cetraria nivalis	1
C. richardsonii	1
C. islandica	1
Cladonia chlorophaea	1
Cetraria pinastri	+
Cladonia cornuta	+
C. gonecha	+
Peltigera pulverulenta	+
R2	
Cetraria cucullata	2
Cladonia amaurocraea	2
Cladina arbuscula	2
Cetraria islandica	1
C. nivalis	1
Cladonia chlorophaea	1
Cladina rangiferina	1
Peltigera aphthosa	1
P. canina	1
Dactylina arctica	1
Cetraria richardsonii	1
C. laevigata	1
Thamnolia subuliformis	1
Asahinea chrysantha	1

Cover classes:
+ = less than 1%
1 = 1 - 5%
2 = 6 - 15%

and *Cetraria cucullata*. Species which are found in either microhabitat for both stands include *C. cucullata*, *Cladina rangiferina* and *Cladonia amaurocraea*. Other generally distributed species are *Cetraria nivalis*, *C. islandica*, *Cladina arbuscula*, *Cladonia chlorophaea*, and *Peltigera aphthosa*. *Cetraria richardsonii* is the only species restricted to a lower hummock microhabitat in both stands.

Fellfields

Fellfields were rarely encountered in the study regions due to the predominance of unsuitable rock types. Only one fellfield site was found in each of the Divide and Ogilvie areas on sandstone and granite, respectively.

The sampling procedure was established for rock surfaces greater than 10 x 10 cm on the most horizontal surface (see Methods). This allowed general description of macrolichen vegetation, without assessing the additional zonation along corners and sides of rocks.

Macrolichen vegetation from both fellfields is summarized in Table 28. Several species appear to be restricted to rock habitats, including *Alectoria minuscula*, *A. pubescens*, *Cetraria hepatizon*, *Hypogymnia oroarctica*, *Parmelia almquistii*, *P. centrifuga*, *P. panniformis*, *P. saxatilis*, *Umbilicaria cylindrica*, *U. hyperborea*, *U. phaea* and *U. proboscidea*. Small pockets of soil on the rock surfaces support the terricolous species *Alectoria ochroleuca*, *Cladonia coccifera/metacorallifera*, *Dactylina ramulosa* and *Thamnolia*

TABLE 28. Cover class values for macrolichen species in fellfield stands O2 and D3, and inter-stand similarity.

	Cover class
O2	
Umbilicaria hyperborea	3
Umbilicaria proboscidea	2
Cetraria hepatizon	2
Parmelia centrifuga	2
Parmelia panniformis	1
Cetraria nigricans	1
Alectoria ochroleuca	1
Parmelia almquistii	1
Cladonia coccifera/metacorallifera	1
Alectoria nigricans	+
Alectoria pubescens	+
Hypogymnia oroarctica	+
Umbilicaria phaea	+
Thamnolia subuliformis/vermicularis	+
D3	
Umbilicaria hyperborea	3
Alectoria minuscula	2
Hypogymnia oroarctica	2
Umbilicaria proboscidea	1
Alectoria pubescens	1
Parmelia saxatilis	+
Umbilicaria cylindrica	+
Dactylina ramulosa	+
Thamnolia subuliformis	+

Cover classes:
+ = less than 1%
1 = 1 - 5%
2 = 6 - 15%
3 = 16 - 30%

Percent Similarity (PS) = 36%
Coefficient of Community (CC) = 43%

subuliformis/vermicularis in the Ogilvie site.

Similarity between fellfields was assessed with coefficient of community and percent similarity indices for macrolichen data (Table 28). The former index produced lower similarity values for fellfields than for other Ogilvie and Divide sites (Table 17). This suggests regional floristic dissimilarity, which is amplified by greater species richness in the Ogilvie fellfield. Low percent similarity between fellfields indicates that species in common do not exhibit importance trends which are sufficiently similar to override importance values from additional species.

Fellfields are characterized by several crustose lichens in addition to macrolichens. The rock surface microhabitat favors crustose lichens over most plant groups, although competitive and successional interactions are not known. It is perhaps more suitable in fellfield studies to describe crustose lichen species and cover values along with macrolichens, than to assess macrolichens alone. Common crustose genera in such habitats include Buellia, Caloplaca, Candelariella, Dimelaena, Haematomma, Lecanora, Lecidea, Rhizocarpon, Sporostatia and Staurothele. Relevant studies of crustose and macrolichen species in fellfields may be found in Bryant and Scheinberg (1970), Bird (1974a, 1974b), Daniëls (1975) and Kuchar (1975).

Integration of Macrolichen and Vascular Plant Communities

Alberta

Partial correspondence of the macrolichen and vascular plant communities is due to an unequal number of designations (Fig. 10). Communities have been independently derived in each data set to provide convenient plant-habitat references. However, these designations tend to conceptually eliminate the original vegetation gradients which are evident in the extensive overlap of communities in Fig. 10.

The major implication of overlapping communities is that responses to environmental factors vary between different groups of plants. In this case, macrolichen community 1 is found in vascular plant communities 1 and 2 in dry habitats with basic substrates. In mesic substrate units of vascular plant community 2 there is a shift to the second macrolichen group. This macrolichen community is most closely associated with mesic and acidic vascular plant group 3, and is also represented in the fourth community. Macrolichen community 3 is also found with both vascular plant groups 3 and 4.

Lichens are long-lived, and may not be influenced directly by the same time factors which affect vascular plants. Thus, macrolichens may not exhibit comparable species groups or communities to those of vascular plants at a given point in time. However terricolous alpine macrolichen species are found in close association with slowly growing

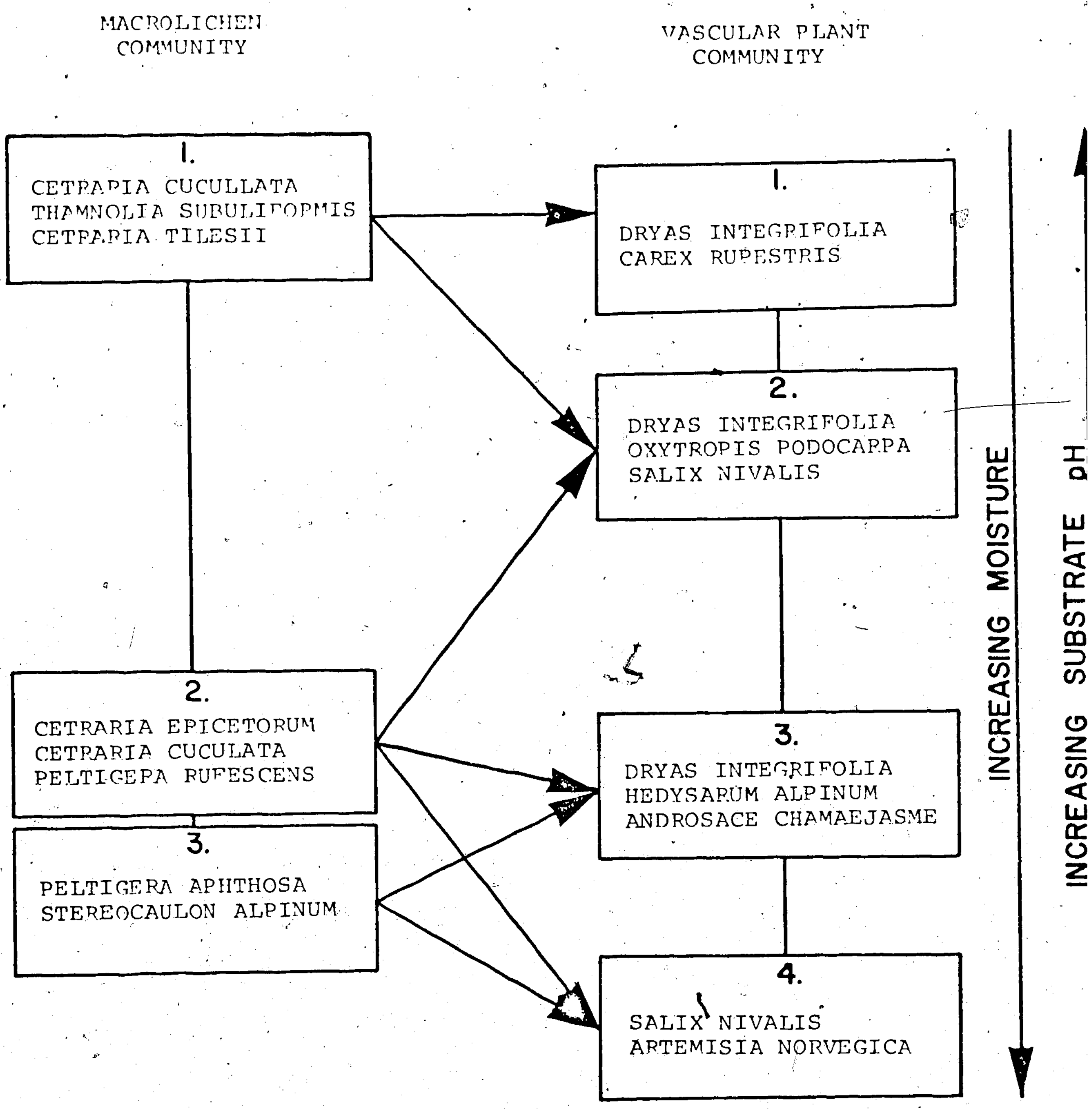


FIGURE 10. Interrelationships of macrolichen and vascular plant communities in Alberta along complex-gradients of moisture and substrate pH.

plants like Dryas spp. which influence several of the physical microhabitat parameters. Therefore, macrolichen communities could be expected to vary with vascular plant vegetation.

The greater number of vascular plants than macrolichen species may be important in the differences between plant communities. Greater competition and narrower ecological amplitudes could be expected for many of the vascular plants than for the small number of more widely distributed macrolichens. This would partially explain the discrepancy between community designations, as well as the greater implied sensitivity of vascular plant species to environmental complex-gradients.

Yukon

Community designations for vascular plants and lichens exhibit a high degree of correspondence in the Yukon areas (Fig. 11). Only two Nahoni substrate units are displaced and both shift from macrolichen community 2 to vascular plant group 1. These wet sites (N2, N5) have comparable similarity values to each of the first two vascular plant communities, so this relocation is not a significant discrepancy.

The correlation between plant communities (Fig. 11) contrasts with results from Alberta. This may be due to a clearly defined moisture complex-gradient and higher macrolichen species richness in the Yukon data. The greater

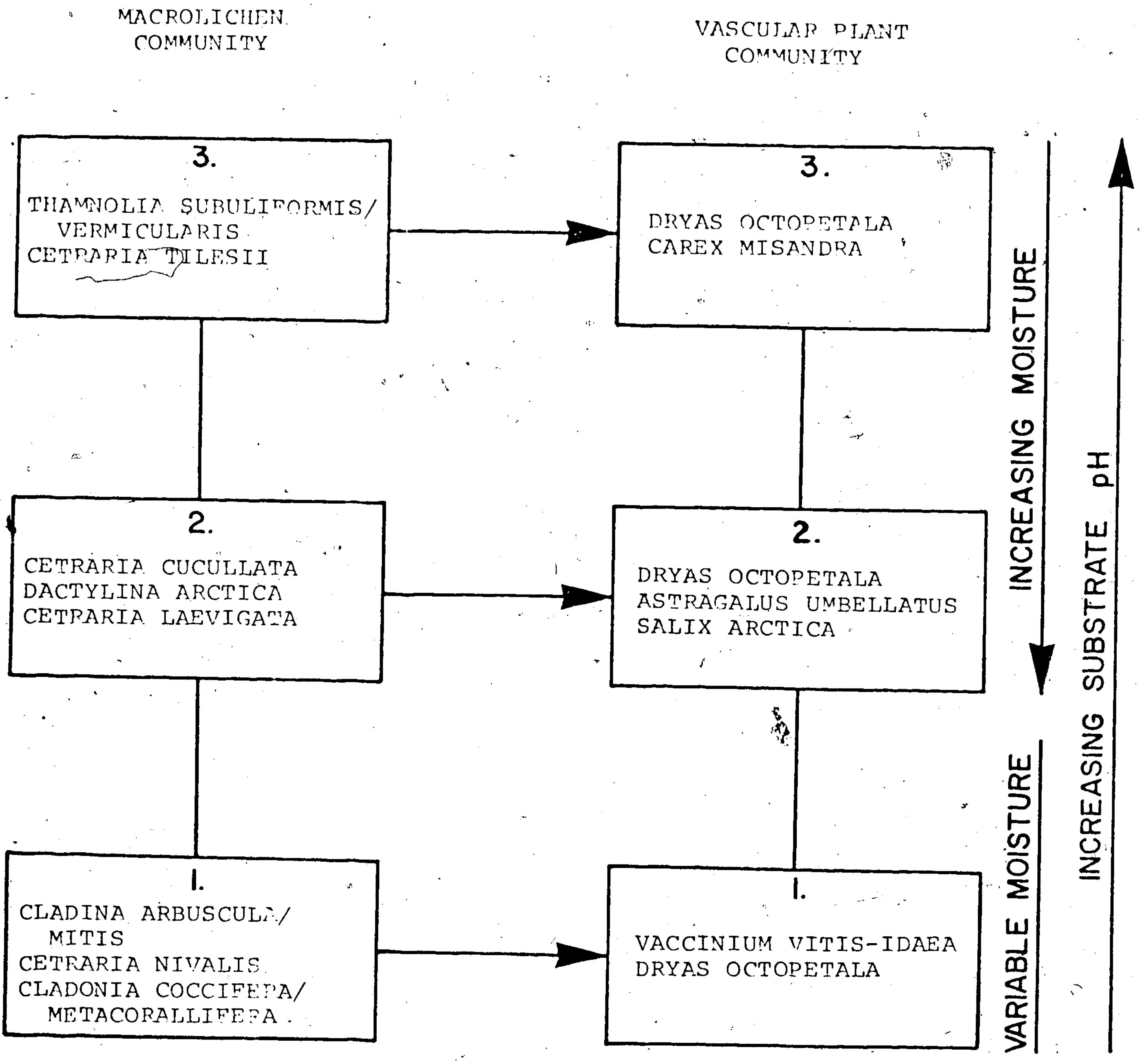


FIGURE 11. Interrelationships of macrolichen and vascular plant communities in the Yukon along complex-gradients of moisture and substrate pH.

number of species suggests that patterns of ecological amplitude are more similar in both groups of plants, which would promote parallel vegetation changes along environmental complex-gradients.

Based upon results from this investigation, vascular plant communities in the Yukon study regions reflect terricolous macrolichen communities. Such correlation may have high predictive value in other northern Yukon regions. In contrast, the Front Range environment in Alberta shows less precise correlation of macrolichen and vascular plant communities. The degree of correspondence is sufficient for general predictive purposes and is most appropriate for dry sites in the Front Ranges.

Species Response Patterns

Introduction

Individual macrolichen species have previously been mentioned in the context of plant communities. In this section, macrolichen species are examined individually with species population response patterns (Whittaker 1973a) derived by plotting cover values on the regional ordinations. Since the ordinations display parallel gradients of moisture and substrate pH for the areas in each region, the ecological importance of these factors can be visually estimated for each species. The ecological amplitude of each species is graphically approximated by the response pattern, and can be compared with those of other species in the area or region.

The ordinations used to construct the species population response patterns are those in Figures 7 and 9, with environmental parameters indicated along the axes. All cover values have been returned to cover classes, and are grouped with isodems (Whittaker 1973a) to facilitate interpretation.

Response patterns of macrolichen species are placed into six ecological groups (Whittaker 1973b) based upon substrate pH association as follows: (1) ubiquist (common with wide ecological amplitude); (2) common on both substrates with greater importance values on acidic substrates; (3) exclusively found on acidic substrates; (4) equally represented on both substrates; (5) common on both substrates with greater importance values on basic substrates; and (6) exclusively found on basic substrates.

Since general differences in areas are indicated in the substrate pH gradients, these values are used instead of moisture regime in determining ecological groups. Species within each of these groups have differing ecological amplitudes which are related to a moisture complex-gradient.

Rare species are included in the six categories of response patterns in one of the two restricted groups (3 and 6). These species can thus be tentatively evaluated, without overestimating importance. The value of including such species in this section is to compare population responses in different regions, especially in cases where a species is significantly more important in one region than in the other.

Alberta

(1) Ubiquists

There are five common and abundant species in the ubiquist group (Fig. 12). Cetraria cucullata and Thamnolia subuliformis are the most evenly distributed across the ordination, and both attain highest cover in the mesic sites. Cetraria nivalis and Cornicularia aculeata are also frequent but have higher cover values in the basic sites. In contrast Cetraria ericetorum has greatest importance in mesic and acidic sites. Of these species, C. cucullata seems to be the most important macrolichen when comparing all sites.

(2) Common Species on Acidic Substrates

All species of this group are relatively infrequent, and occur more often in acidic than in basic sites (Fig. 13). Peltigera rufescens is the most common species with highest cover in mesic and acidic Prospect stands. However, it is most frequent in Divide vegetation substrate units. Cladonia pocillum has a similar but more limited response pattern. Both species are restricted to mineral soil, where they apparently colonize readily and their abundance may be more dependent upon availability of soil rather than soil attributes. Cetraria laevigata (Fig. 13) and Alectoria chalybeiformis are both infrequent, with marked association with acidic substrates.

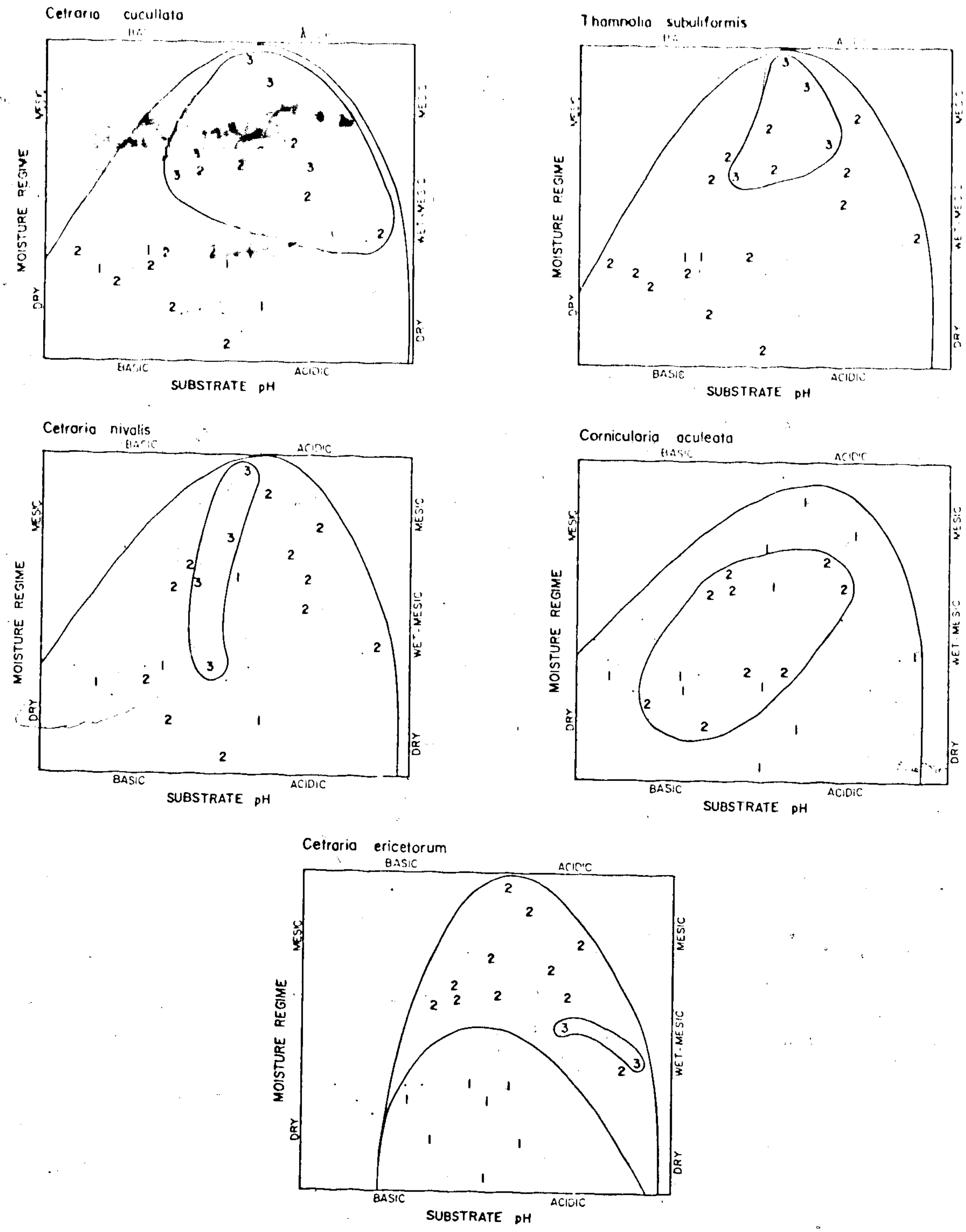


FIGURE 12. Response patterns of macrolichen species in Alberta sites: ubiquists. Cover classes are 1 = 1-5%, 2 = 6-15%, 3 = 16-30%, 4 = 31-50%.

