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THE UNIVERSITY OF ALBERTA

GRADIENT ANALYSIS, HABITATS, AND SPECIES DIVERSITY OF BRYOPHYTES IN JASPER NATIONAL PARK, ALBERTA

by

THOMAS D. LEE ©

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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DEPARTMENT OF BOTANY

EDMONTON, ALBERTA
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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 "Gradient analysis, habitats, and species diversity of bryophytes in Jasper National Park, Alberta" submitted by Thomas Dale Lee in partial fulfilment of the requirements for the degree of Master of Science.

Supervisor

Date 17 June 1976

ABSTRACT

The response patterns or "habitats" of important bryophyte species and the patterns of alpha and beta diversity in bryophyte communities were described along complex elevation and moisture gradients in Jasper National Park, Alberta. Thirty stands were quantitatively sampled including wetlands, forests, rock outcrops, and tundra.

Bryophyte cover was low in xeric communities and high in mesic and hydric communities, reaching a maximum of almost 70% in Engelmann spruce-subalpine fir forests of the subalpine zone.

Direct gradient analysis was used to establish relationships among stands and to ascertain species response patterns. Habitat breadth and overlap were measured for important species. Most species habitats were narrow along the moisture gradient and broad along the elevation gradient. No two species had identical habitats. Many were restricted to one-few substratum types. Species with similar habitats often differed in substratum affinities. A literature survey indicated that species in the Jasper area performed similarly elsewhere.

Species richness of stands was positively correlated with the number of substratum types per stand. Species richness on the most abundant substratum per stand was positively correlated with elevation, and species evenness was positively correlated with both bryophyte cover and

a subjective moisture index, and negatively correlated with elevation. The change in bryophyte species composition, or beta diversity, was highest along the moisture gradient and lowest along the elevation gradient. Trends of bryophyte beta diversity were similar to those of understory vascular plant beta diversity along the moisture gradient, but dissimilar along the elevation gradient especially for mesic and hydric coenoclines.

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INTRODUCTION

The systematic documentation of species distribution and abundance patterns is the first step toward understanding their causes. In community ecology, recent research has sought to describe and explain changes in species composition between communities (Whittaker 1956, 1967, MacArthur 1965, Whittaker, Levin, and Root 1973), and the division of resources by species within communities (Hutchinson 1957, 1959, MacArthur 1964, 1965, McNaughton and Wolf 1970, Whittaker, Levin, and Root 1973). Plant community ecologists have examined changes in species composition and patterns of within-community variables, such as species richness and evenness of abundance, along complex elevation, moisture, and nutrient gradients (e.g. Curtis and McIntosh 1951, Bray and Curtis 1957, Whittaker 1956, 1960, 1967, Monk 1967, Beals 1969, Glenn-Lewin 1975, Westman 1975, Bratton 1975, Marks and Harcombe (1975). The subject of almost all of these studies has been the vascular plant component of the community and only rarely have bryophytes and lichens been included (Slack 1971).

Bryophytes are very different from vascular plants. Since they possess no mechanism to control water loss, lack a well developed vascular system, and have no roots, their water relations are directly regulated by the immediate microclimate; hence, they are poikilohydric (Hosokawa, Odani, and Tagawa 1964). Furthermore, mosses and liverworts are the only important land plants having a dominant gametophyte (haploid) generation. Because of these differences, bryophytes might be expected to play a different role in communities than the vascular plants, and might also respond differently to environmental gradients. Thus, the bryophyte component of the plant community merits its individual scrutiny.

The examination of a specific stratum or synusia within the plant community has become an accepted practice. Lippmaa (1939), who developed the "unistratal concept" of plant communities, believed that synusiae containing plants of similar form and function were valid units of study. Whittaker (1972) has observed that:

> ... species of a particular stratal grouping or synusia are more nearly alike in response to environment and relation to resources, more directly in competition with one another as mature plants, than species of different strata. Division of plants is thus comparable to division of an animal community into guilds.

Early bryophyte ecologists compared species lists and crude abundance estimates to evaluate relationships between species and communities (e.g. Watson 1909, 1932) but eventually quantitative methods were employed, permitting more rigorous data analysis (e.g. Cain and Sharp 1938). European phytosociologists long ago devised schemes for evaluating forest site qualities based on the performance of understory species, including bryophytes (Cajander 1926). The use of this approach by Brinkman (1929), Heimburger (1934), and Crandall (1958) has increased our knowledge of bryophyte communities in North America.

From the beginning, ecologists have recognized that bryophytes are highly sensitive to substratum type and that different bryophyte assemblages develop on different substrata (Scott 1971). Recent studies in bryophyte ecology have focused on particular substrata. For example, corticolous bryophyte and lichen communities have been examined (Billings and Drew 1938, Phillips 1951, Hale 1952, 1955, Culberson 1955, Barkman 1958, Iwatsuki 1960, Hoffman and Kazmierski 1969, Hoffman 1971) as have saxicolous communities on various rock outcrops (Oosting and Anderson 1937, Redfearn 1960, Foote 1966, Yarranton 1967a, b, c, d, Bunce 1967, Nagano 1969, Bates 1975). Bryophytes on decorticated rotting logs have been surveyed in North America only by Cain and Sharp (1938), McCullough (1948), and Lacusta (1970) and the neglect these communities have received is probably a result of their successional nature and obvious sampling difficulties (Scott 1971). Humicolous mosses and liverworts have received little treatment since the days of forest typing, although notable recent studies are those of Davis (1964), Stringer and Stringer

(1973, 1974), and La Roi and Stringer (1976). Wetland bryophyte communities have been intensively investigated and classic studies include those of Sjörs (1959) and Persson and Sjörs (1960), with more recent work being conducted by Vitt and Slack (1975) and Vitt, Achuff, and Andrus (1975).

Much of the bryo-ecological research has concentrated on species composition changes over short gradient segments, usually on one substratum, and thus does not provide perspective on the "habitats" of bryophytes along complex topographic gradients like elevation and exposure. The "habitat" of a species is its population response pattern along such intercommunity gradients (Whittaker, Levin, and Root 1973). Using a framework of elevation and moisture gradients in mountainous areas, Whittaker (e.g. 1956, 1960, 1973a,b) has led the study of vascular plant habitats. However, this 2-gradient approach to the study of plant distribution has not yet been applied to bryophytes.

Both moisture and elevation are important variables for mosses and liverworts. Not only have distinct changes in species presence and abundance been associated with moisture regime (e.g. Gimingham and Birse 1957, Hale 1952, Hamilton 1953, Redfearn 1960) but many autecologists have demonstrated bryophyte sensitivity to this factor (e.g. Clausen 1952, Hosokawa *et al.* 1964, Busby pers. comm.). Elevation, an indirect factor which influences temperature, length of growing season, and other variables, is known to correlate with dramatic changes in the composition of the vascular strata (e.g. Daubenmire 1943, Whittaker 1956), but its influence on bryophytes is less well known. However, Seifriz (1924) on Java, Higinbotham and Higinbotham (1954) in the Cascade Mountains of Washington, Forman (1969) in the White Mountains of New Hampshire, and Slack (1971) in the Adirondack Mountains of New York have described changes in bryophyte species composition with elevation.

In addition to changes in species composition along topographic gradients, trends in species richness and evenness are also of interest, but studies of this kind have again focused mainly on the vascular plants, usually ignoring the bryophytes. Slack (1971) has examined both between- and within-community diversity and community structure for bryophytes in relation to elevation in northern New York, but similar research is lacking for other regions. Furthermore, no one has yet investigated changes in bryophyte species composition and species richness along complex moisture gradients. A description and analysis of such patterns would certainly enhance the understanding of bryophyte communities.

In light of the above discussion the following thesis research objectives were set forth:

1. To characterize the response patterns of bryophytes within a mountain landscape in relation to gradients of moisture and elevation.

2. To measure the habitat breadth and overlap of selected, dominant species.

3. To identify and evaluate trends in species richness and evenness in bryophyte communities along elevation and moisture gradients.

DESCRIPTION OF STUDY AREA

Location

The study area was located in north central Jasper National Park including the northern end of the Maligne Range and the adjacent Athabasca, Maligne, and Miette River valleys (Fig. 1, Plate 1). Easy access via the Signal Mountain fire lookout service road and the gentle slopes, generally free from mass-wasting, were major criteria in selecting the area. The availability of extensive literature concerning vegetation-environment relationships in the region also contributed to the choice.

Climate

Alberta's climate is continental, with cold winters and short, cool summers. However, "winter temperatures at Banff and Jasper ... are generally higher than elsewhere in Alberta because of climatic influences of the Pacific Ocean" (Longley 1967).

Continuous climatic data for the study area were available only for Jasper townsite; however, a series of meteorological stations running from the top of Signal Mountain, across the Athabasca River valley to Pyramid Mountain was operated from 1969 to 1974. Although data from this environmental transect are not yet available,

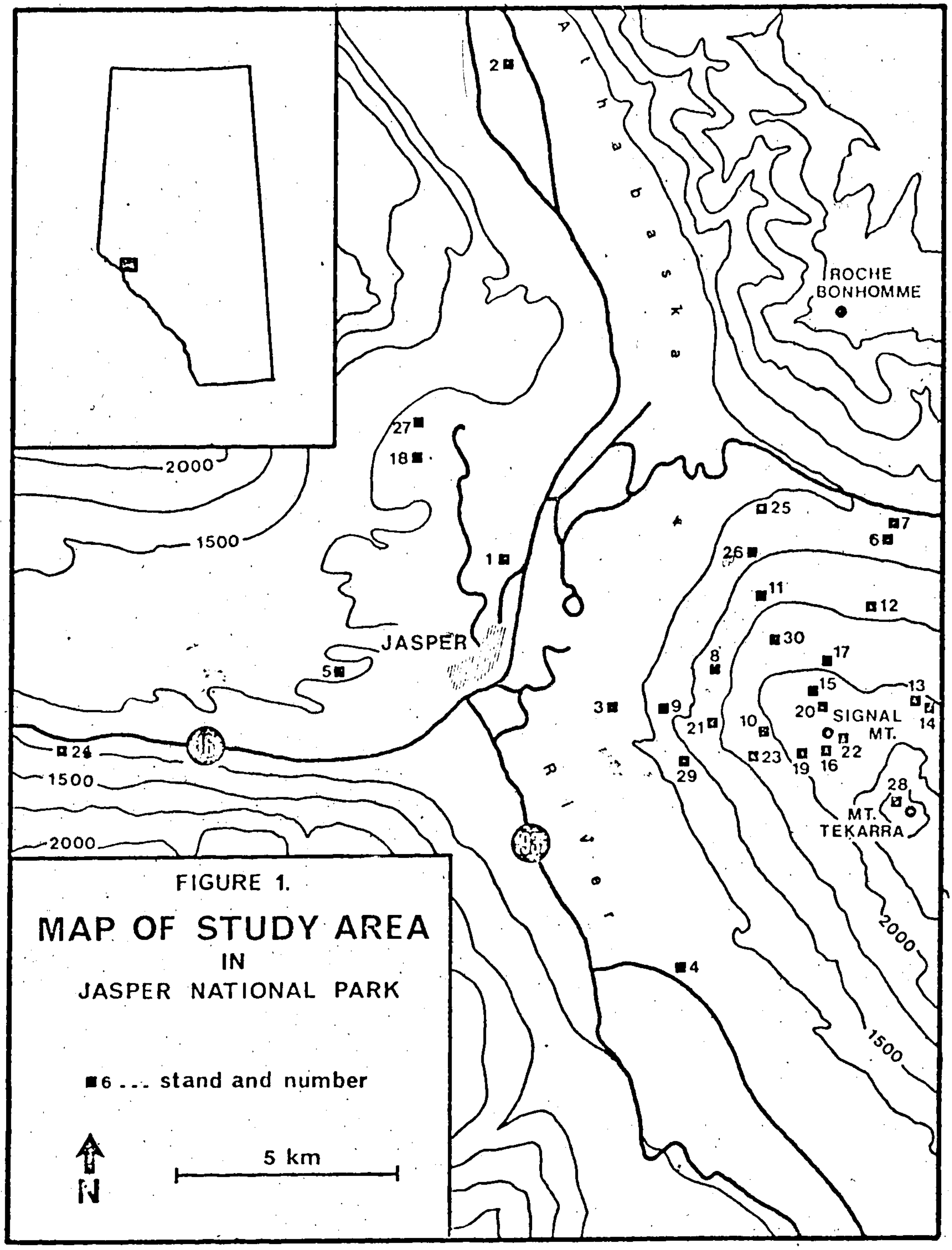

FIGURE 1.