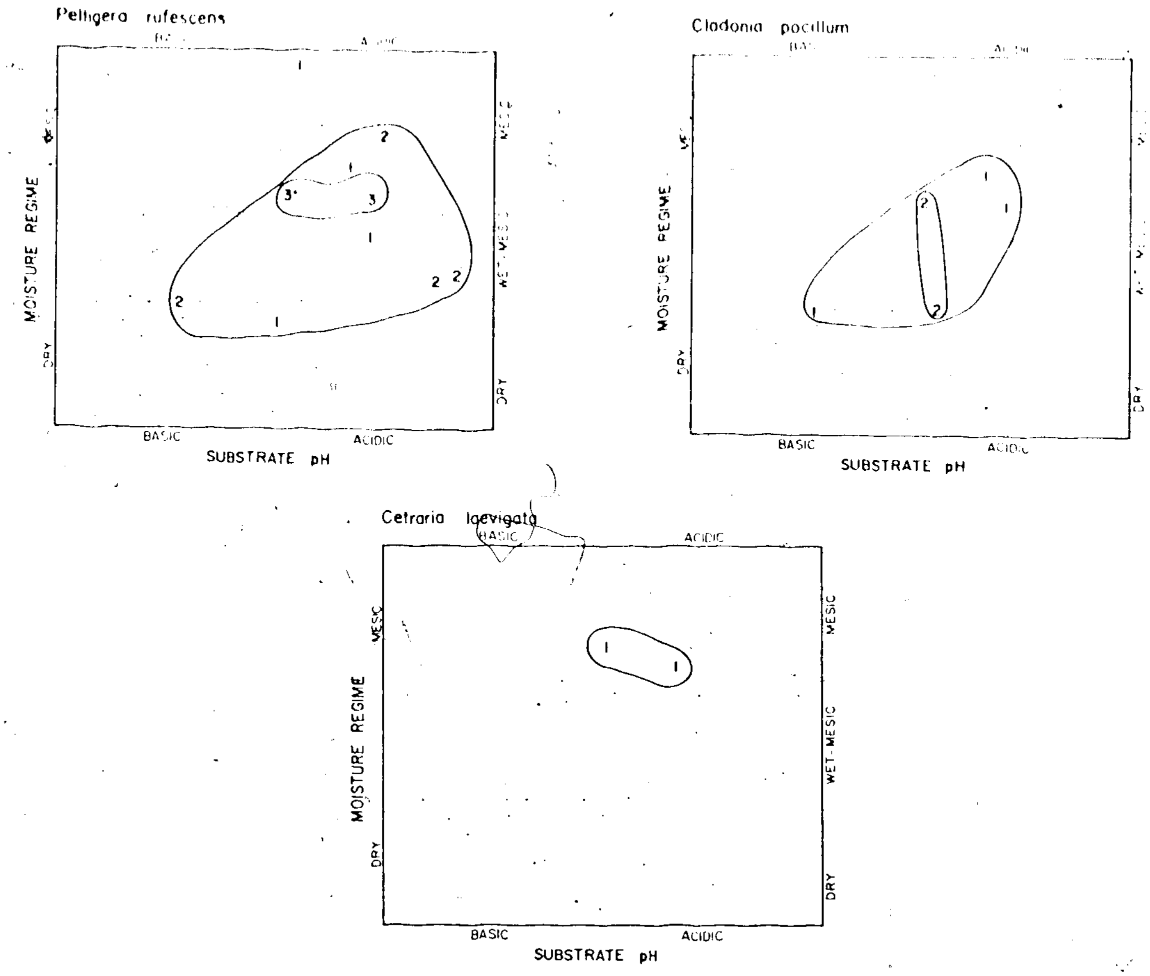


FIGURE 13. Response patterns of macrolichen species in Alberta sites: common on acidic substrates.

(3) Species Exclusively on Acidic Substrates

Stereocaulon alpinum/rivulorum and *Cladonia pyxidata/macrophyllodes* exhibit high frequency on acidic sites (Fig. 14). This is accentuated in each case by combining taxa, which was done because field determinations were not feasible. *Peltigera aphthosa* is of low frequency but high cover in mesic acidic sites (Fig. 14). Species of minor occurrence and importance include *Alectoria nigricans*, *Cetraria islandica* (Fig. 14), *Leptogium saturninum* and *Cladonia ecmocyna/gracilis*.

Three restricted snowbed species *Cladonia coccifera*, *Nephroma expallidum* and *Solorina crocea* are also in this group. *Hypogymnia subobscura* and *Psoroma hypnorum* are found in one mesic Divide stand. Scarcity of acidic areas is partially responsible for low frequencies in this group of species.

(4) Common Species on Both Substrates

The only species of similar response on both substrates is *Dactylina arctica* (Fig. 14). The abundance of this species on mesic sites indicates that moisture is more important than substrate acidity.

(5) Common Species on Basic Substrates

Common species on basic sites include *Alectoria ochroleuca*, *Physconia muscigena* and *Cetraria tilesii* (Fig. 15). All occur on acidic sites as well, but with reduced cover

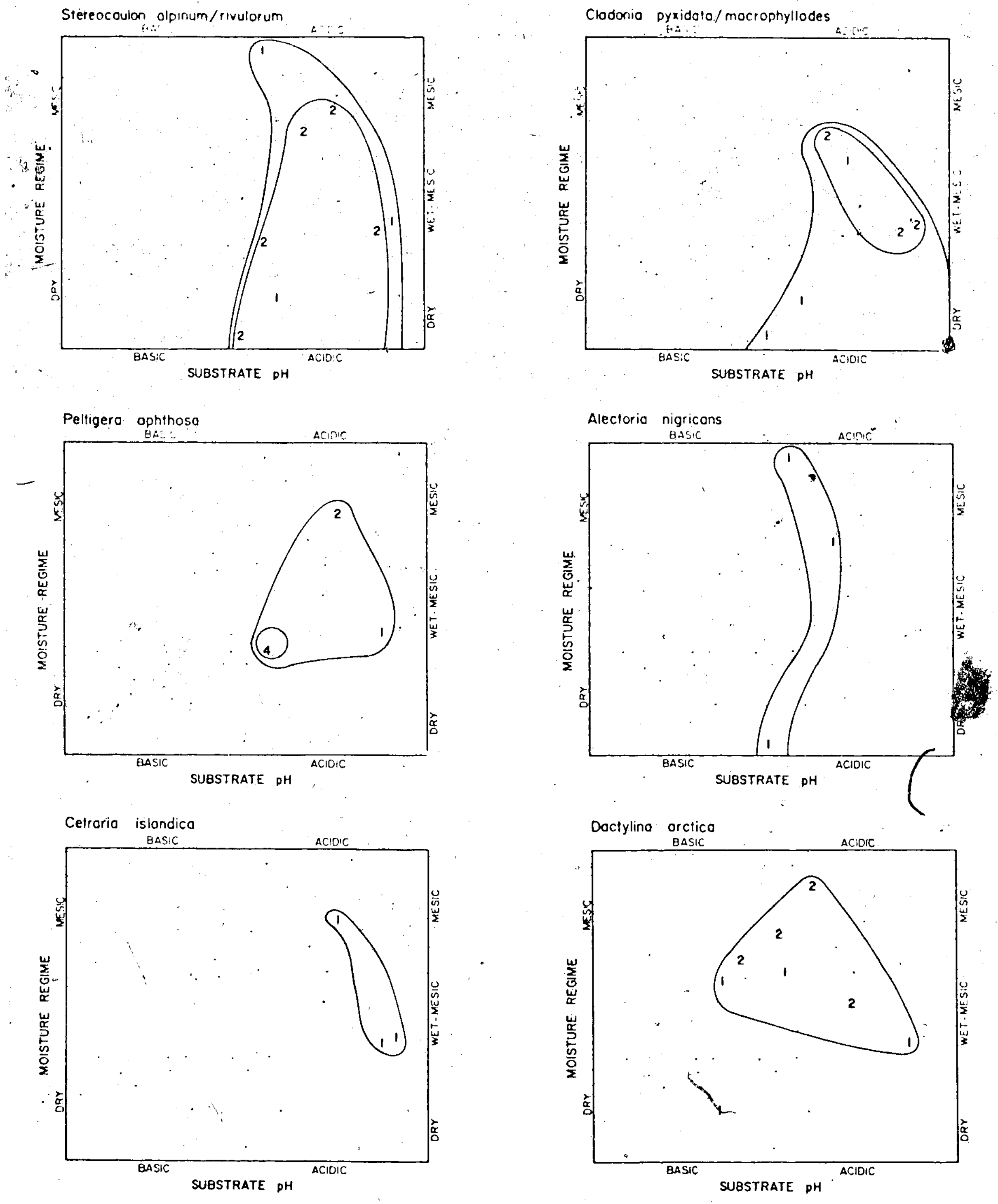


FIGURE 14. Response patterns of macrolichen species in Alberta sites: exclusively on acidic substrates; and common on both substrates (*Dactylina arctica*).

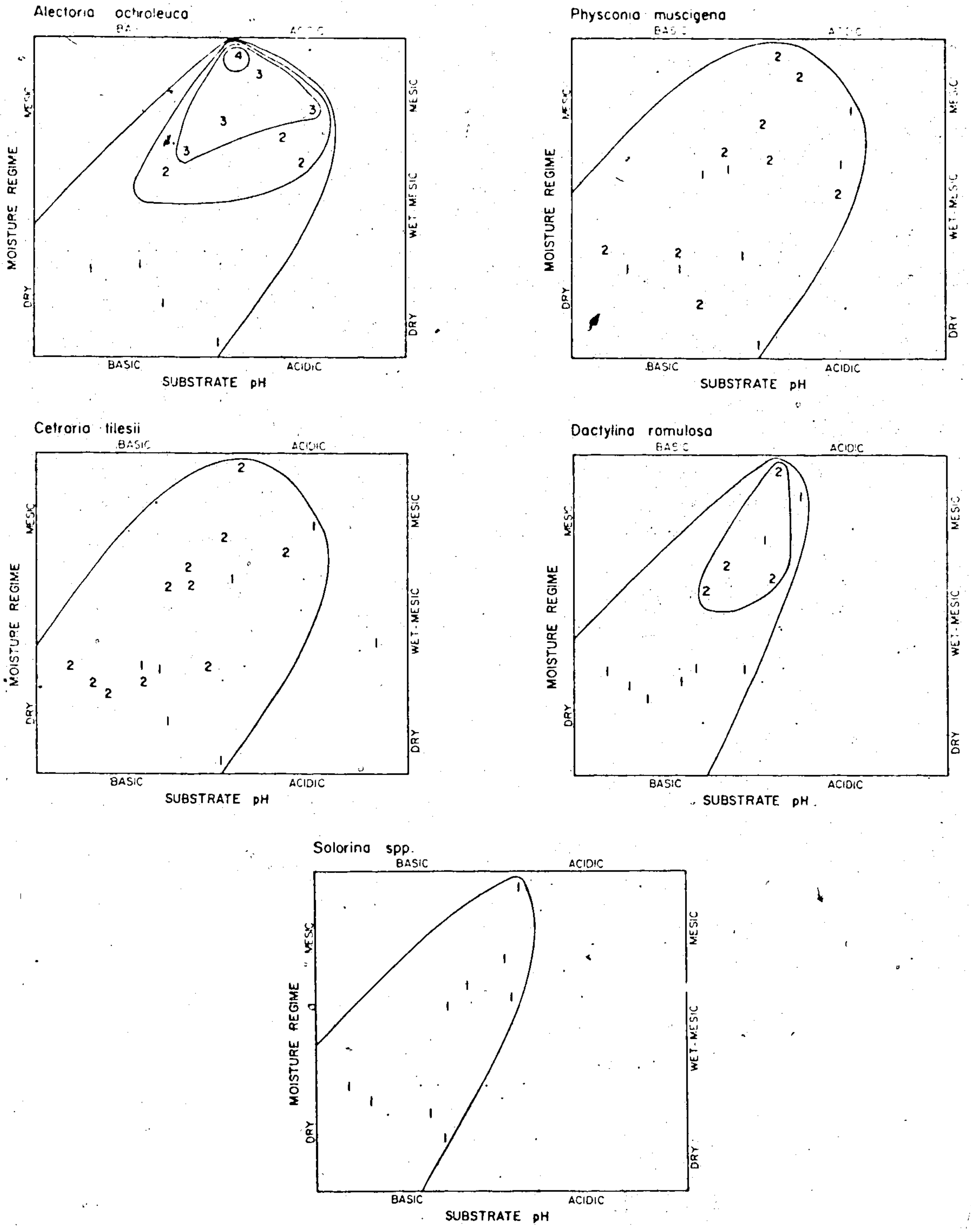


FIGURE 15. Response patterns of macrolichen species in Alberta sites: common on basic substrates; and exclusively on basic substrates (Dactylina ramulosa and Solorina spp.).

and frequency. *Alectoria ochroleuca* is the only species with a distinct arrangement of cover values. The pattern partially correlates with moisture, and is more closely related to increase in total vegetation cover. This is consistent with field observations where *A. ochroleuca* thalli were best developed on stable, well-vegetated mesic slopes.

(6) Species Exclusively on Basic Substrates

The only species restricted to basic substrates are *Dactylina ramulosa* and *Solorina* spp. (Fig. 15). The former is more important in mesic sites, while the latter is evenly distributed. With the addition of group 5 (three species) and two species from group 1, there are fewer species associated with basic than with acidic habitats. This may be due to the prevalence of dry, discontinuous and relatively species-poor vegetation in these areas.

Yukon

(1) Ubiquists

The ubiquist group includes *Dactylina arctica*, *Cetraria islandica*, *C. nivalis* (Fig. 16), *Thamnolia subuliformis/vermicularis*, *C. cucullata*, *C. laevigata*, and *Alectoria ochroleuca* (Fig. 17). Of these, *D. arc[illegible]a* (Fig. 16) shows the strongest association with wet and mesic sites, with lower importance in drier areas. *Cetraria islandica* exhibits a similar tendency, but is not as abundant in wet sites and maintains importance in drier sites. The pattern

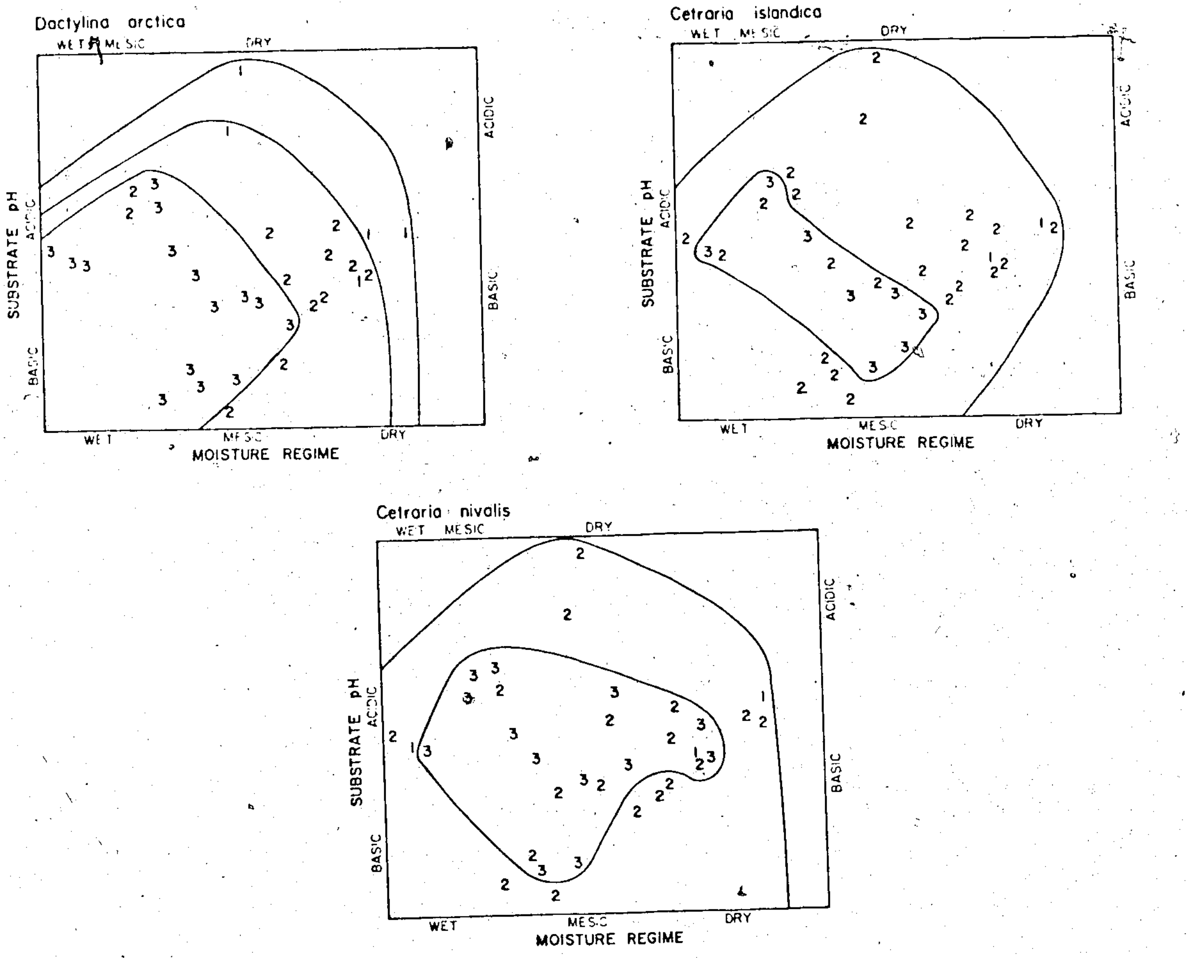
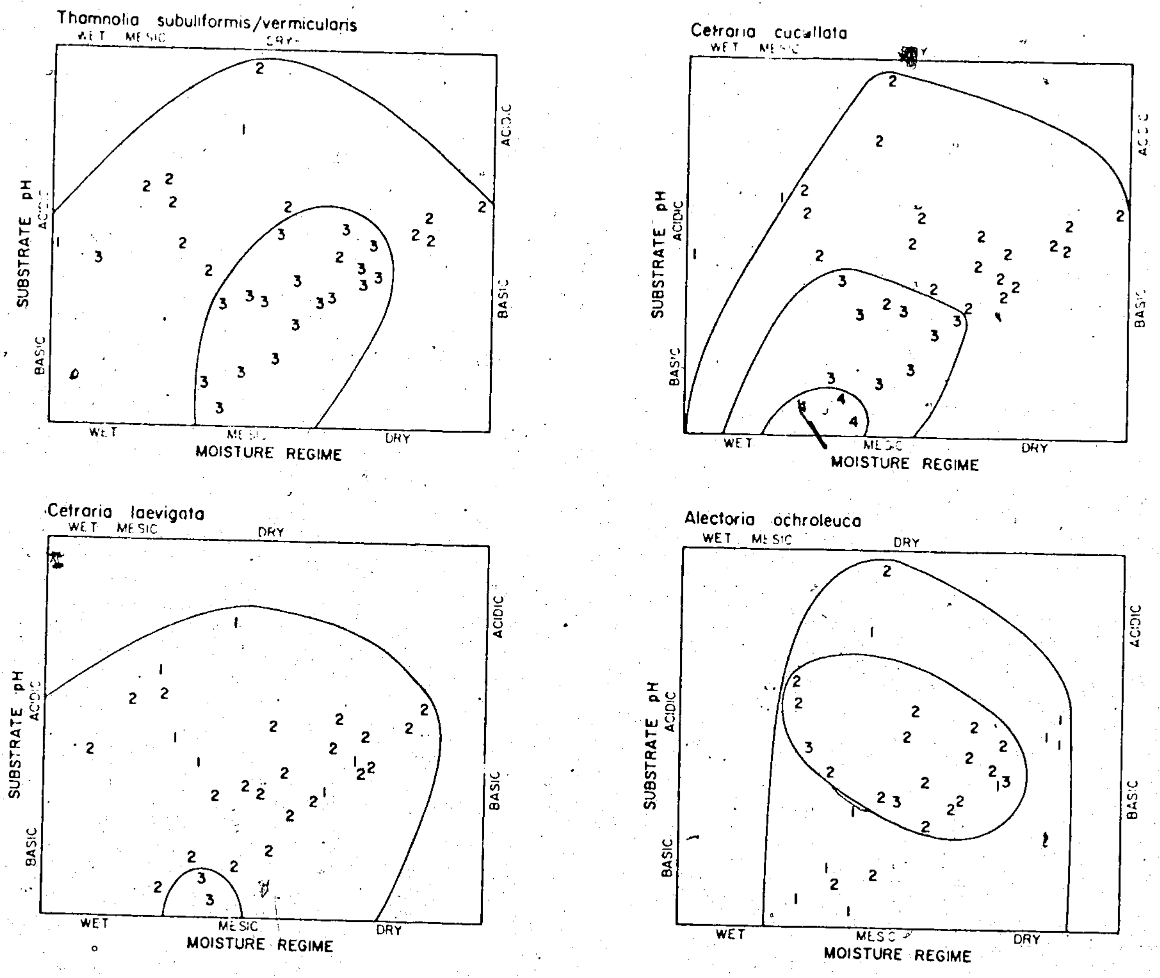


FIGURE 16. Response patterns of macrolichen species in Yukon sites: ubiquists.


Thamnolia subuliformis/vermicularis

Cetraria cucullata

Cetraria laevigata

Alectoria ochroleuca

FIGURE 17. Response patterns of macrolichen species in Yukon sites: ubiquists.

of C. nivalis is similar to that of C. islandica, but the former has higher importance in the entire mesic region of the ordination. These three species are the most pronounced generalists, yet all have distinct and unique habitats in which importance is maximized.

The four remaining species in this group (Fig. 17) show a minor qualitative decrease in Ogilvie sites. The greatest importance of Cetraria cucullata and C. laevigata is in Nahoni snowbeds, with mid-range values in wet to mesic Nahoni sites and lowest values in dry sites of both areas. Thamnolia subuliformis/vermicularis and Alectoria ochroleuca exhibit mesic versions of this pattern. Since none of these species is apparently restricted by either moisture or pH alone, there is some other reason why these generalists are less successful in the Ogilvie sites. One possibility is that competition from a group of specialists limits these generalists on acidic substrates.

(2) Common Species on Acidic Substrates

The largest response pattern in this group is that of Cladonia echinocyna/gracilis (Fig. 18). This may be due to combining the two taxa, if they actually have different habitat requirements. All but one Ogilvie site is included in addition to less than half the Nahoni sites. Most Nahoni occurrences are on acidic substrates.