MAP OF STUDY AREA IN JASPER NATIONAL PARK

Plate 1. View of northern Maligne Range and Athabasca valley from Colin Range in Jasper National Park.

preliminary information provided by La Roi (pers. comm.) suggests the following trends. Annual precipitation, which averages 40.6cm at Jasper townsite (Hrapko 1970), increases with elevation and probably exceeds 80cm above timberline on Pyramid Mountain. A similar trend is expected for Signal Mountain. Mean annual temperatures generally decrease with elevation. Hrapko (1970) has shown that summer diurnal temperature fluctuation is much greater at Jasper townsite than on the summit of Signal Mountain. Higher elevation areas thus have a cooler, wetter, and perhaps less variable climate than do lower elevation areas.

Geology

Since the study included sampling of bryophytes on rock outcrops, and since many bryophytes have been shown to respond to rock type (Nagano 1969), a brief review of geological information for the area is presented here.

The Maligne Range lies in the Main Range Province of the Rocky Mountains and several formations of Precambrian and Cambrian age are exposed in the vicinity. The Old Fort Point Formation, composed of argillaceous slates and siltstones with subsidiary limestone breccias and calcareous sandstones, outcrops frequently in the Athabasca River valley, while the southwest slopes of Signal Mountain exhibit exposures of the Wynd Formation, an arenaceous and argillaceous assortment of conglomerates and sandstones in which calcite is the dominant carbonate (Charlesworth *et al.*

1967 and Charlesworth pers. comm.). The arenaceous Gog group, which is usually found at higher elevations within the study area, including the summit of Mount Tekarra, is composed of feldspathic quartzites and largely non-calcareous sandstones (Charlesworth *et al.* 1967).

Intense glaciation of the region occurred during the Pleistocene (Shaw 1972) and is evidenced by the erratic boulders and roches moutonnées found below 2300m, and by extensive moraines and outwash plains in the river valleys.

Vegetation

On the basis of vegetation and floristics Jasper National Park lies near the boundary between Daubenmire's (1943) northern and far northern Rocky Mountain regions (Beil 1966). Within the park 3 elevational zones of vegetation have been identified: the alpine, subalpine (or spruce-fir) and montane (Daubenmire 1943, Rowe 1972). These units have been divided into subzones and delineated for the Jasper area by La Roi (1975).

Within the alpine zone, which lies between tree line (2070m) and perpetual ice and snow, the pattern of vegetation has been related to environmental factors by Hrapko (1970). In areas with full exposure, early snow release, high wind speed, and coarse soil texture, xerophytic *Dryas octopetala-lichen* and *Dryas*-moss tundra communities are most common. Chionophilous, dwarf shrub-heath communities of *Cassiope tetragona* and *Dryas octopetala* are located in protected places, while *Cassiope mertensiana-Phyllodoce glanduliflora* stands occur in areas of greater snow accumulation or on protected slopes at timberline. *Carex nigricans*-dominated communities are associated with extremely late melting snowbeds, whereas wetland areas with high water tables support wet sedge meadow.

Between approximately 1530m and 2070m the vegetation is subalpine in character with climax Engelmann spruce *(Picea engelmannii)*-subalpine fir *(Abies lasiocarpa)* forests dominating on mesic uplands. The spruce-fir forests maintain extensive bryophyte strata but usually lack well-developed herb and shrub strata (Beil 1966). In the study area much of the subalpine zone is covered by even-aged, post-fire forests of lodgepole pine, which have been classified on the basis of their understory species by Hnatiuk (1969). The *Menziesia glabella, Alnus crispa,* Feathermoss, and *Vaccinium* Types are usually successional to spruce-fir, while the *Elymus innovatus* Type often forms a physiographic climax on xeric, south-facing slopes. In wet situations open Engelmann spruce or black spruce *(Picea mariana)* (at lower elevations) fens are present. At the other end of the moisture gradient south-facing rock outcrops support xerophytic vegetation.

Perhaps the greatest variety of plant communities is found in the montane zone where dry till benches and coarse alluvial gravels support climax stands of old

Douglas-fir *(Pseudotsuga menziesii* var. *glauca)* with *Elymus innovatus* (Stringer and La Roi 1970) in contrast to the mature white spruce *(Picea glauca)*-feathermoss forests found in more mesic sites. At the wet end of the moisture gradient several kinds of *Picea mariana* fen communities have been identified, while *Koeleria cristata-Calamagrostis montanensis* grasslands (Stringer 1973) and rock outcrops represent xeric conditions.

Fire has been a critical factor in shaping the pattern of vegetation and determining canopy species in the montane zone. Widespread fires in the Jasper area in the late Nineteenth Century are apparently responsible for most of the extensive lodgepole pine forests that presently dominate the valleys and slopes in the study area (Tande pers. comm.). Hnatiuk (1969) recognized 3 major montane pine forest types: the *Arctostaphylos uva-ursi* Type, the *Shepherdia canadensis* Type, and the Feathermoss Type; some of these form physiographic climaxes on drier sites.

The bryophyte component of the vegetation is not well known, but many of the researchers mentioned above investigated the ecological relationships of dominant moss species and made statements about the development of the bryophyte stratum.

Bryological research in the Jasper area has been predominantly of a floristic nature and, although the park is far from well known, over 200 species have been reported

(Bird 1973, <u>see</u> ANALYSIS OF THE BRYOPHYTE FLORA, p.22).
Of historical interest is the visit of renowned botanist Thomas Drummond, who explored and collected in the Athabasca and Snake Indian River valleys in 1825 and 1826 and may even have walked the lower slopes of the Signal Mountain.

SITE SELECTION AND SAMPLING PROCEDURE

Site Selection Criteria

An attempt was made to survey as wide a variety of plant communities as possible and to maximize environmental differences between sites. Strictly objective, random site selection would have resulted in excessively replicated sampling of common communities and inadequate sampling of types on less abundant landforms. Thus a subjective approach without preconceived bias was deemed appropriate (Mueller-Dombois and Ellenberg 1974). Since the vegetation-environment relations were well known for the study area, stands could be chosen in an efficient, albeit partially subjective, manner.