Species of local abundance include Cladina stellaris, C. arbuscula/mitis, Cladonia uncialis, and Cladina rangifer-

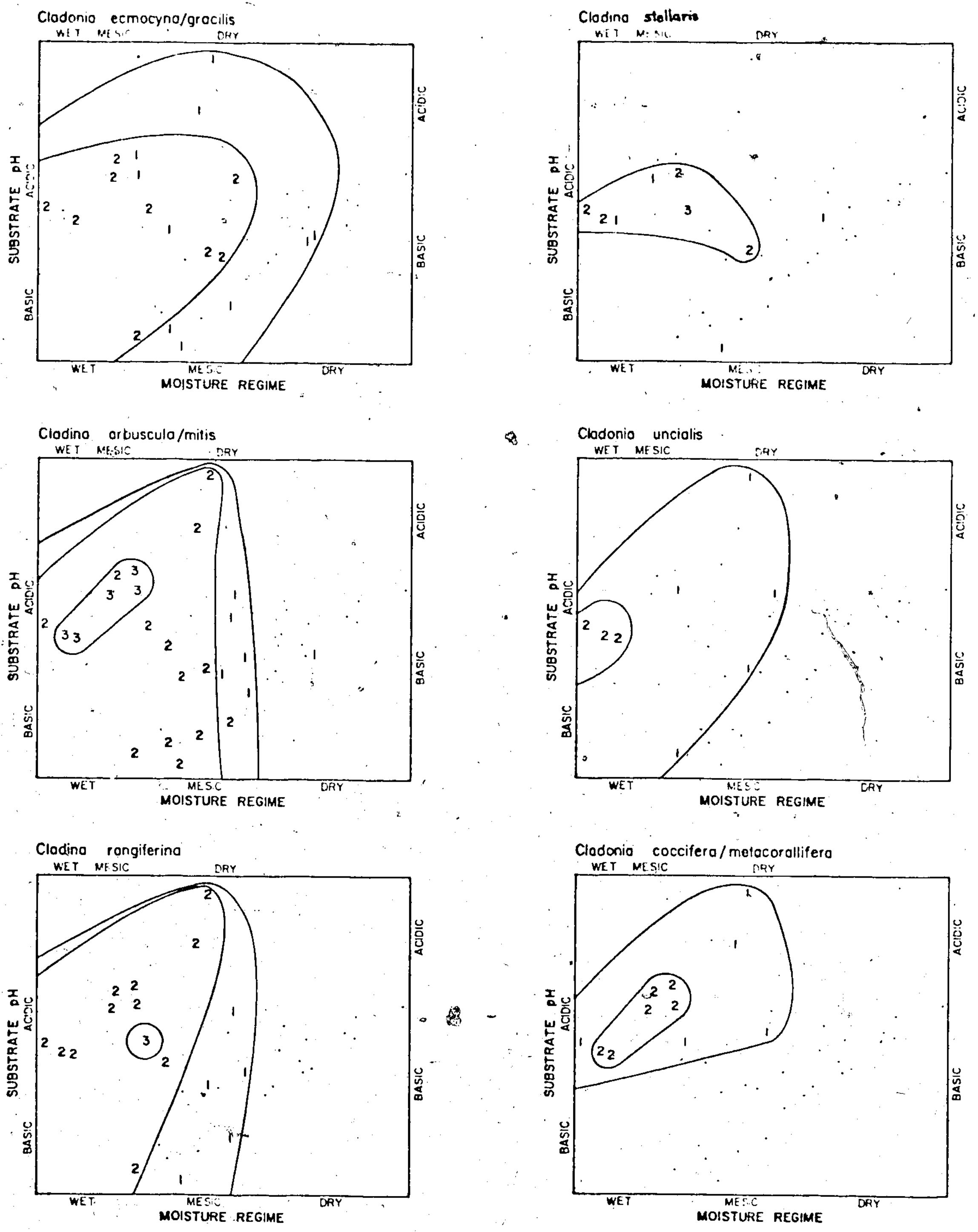


FIGURE 18. Response patterns of macrolichen species in Yukon sites: common on acidic substrates.

ina (Fig. 18). All occur in wet and mesic Nahoni sites, but achieve much greater cover in Ogilvie sites. These species seem to have broader tolerances to different moisture regimes when the substrate is acidic.

A subgroup of four species is completely restricted to the Ogilvie area with the exception of one dry and acidic Nahoni stand (N13). The species are absent from most Nahoni sites due perhaps to specialized habitat requirements. Included are *Cladonia coccifera/metacorallifera* (Fig. 18), *Cetraria nigricans*, *Cladonia amaurocraea* (Fig. 19), and *C. macrophyllodes*.

The remaining four species are *Sphaerophorus globosus*, *Cetraria ericetorum*, *Stereocaulon alpinum* (Fig. 19) and *Peltigera malacea*. These are all relatively uncommon, and occur in some Ogilvie stands as well as in acidic Nahoni stands (e.g. N13, N5). Of these, *S. globosus* is the most common in both areas and is restricted to wet-mesic mineral soil with low pH.

(3) Species Exclusively on Acidic Substrates

The most common species which occur only in the Ogilvie area are *Cladonia crispata*, *Solorina crocea*, *Peltigera pulverulenta* and *C. macrophylla* (Fig. 20). Rare species include *C. bellidiflora*, *Psoroma hypnorum*, and *Peltigera rufescens*.

Groups 2 and 3 include 22 species which are poorly represented or missing outside the Ogilvie sites. These

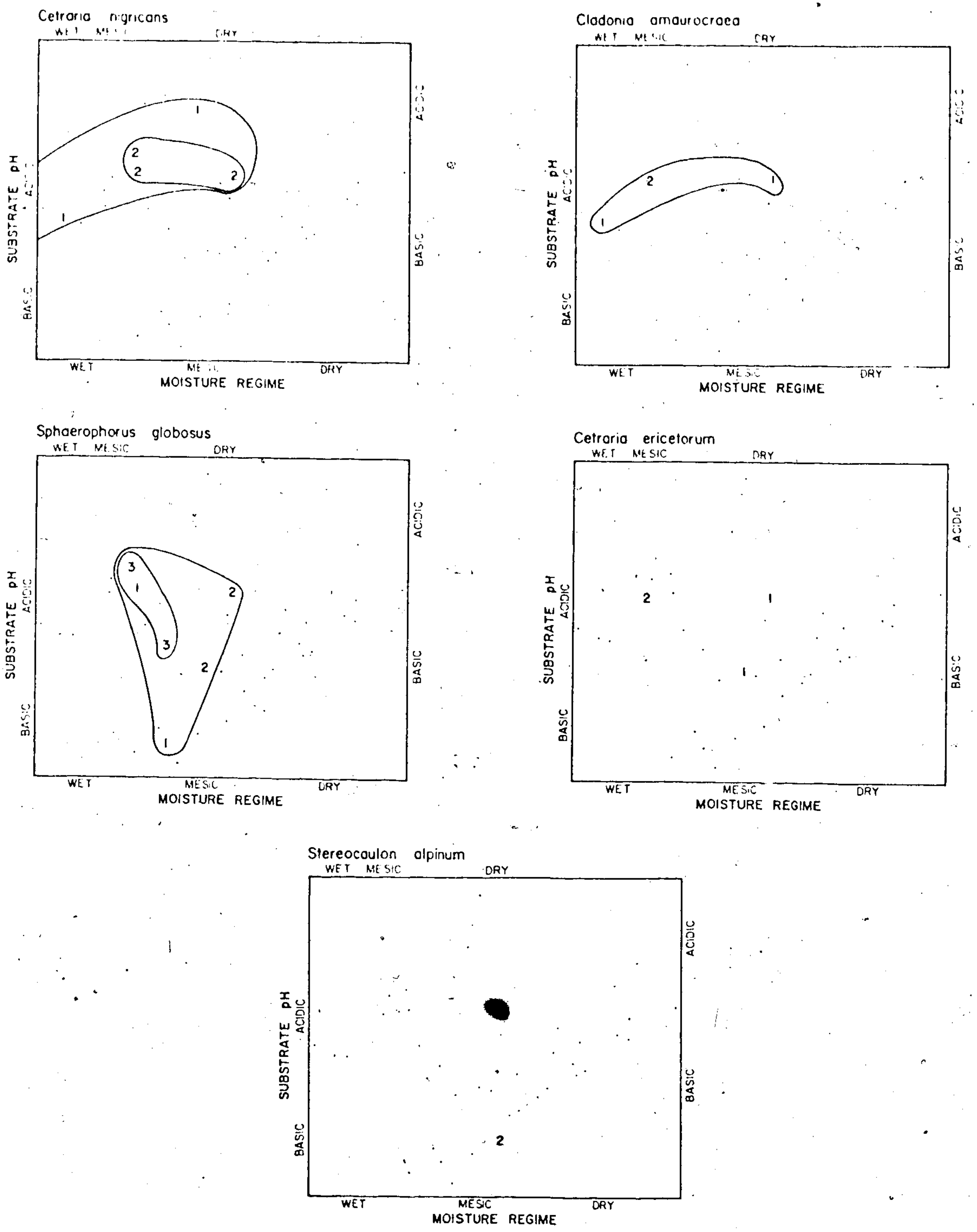


FIGURE 19. Response patterns of macrolichen species in Yukon sites: common on acidic substrates.

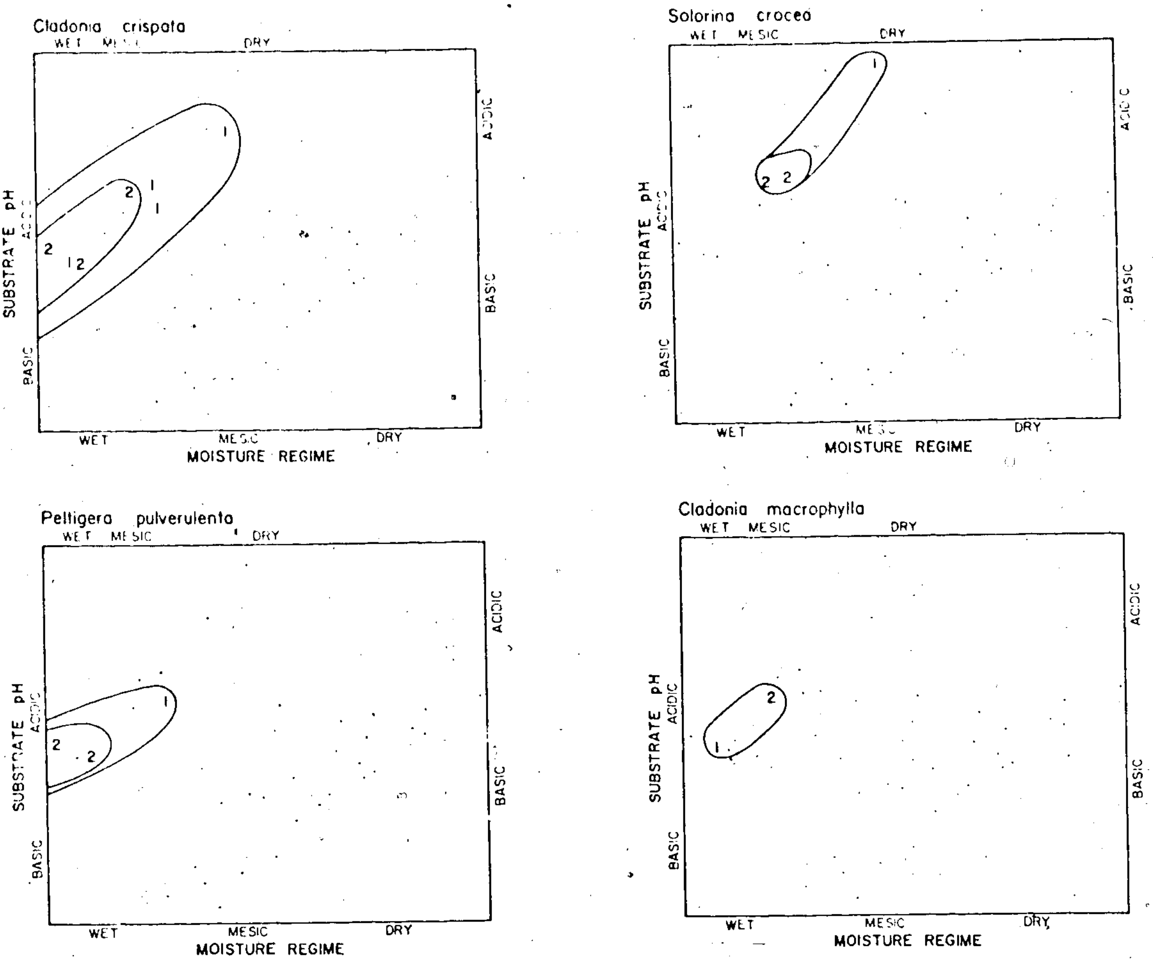


FIGURE 20. Response patterns of macrolichen species in Yukon sites: exclusively on acidic substrates.

populations seem to be specialists for the acidic habitats in this area, which would explain their restricted abundance patterns, as well as the minimal importance of four generalist species from group 1 (Fig. 17).

(4) Common Species on Both Substrates

Three species are equally important in both areas. All are found in wet-mesic habitats and are apparently dependent upon moisture regardless of other environmental factors. Cetraria richardsonii shows the highest importance values of the three species, with negligible cover or frequency in mesic sites (Fig. 21). Peltigera aphthosa is slightly more important in Ogilvie sites. Nephroma expallidum is infrequent in Ogilvie sites and is restricted to very wet Nahoni stands.

(5) Common Species on Basic Substrates

Four species are found commonly in the Nahoni and are less quantitively important in the Ogilvie area. Of these, Dactylina ramulosa is most important in mesic Nahoni sites, with a broader moisture tolerance or requirement in Ogilvie sites (Fig. 22). Since populations of D. ramulosa respond differently in these areas, the group designation for this species was based upon greater total importance values in the Nahoni area.

Cornicularia divergens, Cladonia pyxidata/pocillum and Alectoria nigricans are abundant in the mesic Nahoni region

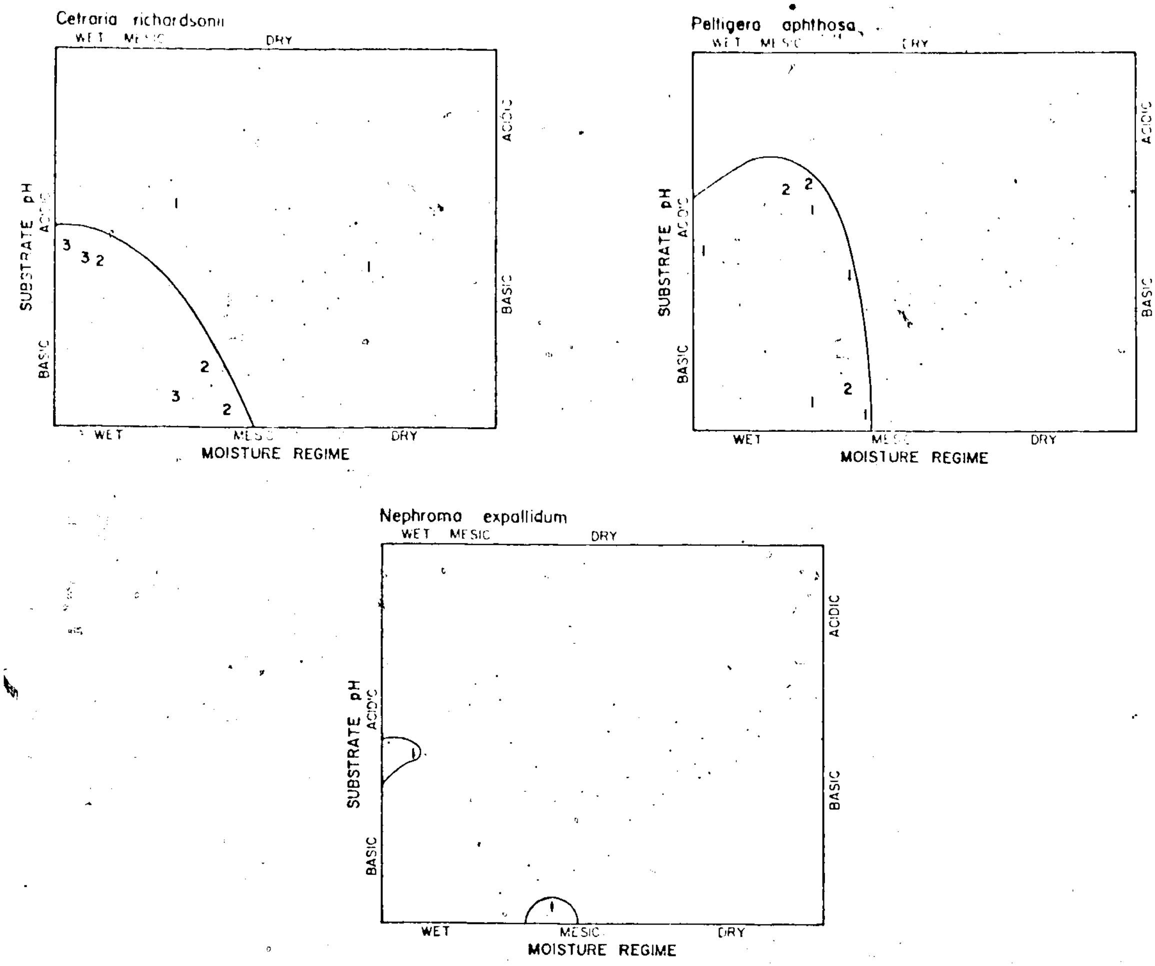


FIGURE 21. Response patterns of macrolichen species in Yukon sites: common on acidic and basic substrates.

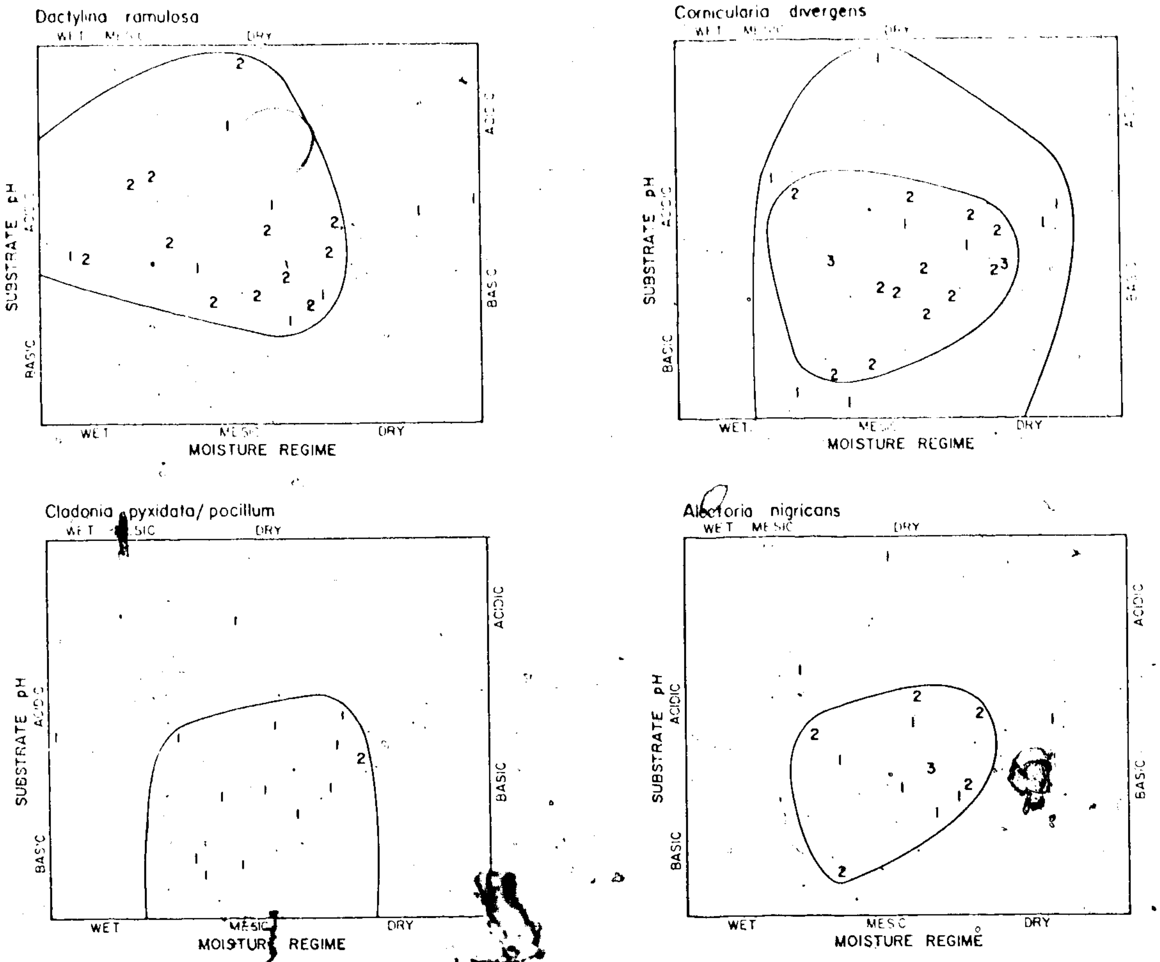


FIGURE 22. Response patterns of macrolichen species in Yukon sites: common on basic substrates.

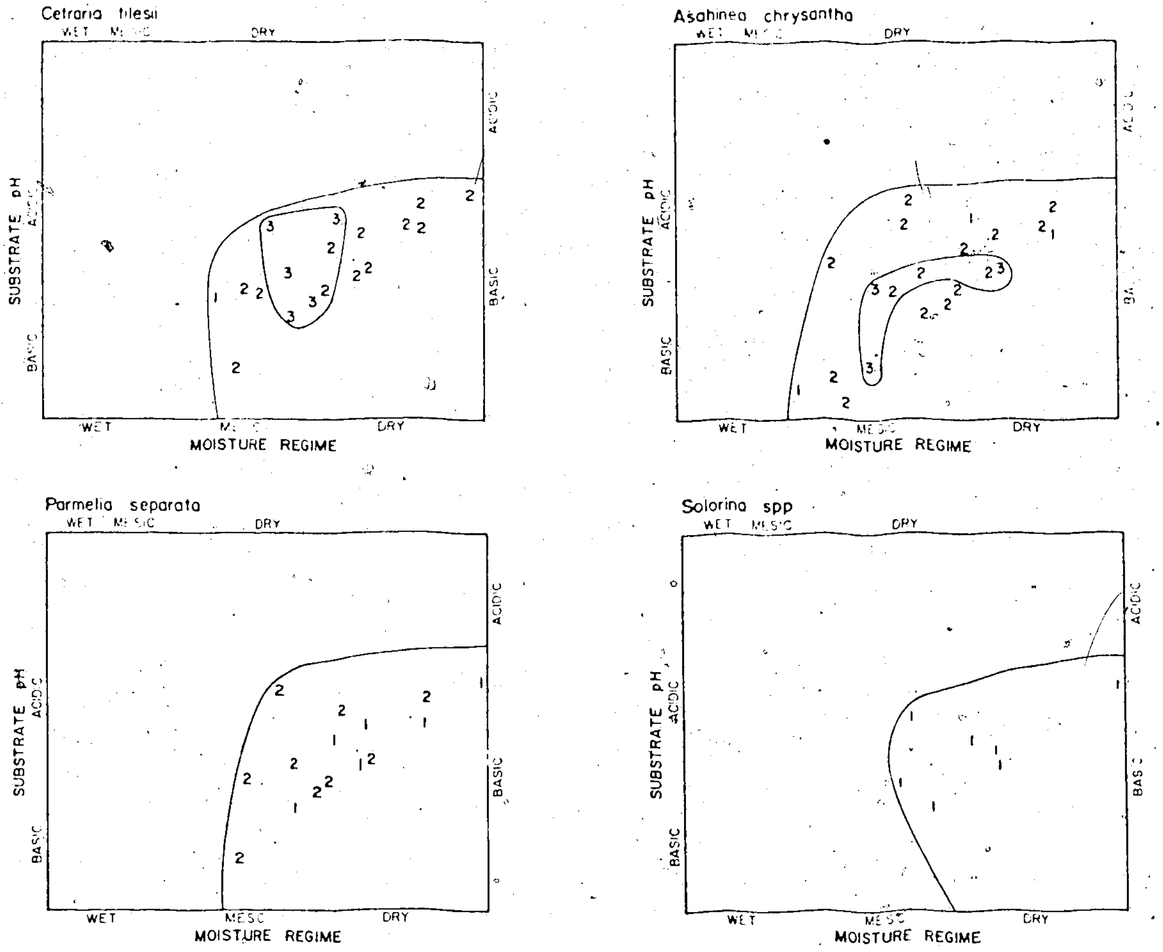
of the ordination (Fig. 22). *Alectoria nigricans* shows a tendency toward greater importance in less basic and mesic-wet sites.