The three major vegetation zones and their subzones were utilized to guide strategic location of stands with elevation. Information on intrazonal variation in plant communities relating to moisture supply was extracted from previous studies of the vegetation (Beil 1966, Stringer and La Roi 1970, Stringer 1971, Hnatiuk 1969, Laidlaw 1971) and proved invaluable in selecting appropriate stands. The extreme ends of the moisture gradient are not well known in the Jasper region so I used personal judgement in choosing suitable rock outcrop and wetland communities.

With specific, yet flexible, concepts of the major plant community types in mind, 30 stands were chosen, all of which met the following criteria:

1. An important quality of each stand was maximal, internal homogeneity; it had to have minimal microtopographic variation, consistent aspect and slope angle, and even distribution of vascular plant strata.

2. Stands had to have reached a mature or stable condition (requires ca. 40 years for the bryophyte stratum [Hnatiuk 1969]). Stands younger than 40 years (based on increment cores) were not sampled.

3. Stands had to show little or no disturbance by man or other agents.

The 30 study sites included 5 rock outcrops, 1 grassland, 15 montane and subalpine forest communities, 5 fens, and 4 tundra communities, whose main characteristics are described in Table 1. Approximate locations of stands are shown in Figure 1.

Sampling Procedure

A crude co-ordinate system was established in each stand and random numbers were used to locate a single, 10 x 50m macroplot. Four corner stakes and a center stake were placed and 6, 5m transects were located along the plot diagonals, 1 beginning in each corner of the macroplot and 2 radiating from the center. The line-intercept technique was used along the transects to estimate cover of the

Table 1. Location and selected attributes of the 30 stands sampled in the Jasper study area.

	STAND NO.	GENERAL DESCRIPTION	DOMINANT SPECIES	LAT.-LONG.	ELEV. (m)	AS-PECT	COVER (%) TREE	COVER (%) HERB-SHRUB	COVER (%) BRYO-PHYTE
MONTANE ZONE	2	grassland	*Calamagrostis montanensis* *Koeleria cristata*	52°59'15" 118°04'15"	1052	-	-	42	2
	3	rock outcrop[1]	*Koeleria cristata* *Calamagrostis purpurescens*	52°51'50" 118°47'00"	1128	NE	-	9	6
	9	rock outcrop[2]	*Rosa acicularis*	52°51'40" 118°01'25"	1451	SW	-	9	1
	1	forest	*Pseudotsuga menziesii* *Elymus innovatus*	52°53'50" 118°04'35"	1089	SE	55	19	10
	4	forest	*Pinus contorta* *Shepherdia canadensis* *Arctostaphylos uva-ursi*	52°51'10" 118°09'00"	1067	SE	54	42	6
	29	forest	*Pinus contorta* *Shepherdia canadensis* *Elymus innovatus*	52°50'55" 118°00'25"	1402	SW	45	29	3
	5	forest	*Pinus contorta* *Elymus innovatus*	52°52'25" 118°07'20"	1219	E	49	30	35
	24	forest	*Picea glauca* *Hylocomium splendens*	52°51'20" 118°08'50"	1112	N	60	15	53
	25	forest	*Pinus contorta* *Alnus crispa* *Cornus canadensis*	52°54'20" 117°59'10"	1295	N	53	76	24
	6	forest	*Picea glauca* *Hylocomium splendens*	52°54'00" 117°56'45"	1326	N	73	17	48
	18	wooded fen	*Picea mariana* *Alnus tenuifolia*	52°55'05" 118°06'15"	1143	-	35	42	32

Table 1 - Continued

	STAND NO.	GENERAL DESCRIPTION	DOMINANT SPECIES	LAT.- LONG.	ELEV. (m)	AS- PECT	COVER (%)		
							TREE	HERB- SHRUB	BRYO- PHYTE
	7	wooded fen	*Picea mariana* *Ledum groenlandicum* *Carex aquatilis*	52°54'05" 117°56'30"	1295	-	23	50	49
	27	fen	*Betula glandulifera* *Carex aquatilis*	52°55'30" 118°06'15"	1180	-	-	65	58
SUBALPINE ZONE	21	rock outcrop[2]	*Rosa acicularis* *Arctostaphylos uva-ursi*	52°51'15" 117°59'40"	1661	SW	-	17	1
	10	rock outcrop[2]	*Juniperus communis* *Dryas octopetala*	52°51'35" 117°59'45"	1981	W	-	14	1
	8	forest	*Pinus contorta* *Shepherdia canadensis* *Linnaea borealis*	52°52'15" 118°00'05"	1676	W	66	13	14
	23	forest	*Pinus contorta* *Juniperus communis* *Vaccinium scoparium*	52°51'13" 117°59'30"	1798	SW	47	27	6
	19	forest	*Picea engelmannii* *Juniperus communis* *Elymus innovatus*	52°51'10" ~~117°58'10"~~	2072	S	41	22	4
	26	forest	*Pinus contorta* *Alnus crispa* *Arnica cordifolia*	52°53'40" 117°59'35"	1509	N	48	65	23
	11	forest	*Pinus contorta* *Ledum groenlandicum* *Arnica cordifolia*	52°53'25" 117°59'45"	1692	NW	51	27	23
	13	heath tundra	*Cassiope mertensiana* *Phyllodoce glanduliflora*	52°51'50" 117°55'50"	2042	NE	-	66	11

Table 1 - Continued

	STAND NO.	GENERAL DESCRIPTION	DOMINANT SPECIES	LAT.- LONG.	ELEV. (m)	AS-PECT	COVER (%)		
							TREE	HERB-SHRUB	BRYO-PHYTE
	30	forest	*Picea engelmannii* *Hylocomium splendens*	52°52'35" 117°59'15"	1844	NW	46	24	61
	14	forest	*Abies lasiocarpa* *Hylocomium splendens*	52°51'55" 117°55'45"	2014	NE	53	13	32
	12	forest	*Picea engelmannii* *Hylocomium splendens*	52°53'00" 117°55'15"	1684	NE	64	10	68
	17	wooded fen	*Picea engelmannii* *Carex aquatilis*	52°51'25" 117°52'50"	1950	-	18	26	33
ALPINE ZONE	16	rock outcrop[2]	*Dryas octopetala*	52°51'25" 117°57'55"	2224	SW	-	14	1
	28	alpine desert[3]	*Rhizocarpon sp.* *Rhacomitrium lanuginosum*	52°50'30" 117°56'30"	2676	SW	-	1	4
	15	cushion plant tundra	*Dryas octopetala*	52°51'35" 117°58'15"	2197	NW	-	21	2
	20	heath tundra	*Cassiope tetragona* *Dryas octopetala*	52°51'30" 117°58'10"	2227	N	-	36	5
	22	wet sedge tundra	*Carex phaeocephala* *Salix arctica*	52°21'25" 117°57'20"	2227	-	-	25	36

[1] Old Fort Point Formation (see DESCRIPTION OF STUDY AREA, p. 7.)

[2] Wynd Formation (see DESCRIPTION OF STUDY AREA, p. 7)

[3] Gog Group (see DESCRIPTION OF STUDY AREA, p. 7.)

vascular plants and major substratum types (humus, wood, rock, bark, soil and water). Canopy cover was measured at five points along the plot diagonal using a spherical densiometer, and measurements of altitude (altimeter), slope angle (clinometer), and aspect (compass) were taken.

Fifty 0.2m^2 quadrats were set out within the macroplot (i.e. 2% sampling intensity) to sample the bryophytes. To insure that all substratum types were sampled, the quadrats were allocated proportionately to different substratum types based on the line-intercept data for substratum abundance. Random numbers determined which of the 50 quadrats would be used to sample each substratum. At each meter mark along the 50m baseline a random number, n, was drawn from 0-9, and a stake was located n meters into the plot, perpendicular to the baseline. The closest patch of the appropriate substratum in the plot was sampled using a 20 x 100cm quadrat. For small, patchy substrata 20 x 50cm or 10 x 10cm quadrats were utilized in various combination until the 0.2m^2 area was sampled.

Initially, cover estimates in cm^2 for bryophytes were obtained for each quadrat using a metric ruler, but experience allowed use of ocular estimates later in the field season. Measurements were made to the nearest cm^2 and were repeatable to within 10% accuracy. The presence or absence of sporophytes was noted in each quadrat for each species.

When quantitative sampling had been completed a search of the macroplot revealed rarer bryophytes which were collected and added to the species list for that stand. Voucher specimens were taken of all bryophytes and unknown vascular plants. Rock samples were procured from all rock outcrops and each of the study sites was photographed.

ANALYSIS OF THE BRYOPHYTE FLORA

Introduction

In 1962 Bird observed that only 107 moss species had been reported from Jasper National Park but he noted that the area was still relatively unexplored, bryologically. In the most recent *Catalogue of the Bryophyte Reported from Alberta, Saskatchewan, and Manitoba*, Bird (1973) listed 184 moss species, 31 hepatics, and 1 hornwort in the Jasper flora. Six mosses and 1 liverwort were added by Vitt (1973). I have surveyed recent vegetation research in the Jasper area (i.e. Hrapko 1970, Kuchar 1975, Hettinger 1975) to find 26 moss and 16 hepatic species newly reported for the park. Recent studies of the Hepaticae in the Jasper region have added 40 species (Bird and Hong 1975, Hong and Vitt 1976). Thus, prior to this writing, the known bryophyte flora of Jasper National Park included approximately 216 mosses, 88 liverworts and 1 hornwort for a total of 305 species.

Results and Discussion

In the present study 144 bryophyte species, including 129 mosses and 15 hepatics, were collected and identified (*see* APPENDIX A). Twenty-four of the moss species were new records for Jasper Park and as a result of these additions, the moss and total bryophyte floras of the park may be estimated at 240 and 329 species respectively.

The size of the Jasper bryophyte flora compares favorably with those of other areas in the northern and far northern Rocky Mountain regions. Banff National Park, for example, supports over 250 bryophyte species (Bird 1973), but this area has not been as intensively collected as Jasper Park in recent years and a substantial increase in this number should be expected with future exploration. Hermann (1969) has estimated 390 bryophyte taxa to be present within Glacier National Park, Montana, which is smaller in size than both Banff and Jasper. If only mosses are considered, the relative sizes of these floras remain the same; Jasper has 240 species, Banff, 193 and Glacier, 303. Vitt and Koponen (1976) have reported 177 mosses from the Grande Cache area, just north of Jasper Park. Vitt (unpublished data)believes the Ogilvie Mountains of the Yukon to contain approximately 200 moss species, while farther south in the Rockies Weber (1973) has reported 292 species from the entire state of Colorado.

Since the areas mentioned are of different sizes, detailed comparison of floras is impossible. However, Glacier National Park appears to be the most bryophyte rich section of the Rocky Mountains since the bryofloras are generally smaller both north and south of this region, even for geographical units of larger size.

Crum (1966) has observed that:

> At least as far as mosses are concerned there is no distinctive flora of the Canadian Rocky Mountains. It is rather a fairly rich assemblage of widespread calciphiles derived in post-Pleistocene times from the American Rockies and the unglaciated mountains of Alaska and Yukon.

An analysis of floristic elements within the Jasper flora largely supports this view. Table 2 presents a breakdown of the major floristic elements and Table 3 lists the species representing each. Nomenclature is from Crum, Steere and Anderson (1973) for all mosses except Mniaceae, for which Koponen (1974) is used, and *Sphagnum*, for which Isoviita (1966) is used. Information on species distributions was obtained from Bird (1974a,b), Crum (1973), Flowers (1973), Koponen (1974), Lawton (1971), Schofield (1969, 1972), and Vitt (1973, pers. comm.).

The circumboreal element, which includes species whose ranges are primarily in the boreal zone of the northern hemisphere, is the largest single element with over 42% of the species. Together, widespread species and weeds, which are distributed throughout the northern hemisphere and in many cases throughout the world, account for over 15% of the flora. There is a large arctic-alpine component as well as a number of arctic-alpine-montane species; the latter differ from the former in being present below timberline in the mountains. The western North American element is small, including about 8% of the species of which 2.9%

Table 2. Major floristic elements in the moss flora of Jasper National Park.