These species characterize well-vegetated dry to mesic Nahoni areas. *Cladonia pocillum* and *C. pyxidata* are usually found on mineral soil, which is continually available due to frost action and animal activity. This habitat represents a patchy microenvironment within vegetated sites.

(6) Species Exclusively on Basic Substrates

A group of seven species is restricted to mesic and dry habitats in Nahoni sites. *Cetraria tilesii* and *Asahinea chrysantha* are the most common species, and both attain high importance values in mesic sites (Fig. 23). *Parmelia separata* and *Solorina* spp. are also common with even patterns of importance values. The other three species are less frequent (Fig. 24) and *Cornicularia aculeata* shows the driest association of these. *Hypogymnia subobscura* and *Alectoria nitidula* are both centred in mesic stands. The pattern of *A. nitidula* closely resembles that of *A. nigricans* (Fig. 22) but shows a narrower ecological amplitude.

This group may include calcicoles as well as Beringian populations which have not dispersed into the Ogilvie area. *Cetraria tilesii*, *Asahinea chrysantha*, *Parmelia separata*, *Solorina* spp., and *Cornicularia aculeata* may be calcicoles based upon these data. *Alectoria nitidula* and *Hypogymnia subobscura* are not because the former is found on dead sedge



Cetraria tilesii

Asahinea chrysantha

Parmelia separata

Solorina spp

FIGURE 23. Response patterns of macrolichen species in Yukon sites. exclusively on basic substrates.

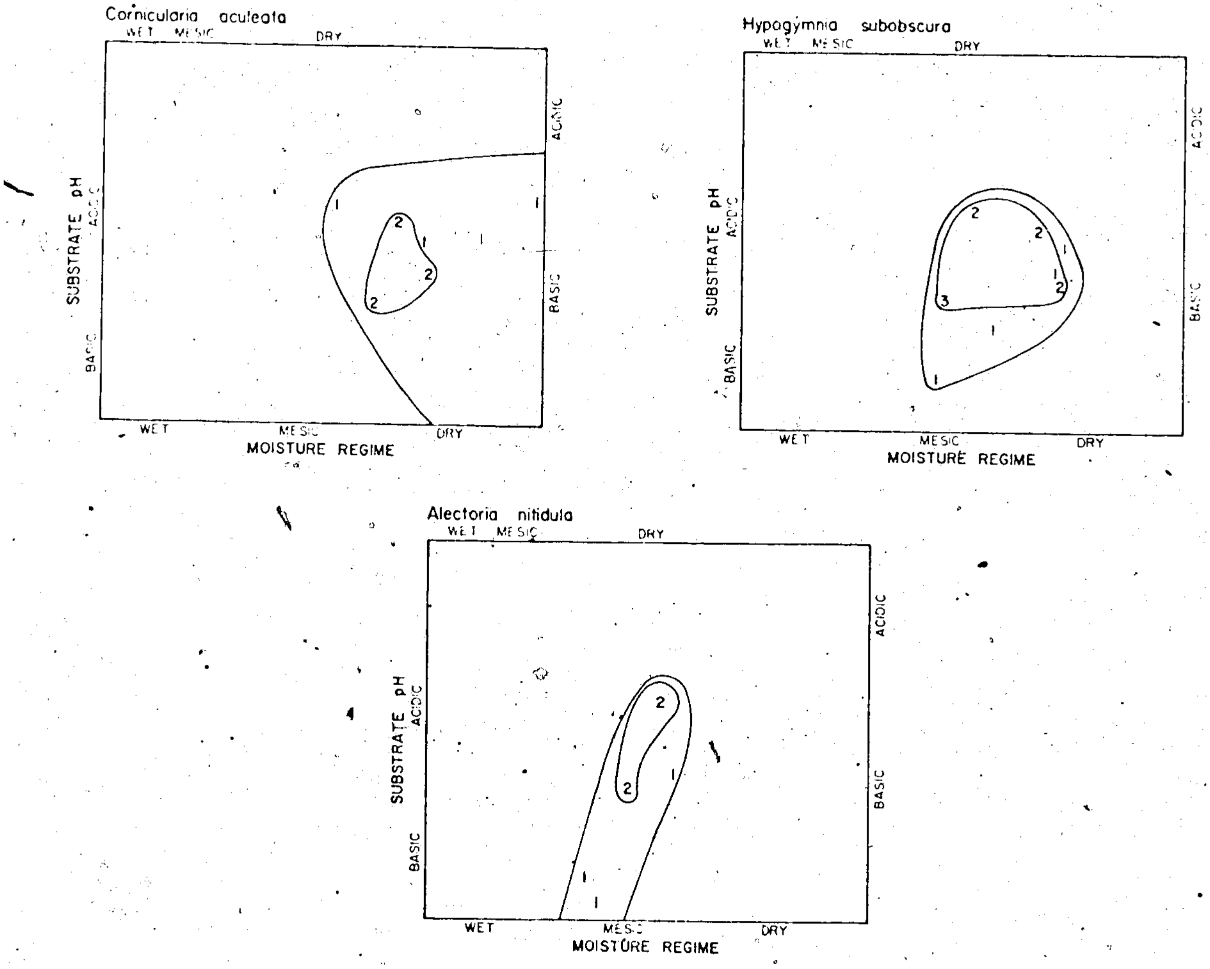


FIGURE 24. Response patterns of macrolichen species in Yukon sites exclusively on basic substrates.

mats, and the latter is associated with slate areas or mesic sites.

Asahinea chrysantha, P. separata and H. subobscura are probably restricted to the Nahoni area due to poor dispersal ability. None of these species has reproductive structures, and all possess a thick thallus which does not fragment easily. One tiny thallus of A. chrysantha was found in the Ogilvie area, but its lack of success could be due to a variety of factors, including recent establishment.

Integration

The six categories of species response patterns in each region are compared in Table 29. Of the 23 taxa common to both regions, [illegible] ubiquists and three species from other groups exhibit comparable substrate relationships. The remaining ubiquists are less frequent in the other region due to narrower moisture range or substrate pH association.

The ubiquist pattern of Cetraria ericetorum in Alberta may be due to the greater tolerance this species has to the arid southern Rocky Mountain environment in the Front Ranges. This type of habitat restricts congeners C. islandica and C. laevigata. Another species, C. richardsonii is missing altogether from Alberta. Cetraria ericetorum is not as important in cover nor as widely distributed in the Yukon where there are several other Cetraria species including C. nigricans, C. delisei, C. andrejevii, C. elenkinii, C. islandica,

TABLE 29. Ecological groups of macrolichen species in both study regions based upon substrate associations of population response patterns.

ALBERTA	YUKON
Ubiquists	
Cetraria cucullata	Cetraria cucullata
Cetraria nivalis	Cetraria nivalis
Thamnolia subuliformis	Thamnolia subuliformis/vermicularis
Cetraria ericetorum	
Cornicularia aculeata	
	Alectoria ochroleuca
	Cetraria islandica
	Cetraria laevigata
	Dactylina arctica
Common on acidic substrates	
Alectoria chalybeiformis	
Cetraria laevigata	
Cladonia pocillum	
Peltigera rufescens	
	Cetraria ericetorum
	Cetraria nigricans
	Cladina arbuscula/mitis
	Cladina rangiferina
	Cladina stellaris
	Cladonia amaurocraea
	Cladonia coccifera/metacorallifera
	Cladonia ecmocyna/gracilis
	Cladonia macrophyllodes
	Cladonia uncialis
	Peltigera malacea
	Sphaerophorus globosus
	Stereocaulon alpinum
Exclusively on acidic substrates	
Solorina crocea	Solorina crocea
Psoroma hypnorum	Psoroma hypnorum
Alectoria nigricans	
Cetraria islandica	
Cladonia coccifera	
Cladonia ecmocyna/gracilis	
Cladonia pyxidata/macrophyllodes	
Hypogymnia subobscura	
Leptogium saturninum	
Nephroma expallidum	
Peltigera aphthosa	
Stereocaulon alpinum	
	Cladonia bellidiflora
	Cladonia crispata
	Cladonia macrophylla
	Peltigera pulverulenta
	Peltigera rufescens
Common on both substrates	
Dactylina arctica	
	Cetraria richardsonii
	Nephroma expallidum
	Peltigera aphthosa
Common on basic substrates	
Alectoria ochroleuca	
Cetraria tilesii	
Physconia muscigena	
	Alectoria nigricans
	Cladonia pyxidata/pocillum
	Cornicularia divergens
	Dactylina ramulosa
Exclusively on basic substrates	
Solorina spp.	Solorina spp.
Dactylina ramulosa	
	Alectoria nitidula
	Asahinea chrysantha
	Cetraria tilesii
	Cornicularia aculeata
	Hypogymnia subobscura
	Parmelia separata

C. laevigata, C. richardsonii and C. kamchatica.

Cornicularia aculeata in Alberta may be similarly better adapted to the southern mountains in comparison with C. divergens. Where these are allopatric, their responses to dry, basic substrates are similar. However, where they are sympatric, C. aculeata is limited to the driest sites.

The Yukon ubiquist Cetraria laevigata shows greatest cover in Nahoni snowbeds, and is restricted in Alberta to one Divide site and a mesic Prospect site. This suggests that the species responds as a mesophyte in both regions, and has a broad tolerance of substrate variability. This mesophyte response is also evident for Dactylina arctica in both regions. Cetraria islandica may be less tolerant of basic conditions in Alberta, as it is a general mesophyte in Yukon sites but is only abundant in Divide stands.

Dactylina ramulosa and Cetraria tilesii shift habitat groups in the two regions, with the former being more widespread in the Yukon. Both Dactylina species maintain their substrate relationships in the two regions, while both change categories due to lower frequencies in Alberta. Microclimate may be less favorable in the Front Ranges for D. ramulosa than for C. tilesii, since the latter is more widespread in dry spotted tundra in Alberta sites. Another regional difference is that C. tilesii occurs as small scattered thalli in the southern areas instead of large clumps which are commonly found in northern areas. These aggregations can be as much as 6 cm in diameter and are found as far north as southern Victoria Island (S. Wolf, pers. comm.).

The distinct species assemblage in the Ogilvie sites is due to the presence of 11 species within the Cladoniaceae. In group 3, three of the seven species are in this family, as are eight of the 13 species in group 2. This group of acid-tolerant specialists has a high degree of overlap in niche parameters, at least in the context of the two environmental gradients presented here. However no two species in this group have identical habitat response patterns. These species are minimally represented in Nahoni sites through lack of suitable habitat, poor competitive abilities, or both.

The only other Cladonia species in the study are C. pyxidata and C. pocillum found in Nahoni sites. Response patterns for these closely related species (Fig. 22) show significant habitat divergence from the other Yukon species of Cladoniaceae.

Most remaining differences in species ecological amplitudes are due to minor regional shifts in frequency, on the same substrate. One example is Alectoria ochroleuca which is a minor Yukon ubiquist with lower frequencies in Ogilvie sites. In Alberta this species has a very similar substrate pattern, but has too few occurrences to be considered a ubiquist.

Other examples may be found in species associated with low substrate pH which are more common in Yukon than in Alberta sites. *Stereocaulon alpinum*, *Cladonia ecmocyna/gracilis* and *C. coccifera/metacorallifera* all follow this trend due to the limited occurrence of comparable sites in Alberta study areas. The reverse pattern is found only with *Peltigera rufescens*, which is common in Divide and Prospect stands but is only found in one Ogilvie stand. In Alberta, *P. rufescens* seems to be an important colonizing species on frost-disturbed soils, and dead thalli have often been observed underneath other species of lichens and bryophytes. However, the northern ecological role of this species remains unclear due to its rareness.

Regional substrate reversals are suggested in the two species *Hypogymnia subobscura* and *Alectoria nigricans*. The former is common on basic Nahoni sites and is found in one Divide stand, although it also was encountered once outside a Prospect stand. This species probably does not disperse well and these populations may be relicts, or evidence of recolonization from western mountains. Substrate relationships of *H. subobscura* in the southern areas cannot adequately be determined until more populations have been encountered.

Alectoria nigricans is not as rare in Alberta as is *H. subobscura*, but is also unlikely to provide an example of a major shift in substrate association. In the Yukon *A. nigricans* is grouped with species which are more common and have higher cover values in basic sites. It also occurs in the more acidic Nahoni sites as well as in four Ogilvie sites. In general, greatest importance of A. nigricans is in sites with dry-mesic moisture regime and well-developed vegetation. Association with low substrate pH may be evidence of narrower ecological amplitude in southern populations, rather than a complete divergence in substrate relations.

In summary, macrolichen species responses to environmental gradients in the study regions can be grouped into six major substrate pH patterns: ubiquists; common on acidic substrates; exclusively on acidic substrates; common on both substrates; common on basic substrates; and exclusively on basic substrates. Minor shifts in ecological amplitudes are common for species populations compared in the two study regions. Regionally distinct species habitats are partially due to the prevalence of dry, basic sites in the southern areas, and to differences in species richness. No major changes in inter-regional species and substrate relationships are found.

Diversity

Introduction

Diversity measures of plant communities can be used to assess the relationship of species to each other and to resources. Different aspects of diversity can be considered using two distinct categories. Alpha diversity concerns species responses within communities, and beta diversity represents the differentiation of communities along habitat gradients. (Whittaker 1972, 1975).

Beta diversity can be examined by calculating the change in composition of samples along an environmental gradient (Whittaker 1972). The general beta diversity differences in samples are represented in this study by percent similarity and coefficient of community values for macrolichen vegetation. These measures provide an ecological distance between samples, which relates to separation along environmental gradients (Whittaker 1975). Graphical representation of ecological distance is provided by ordinations (Figs. 7, 9).

Alpha diversity can be assessed by determining species richness (S) and evaluating relative species importance or evenness (J). These two components can also be combined into a single diversity measure H' (Whittaker 1972).

Studies of alpha diversity aid in determining how many species co-occur, and to what extent they evenly divide resources. Selected factors such as substrate pH and macrolichen cover are compared to diversity values to further elucidate species relationships. In this section, particular emphasis is placed upon richness, evenness and diversity differences in areas and regions.

Regional Results

All substrate unit values for S, J, H' and total macrolichen cover are summarized in Table 30. Individual values

TABLE 30. Means and ranges of values for macrolichen species cover, richness, evenness, and diversity in all vegetation (veg), stone stripe (str) and combined (all) substrate units from Alberta and Yukon study areas.

AREA	SU	N	COVER		RICHNESS		EVENNESS		DIVERSITY	
			$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Prospect	veg	11	24.38	5.40-43.90	10.27	5-14	0.823	0.730-0.905	1.90	1.39-2.28
"	all	21	15.37	0.37-43.90	9.43	3-14	0.781	0.070-0.905	1.82	0.99-2.28
Divide	veg	6	40.28	12.45-61.56	14.00	7-21	0.702	0.490-0.842	1.94	0.97-2.48
"	all	10	27.86	2.65-61.56	13.10	6-21	0.731	0.490-0.870	1.93	0.92-2.59
Nahoni	veg	17	56.57	39.31-71.87	19.53	14-31	0.817	0.667-0.900	2.42	1.94-2.97
"	all	27	43.79	13.73-71.87	17.78	12-31	0.826	0.667-0.920	2.38	1.81-2.97
Ogilvie	veg	10	46.72	17.13-64.03	18.90	15-23	0.831	0.760-0.878	2.46	2.07-2.86
"	all	11	44.30	17.13-64.03	19.09	15-23	0.836	0.760-0.890	2.48	2.07-2.86
Alberta	veg	17	29.99	5.40-61.56	11.58	5-21	0.781	0.490-0.905	1.91	0.97-2.48
"	str	14	6.54	0.37-16.80	9.43	3-19	0.747	0.070-0.900	1.78	0.92-2.59
"	all	31	19.40	0.37-61.56	10.61	3-21	0.765	0.490-0.905	1.85	0.92-2.59
Yukon	veg	27	52.92	17.13-71.87	19.30	14-31	0.822	0.667-0.900	2.43	1.94-2.97
"	str	11	21.87	13.73-43.06	15.36	12-21	0.846	0.720-0.920	2.31	1.81-2.71
"	all	38	43.93	13.73-71.87	18.16	12-31	0.829	0.667-0.920	2.40	1.81-2.97

are grouped by substrate unit, area, and region for comparison.

Macrolichen species richness (Table 31) and cover values (Table 32) are significantly higher in the Yukon than in Alberta for both types of substrates. The differences are greatest between vegetation substrate units in Prospect and the two Yukon areas.

Macrolichen diversity is also significantly higher for both types of substrates in the Yukon than in Alberta (Table 33). However, evenness values (Table 34) indicate that none of the areas are significantly different, which contrasts with trends in H' and S values.

Correlations between S, J, H', cover and substrate pH are summarized in Table 35. Richness and cover are positively correlated in pooled substrate unit data for Nahoni and Prospect areas, and for vegetation substrate units from Prospect.

Other correlated values are those for J and substrate pH in pooled Nahoni substrate units. Nahoni sites with low evenness are those with lower pH and wetter conditions (SN1, N1, N2, N4, N14 Appendix C). In contrast, stone stripes and upland vegetation substrate units have high evenness. Low evenness in wetter sites occurs when there are few species with high cover and many with low cover. In well-vegetated upland areas, high evenness is due to the presence of several species which all have low or at least similar

TABLE 31. Macrolichen species richness (S) compared for Yukon and Alberta areas, using the T test for unequal variances (Sokal and Rohlf 1969).

Vegetation Substrate Units

	Prospect	Divide	Nahoni
Ogilvie	***	NS	NS
Nahoni	***	NS+	
Divide	NS		

	Yukon
Alberta	**

Stone Stripe Substrate Units

	Yukon
Alberta	**

** = P<.01
*** = P<.001
NS = no significant difference
NS+ = borderline significance (P≥.05)

TABLE 32. Macrolichen cover totals compared for Yukon and Alberta areas, using the T test for unequal variances (Sokal and Rohlf 1969).

Vegetation Substrate Units

	Prospect	Divide	Nahoni
Ogilvie	**	NS	NS
Nahoni	***	NS	
Divide	NS		

	Yukon
Alberta	**

Stone Stripe Substrate Units

	Yukon
Alberta	**

** = P .01
*** = P .001
NS = no significant difference

TABLE 33. Macrolichen diversity (H') values compared for Yukon and Alberta areas, using the T test for unequal variances (Sokal and Rohlf 1969).

Vegetation Substrate Units

	Prospect	Divide	Nahoni
Ogilvie	***	NS	NS
Nahoni	***	NS	
Divide	NS		

	Yukon
Alberta	***

Stone Stripe Substrate Units

	Yukon
Alberta	**

All Substrate Units

	Prospect	Divide	Nahoni
Ogilvie	***	*	NS
Nahoni	***	*	
Divide	NS		

	Yukon
Alberta	***

* = P<.05
** = P<.01
*** = P<.001
NS = no significant difference

TABLE 34. Macrolichen evenness (J) values compared for Yukon and Alberta areas, using the T test for unequal variances (Sokal and Rohlfe 1969).

Vegetation Substrate Units

	Prospect	Divide	Nahoni
Ogilvie	NS	NS$^+$	NS
Nahoni	NS	NS	
Divide	NS		

	Yukon
Alberta	NS

Stone Stripe Substrate Units

	Yukon
Alberta	NS

All Substrate Units

	Prospect	Divide	Nahoni
Ogilvie	NS	NS$^+$	NS
Nahoni	NS	NS	
Divide	NS		

	Yukon
Alberta	NS$^+$

NS = no significant difference
NS$^+$ = borderline significance ($P \geq .05$)

TABLE 35. Comparisons between macrolichen species richness, evenness, diversity, total cover, and substrate pH in all substrate units using Spearman's Rank Correlation Coefficient (Sokal and Rohlf 1969). Values are for both vegetation and stone stripe substrate units unless otherwise indicated.

	pH	Degrees Freedom	Cover	Degrees Freedom
RICHNESS				
Prospect[1]	–	--	*	11
Divide	–	–	NS	6
Nahoni	–	–	NS	17
Ogilvie	–	–	NS	10
Prospect	NS	11	**	21
Divide	NS	5	NS	10
Nahoni	NS	19	**	27
Ogilvie	NS	7	NS	11
COVER				
Prospect	NS	11		
Divide	NS	5		
Nahoni	NS	19		
Ogilvie	NS	7		
DIVERSITY				
Prospect[1]	NS	7		
Divide	NS	3		
Nahoni	NS	10		
Ogilvie	NS	6		
EVENNESS				
Prospect[1]	NS	7		
Divide	NS	3		
Nahoni	*	10		
Ogilvie	NS	6		

[1] vegetation substrate units only, for all four areas.