FLORISTIC ELEMENT	% OF FLORA
CIRCUMBOREAL	42.5
WIDESPREAD	13.3
ARCTIC-ALPINE	12.5
BOREAL-MONTANE	8.2
WESTERN NORTH AMERICAN	5.2
ARCTIC-ALPINE-MONTANE	4.7
MONTANE	4.2
WESTERN NORTH AMERICAN (endemic)	2.9
WEEDS	2.6
ALPINE-MONTANE	1.8
BOREAL-TEMPERATE	0.9
TEMPERATE-MONTANE	0.4
BOREAL-ALPINE	0.4
LOW ARCTIC	0.4
	Σ = 100.0

Table 3. Species lists for the major floristic elements in the Jasper National Park moss flora.

A. CIRCUMBOREAL ELEMENT

*Aulacomnium palustre (Hedw.)Schwaegr.
Barbula acuta (Brid.)Brid.
Brachythecium albicans (Hedw.)B.S.G.
**B. curtum (Lindb.)Limpr.
*B. turgidum (C.J.Hartm.)Kindb.
*B. velutinum (Hedw.)B.S.G.
*Bryum pseudotriquetrum (Hedw.)Gaertn., Meyer&Scherb.
Bryum turbinatum (Hedw.)Turn.
**Bryum weigelii Spreng.
Buxbaumia aphylla Hedw.
*Calliergon giganteum (Schimp.)Kindb.
C. richardsonii (Mitt.)Kindb. ex Warnst.
*C. sarmentosum (Wahlenb.)Kindb.
*C. stramineum (Brid.)Kindb.
C. trifarium (Web & Mohr)Kindb.
Campylium hispidulum (Brid.)Mitt.
*C. stellatum (Hedw.)C.Jens.
*Catoscopium nigritum (Hedw.)Brid.
Cirriphyllum cirrosum (Schwaegr. ex Schultes)Grout
Climacium dendroides (Hedw.)Web & Mohr
Cratoneuron filicinum (Hedw.)Spruce
Dicranella crispa (Hedw.)Schimp.
D. subulata (Hedw.)Schimp.
D. varia (Hedw.)Schimp.
Dicranum bonjeanii De Not. ex Lisa
*D. fuscescens Turn.
D. groenlandicum Brid.
*Dicranum polysetum Sw.
D. undulatum Brid.
Distichium inclinatum (Hedw.)B.S.G.
Drepanocladus exannulatus (B.S.G.)Warnst.
D. fluitans (Hedw.)Warnst.
*D. revolvens (Sw.)Warnst.
*D. uncinatus (Hedw.)Warnst.
D. vernicosus (Lindb. ex C.Hartm.) Warnst.
**Helodium blandowii (Web & Mohr)Warnst.
Hygrohypnum luridum (Hedw.)Jenn.
H. molle (Hedw.)Loeske
Hylocomium pyrenaicum (Spruce)Lindb.
*H. splendens (Hedw.)B.S.G.
*Hypnum cupressiforme Hedw.
H. lindbergii Mitt.
*H. revolutum (Mitt.)Lindb.
**Isopterygium pulchellum (Hedw.) Jaeg.& Sauerb.
Meesia longiseta Hedw.
*M. uliginosa Hedw.
*Mnium marginatum (With.)P.-Beauv.
*M. spinulosum B.S.G.
*M. thomsonii Schimp.
*Oncophorus virens (Hedw.)Brid.
**O. wahlenbergii Brid.
Orthothecium chryseum (Schwaegr. ex Schultes) B.S.G.
**Orthotrichum obtusifolium Brid.
*O. speciosum Nees ex Sturm
*Paludella squarrosa (Hedw.)Brid.
**Plagiomnium ciliare (C.Muell.)Kop.
**P. drummondii (Bruch. & Schimp.)Kop.
**P. ellipticum (Laur.)Kop.
*P. medium (B.S.G.)Kop.
Plagiothecium denticulatum (Hedw.)B.S.G.
**P. laetum B.S.G.
Platydictya jungermannioides (Brid.)Crum
P. minutissima (Sull. & Lesq. ex Sull.)Crum
*Pleurozium schreberi (Brid.)Mitt.
Pogonatum urnigerum (Hedw.)P.-Beauv.
Pohlia annotina (Hedw.)Lindb.
P. atropurpurea (Wahlenb.)H.Lindb.
*P. cruda (Hedw.)Lindb.
P. drummondii (C.Muell.)Andr.
*Ptilium crista-castrensis (Hedw.)De Not
*Pylaisiella polyantha (Hedw.)Grout
*Rhizomnium gracile (Steere)Kop.
*R. pseudopunctatum (Bruch. & Schimp.)Kop.
Rhytidiadelphus loreus (Hedw.)Warnst.
R. squarrosus (Hedw.)Warnst.
*R. triquetrus (Hedw.)Warnst.
Scorpidium scorpioides (Hedw.)Limpr.
S. turgescens (T.Jens.)Loeske
Seligeria campylopoda Kindb.ex Macoun & Kindb.
Sphagnum angustifolium (Russow)C.Jens.
S. compactum DC.ex Lam. & DC.
S. fuscum (Schimp.)Klinggr.
S. girgensohnii Russ.
S. nemoreum Scop.
Sphagnum riparium Angst.
S. russowii Warnst.
S. squarrosum Crome
*S. warnstorfii Russ.
Splachnum luteum Hedw.
S. rubrum Hedw.
*S. sphaericum Hedw.
*S. vasculosum Hedw.
*Tayloria lingulata (Dicks.)Lindb.
T. serrata (Hedw.)B.S.G.
Tetraphis pellucida Hedw.
*Tetraplodon angustatus (Hedw.)B.S.G.
*T. mnioides (Hedw.)B.S.G.
*Thuidium abietinum (Hedw.)B.S.G.
*T. recognitum (Hedw.)Lindb.
*Tomenthypnum nitens (Hedw.)Loeske

Table 3 - Continued

B. WIDESPREAD ELEMENT

*_Amblystegium serpens_ (Hedw.)B.S.G.
Atrichum undulatum (Hedw.) P.Beauv.
**_Barbula convoluta_ Hedw.
Barbula fallax Hedw.
*_Brachythecium salebrosum_ (Web & Mohr)B.S.G.
*_Bryoerythrophyllum recurvirostrum_
(Hedw.)Chen
**_Bryum angustirete_ Kindb. _ex_ Macoun
*_B. capillare_ Hedw.
**_Campylium chrysophyllum_ (Brid.)J.Lange
C. polygamum (B.S.G.)C.Jens.
*_Dicranum scoparium_ Hedw.
*_Drepanocladus aduncus_ (Hedw.)Warnst.
*_Eurhynchium pulchellum_ (Hedw.)Jenn.
*_Fissidens osmundoides_ Hedw.
*_Grimmia alpicola_ Hedw.
*_G. apocarpa_ Hedw.

Gymnostomum recurvirostrum Hedw.
*_Hedwigia ciliata_ (Hedw.)P.Beauv.
Leptodictyum riparium (Hedw.)Warnst.
*_Philonotis fontana_ (Hedw.)Brid.
*_Pohlia nutans_ (Hedw.)Lindb.
P. wahlenbergii (Web & Mohr)Andr.
Polytrichum commune Hedw.
*_P. juniperinum_ Hedw.
P. longisetum Brid.
*_P. piliferum_ Hedw.
*_P. strictum_ Brid.
*_Rhacomitrium canescens_ (Hedw.)Brid.
R. fasciculare (Hedw.)Brid.
*_R. heterostichum_ (Hedw.)Brid.
*_Tortula ruralis_ (Hedw.)Gaertn., Meyer &
Scherb.

C. ARCTIC-ALPINE ELEMENT

*_Andreaea rupestris_ Hedw.
*_Aulacomnium turgidum_ (Wahlenb.)Schwaegr.
*_Bartramia ithyphylla_ Brid.
Blindia acuta (Hedw.)B.S.G.
Bryum stenotrichum C.Muell.
Conostomum tetragonum (Hedw.)Lindb.
*_Desmatodon latifolius_ (Hedw.) Brid.
**_Dicranum angustum_ Lindb.
Dicranum spadiceum Zett.
**_Drepanocladus badius_ (C.J.Hartm.)Roth
Dryptodon patens (Hedw.)Brid.
Grimmia torquata Hornsch. _ex_ Grev.
Hypnum bambergeri Schimp.
H. callichroum Funck _ex_ Brid.
H. hamulosum B.S.G.
H. procerrimum Mol.
Kiaeria blyttii (Schimp.)Broth.

Mielichhoferia macrocarpa (Hook. _ex_ Drumm.)
Bruch. & Schimp. _ex_ Jaeg. & Sauerb.
*_Mnium blyttii_ B.S.G.
Myurella tenerrima (Brid.)Lindb.
*_Paraleucobryum enerve_ (Thed. _ex_ C.J.Hartm.)
Loeske
Plagiobryum demissum (Hook.)Lindb.
*_P. zieri_ (Hedw.)Lindb.
*_Pogonatum alpinum_ (Hedw.)Roehl.
*_P. dentatum_ (Brid.)Brid.
*_Polytrichum sexangulare_ Brid.
*_Rhacomitrium lanuginosum_ (Hedw.)Brid.
Stegonia latifolia (Schwaegr._ex_ Schultes)
Vent. _ex_ Broth.
*_Tortula norvegica_ (Web.)Wahlenb. _ex_
Lindb.

D. BOREAL-MONTANE ELEMENT

Aloinia brevirostris (Hook.&Grev.)Kindb.
*_Bryum pallescens_ Schleich. _ex_ Schwaegr.
Desmatodon cernuus (Hueb.)B.S.G.
*_Dichodontium pellucidum_ (Hedw.)Schimp.
Didymodon rigidulus Hedw.
*_Distichium capillaceum_ (Hedw.)B.S.G.
*_Ditrichum flexicaule_ (Schwaegr.)Hampe
*_Encalypta procera_ Bruch
*_E. rhaptocarpa_ Schwaegr.
*_E. vulgaris_ Hedw.
*_Grimmia affinis_ Hoppe&Hornsch. _ex_ Hornsch.
G. agassizii (Sull & Lesq. _ex_ Sull.)
Jaeg. & Sauerb.
**_G. anodon_ B.S.G.

Grimmia donniana Sm.
*_Grimmia tenerrima_ Ren.& Card.
**_Leskeella nervosa_ (Brid.)Loeske
*_Myurella julacea_ (Schwaegr.)B.S.G.
**_Orthotrichum anomalum_ Hedw.
Plagiopus oederiana (Sw.)Limpr.
*_Pseudoleskea radicosa_ (Mitt.)Macoun & Kindb.
**_Pseudoleskeella tectorum_ (Funck _ex_ Brid.)
Kindb. _ex_ Broth.
*_Rhytidium rugosum_ (Hedw.)Kindb.
*_Saelania glaucescens_ (Hedw.)Bomanss. & Broth.
*_Timmia austriaca_ Hedw.
*_Tortula mucronifolia_ Schwaegr.

Table 3. - Continued

E. WESTERN NORTH AMERICAN ELEMENT

**Brachythecium collinum* (Schleich. *ex* C.Muell.)B.S.G.
***Dicranum fragilifolium* Lindb.
**Dicranum muehlenbeckii* B.S.G.
***Encalypta mutica* Hag.
Funaria muhlenbergii R.Hedw. *ex* Turn.
Grimmia pulvinata (Hedw.)Sw.
Kiaeria falcata (Hedw.)Hag.
Metaneckera menziesii (Hook.*ex* Drumm.) Steere
Oligotrichum aligerum Mitt.
O. hercynicum (Hedw.)DC.
Orthotrichum laevigatum Zett.
Pseudoleskea incurvata (Hedw.)Loeske
Rhizomnium nudum (Britt. & Williams)Kop.