* = P .05, positive correlation

** = P .01, positive correlation

NS = no significant correlation

cover values. Therefore, evenness changes with both pH and moisture complex-gradients in the Nahoni area.

Evenness values for the Ogilvie area do not correlate with pH values, although the relationship of moisture and evenness is very similar to that in Nahoni sites. Highest evenness is in upland sites (SO1, O1-O3, O5c Appendix C) with lowest values in the mesic-wet substrate units (O4, O5v, O6, O8).

This trend of higher evenness under drier conditions is evident in the Divide as well as in the Yukon areas. Highest evenness on the Divide is found in SD1, SD2, D3, SD5, and D5 which are dry substrate units. The wetter stands D4 and D6 have the lowest evenness values.

Evenness on Prospect is also related to a moisture complex-gradient. The highest values are those for dry and mesic substrate units (SP1, P1, P3, P8, SP9, P10, P11). These have high species richness and moderate macrolichen cover with the exception of species-poor stand P3. The lowest evenness values are found in substrate units which are species-poor (SP2, P2, SP3, SP5, P9, P10). In these habitats one or two species have slightly higher cover than the rest.

Trends in evenness values for Prospect reflect a predominance of distinct dry habitats and a paucity of wet sites. The highest evenness values represent upland vegetation comparable to that in the other three areas. However, the lower evenness values on Prospect are related more to the driest species-poor habitats, instead of wet sites as in the other study areas. If major snowbed or wet areas were encountered on Prospect, it is likely that evenness would follow the moisture related trends found in the other study areas. Conversely, dry species-poor sites in the other three areas would probably have low evenness. These instances remain hypothetical until the macrolichens in these regions have been studied in more areas.

DISCUSSION

Diversity

Diversity calculations in this study indicate that increases in macrolichen cover, species richness (S) and diversity (H') are correlated with a shift from southern to northern latitudes. A prediction of regional trends in macrolichen values of S, H' and cover can be made by assessing any of the three, in both regions. These results contrast with those of Slack (1971) in which S had no predictive value for H' in bryophyte data from the Adirondack Mountains. In a bryophyte study within Jasper National Park (Lee 1976) S and diversity were not correlated with absolute bryophyte cover, but correlated instead with an elevation complex-gradient.

Macrolichen evenness (J) is not significantly different between any of the study areas, even with differences in species richness. This has already been shown qualitatively in the comparibility of inter-region population response patterns. However, evenness values vary along a moisture complex-gradient within Nahoni, Ogilvie, Divide and Prospect areas. In the first three areas, lowest evenness is in wet sites; at Prospect the lowest evenness is in dry, species-poor sites. The trend suggests that wet habitats in the Prospect area would also exhibit low evenness. Evenness data are dissimilar to those for bryophytes (Lee 1976) in which values correlated with a subjective moisture index were highest at the wet end of a moisture complex-gradient.

Other investigators have suggested the use of separate indices for species richness and evenness in diversity studies (Whittaker 1972, Addicott 1974). In the present study, inter- and intra-regional trends of S, J, and H' are clearly more informative than for H' alone.

Implications of Regional Trends

Regional differences in values for macrolichen cover, S, and H' may be related to several factors. The major environmental distinction between regions is climate, which in turn influences a wide variety of abiotic and biotic habitat factors along a latitudinal gradient. Abiotic factors affecting macro- and microhabitats include soil and air temperatures; relative humidity; annual precipitation; length of growing season; permafrost; and intensity of frost action. Biotic factors which influence microhabitats include type and amount of plant cover; presence and activity of soil microorganisms; and species and densities of herbivorous fauna. Due to interactions of these many factors, the northern study areas have habitats which are more favorable for macrolichens than those found further south in the Canadian Cordillera. Physiological adaptations of macrolichens to northern climates may partially explain these regional differences.

Many macrolichens are adapted to cold temperatures at high latitudes by having low temperature optima (Ahmadjian 1970, Greene and Longton 1970, Lamb 1970, Kappen 1973).

However, macrolichens in habitats of some low-arctic and alpine environments have comparable temperature responses to those in more temperate areas (Bliss and Hadley 1964, Kershaw 1977). Some macrolichens apparently do not need a specialized low temperature response in such habitats, although several species can acclimate rapidly to seasonal temperature patterns (K[illegible]lio and Heinonen 1971, Larson and Kershaw 1975b, 1975c, 1975d). The different physiological mechanisms which allow macrolichens to thrive in high latitudes may be related to high abundance in the Yukon study region. Likewise, the warm and dry environments in the Alberta Front Ranges may be unfavorable for many northern macrolichens.

Another physiological consideration is that vascular plant species which are not as well-adapted to the northern environments may exhibit reduced species richness and cover, and thereby potentially reduce competition with macrolichens. Lower importance and competition of arctic and alpine vascular plants has also been attributed to selective herbivory (Thomson 1972). This theory is based on an assumption of macrolichen unpalatability due to lichen substances, but unfortunately has not been tested.

Competition between macrolichens and vascular plants may also involve allelopathy. Experiments with extracts of *Peltigera canina* have shown inhibition of several grass species (Pyatt 1967), and such allelopathic capabilities may occur in the closely related alpine species P. rufescens. Kershaw (1977) reviews experimental evidence for inhibition of pine and spruce seedlings by Cladina stellaris, yet he cautions that the results are subject to multiple interpretation. These initial studies suggest that allelopathy may be important to macrolichen species in certain habitats, and this possibility should be examined for northern populations. However, so few examples have been documented that it is premature to predict the importance of allelopathy in most macrolichen taxa, or to infer allelopathic capacity of species or populations for different regions in this study.

A final consideration of regional diversity differences is that glacial history may have restricted or eliminated macrolichen biotypes from the southern study region, and that only limited recolonization has occurred. While some macrolichen species from northern (Yukon) or southern (U.S.) unglaciated regions have colonized the formerly glaciated areas, many northern species are absent in the southern Canadian Rocky Mountains. Limited dispersal mechanisms and prevailing northwesterly winds may be unfavorable for southward dispersal of northern macrolichen populations. It is also possible, however, that the climatic regime of the southern Rocky Mountains has been unfavorable for establishment of propagules from northern species.

The question of why lichens are more successful in study areas in the Yukon than in Alberta cannot be fully answered due to limited available data, but some hypotheses can be reviewed. Physiological relations and adaptations to northern habitats are well-documented factors, and may confer competitive advantages to macrolichens over vascular plant species. Physiological limits of some macrolichen populations could restrict occurrences in hotter, drier climates. The influences of herbivory and allelopathy in macrolichens are also suggested as factors which should be investigated in relation to regional diversity and importance differences.

Macrolichen Distribution

The predominance of circumpolar distributions of North American arctic lichens has been documented by Thomson (1972). Circumpolar distributions represent 88.4% (Bird 1974a) and 91.8% (Bird 1974b) of the lichen species in studies from the Yukon and Northwest Territories. Results from these studies indicate that widely distributed lichen species have colonized northern areas since the last extensive glaciation which ended 11,000-9,000 years ago. The historical influence of glaciation is therefore not responsible for most current macrolichen distributions in northern areas. However, the minority of endemic or other species with narrow distributions could hypothetically indicate relict or relict-derived populations.

In the initial phases of research this endemism hypothesis was accepted in principle, and the number of narrowly distributed macrolichen species was expected to constitute a significant proportion of regional species. To test this theory, distribution elements of macrolichen taxa in the study areas and regions have been compiled (Table 36) from Imshaug (1957), Hale (1969), Bird and Marsh (1973a, 1973b), Dahl and Krog (1973), Bird (1974a, 1974b), Krog (1974) and Bird (1975).

Macrolichen floras from both Alberta and the Yukon are predominantly circumpolar with values of 92.8% and 86.4%, respectively. (Table 37). The majority of these species are

TABLE 36. Distribution elements for macrolichen species found in Alberta and Yukon regions; groups determined primarily from this study and from Bird (1974a, 1974b).

DISTRIBUTION/MACROLICHEN SPECIES

CIRCUMPOLAR	PDNO
Arctic Alpine	
Alectoria minuscula	+++
A. nigricans	+++
A. nitidula	+
A. ochroleuca	++++
A. pubescens	+++
Cetraria delisei	+
C. laevigata	++++
C. nigricans	++
C. tilesii	+++
Coriscium viride	+
Cornicularia divergens	++
Dactylina arctica (P-)	++
D. ramulosa	++++
Hypogymnia oroarctica	++ +
H. subobscura	+++
Nephroma expallidum	+++
Parmelia almquistii	+
P. centrifuga	+
P. panniformis	++
Sphaerophorus globosus	++
Stereocaulon alpinum	+++
S. rivulorum	+
Thamnolia subuliformis	++++
T. vermicularis	++
Umbilicaria proboscidea	+ +
Arctic-Boreal	
Alpine-Montane	
Cetraria commixta	+
C. cucullata	++++
C. hepatizon	+
C. nivalis	++++
Cladina mitis	++
C. stellaris	++
Cladonia amaurocraea	++
C. coccifera	+++
C. cornuta	+
C. crispata	+
C. ecmocyna	+++
C. gracilis	+++
C. macrophylla	+
C. macrophyllodes	+++
C. phyllophora	+
C. pyxidata	++++
Con't.	PDNO
Cladonia uncialis	++
Hypogymnia physodes	+ +
Lecanora chrysoleuca	+
Leptogium saturninum	++
Nephroma arcticum	++
Parmelia omphalodes	++
P. saxatilis	+
Peltigera aphthosa	+++
P. malacea	++
P. pulverulenta	+
Solorina crocea	+ +
Umbilicaria cylindrica	+
U. hyperborea	+ +
U. virginis	+
Arctic-Temperate	
Alpine-Montane	
Alectoria chalybeiformis	++
Cetraria ericetorum	++++
C. islandica	+++
Cladina rangiferina	++
Cladonia chlorophaea	+
C. pocillum	+++
Cornicularia aculeata	+++
Peltigera rufescens	++ +
P. spuria	++
Boreal Montane	
Cetraria pinastri	+
Boreal-Temperate Montane	+
Parmelia taractica	+
AMPHI-BERINGIAN	
Arctic Alpine	
Cladina aberrans	+
C. arbuscula	++
Cladonia metacorallifera	+++
Dactylina arctica (P+)	++++
Evernia perfragilis	+
Parmelia separata	+
Western Arctic Alpine	
Asahinea chrysantha	++
Cetraria richardsonii	++
Western Arctic-Boreal	
Alpine	
Asahinea scholanderi	+
AMERICAN	
Alpine Montane	
Parmelia wyomingica	+

P = Prospect
D = Divide
N = Nahoni
O = Ogilvie

TABLE 37. Compiled totals and percentages of distribution elements for alpine macrolichen species. Values are for each area, region, and both regions combined.

DISTRIBUTION	ALBERTA P	%	D	%	ST	%	YUKON N	%	O	%	ST	%	T	%
Circumpolar														
Arctic Alpine	9	41.4	14	35.0	14	33.3	19	38.8	18	34.6	24	36.4	25	32.9
Arctic-Boreal Alpine-Montane	6	27.2	15	37.5	17	40.5	16	32.7	23	44.2	25	37.9	30	39.6
Arctic-Temperate-Alpine-Montane	6	27.2	7	17.5	7	16.6	5	10.2	5	9.6	7	10.6	9	11.8
Boreal Montane	-	-	-	-	-	-	1	2.0	-	-	1	1.[illegible]	1	1.3
Boreal-Temperate-Montane	-	-	1	2.5	1	2.4	-	-	-	-	-		1	1.3
Amphi-Beringian														
Arctic Alpine	1	4.5	2	5.0	2	4.8	5	10.2	4	7.7	6	9.1	6	7.9
Western Arctic-Alpine	-	-	-	-	-	-	2	4.1	2	3.9	2	[illegible]0	2	2.6
Western Arctic-Boreal Alpine	-	-	-	-	-	-	1	2.0	-	-	1	1.5	1	1.3
American														
Alpine Montane	-	-	1	2.5	1	2.4	-	-	-	-	-	-	1	1.3
Total species	22		40		42		49		52		66		76	

Macrolichen species: P = Prospect; D = Divide; N = Nahoni; O = Ogilvie
ST = Regional subtotal; T = Total for both regions

included in the broad subdivision Arctic-Boreal Alpine-Montane. There are more species in the Arctic Alpine subdivision in Yukon areas, and more Arctic-Temperate Alpine-Montane species in Alberta. A minor distribution component of Amphi-Beringian species is found in Alberta (4.8%) with higher values in the Yukon (13.6%). The American distribution element is insignificant in both regions.

Within the Alberta data (Table 37), distribution elements for Prospect exhibit parallel trends to those in the Divide sites. The lower percentage of Circumpolar Arctic Alpine species in the Divide area is due primarily to more species in the Arctic-Boreal Alpine-Montane category.

Parallel distribution trends are also evident between the two areas in the Yukon region. A greater number of total Amphi-Beringian species occur in the Nahoni area. Conversely, the Ogilvie area has a higher number and percentage of Arctic-Boreal Alpine-Montane species within the circumpolar distribution pattern.

Seven of the nine Amphi-Beringian macrolichen species in this study are restricted to the Yukon (Table 36). This may be related to the geographic proximity of the northern study areas to past species distribution centres in unglaciated regions of Alaska and the Yukon. However, this may also be related to more favorable environmental factors for these species in northern sites.

One of the Amphi-Beringian species is found only in the

Ogilvie area; three are restricted to the Nahoni sites; and three are common to both areas (Table 36). It is tempting to interpret the restricted Nahoni distributions as examples of limited post-glacial dispersal in relict populations of *Evernia perfragilis*, *Parmelia separata*, and *Asahinea chrysantha*. However, *E. perfragilis* and *A. chrysantha* are known from many northern calcareous alpine areas regardless of glaciation history (Thomson 1972, Bird 1974c). *Parmelia separata* has not been found in glaciated uplands in this or other Yukon studies (Bird 1974a, 1974b), yet it is reported from such habitats on Devon Island (Barrett and Thomson 1975), and from the Northwest Territories (Scotter and Thomson 1966, Thomson et al. 1969). These results show that the original hypothesis is unfounded because narrow macrolichen species distributions are not correlated with glacial history in the study areas.

Therefore, on the basis of macrolichen distributions from species in this study, there is no evidence which supports either the refugial status of Mountain Park alpine areas (Packer and Vitt 1974), or the determination of present-day northern macrolichen distributions due to glaciation history. As Thomson (1972) points out, arctic lichen species disjunctions are often caused by disjunctions of habitat factors rather than historical factors.

The overwhelming dominance of circumpolar distributions characterizes not only the macrolichens of this study, but also the hepatic flora of Alberta (Bird and Hong 1975, Hong and Vitt 1976) and the moss flora of Jasper National Park (Lee 1976). Widespread dispersal is implied by distributions of mosses and liverworts in these studies. Likewise, Thomson (1972) concludes that distribution patterns of most northern lichens indicate widespread dispersal within the past 10,000 years. The results of the present study are in agreement with this view, and thus support long-distance dispersal as an important and viable process affecting distributions of many alpine macrolichen species.

Substrate Relationships

Habitat selection by lichens for specific microenvironmental factors has been suggested by several investigators (Culberson and Culberson 1967, 1973, Garty, Gal and Galun 1974, Garty and Galun 1974). These studies have all relied upon correlation of lichen presence and microhabitat factors, rather than using an experimental approach to the implied physiological relationships. In the present investigation, species-habitat correlations are used to examine reliability of substrate relationships and to evaluate the evidence for obligate acidicoly and calcicoly.

Substrate relationships of terricolous macrolichens encountered in this study (Table 38) have been compiled primarily from Bird (1974a, 1974b), as well as Gelting (1955), Thomson (1967), Barrett and Thomson (1975), and Bird (1975). The substrate categories are: (1) acidic soils and rocks; (2) calcareous (basic) soils and rocks; and (3) acidic and calcareous soils and rocks.

Macrolichen species in the Alberta and Yukon regions (Table 39) exhibit parallel trends in substrate relationships. The largest group includes species on both substrates, with decreasing percentages of acidic, and calcareous substrate-associated species groups, respectively. Within the context of these categories, the majority of species do not exhibit marked substrate preference or selectivity.

TABLE 38. Substrate relations for macrolichen species found in Alberta and Yukon regions; groups determined primarily from this study and from Bird (1974a, 1974b).

SUBSTRATE/MACROLICHEN SPECIES	PDNO
Acidic soils and rocks	
Alectoria chalybeiformis	++
Cetraria nigricans	+++
Cladonia chlorophaea	+
C. macrophylla	+
C. macrophyllodes	+++
C. metacorallifera	+++
C. crispata	+
C. phyllophora	+
Coriscium viride	+
Nephroma arcticum	++
N. expallidum	+++
Peltigera malacea	++
P. pulverulenta	+
Solorina crocea	+ +
Sphaerophorus globosus	++
Calcareous soils and rock	
Evernia perfragilis	+
Hypogymnia physodes	+ +
H. subobscura	+++
Parmelia separata	+
Acidic and calcareous soils and roc[illegible]	
Alectoria ni[illegible]s	+++
A. nitidula	+
A. ochroleuca	++++
Asahinea chrysantha	++
Cetraria cucullata	++++
C. delisei	+
C. ericetorum	++++
Cetraria islandica	+++
C. laevigata	++++
C. nivalis	++++
C. richardsonii	++
C. tilesii	+++
Cladina aberrans	+
C. arbuscula	++
C. mitis	++
C. rangiferina	++
C. stellaris	++
Cladonia amaurocraea	++
C. coccifera	+++
C. cornuta	+
C. ecmocyna	+++
C. gracilis	+++
C. pocillum	+++
C. pyxidata	++++
C. uncialis	++
Cornicularia aculeata	+++
C. divergens	++
Dactylina arctica (P+)	++++
D. arctica (P-)	++
D. ramulosa	++++
Peltigera aphthosa	+++
P. rufescens	++ +
P. spuria	++
Stereocaulon alpinum	+++
S. rivulorum	+
Thamnolia subuliformis	++++
T. vermicularis	++

P = Prospect
D = Divide
N = Nahoni
O = Ogilvie

TABLE 39. Compiled totals and percentages of alpine macrolichen species from different substrates. Values are for each area, region, and both regions combined.

SUBSTRATE	ALBERTA						YUKON							
	P	%	D	%	ST	%	N	%	O	%	ST	%	T	%
Acidic soils and rocks	2	11.1	6	20.7	6	20.0	7	15.9	13	30.2	14	25.9	15	26.8
Calcareous soils and rocks	2	11.1	1	3.5	2	6.7	4	9.1	-	-	4	7.4	4	7.1
Acidic and calcareous soils and rocks	14	77.7	22	75.8	22	73.3	33	75.0	30	69.9	36	66.7	37	66.1
Total species	18		29		30		44		43		54		56	

P = Prospect macrolichen species
D = Divide " "
N = Nahoni " "
O = Ogilvie " "
ST = Regional subtotal of macrolichen species
T = Total for both regions of macrolichen species

Of the two specific substrates, the acidic soils and rocks category is better represented in the Divide, Nahoni, and Ogilvie areas (Table 39). The greatest number in this category is found in Ogilvie sites, corresponding to the response patterns of species which are restricted or more common in acidic habitats (Figs. 18-20).

Macrolichen species with calcareous or basic substrate associations are least frequent in Divide and Ogilvie areas, with increasing representation in Prospect and Nahoni sites (Table 39). The low total number of species in this group is due to the exclusion of species which are usually but not always associated with basic substrates, such as Alectoria nitidula, Asahinea chrysantha, Cetraria tilesii, Cornicularia aculeata, and Solorina spp. excluding S. crocea (Figs. 12,11, 15, 23, 24). These species are therefore grouped in the acidic and calcareous substrate category, although in acidic sites each may occur with greatly reduced frequency and cover (Hrapko 1970, Bird [illegible] 1974b).

The relationship of species and habitats (Table 39) provides greater evidence for obligate acidicoly than for obligate calcicoly. Preferential physiological mechanisms for basic, calcareous substrates may well exist in species most commonly found in such habitats, but few species appear to be completely dependent upon this substrate. Unfortunately, the degree of inter- and intraspecific physiological variability in obligate and preferential substrate requirements is poorly known for macrolichens.

The large proportion of species found on both substrates (Table 39) reflects the importance of ubiquist species, including epiphytes which may respond more to the microhabitat of ground vegetation than to substrate pH. Also, some of the species included are preferential but not restricted to either substrate. The lack of correlation with substrate pH in this group provides indirect evidence of other overriding habitat factors.

Several microhabitat factors are likely to be equally or more important than those associated with substrate pH in macrolichen habitat selection and subsequent population-habitat interactions. Important documented factors include: topography (Kershaw 1974); organic substrate (Rouse and Kershaw 1973, Larson and Kershaw 1974, Maikawa and Kershaw 1976); wind speed and boundary layer (Kershaw 1975a); moisture regime (Lechowicz and Adams 1974b, Kershaw and Rouse 1971, Rouse and Kershaw 1973, Larson and Kershaw 1976); and snow cover (Larson and Kershaw 1975a, Kershaw 1975b).

The implications of these results to other alpine vegetation studies can be summarized in predictive terms. The presence of northern alpine macrolichen species with restricted substrate relationships is likely to indicate specific acidic or basic habitats. In addition, several species with broader substrate associations exhibit greater quantitative importance in one of the two specific substrate pH regimes.

The combined occurrence of species in these habitat groups should indicate substrate pH characteristics, within the context of the regions investigated. However, a large proportion of species encountered indicate factors such as moisture regime, rather than substrate pH.

Plant Communities

Introduction

North American alpine vegetation studies have generally included conspicuous lichens rather than specifically determining lichen vegetation communities. In the course of distinguishing alpine vascular plant communities, several investigators have included macrolichen data which can be compared to those in this study. Pertinent macrolichen vegetation studies are also compared, although few have been carried out. All comparisons of investigations are based, whenever possible, upon quantitative importance values of frequency, cover or both, for species under consideration.

This section presents separate community discussions for the Alberta and Yukon regions. The main reason for this is that qualitative and quantitative vegetation data for macrolichens and vascular plants are regionally distinct. Lack of intermediate sampling areas either from this or other studies also justifies this treatment.

Within the Alberta discussion, macrolichen and vascular plant communities are considered separately due to their limited correlation (Fig. 10). Comparable Yukon plant communities are highly correlated (Fig. 11) and are therefore combined for discussion.

Alberta

Macrolichens

(1) Cetraria cucullata - Thamnolia subuliformis - Cetraria tilesii

This macrolichen community has few described counterparts. The differential-species Solorina spp., Dactylina ramulosa and Cetraria tilesii are characteristic of spotted tundra and discontinuous stone stripes found at Prospect on dry, unstable slopes (Fig. 25).

Spotted tundra consists of discontinuous patches of either Dryas integrifolia or D. octopetala (Bamberg and Major 1968) with a variety of associated small vascular plants, lichens and mosses. While such patchy areas may be successional to shrub and tree establishment at treeline (Broad 1973), they are probably maintained in higher alpine sites (Kuchar 1975).

This community is most similar to Dryas octopetala islands on scree on Signal Mountain, Jasper National Park (Hrapko 1970). The islands on scree are considered here to be equivalent to scattered stone stripes or spotted tundra. Of all vascular plant communities designated on Signal Mountain, this has the highest lichen and vascular plant species richness. The relative species importance for macrolichens (Table 40) is similar to that in Prospect sites, although Thamnolia subuliformis is less important in the Signal community.

Cetraria tilesii is common on Dryas islands with south-

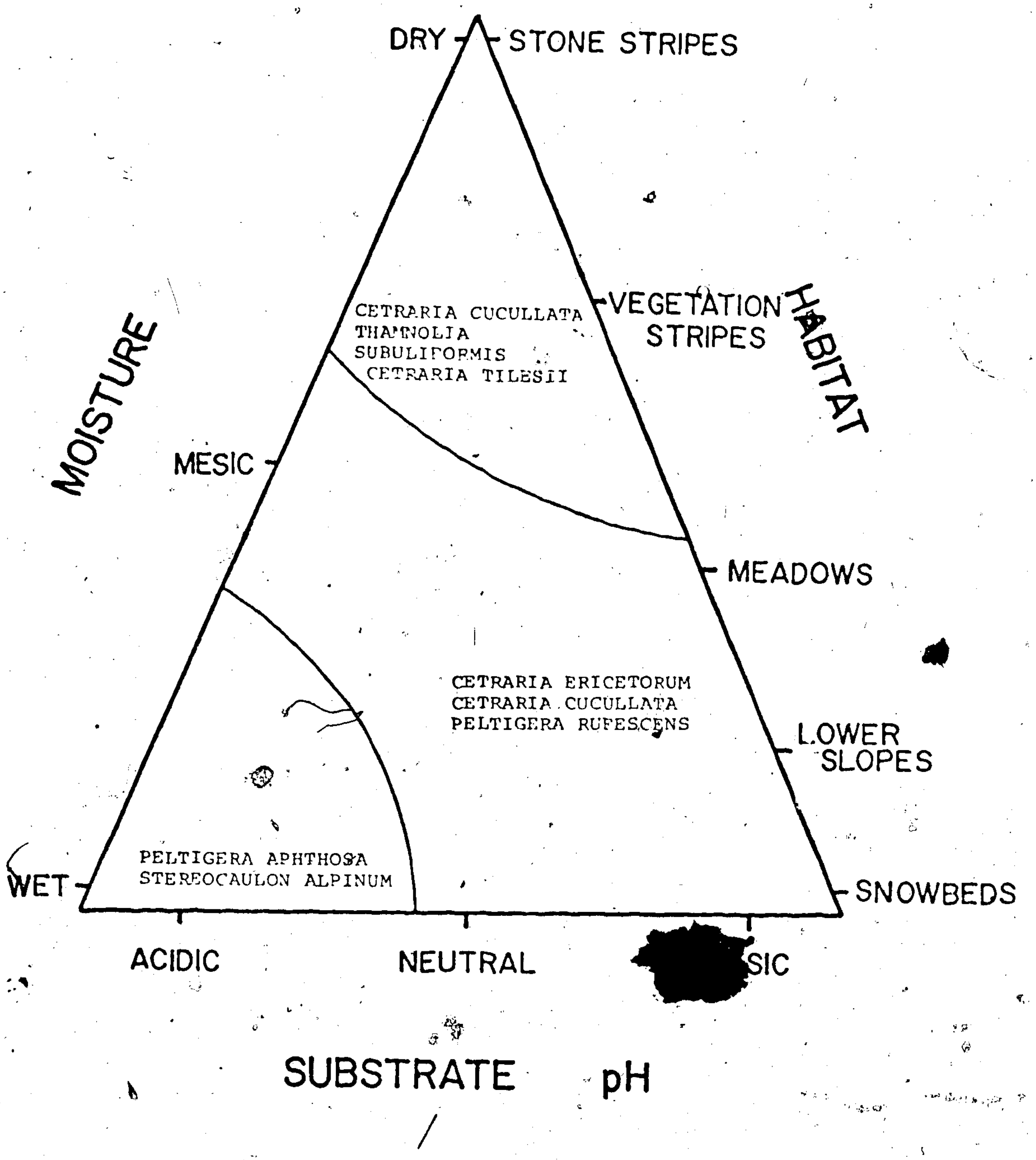


FIGURE 25. Habitat relations of alpine macrolichen communities from Alberta study areas.

TABLE 40. Vascular plant communities with similar macrolichen vegetation to the *Cetraria cucullata - Thamnolia subuliformis - Cetraria tilesii* community (#1) in Alberta.

Community/Important Macrolichens	Location
1) *Dryas octopetala islands on scree* Cetraria cucullata, *C. nivalis, C.* tilesii, Cornicularia aculeata, Cladonia pocillum, Cetraria islandica, Alectoria ochroleuca.	$52^{\circ}51'$N, $117^{\circ}59'$W Signal Mountain, Maligne Range, Jasper National Park, Alberta (Hrapko 1970)
2) *Dryas integrifolia - lichen* Alectoria nitidula*, Cetraria nivalis, C. ericetorum, Physconia muscigena, Thamnolia subuliformis, Cladonia pyxidata, Cetraria cucullata.	$69^{\circ}52'$N, $54^{\circ}22'$W Disko Island, Western Greenland (Gelting 1955)

* possibly with Alectoria chalybeiformis.

erly aspect on Si[illegible]l Mountain, although it is absent from comparable north-facing stands, and from similar communities in other Main Range areas. It appears that the hot, dry microhabitat of south-facing slopes on Signal Mountain overrides the correlation with basic substrate for this species, since the associated soils have a pH range from 5.9-6.2.

Macrolichen data are not available from vascular plant communities most closely resembling the associated Dryas integrifolia - Carex rupestris and D. integrifolia - Oxytrop[illegible] podocarpa - Salix nivalis communities on Prospect Mounta[illegible] The similarity of vascular plant communities in dry, calcareous habitats makes it likely that macrolichen vegetatio[illegible] will also be similar. However, southern Rocky Mountain alpine areas in Colorado (Langenheim 1962) and Montana (Bamberg and Major 1968) have lower macrolichen species richness and cover. There is probably an extensive geographic gradient of decreasing macrolichen importance and species richness from north to south in the Rocky Mountains, just as there appears to be from the northern Cordillera to the Alberta study areas.

Gelting (1955) has described an arctic plant community from western Greenland which shows noticeable similarity to the Cetraria cucullata - Thamnolia subuliformis - C. tilesii community of Prospect Mountain (Table 40). The characteristic vascular plants include Carex rupestris, Polygonum viviparum, Salix cf. glauca, Vaccinium uliginosum, Draba spp., *Saxifraga oppositifolia*, *S. tricuspidata* and *Silene acaulis*. Although species-poor, there is [illegible] correspondence in this community with species of *Dryas integrifolia - Carex rupestris* and *D. integrifolia - Oxytropis podocarpa - Salix nivalis* communities (Table 7). Limited crustose lichen data from Prospect also includes species in Gelting's community such as *Caloplaca jungermanniae*, *Lecanora epibryon*, *Ochrolechia upsaliensis*, and *Pertusaria dactylina*.

Elements of prairie lichen communities are also found in Front Range alpine areas, yet none of the communities recognized by Looman (1964a, 1964b) are directly comparable to those at higher elevations. One type which represents a subgroup within the *Cetraria cucullata - Thamnolia subuliformis - C. tilesii* community is the Physcietum muscigenae, composed of epiphytic and crustose lichens and macrolichens *Physconia muscigena* and *Physcia constipata*. Looman (1964a, 1964b) describes this community from overgrazed prairie, and recognizes the alpine affinities of the two macrolichens as well as crustose species *Caloplaca jungermanniae*, *Ochrolechia upsaliensis* and *Lecanora epibryon*. As in prairie habitats, these species in alpine areas are found on dead mosses or roots with high frequency but very low cover.

The Front Ranges are in close proximity to prairie, especially in the southern mountains of Alberta, and have similar habitat factors of calcareous substrate, high levels of incoming radiation, low humidity, and disturbance. Such factors are probably responsible for the inhabitation of prairie and alpine environments by several common xerophytic species.

(2) Cetraria ericetorum - C. cucullata - Peltigera rufescens

This type of vegetation is commonly represented in other alpine community studies in which constant species Cetraria cucullata, C. ericetorum, C. nivalis and Thamnolia subuliformis are the most important. Because of this, presence and relative importance of character-species such as Stereocaulon alpinum, Peltigera rufescens, Cladonia pyxidata and C. pocillum are used to establish a basis of community similarity.

The community exhibits a consistent relationship with upland Dryas octopetala communities in the Rocky Mountains from central Alberta to northern Montana (Table 41). Carex nardina vegetation on Plateau Mountain represents a related community which is thought to succede that of D. octopetala (Bryant and Scheinberg 1970).

Within the geographic range of this macrolichen community there is a divergence in associated vascular plant communities. The Dryas integrifolia vegetation on Prospect appears to characterize Front Range upland environments, and is considerably modified in species composition and importance values from D. octopetala communities in the Main Ranges.

While major shifts in macrolichen species do not appear between upland Dryas-lichen communities in the Main and

TABLE 41. Alpine vascular plant communities with similar macrolichen vegetation to the Cetraria ericetorum - C. cucullata - Peltigera rufescens community (#2) in Alberta. All communities are in Alberta unless otherwise indicated.

Community/Important Macrolichens	Location
1) Dryas octopetala - lichen+ Stereocaulon alpinum, Thamnolia subuliformis, Cladonia macrophyllodes, C. ecmocyna, Cladina mitis, Cetraria ericetorum, C. cucullata, Peltigera rufescens.	52°40'N, 117°41'W Bald Hills, Maligne Range, Jasper National Park (Kuchar 1975)
2) Dryas octopetala - Empetrum nigrum Cladina mitis, Cetraria ericetorum, C. cucullata, C. islandica, Thamnolia subuliformis, Cladonia pyxidata, Peltigera rufescens.	51°42'N, 116°30W Bow Summit, Banff National Park (Broad 1973)
3) Dryas octopetala Peltigera rufescens, Cetraria ericetorum, C. islandica, C. nivalis, C. cucullata.	50°35'N, 115°10'W Highwood Pass, Southern Front Ranges (Trottier 1972)
4) Carex nardina (types 3-5) Cetraria cucullata, C. ericetorum, Cornicularia aculeata, Peltigera canina*.	40°15'N, 114°31'W Plateau Mountain, Southern Front Ranges (Bryant and Scheinberg 1970)
5) Dryas octopetala Cetraria islandica, Peltigera canina*, Dermatocarpon miniatum, Thamnolia subuliformis.	49°48'N, 113°35'W Siyeh Pass, Glacier National Park, Montana (Bamberg and Major 1968)

+ = species from original study and from resampling by See in 1976.

* = probably is Peltigera rufescens.

Front Ranges, minor changes are evident. Greater species richness and abundance of Cladoniaceae is found in the Main Ranges, including *Cladina mitis*, *Cladonia coccifera*, *C. coniocraea*, *C. pyxidata*, *C. macrophyllodes*, and *C. uncialis* (Hrapko 1970, Kuchar 1975). Reasons for these species shifts may include differences in substrate pH, amount of snow cover and runoff, summer precipitation, and relative humidity. The increased cover of heath species in the Main Range alpine uplands also provides a suitable microhabitat for *Cladina* and *Cladonia* species by an increased boundary layer which minimizes wind damage and desiccation.

As in the *Cetraria cucullata - Thamnolia subuliformis - C. tilesii* community, several species of this macrolichen group are found in lichen associations on western prairies and parklands. The Cladonietum nemoxynae of grassland or parkland includes *Cladonia macrophyllodes*, *Peltigera rufescens* and *Cornicularia aculeata*, although the association is dominated by non-alpine species. Other alpine species are found in the Cladonietum multiformis association which occurs with aspen or pine. This vegetation type is also dominated by *Cladonia* species, and includes *Cladonia coccifera*, *C. gracilis*, *Cetraria ericetorum*, *C. nivalis* and *Peltigera spuria*. A major distinction between these low and high elevation communities is the increasing importance of *Cetraria* species in the alpine, and the correlated decrease of lowland *Cladonia* species.

(3) Peltigera aphthosa - Stereocaulon alpinum

The mesic-wet habitats where this community occurs (Fig. 25) are not widely represented in the Alberta study area. Indicators of this vegetation type include the crustose lichen Lepraria neglecta, and mosses Polytrichum juniperinum, P. piliferum and Pogonatum alpinum. Vascular plant communities with similar macrolichen species composition and abundance are compiled in Table 42.

In examining these communities, it is important to distinguish between habitats which melt out and experience very dry conditions (early snowbed) and those which melt out only in some years and remain wet (late snowbed). The latter sites are often dominated by Carex nigricans with few or no lichens (Hrapko 1970, Kuchar 1975). Macrolichen species richness is negatively correlated with snow depth and bryophyte cover in the Bald Hills (Kuchar 1975), and similar conditions are found at Highwood Pass (Trottier 1972).

Early snowbed areas support many species such as Sibbaldia procumbens, Salix nivalis, Antennaria lanata, Stereocaulon alpinum, Solorina crocea and Lepraria neglecta. Areas of moderate-heavy snow accumulation, mid-season melt and sustained summer moisture may support Dryas octopetala with one to several species of heaths, herbs and willows. These communities often exhibit a small group of macrolichen species within the genera Cladonia, Peltigera and Cetraria which together may contribute high cover values. An example

TABLE 42. Alpine vascular plant communities with similar macrolichen vegetation to the Peltigera aphthosa - Stereocaulon alpinum community (#3) in Alberta! All communities are in Alberta unless otherwise indicated.

Community/Important Macrolichens	Location
1) Carex phaeocephala - Salix nivalis Cladonia pyxidata, C. coccifera, Peltigera rufescens, Lepraria neglecta	50°35'N, 115°10'W Highwood Pass, Southern Front Ranges (Trottier 1972)
2) Lepraria neglecta subtype of Cassiope tetragona - Dryas octopetala Cladina mitis, Cetraria ericetorum/islandica, Stereocaulon alpinum, Cladonia ecmocyna, Solorina crocea, Dactylina arctica, Peltigera aphthosa.	52°40'N, 117°41'W Bald Hills, Maligne Range, Jasper National Park (Kuchar 1975)
3) Cassiope tetragona - Dryas octopetala Cetraria ericetorum, Cladina mitis, Dactylina arctica, Cetraria nivalis, C. cucullata, Peltigera aphthosa, Stereocaulon alpinum.	52°51'N, 117°59'W Signal Mountain, Maligne Range, Jasper National Park (Hrapko 1970)
4) Salix arctica - Antennaria lanata Peltigera aphthosa, P. canina, P. malacea, Cladonia cariosa, C. pocillum, C. pyxidata, Cetraria ericetorum, C. islandica.	"
5) Antennaria lanata - Sibbaldia procumbens Stereocaulon alpinum, Cetraria islandica, C. ericetorum, Cladonia ecmocyna, C. macrophyllodes, Solorina crocea.	49°35'N, 119°25'W Big White Mountain, Okanagan Valley, B.C. (Eady 1971)

of this is found in the Salix arctica - Antennaria lanata community (Hrapko 1970) which has the greatest macrolichen prominence of all plant communities of Signal Mountain. In contrast, species richness is very low. Although evenness values are not available for the Signal Mountain plant communities, evenness of macrolichens in Salix - Antennaria vegetation may parallel the trend of low values in wetter habitats as found in both Alberta and Yukon study regions.

Variability of snow accumulation and time of snow melt in snowbeds is known to be of primary importance in determining distributions of associated alpine vascular plants (Billings and Bliss 1959) and arctic macrolichens (Larson and Kershaw 1975a, Kershaw 1975a). The community data (Table 42) indicate that several species of both plant groups are characteristically found in mesic-wet habitats, but the degree of predictability for a particular macrolichen species appears to be very low. This may be due to the lack of extensive data for the variety of habitats represented, as well as the potential existence of ecotypic differentiation in snowbed macrolichen populations.

Vascular Plants

The upland alpine vascular plant communities in the Alberta study areas can be compared with several other communities in Rocky Mountain localities. The most similar are those dominated by Dryas integrifolia in the Front Ranges, and by D. octopetala in the Main Ranges.

Dryas integrifolia is an important upland component of some arctic plant communities (Gelting 1955, Barrett and Thomson 1975, Bird 1975, Bliss 1975) but seems to be restricted in the southern Canadian Rocky Mountains. Dryas integrifolia communities from Montana (Bamberg and Major 1968) and from the southern Front Range in Alberta (Johnson 1975) exhibit the closest relationship to those described on Prospect Mountain.

Dryas octopetala communities in Alberta are found in Waterton (Kuchar 1973), Highwood Pass (Trottier 1972), Banff National Park (Beder 1967, Broad 1973) and Jasper National Park (Hrapko 1970, Kuchar 1975). These communities are generally found on acidic soils, in areas of regionally high precipitation. In each of the above studies Dryas octopetala communities represent the drier, more exposed habitats. Associated species include Cassiope tetragona, Empetrum nigrum, Vaccinium vitis-idaea, Artemisia norvegica, and Salix arctica.

(1) *Dryas integrifolia - Carex rupestris*

(2) *D. integrifolia - Oxytropis podocarpa - Salix nivalis*

These communities resemble alpine stands from the Big Snowy Mountains, Montana (Bamberg and Major 1968). Many dominant species are common to both Prospect and the Big Snowy Mountains including *Dryas integrifolia*, *Carex rupestris*, *Polygonum viviparum*, *Androsace chamaejasme*, *Potentilla fruticosa*, and species of *Oxytropis* and *Hedysarum*. Differences between these areas involve species shifts due to the regional isolation of the Montana site, as well as its proximity to the southern (U.S.) Rocky Mountains.

(3) *Dryas integrifolia - Hedysarum alpinum -Androsace chamaejasme*

The most similar vegetation to this community is fo[illegible] in Siyeh Pass, Glacier National Park, Montana (Bamberg and Major 1968). The dominant species on Siyeh Pass are *Dryas octopetala* and *Salix reticulata*, yet the associated plants include important Prospect species such as *Polygonum viviparum*, *Carex rupestris*, *Smelowskia calycina* and *Potentilla diversifolia*. As in the previous comparisons, southern (U.S.) Rocky Mountain plant species distinguish the Siyeh Pass vegetation in common genera such as *Oxytropis*, *Hedysarum* and *Astragalus*.

(4) *Salix nivalis - Artemisia norvegica*

The Divide stands representing this community are few in number to make accurate comparisons. On a tentative basis, the closest similarity is with communities in the Maligne Range of Jasper National Park, specifically with the Herb Meadow group (Kuchar 1975) and the Salix arctica - Antennaria lanata community (Hrapko 1970). Within the Herb Meadow group the Artemisia norvegica - Salix arctica and A. norvegica - Antennaria lanata types are similar to the Divide community. However, the Divide community is depauperate in relation to all community types mentioned. Perhaps the best comparison is within the Heath Group (Kuchar 1975) in the Lepraria neglecta subtype of the Cassiope tetragona - Dryas octopetala community. This subtype has low richness and includes several species in common with the Salix nivalis - Artemisia norvegica community from the Divide. These include S. arctica, A. norvegica, Sibbaldia procumbens, Antennaria lanata, Salix nivalis, Potentilla diversifolia, and Trisetum spicatum. The low species richness of the Salix nivalis - Artemisia norvegica community may be due to the infrequency of suitable habitat in comparison with the study areas of Hrapko (1970) and Kuchar (1975). The well-drained Front Range environment does not promote large-scale development of wet meadows and snowbeds, and the low species richness of mesic-wet stands in this study area may reflect insular, small, and widely distributed habitats.

Yukon

Macrolichens and Vascular Plants

The importance of cryptogams in northern plant communities is evident in the combined use of macrolichen, bryophyte and vascular plant species to designate communities (Kershaw and Rouse 1973, Kojima 1973, Neal and Kershaw 1973a, 1973b). Such recognition of the most conspicuous macrolichens provides qualitative and quantitative descriptions for common species, although detailed information on other species may be lacking. Differences in macrolichen vegetation descriptions seems to be a function of the skills of the investigator, which in turn makes some data comparisons less reliable. This problem has been enhanced by the lack of a standardized northern lichen identification guide, which has forced plant ecologists into choosing from a variety of taxonomic treatments and concepts. The upcoming publication on northern lichens (Thomson, in press) should greatly alleviate inconsistency in northern lichen studies.

The most reliable and detailed studies of comparable alpine vascular plant and macrolichen vegetation are those by Bird (1974a, 1974b) for mountain ranges in the Yukon and Northwest Territories. In these field expeditions, lichen, vascular plant and bryophyte vegetation data were obtained from sites where geologists were simultaneously collecting substrate samples and glacial history data. Rapid vegetation survey techniques were based upon cover estimates from small plots (Bird 1974a, 1974b). I have compared all the unanalyzed stand data from Bird's studies to communities designated in the present study. Of 76 upland alpine stands from 13 sites (Table 43), close correspondence of macrolichen species composition and abundance was found between the following: 12 stands with community 1 (Table 23); 16 stands with community 2 (Table 24); and 48 stands with community 3 (Table 25). The comparability of these data support ~~the geo~~graphic validity of the community designations, as discussed in detail for each vegetation type.

(1) *Cladina arbuscula/mitis - Cetraria nivalis - Cladonia coccifera/metacorallifera*
Vaccinium vitis-idaea - Dryas octopetala

This community is characteristically found on acidic substrates in glaciated terrain, such as in the Ogilvie Mountains (this study, Kojima 1973), and in the McConnell Range of the Franklin Mountains (Bird 1974a, sites 6,8,9, Table 43). The only unglaciated stands of this community type are reported from the Plains of Abraham on chert substrate (Bird 1974b). The interpretive question thus arises whether glaciation is merely coincident with substrate attributes, or is an equal or more important influence on this plant community. Examination of other investigations will help resolve this question.

The *Ledum palustre - Hierochloe alpina - Cladina stellaris - Cetraria nivalis* association of Kojima (1973) is

TABLE 43. Site descriptions from Bird (1974a, 1974b) for alpine areas in the Yukon and Northwest Territories.

LOCATION	#	LATITUDE-LONGITUDE	GLACIATED	ROCK TYPES
YUKON				
Knorr Range	1	65°26'N, 134°29'W	no	dolomite, limestone, shale
Wernecke Mountains	2	65°15'N, 135°50'W	no	limestone, quartzite, chert
Richardson Mountains	3	65°03'N, 135°47'W	no	limestone, siltstone
Mount Deception	4	65°37'N, 135°30'W	yes	-
NORTHWEST TERRITORIES				
Franklin Mountains, McConnell Range	5	63°18'N, 123°11'W	yes	limestone, sandstone
" "	6	63°24'N, 123°14'W	yes	sandstone
" "	7	63°10'N, 123°07'W	yes	limestone
" "	8	63°22'N, 123°01'W	yes	-
Mount Clark	9	64°25'N, 124°13'W	yes	schist, granite
Mackenzie Mountains, Canyon Ranges	10	63°05'N, 125°09'W	yes	-
Backbone Ranges	11	63°08'N, 125°45'W	both	limestone
Camsell Range	12	63°07'N, 123°40'W	yes	limestone
Plains of Abraham	13	64°33'N, 127°43'W	no	schist, granite

similar to the Ogilvie community in this study (Table 44). Vascular plant species in common include *Empetrum nigrum*, *Luzula multiflora*, *Cassiope tetragona*, *Dryas octopetala* and *Vaccinium vitis-idaea*. This association is described from well-drained north-facing slopes, with *Cassiope tetragona* occurring in late snowbed habitats. The combination of good drainage and snowbed moisture regime seems contradictory, but northern aspect and topographic position can interact to promote snow accumulation and late melting on otherwise well-drained slopes. For this reason, moisture regime of individual stands in this community is difficult to assess without observing winter and spring conditions.

The moisture complex-gradient in this community (Fig. 26) is reflected in subtle shifts in species importance rather than in major compositional differences between stands. Examples include the decrease in cover values for *Cetraria richardsonii*, *Cladonia uncialis* and *C. crispata* from mesic-wet to drier sites (Table 22). In exposed sites the moss *Rhacomitrium lanuginosum* attains high importance with *Alectoria nitidula*, *A. ochroleuca*, *Cetraria nigrescens* and *C. nivalis*. *Cassiope tetragona* is most important in mesic-wet snowbed or polygon sites and is frequently associated with high species richness of the genera *Cladonia* and *Cladina*.

The *Cladina - Cetraria - Cladonia - Vaccinium - Dryas* vegetation in this study is similar to arctic lichen-heath associations in the Hudson Bay Lowlands (Table 44). Lichen-

TABLE 44. Alpine and low-arctic plant communities with similar macrolichen vegetation to the *Cladina arbuscula/mitis* - *Cetraria nivalis* - *Cladonia coccifera/ metacorallifera* community (#1) in the Yukon.

Community/Important Macrolichens	Location
1) *Ledum palustre* - *Hierochloe alpina* - *Cladina stellaris* - *Cetraria nivalis* Cetraria cucullata, C. islandica, Cladonia amaurocraea, C. gracilis, Cladina rangiferina, Dactylina arctica, Cornicularia divergens.	64°34'N, 138°14'W North Fork Pass, Ogilvie Mountains, Y.T. (Kojima 1973)
2) *General Lichen-Heath II* Cetraria nivalis, Cladina arbuscula, Cornicularia divergens, Cladina rangiferina, Alectoria ochroleuca, Thamnolia vermicularis, Cetraria islandica.	56°46'N, 88°46'W East Pen Island Area, Hudson Bay Lowlands, Ont. (Kershaw and Rouse 1973)
3) *Central Lichen-Heath 2* Cladina rangiferina, C. arbuscula, Cetraria nivalis, Cornicularia divergens, Alectoria ochroleuca, Cetraria islandica, C. cucullata, Sphaerophorus globosus	54°47'N, 82°23'W Cape Henrietta Maria, Hudson Bay Lowlands, Ont. (Neal and Kershaw 1973a, 1973b)

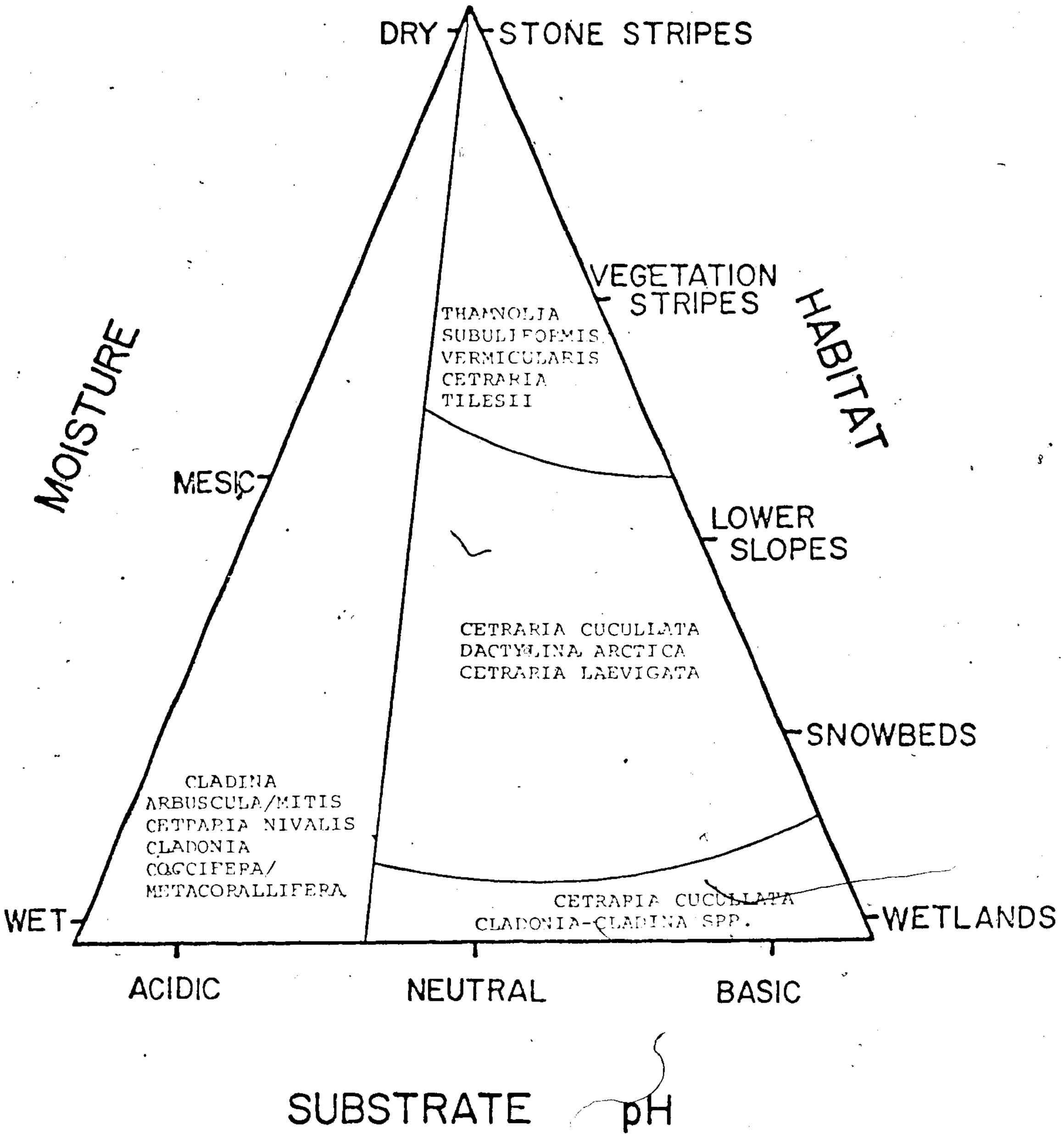


FIGURE 26. Habitat relations of alpine macrolichen communities from Yukon study areas.

heath associations are found on more neutral-basic substrates and exhibit reduced macrolichen species richness, in contrast to this community. However, intensive ecophysiological research in the Lowlands has shown the importance of peat substrate for macrolichen growth in lichen-heath associations (Rouse and Kershaw 1973, Larson and Kershaw 1974, Kershaw 1975a, Larson and Kershaw 1976). Thus, the peat build-up provides similar acidic microhabits in the Lowlands. The increased moisture regime for macrolichens on peat layers is associated with increased importance of species such as _Cladina_ _arbuscula_, _C_. _rangiferina_, _C_. _stellaris_, _Cetraria_ _nivalis_ and _Alectoria_ _ochroleuca_ (Kershaw and Rouse 1971, 1973, Rouse and Kershaw 1973, Larson and Kershaw 1974).

One of the distinguishing features of the Ogilvie macrolichen community is the importance and restricted distribution of species in the Cladoniaceae (Figs. 18-20). Common occurrences of alpine _Cladonia_ species on acidic and peaty substrates are described by Thomson (1967), and similar trends are documented for woodland _Cladonia_ communities (Looman 1964a, 1964b, Ahti 1967, Lambert and Maycock 1968, Lechowicz and Adams 1974a, Kershaw 1977). The evidence strongly suggests greater importance of an acid substrate for the alpine _Cladina - Cetraria - Cladonia - Vaccinium - Dryas_ community, with coincidental history of recent glaciation.

(2) Cetraria cucullata - Dactylina arctica - Cetraria laevigata

Dryas octopetala - Astragalus umbellatus - Salix arctica

These macrolichen and vascular plant communities are closely correlated in the Nahoni and Ogilvie areas; the Knorr Range; the Richardson, Franklin and Mackenzie Mountains; and the Plains of Abraham (sites 1,3-6,9,11-13, Table 43).

Few alpine macrolichen communities have been described which are equivalent to this type of vegetation (Table 45). It is apparent, however, that high relative importance of Cetraria cucullata is a reliable indicator of mesic and snow-bed habitats in alpine and arctic areas of the Yukon and Northwest Territories (this study, Bird 1974a, 1974b), Devon Island (Barrett and Thomson 1975), and western and southern Greenland respectively (Gelting 1955, Hansen 1971).

Dryas integrifolia or D. octopetala is the most frequent vascular plant species. Associated species and their relative importance values distinguish this community, including Salix arctica, S. reticulata, Cassiope tetragona, Rhododendron lapponicum, Astragalus umbellatus, Arctostaphylos rubra, Carex misandra and C. scirpoidea. Bryophyte cover is also important, and common species include Hylocomium splendens and Rhytidium rugosum.

As in the Cladina - Cetraria - Cladonia - Vaccinium - Dryas community (#1), glaciation history does not seem to

TABLE 45. Arctic plant communities with similar macrolichen vegetation to the *Cetraria cucullata - Dactylina arctica - Cetraria laevigata* community (#2) in the Yukon.

Community/Important Macrolichens	Location
1) *Cassiope tetragona* *Cetraria cucullata, Stereocaulon alpinum, Peltigera malacea, Cetraria delisei.*	69°52'N, 54°22'W Disko Island, Western Greenland, (Gelting 1955)
2) *Raised beach foreslopes* *Cetraria cucullata, C. nivalis, Dactylina arctica, C. ramulosa, Parmelia omphalodes, Cetraria delisei.*	74°41'N, 84°33'W Truelove Lowland, Devon Island, N.W.T. (Barrett and Thomson 1975)

affect distribution of this vegetation type. Glaciated and unglaciated sites are almost equally represented in comparable vegetation data (Bird 1974a, 1974b). Also, the type of substrate shows no relationship to this community either. The main factors thus appear to be the moderate to high amount of snow accumulation and the mid-season time of melt. The soil moisture regime is the most important factor affecting snowbed vegetation in several other studies (Billings and Bliss 1959, Johnson and Billings 1962, Bliss 1963, Kershaw and Rouse 1973). The widespread occurrence of this community in mesic sites and snowbeds seems to be a function of microtopography and microclimate, regardless of regional trends in elevation or substrate.

(3) Thamnolia subuliformis/vermicularis - Cetraria tilesii Dryas octopetala - Carex misandra

The most distinctive species of this upland community is Cetraria tilesii, in association with Dryas spp. This plant community is well represented in upland stands from the Nahoni Range and from the majority of Bird's stands (1974a, 1974b) in the Mackenzie, Franklin and Wernecke Mountains, the Knorr Range and the Plains of Abraham (sites 1,2, 5,7,10-13, Table 43).

When all substrate data from Bird (1974a, 1974b) and this study were compared, it became evident that this community consistently characterizes limestone, dolomite or chert substrates in dry unstable habitats, regardless of glaciation history. Unglaciated sites include the Nahoni and Knorr Ranges; Wernecke and Mackenzie Mountains; and the Plains of Abraham (sites 1,2,11,13, Table 43). This community is also represented by ten stands in glaciated regions of the Mackenzie Mountains (sites 5,7,10,11,12, Table 43).

The differences between stands in the unglaciated and glaciated areas are qualitatively and quantitatively minor. Species absent from glaciated sites include *Parmelia separata* and *Hypogymnia subobscura*, with infrequent occurrence of *Asahinea chrysantha* and *Cornicularia divergens*. Neither of the northern species *Cetraria richardsonii* nor *Evernia perfragilis* are noticeably diminished in frequency or cover in glaciated stands. The species differences are due perhaps to poor dispersal, but are of minor consequence to the overall species composition and relative abundance values in the community.

Dryas species indicating this community include both *D. integrifolia* and *D. octopetala* in the Wernecke Mountains and Knorr Ranges. The latter species is encountered in the Nahoni Range, while all other sites are characterized by *D. integrifolia* in glaciated and unglaciated areas. A suggested pattern is that *D. integrifolia* occurs in the eastern ranges (e.g. Franklin Mountains), shifting to mixtures in the central and western Mackenzie Mountains, and then is replaced by *D. octopetala* in the western and northern Ogilvie and Porcupine Mountains (e.g. Nahoni Range) extending northward to the Richardson Mountains. This may be an oversimplification of Dryas distribution, and the species of Dryas should not be predicted for this community in a given northern site based solely upon data presented here.

Other northern vegetation studies from Greenland (Gelting 1955) and the Hudson Bay Lowlands (Kershaw and Rouse 1973, 1973) have basic-neutral substrates, yet show limited correspondence to this community. Cetraria tilesii is absent from the Alectoria nitidula - Dryas integrifolia associations of both other studies, and only ubiquist species are found in common with the Yukon community. Species in all three studies include Cetraria nivalis, Alectoria ochroleuca, Thamnolia vermicularis and C. cucullata, although relative importance values from the two other studies do not correspond to those of the Yukon community.

It is likely that upland vegetation from the Greenland and Hudson Bay Lowland studies is influenced substantially by local maritime climate. The correlation of macrolichen species composition and relative importance to Yukon uplands may not be as dependent upon substrate attributes alone as on location of such habitats in interior North American mountains where continental climate prevails.

Nahoni Slate Outcrop Stand

The high cover of Stereocaulon alpinum on a gravelly Nahoni slate coutcrop is atypical of other Nahoni or Ogilvie

(Kojima 1973) areas, and of other northern alpine studies (Bird 1974a, 1974b). Ricker (1967), however, found similar stands while working on low alpine tundra dwarf birch communities in the same region of the Ogilvies as Kojima (1973). He describes a gravel-hummock community which occurs on well-drained sites with high cover of *Stereocaulon tomentosum*. The high combined importance of *Stereocaulon* and *Betula glandulosa* is similar to the Nahoni slate outcrop area, and suggests possible misidentification of *S. alpinum*. Dwarf birch communities have been found in Greenland (Hansen 1971) with *Stereocaulon alpinum* dominating the ground strata, although the distribution of this vegetation type in the Yukon or Northwest Territories needs further documentation.

Nahoni Wetland Stands

The two Nahoni stands in poorly-drained sites correspond to two associations described by Kojima (1973) in the North Fork Pass area. The *Betula glandulosa - Rubus chamaemorus - Ledum palustre* vegetation (R1) is similar to the *B. glandulosa - Artemisia arctica - Hylocomium splendens ssp. alaskanum* association of Kojima (1973). In both communities *Nephroma arcticum* and *Peltigera aphthosa* are conspicuous indicator species. Valley bottoms in the Nahoni area exhibit large expanses of *Eriophorum vaginatum* (R2) comparable to the *Ledum palustre - Eriophorum vaginatum - Sphagnum spp.* association at North Fork Pass. In the *Betula glandulosa* and Eriophorum vaginatum communities bryophytes attain virtually 100% cover, and contrast with reduced lichen importance.

Macrolichen and vascular plant data from Nahoni wetlands were compared to other stands in the Yukon and Northwest Territories (Bird 1974a, 1974b, sites 6,7,9,12,13, Table 43). While vascular plant communities are all dominated by Eriophorum spp. or Carex spp., the macrolichen assemblages are not as clearly delineated. The most important macrolichen species in both wetlands is Cetraria cucullata (Table 27); therefore the community distinctions are based upon the increased importance of Cladonia species in Betula stands, and of increased Cladina importance in Eriophorum stands. This quantitative difference is not as clear in the other sites (Bird 1974a, 1974b) due to equally low cover values for all macrolichen species other than C. cucullata.

The rich microhabitat variability in Eriophorum sp. tussocks may partially explain the difficulty of determining associated macrolichen communities, although sample size in this and related studies are low. Dynamic aspects of water availability, peat accumulation, pH modification, exposure and shading from the tussocks are expected to account for much of the variability in macrolichen vegetation (Rouse and Kershaw 1973, Larson and Kershaw 1974, Kershaw 1974).

Low similarity of wetland macrolichen stands to those in upland communities merits more thorough investigation.

Higher macrolichen similarity is generally found between Nahoni wetlands and *Picea mariana* lowlands (Bird 1974a, 1974b). Common species include *Cladonia amaurocraea*, *C. bacillaris*, *C. botrytes*, *C. cenotea*, *C. chlorophaea* s.l., *C. coniocraea*, *C. cornuta*, *C. deformis*, *C. gonecha*, *C. pleurota*, *Cladina* species, *Nephroma arcticum*, *Peltigera canina* and *P. malacea*. These species can be considered as Boreal Forest outliers, or species which were possibly associated with an advance of forest over the tundra about 1,000 years ago (Thomson 1972). The community similarity between alpine and boreal wetlands suggests that the wetland habitat overrides other factors such as glacial history, type of mineral substrate or elevation.

Alectoria ochroleuca Communities

An important variant of northern alpine upland vegetation is that dominated by *Alectoria ochroleuca*. Dominance of *A. ochroleuca* is reported from stands in the McConnell Range, the Plains of Abraham and the Richardson Mountains (Bird 1974a, 1974b), although it was not as important in Nahoni or Ogilvie sites in this study. *Cetraria cucullata* is found as a secondary species along with species of the *C. cucullata - Dactylina arctica - C. laevigata* community and additional species *Cladina arbuscula*, *C. mitis* and *C. stellaris*. The relative importance of *Cladina* species indicates a relationship to the *Cladina arbuscula/mitis - Cetraria nivalis - Cladonia coccifera/metacorallifera* community.

No relationship between substrate or glaciation history is evident in the distribution of the *Alectoria ochroleuca* vegetation based upon Bird's data. In regard to moisture regime, Kojima (1973) has included this species in a designation with *Arctostaphylos rubra* and *Cornicularia divergens* for dry ridges in the Ogilvie Mountains. *Alectoria ochroleuca* is also characteristic of exposed ridges in lichen heath on the Hudson Bay Lowlands (Kershaw and Rouse 1973). Associated plant species in the Mackenzie and Richardson Mountains span a moisture gradient from dry sites with *Rhacomitrium lanuginosum*, *Dryas integrifolia*, and *D. octopetala*, to wetter habitats with *Vaccinium vitis-idaea*, *Betula glandulosa* and *Cassiope tetragona*.

The limited data suggest that there may be regionally distinct communities characterized by *Alectoria ochroleuca*. This species exhibits a very broad habitat response pattern in both study regions (Fig. 15, 17) with highest cover in mesic-dry sites with basic substrates, and frequent occurrence in other habitats (Kershaw and Rouse 1973, Kojima 1973, Bird 1974a, 1974b, Larson and Kershaw 1975b, 1975c).

Recent physiological investigations have shown that net photosynthesis in *A. ochroleuca* varies intraspecifically in plants from different geographic locations but does not vary in plants from a local topographic gradient (Larson and Kershaw 1975b, 1975c). It is therefore possible that the differences in vegetation associated with this species may reflect the distribution of its physiologically distinct populations.

SUMMARY AND CONCLUSIONS

Alpine macrolichen vegetation was studied in Cordilleran regions in west central Alberta and north central Yukon Territory. The four study areas included Prospect Mountain and the Divide in the Mountain Park region, Alberta, and the Nahoni Range and Ogilvie Mountains in the Yukon.

Macrolichen species were more important in the Yukon study areas in terms of increased cover, species richness (S) and overall diversity (H'). Values for species evenness (J) were not significantly different between the four study areas, indicating that increased species richness does not affect trends in habitat utilization by different species. Within regions, evenness values varied with different moisture regime. Lowest evenness was found in mesic-wet sites and in extremely dry, depauperate stands, while highest evenness occurred in well-vegetated upland sites in all areas.

Population response patterns for macrolichen species elucidated the following ecological groups in both regions which were related to a complex-gradient of substrate pH: (1) ubiquists; (2) common on acidic substrates; (3) exclusively on acidic substrates; (4) common on both substrates; (5) common on basic substrates: and (6) exclusively on basic substrates. Species in the ubiquist group from each region were comparable, while most other species shifted in breadth of distribution over moisture and substrate gradients. This was partially due to the prevalence of dry, basic substrates in the Alberta region. The most significant regional difference in response patterns was the large group of Yukon species which were specialized on acidic substrates and were most frequent or were restricted in Ogilvie sites. The highest importance of these species corresponded with lowest importance of regional ubiquist species.

Macrolichen species groups were also examined in each region through the use of ordinations and were found to be related to both moisture and substrate pH complex-gradients. Three macrolichen communities were delineated in the vegetation of each region by grouping similar stands. Communities were also designated for vascular plant data, and the two plant groups were compared.

Macrolichen communities from Alberta in order of increasing moisture and increasing substrate acidity are: (1) *Cetraria cucullata - Thamnolia subuliformis - Cetraria tilesii*; (2) *Cetraria ericetorum -Cetraria cucullata - Peltigera rufescens*; and (3) *Peltigera aphthosa - Stereocaulon alpinum*. The vascular plant communities also follow these gradients: (1) *Dryas integrifolia - Carex rupestris*; (2) *Dryas integrifolia - Oxytropis podocarpa - Salix nivalis*; (3) *Dryas integrifolia - Hedysarum alpinum - Androsace chamaejasme*; and *Salix nivalis - Artemisia norvegica*. There is a sequential overlap of vascular plant and macrolichen vegetation which results in partial correlation of these designations along complex-gradients of substrate pH and moisture.

In the Yukon data, the macrolichen communities are ranked in order of decreasing substrate acidity: (1) *Cladina arbuscula/mitis - Cetraria nivalis - Cladonia coccifera/metacorallifera*; (2) *Cetraria cucullata - Dactylina arctica - Cetraria laevigata*; and (3) *Thamnolia subuliformis/vermicularis - Cetraria tilesii*. Moisture regime is variable in the first community, and grades from mesic-wet in the second, to dry in the third community. These communities correspond to the following vascular plant communities: (1) *Vaccinium vitis-idaea - Dryas octopetala*; (2) *Dryas octopetala - Astragalus umbellatus - Salix arctica*; and (3) *Dryas octopetala - Carex misandra*.

Communities were compared with those of other studies in order to evaluate environmental factors in relation to vegetation distribution patterns.

Macrolichen communities in Alberta are similar in the region from Mountain Park and Jasper National Park south to Waterton, and into Montana. Specifically, the *Cetraria cucullata - Thamnolia subuliformis - Cetraria tilesii* community (#1) is characteristic of dry upland habitats with basic substrate pH. Such environments can be found in the Front Ranges extending south to mountains in Montana.

The second community, *Cetraria ericetorum - Cetraria cucullata - Peltigera rufescens* is represented in several alpine vegetation studies of Main Range areas. It is most frequently associated with upland *Dryas* spp. communities. This community has higher importance of *Cladonia* and *Cladina* species in Main Range than in Front Range areas.

The *Peltigera aphthosa - Stereocaulon alpinum* community (#3) is documented from few comparable vegetation types in the Main Ranges. The limited extent of suitable snowbed habitat in the study areas is responsible for the depauperate nature of this vegetation. The most similar community is described from Jasper National Park, but the regional distribution is not known.

In the Yukon, a distinct macrolichen community occurs in the Ogilvie area over a wide range of moisture regime. This *Cladina arbuscula/mitis - Cetraria nivalis - Cladonia coccifera/metacorallifera* community (#1) is also found in the Franklin and Mackenzie Mountains as well as in the Hudson Bay Lowlands. These communities are consistently associated with low substrate pH.

The *Cetraria cucullata - Dactylina arctica - Cetraria laevigata* community (#2) is found in the Knorr Range, the Ogilvie, Richardson, Franklin and Mackenzie Mountains, and is encountered in both Nahoni and Ogilvie study areas. Similar vegetation also occurs on Devon Island and in western Greenland. This type of vegetation is strongly correlated with mesic sites and snowbed habitats. Distribution of the community thus reflects the habitat distribution in alpine environments.

Dry upland habitats in the Nahoni study area are characterized by the Thamnolia subuliformis/vermicularis - Cetraria tilesii community (#3). It also occurs consistently on limestone and dolomite in the Knorr Range, Wernecke and Mackenzie Mountains. The strong correlation of this upland community with basic soil pH suggests that this type of mineral substrate determines the macrolichen vegetation.

The general distribution trends of all communities were related to environmental complex-gradients such as moisture and substrate pH. The results indicated that glaciation history alone does not explain macrolichen vegetation distribution in the Canadian Cordillera. Investigations of individual macrolichen species distributions confirmed that widespread dispersal has obscured the boundaries between past refugia and glaciated regions.

The question remains of why macrolichen importance and diversity is significantly higher in the northern Cordillera. The proximity of northern areas to past unglaciated regions may, of course, be involved. However it is suggested that the microhabitat factors in the southern Rocky Mountains are unsuitable for species currently restricted to northern Cordilleran areas. The resolution of this question will require intensive examination of macrolichen physiology.

Alpine macrolichen vegetation has been outlined for certain northern and southern Cordilleran regions, yet no information is available for intermediate mountain areas. The correspondence of macrolichen and vascular plant data to environmental factors in this study are considered to be suitable for predictive purposes in such uninvestigated regions.

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APPENDIX A. Macrolichens encountered in the Yukon and Alberta study areas: Nahoni (N), Ogilvie (O), Prospect (P), and Divide (D).

ASCOMYCETES	PDNO
Collemataceae	
Leptogium saturninum (Dicks.) Nyl.	++--
Pannariaceae	
Psoroma hypnorum (Vahl) S.Gray	-+++
Peltigeraceae	
Peltigera aphthosa (L.) Willd.	-+++
P. canina (L.) Willd.	-++-
P. malacea (Ach.) Funck	+-++
P. pulverulenta (Hook.) Nyl.	+-++
P. rufescens (Weis.) Humb.	+++-
P. spuria (Ach.) DC.	++--
Nephroma arcticum (L.) Torss.	--++
N. expallidum (Nyl.) Nyl.	+++-
Solorina crocea (L.) Ach.	-+-+
S. spp.	++++
Stictaceae	
Lobaria linita (Ach.) Rabh.	---+
Stereocaulaceae	
Stereocaulon alpinum Laur.	++++
S. rivulorum Magn.	-+--
Cladoniaceae	
Cladina aberrans (Abb.) Hale & W.Culb.	---+
C. arbuscula (Wallr.) Hale & W.Culb.	--++
C. mitis (Sandst.) Hale & W.Culb.	-+++
C. rangiferina (L.) Harm.	--++
C. stellaris (Opiz) Brodo	--++
Cladonia amaurocraea (Flörke) Schaer.	--++
C. bellidiflora (Ach.) Schaer.	---+
C. chlorophaea (Flörke) Spreng.	--++
C. coccifera (L.) Willd.	-+++
C. cornuta (L.) Hoffm.	---+
C. crispata (Ach.) Flot.	---+
C. ecmocyna (Ach.) Nyl.	-+++
C. gonecha (Ach.) Asah.	--++
C. gracilis (L.) Willd.	-+++
C. macrophylla (Schaer.) Stenham	--++
C. macrophyllodes Nyl.	-+++
C. metacorallifera Asah.	--++
C. phyllophora Hoffm.	-+-+
C. pocillum (Ach.) O.Rich.	+++-
C. pyxidata (L.) Hoffm.	++++
C. uncialis (L.) Wigg.	--++
Umbilicariaceae	
Umbilicaria cylindrica (L.) Del.	-+--
U. hyperborea (Ach.) Ach.	-+-+
U. lambii Imsh.	-+--
U. phaea Tuck.	---+
U. proboscidea (L.) Schrad.	-+-+
U. virginis Schaer.	---+

APPENDIX A. CONTINUED.

	PDNO
Lecanoraceae	
Lecanora chrysoleuca (Sm.) Ach.	+---
Parmeliaceae	
Asahinea chrysantha (Tuck.) W.Culb. & C.Culb	--++
A. scholanderi (Llano) W.Culb & C.Culb.	--+-
Cetraria commixta (Nyl.) Th.Fr.	-+--
C. cucullata (Bell) Ach.	++++
C. delisei (Bory ex Schaer.) Th.Fr.	--+-
C. ericetorum Opiz	++++
C. hepatizon (Ach.) Vain.	---+
C. islandica (L.) Ach.	++++
C. laevigata Rass.	++++
C. nigricans (Retz.) Nyl.	--++
C. nivalis (L.) Ach.	++++
C. pinastri (Scop.) S.Gray	--+-
C. richardsonii Hook.	--++
C. tilesii Ach.	+++-
Hypogymnia oroarctica Krog	++++
H. physodes (L.) W.Wats.	+-+-
H. subobscura (Vain.) Poelt	+++-
Parmelia almquistii Vain.	---+
P. centrifuga (L.) Ach.	---+
P. chlorochroa Tuck.	-+--
P. omphalodes (L.) Ach.	-++-
P. panniformis (Nyl.) Vain.	--++
P. saxatilis (L.) Ach.	-++-
P. separata Th.Fr.	--+-
P. sulcata Tayl.	---+
P. taractica Kremp.	-+--
P. wyomingica (Gyeln.) Hale	-+--
Usneaceae	
Alectoria chalybeiformis (L.) S.Gray	++--
A. minuscula Nyl.	+++-
A. nigricans (Ach.) Nyl.	++++
A. nitidula (Th.Fr.) Vain.	--+-
A. ochroleuca (Hoffm.) Mass.	++++
A. pubescens (L.) R.H.Howe	-+++
Cornicularia aculeata (Schreb.) Ach.	+++-
C. divergens Ach.	--++
Dactylina arctica (Hook.) Nyl.	++++
D. ramulosa (Hook.) Tuck.	++++
Evernia perfragilis Llano	--+-
Thamnolia subuliformis (Ehrh.) W.Culb.	++++
T. vermicularis (Sw.) Ach. ex Schaer.	--++
Physciaceae	
Physcia constipata (Nyl.) Norrl. & Nyl.	++--
Physconia muscigena (Ach.) Poelt	++--
Verrucariaceae	
Dermatocarpon intestiniforme (Korb.) Hasse	+---
Sphaerophoraceae	
Sphaerophorus globosus (Huds.) Vain.	--++
BASIDIOMYCETES	
Tricholomataceae	
Coriscium viride (Ach.) Vain.	---+

APPENDIX B. Vascular plants encountered in the Yukon and Alberta study areas: Nahoni (N), Ogilvie (O), Prospect (P), and Divide (D).

	PDNO
Equisetaceae	
Equisetum scirpoides Michx.	+++-
Lycopodiaceae	
Lycopodium clavatum L.	---+
L. selago L.	---+
Gramineae	
Bromus inermis var. pumpellianus (Scribner) Wagnon	∓+--
Calamagrostis purpurascens R.Br.	-+-+
Elymus innovatus Beal	++--
Festuca baffinensis Polunin	++--
F. ovina var. brevifolia (R.Br.) Watson	++--
Hierochloe alpina (Sw.) Roem. & Schult.	--++
Poa spp.	++++
Trisetum spicatum (L.) Richt.	++--
Cyperaceae	
Carex atrosquama Mack.	++--
C. capillaris L.	--+-
C. macrochaeta C.A.Mey.	---+
C. membranacea Hook.	--+-
C. microchaeta Holm	--++
C. misandra R.Br.	+-++
C. nardina Fries	++--
C. oederi ssp. viridula (Michx.) Hult.	--+-
C. petricosa Dewey	+---
C. rupestris All.	+++-
C. scirpoidea Michx.	--+-
Eriophorum vaginatum L.	--+-
Kobresia bellardii (All.) Degl.	+++-
K. simpliciuscula (Wahlenb.) Mack.	+---
Juncaceae	
Luzula multiflora (Retz.) Lej.	--++
Liliaceae	
Tofieldia coccinea Richards.	--+-
T. pusilla (Michx.) Pers.	+---
Zygadenus elegans Pursh	++--
Salicaceae	
Salix alaxensis (Anderss.) Coville	+-+-
S. arctica Pall.	++++
S. drummondiana Barrett	+---
S. glauca L.	++--
S. interior Rowlee	---+
S. nivalis Hook.	++--
S. phlebophylla Anderss.	--+-
S. reticulata L.	--++
S. vestita Pursh	+---
Betulaceae	
Betula glandulosa Michx.	++++

APPENDIX B. CONTINUED.

	PDNO
Polygonaceae	
Polygonum bistorta L.	--++
P. viviparum L.	++++
Caryophyllaceae	
Cerastrium beeringianum Cham. & Schlecht.	-+++
Lychnis apetala L.	+-+-
Minuartia arctica (Stev.) Aschers. & Graebn.	--+-
M. austromontana Wolf & Packer	++--
M. elegans (Maguire) Wolf	--+-
M. rossii (R.Br.) Graebn.	++--
M. rubella (Wahlenb.) Graebn.	-+--
M. sajanensis (Willd.) Wolf	-+--
Silene acaulis L.	++++
Stellaria laeta (Richards.) Wats.	++--
S. monantha Hult.	+---
Ranunculaceae	
Aconitum delphinifolium DC.	+--+
Anemone narcissiflora L.	--++
A. parviflora Michx.	+-+-
Delphinium brachycentrum Ledeb.	-+--
Trollius albiflorus (A.Gray) Rydb.	+---
Papaveraceae	
Papaver macounii Greene	--+-
Cruciferae	
Arabis drummondii Gray	+---
Cardamine bellidiflora L.	---+
C. purpurpea Cham. & Schlecht.	--++
Draba incerta Payson	+---
D. lonchocarpa Rydb.	+---
D. oligosperma Hook.	+---
D. porsildii G.A.Mulligan	+-+-
Lesquerella arctica (Wormsk.) S.Wats.	+-+-
Parrya nudicaulis (L.) Regel	--++
Smelowskia calycina (Stephan) C.A.Mey.	++--
Crassulaceae	
Sedum rosea (L.) Scop.	---+
S. stenopetalum Pursh	-+--
Saxifragaceae	
Boykinia richardsonii (Hook.) Gray	--+-
Chrysosplenium wrightii Fr. & Sav.	--[illegible]+
Saxifraga aizoides L.	+---
S. caespitosa L.	-+--
S. davurica Willd.	--++
S. flagellaris Willd.	---+
S. hieracifolia Waldst. & Kit.	---+
S. nivalis L.	-+--
S. oppositifolia L.	++--
S. punctata L.	--+-
S. serpyllifolia Pursh	---+
S. tricuspidata Rottb.	++--

APPENDIX B. CONTINUED.

	PDNO
Rosaceae	
Dryas integrifolia M.Vahl	++--
D. octopetala L.	++++
Geum glaciale Adams	--+-
G. rossii (R.Br.) Ser.	--++
Potentilla biflora Willd.	--+-
P. diversifolia Lehm.	+++-
P. fruticosa L.	+---
P. nivea L.	++--
Rubus chamaemorus L.	--+-
Sibbaldia procumbens L.	-+--
Leguminosae	
Astragalus aboriginum Richards.	++--
A. alpinus L.	+---
A. umbellatus Bunge	--++
Hedysarum alpinum L.	+++-
H. mackenzii Richards.	+-+-
Lupinus arcticus S.Wats.	--+-
Oxytropis campestris (L.) DC.	++--
O. maydelliana Trautv.	--++
O. nigrescens (Pall.) Fisch. ssp. bryophila (Greene) Hult.	--+-
O. podocarpa A.Gray	++--
O. viscida Nutt. var. viscida Barneby	--+-
Empetraceae	
Empetrum nigrum L.	--++
Pyrolaceae	
Pyrola asarifolia Michx.	--+-
P. grandiflora Radius	++--
Ericaceae	
Andromeda polifolia L.	--+-
Arctostaphylos rubra (Rehd. & Wilson) Fern.	+++-
Cassiope tetragona (L.) D.Don	-+++
Ledum palustre L.	--++
Phyllodoce empetriformis (Smith) D.Don	-+--
P. glandulifera (Hook.) Coville	-+--
Rhododendron lapponicum (L.) Wahlenb.	--+-
Vaccinium uliginosum L.	--++
V. uliginosum L. ssp. microphyllum Lange	--++
V. vitis-idaea L.	--++
Primulaceae	
Androsace chamaejasme Host.	++--
A. septentrionalis L.	+---
Dodecatheon frigidum Cham. & Schlecht.	---+
Gentianaceae	
Gentiana propinqua (Richards.) J.M.Gillett	-+--
G. prostrata Haenke	++-+
Boraginaceae	
Eritrichium chamissonis DC.	--+-
Mertensia paniculata (Ait.) G.Don	+---
Myosotis alpestris Schmidt	++++

APPENDIX B. CONTINUED.

	PDNO
Scrophulariaceae	
Castilleja hispida Benth.	+---
C. hyperborea Pennell	--++
C. miniata Dougl.	+---
C. occidentalis Torr.	-+--
Lagotis glauca Gaertn.	--++
Pedicularis capitata Adams	+++-
P. flammea L.	++--
P. groenlandicum Retz.	++--
P. lanata Cham. & Schlecht.	++++
P. sudetica Willd.	--++
Lentibulariaceae	
Pinguicula vulgaris L.	--+-
Valerianaceae	
Valeriana capitata Pall.	---+
Campanulaceae	
Campanula lasiocarpa Cham.	++-+
C. rotundifolia L.	++--
C. uniflora L.	+---
Compositae	
Antennaria alpina (L.) Gaertn.	++--
A. lanata (Hook.) Greene	-+--
A. monocephala DC.	---+
A. umbrinella Rydb.	-+--
Arnica alpina (L.) Olin	++--
A. frigida C.A.Mey.	--+-
Artemisia norvegica Fries	-+-+
Aster alpinus L.	++--
Chrysanthemum integrifolium Richards.	--+-
Erigeron grandiflorus Hook.	++--
E. humilis Grah.	+---
E. lanatus Hook.	+---
E. peregrinus (Pursh) Greene	-+--
E. radicatus Hook.	+---
Saussurea angustifolia (Willd.) DC.	--++
S. densa (Hook.) Rydb.	+---
Senecio atropurpureus (Ledeb.) Fedtsch.	---+
S. lugens Richards.	-+--
S. yukonensis Pors.	---+
Solidago multiradiata Ait.	++--

APPENDIX C. Values for macrolichen cover, species richness (S), evenness (J), and diversity (H') in Alberta and Yukon stands.

COVER

Prospect Stand	Substrate Unit veg.	Substrate Unit stripe
1	28.77	12.09
2	5.40	2.11
3	9.98	.37
4	14.96	1.23
5	29.57	1.17
6	32.32	2.74
7	16.90	-
8	28.82	10.82
9	43.90	13.48
10	19.14	4.16
11	38.44	6.52
Ogilvie		
1	38.27	20.04
2	17.13	-
3	85.88	-
4	31.31	-
5v	49.03	-
5b	43.30	-
5c	39.87	-
6	64.03	-
7	45.79	-
8	52.61	-

Divide Stand	Substrate Unit veg.	Substrate Unit stripe
1	50.88	13.30
2	37.70	4.14
3	53.04	-
4	26.06	2.65
5	61.80	16.80
6	12.45	-
Nahoni		
1	39.31	14.24
2	64.29	-
3	71.96	17.72
4	69.49	-
5	53.67	-
6	57.00	43.06
7	43.63	29.15
8	60.45	24.11
9	54.06	13.73
10	50.98	15.06
11	59.55	15.89
12	63.12	21.79
13	60.73	-
14	56.11	-
15	71.87	25.78
R1	42.45	-
R2	43.00	-

SPECIES RICHNESS

Prospect		
1	11	11
2	8	6
3	5	4
4	10	8
5	9	3
6	13	8
7	8	-
8	11	8
9	11	12
10	13	12
11	14	13

Divide		
1	21	19
2	14	11
3	9	-
4	7	6
5	15	11
6	18	-
Nahoni		
1	14	13
2	18	-
3	17	13
4	23	-
5	22	-

APPENDIX C. CONTINUED.

SPECIES RICHNESS

Ogilvie Stand	Substrate Unit veg.	Substrate Unit stripe	Nahoni Stand	Substrate Unit veg.	Substrate Unit stripe
1	26	21	6	20	16
2	21	-	7	15	17
3	17	-	8	19	18
4	15	-	9	19	12
5v	19	-	10	21	13
5b	21	-	11	16	12
5c	17	-	12	19	15
6	23	-	13	31	-
7	16	-	14	21	-
8	19	-	15	25	19
			R1	17	-
			R2	15	-

EVENNESS

Prospect		
1	.90	.90
2	.77	.64
3	.86	.71
4	.77	.85
5	.73	.07
6	.80	.89
7	.85	-
8	.90	.83
9	.76	.90
10	.85	.77
11	.86	.80

Ogilvie		
1	.88	.89
2	.87	-
3	.84	-
4	.76	-
5v	.82	-
5b	.83	-
5c	.87	-
6	.82	-
7	.83	-
8	.79	-

Divide		
1	.78	.88
2	.67	.86
3	.84	-
4	.49	.49
5	.78	.87
6	.65	-

Nahoni		
1	.79	.79
2	.67	-
3	.81	.85
4	.75	-
5	.83	-
6	.84	.87
7	.77	.89
8	.87	.85
9	.88	.92
10	.86	.82
11	.85	.72
12	.82	.88
13	.86	-
14	.67	-
15	.85	.83
R1	.86	-
R2	.90	-

APPENDIX C. CONTINUED.

DIVERSITY

Prospect	Substrate Unit	
Stand	veg.	stripe
1	2.17	2.16
2	1.62	1.21
3	1.39	.99
4	1.79	1.82
5	1.60	1.17
6	2.07	1.86
7	1.78	-
8	2.17	1.73
9	1.83	2.25
10	2.18	1.96
11	2.28	2.09
Ogilvie		
1	2.86	2.71
2	2.66	-
3	2.38	-
4	2.07	-
5v	2.42	-
5b	2.53	-
5c	2.46	-
6	2.58	-
7	2.29	-
8	2.33	-

Divide	Substrate Unit	
Stand	veg.	stripe
1	2.37	2.59
2	1.78	2.09
3	2.48	-
4	.97	.92
5	2.12	2.08
6	1.90	-
Nahoni		
1	2.09	2.04
2	1.94	-
3	2.31	2.18
4	2.36	-
5	2.58	-
6	2.52	2.42
7	2.10	2.54
8	2.57	2.45
9	2.59	2.30
10	2.63	2.12
11	2.37	1.81
12	2.42	2.38
13	2.97	-
14	2.05	-
15	2.74	2.43
R1	2.44	-
R2	2.44	-