F. ARCTIC-ALPINE MONTANE ELEMENT

Amphidium lapponicum (Hedw.)Schimp.
Cynodontium alpestre (Wahlenb.)Milde
C. schisti (Web. & Mohr)Lindb.
**C. strumiferum* (Hedw.)Lindb.
Desmatodon heimii (Hedw.)Mitt.
**Dicranoweisia crispula* (Hedw.)Lindb. *ex* Milde
**Dicranum acutifolium* (Lindb. & Arnell) C. Jens. *ex* Weinm.
**Dicranum elongatum* Schleich. *ex* Schwaegr.
**Kiaeria starkei* (Web.& Mohr) Hag.
**Tortella fragilis* (Drumm.)Limpr.
**T. tortuosa* (Hedw.)Limpr.

G. MONTANE ELEMENT

Encalypta affinis R. Hedw.
Encalypta ciliata Hedw.
Grimmia atricha C.Muell.&Kindb. *ex* Macoun & Kindb.
**Hypnum vaucheri* Lesq.
***Mnium arizonicum* Amann
**Orthotrichum alpestre* Hornsch.*ex* B
**O. rupestre* Schleich.*ex* Schwaegr.
**Pterigynandrum filiforme* Hedw.
Rhacomitrium aciculare (Hedw.)Brid.
Seligeria donniana (Sm.)C.Muell.

H. WESTERN NORTH AMERICAN ENDEMIC ELEMENT

Cratoneuron williamsii Grout
***Grimmia calyptrata* Hook. *ex* Drumm.
Homalothecium aeneum (Mitt.)Lawt.
Oligotrichum parallelum (Mitt.)Kindb.
**Orthotrichum jamesianum* Sull. *ex* James
Polytrichum lyallii (Mitt.)Kindb.
Scleropodium obtusifolium (Jaeg. & Sauerb.) Kindb. *ex* Macoun & Kindb.

I. WEEDS

**Bryum argenteum* Hedw.
**Bryum caespiticium* Hedw.
**Bryum creberrimum* Tayl.
**Ceratodon purpureus* (Hedw.)Brid.
Funaria hygrometrica Hedw.
**Leptobryum pyriforme* (Hedw.)Wils.

J. OTHER

Aongstroemia longipes (Somm.)B.S.G. (BOREAL-ALPINE)
Campylium halleri (Hedw.)Lindb. (ALPINE-MONTANE)
Desmatodon obtusifolius (Schwaegr.)Schimp. (TEMPERATE-MONTANE)
Dichelyma falcatum (Hedw.)Myr. (BOREAL-TEMPERATE)
Encalypta brevicolla (B.S.G.)Bruch. *ex* Angstr. (ALPINE-MONTANE)
Fontinalis hypnoides C.J.Hartm. (BOREAL-TEMPERATE)
***Grimmia incurva* Schwaegr. (ALPINE-MONTANE)
Hygrohypnum smithii (Sw. *ex* Lilj.)Broth. (ALPINE-MONTANE)
Ulota curvifolia (Wahlenb.)Lilj. (LOW-ARCTIC)

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*Species collected during the present study.

**Species collected during the present study and new to Jasper National Park.

are endemic. Another small group of species (4.2%) is limited to mountain habitats on the continent. Other distribution patterns represented in the flora are listed in Table 2.

Bird and Hong (1975) examined the phytogeographic relationships within the hepatic flora of Alberta and reported that the largest floristic unit was arctic-boreal, alpine-montane. Likewise, Hong and Vitt (1976) observed that most of the hepatic species in west-central Alberta were widely distributed in the northern portion of the northern hemisphere. These results closely parallel those described above for Jasper mosses.

GRADIENT ANALYSIS

Introduction

Data analysis and interpretation in bryophyte phytosociology have utilized many of the techniques developed for studies of the vascular plant component of vegetation. Cain and Sharp (1938), for example, and Yarranton (1962) have employed bryophyte association tables to exhibit data and infer relationships between species and stands.

Indirect gradient analysis (Whittaker 1967) has been an attractive method for those studying bryophyte and lichen communities on rock outcrops where gradients are not obvious. Foote (1966) utilized the Bray and Curtis (1957) technique on outcrops in southern Wisconsin, while principal components analysis has been a popular method with British ecologists (Bunce 1967, Yarranton 1967a).

Direct gradient analysis (Whittaker 1967) has been used infrequently by bryophyte phytosociologists, although crude environmental measurements allowed Redfearn (1960) to ordinate moss communities along a moisture gradient on a Florida rock outcrop, and Hale (1955) used the climax adaptation numbers of arboreal species from Curtis and McIntosh (1951) to ordinate hardwood stands and establish a complex gradient from mesophytic maple-basswood forest to dry oak openings. In Hale's study the distribution of epiphytic mosses and lichens was then examined along the gradient, which had been constructed solely on the basis of the arboreal species.

Where environmental gradients are obvious and vegetation data heterogeneous direct gradient analysis provides a proven, reliable method for presentation of stand relationships (Whittaker 1973, Whittaker and Gauch 1973), whereas indirect gradient analysis is subject to increasing distortion as floristic differences increase (Beals 1973, Gauch 1973a, Gauch and Whittaker 1972). Whittaker and Gauch (1973) have suggested that direct and indirect ordination can be used to check and complement one another.

In this study, direct gradient analysis was selected as the primary means of establishing stand relationships since the sampling units were drawn from a broad spectrum of communities yet were aligned along relatively obvious gradients. A Bray and Curtis (1957) ordination was performed on 19 of the 30 stands as a check on the direct technique and was chosen over the mathematically more elegant principal components analysis (also performed) due to the more pronounced distortive powers of the latter (Whittaker and Gauch 1973).

Methods

Direct ordination. In the direct gradient analysis stands were positioned along moisture and elevation gradients. Although stands were easily placed along the elevation gradient using field measurements of altitude, the evaluation of moisture regime was more difficult. Utilizing the indicator species concept of Rowe (1956) and Looman (1964) and the methods of Whittaker (1973a), a means for computing moisture indices for all stands was devised.

Since the vegetation of the study area and the environmental response patterns of its major vascular plant species were fairly well known, I felt that an estimation of stand moisture regime based on the moisture affinities of the vascular species would be valid. Each stand was assigned a tentative moisture index from 1 to 5 (xeric to hydric), where 1 = rock outcrops and grassland, 3 = mesic forest communities, and 5 = hydric fens. A moisture index was then computed for each species by averaging the moisture indices for all the stands in which the species was present. A subjective estimate was made of the moisture indices for rarer species (i.e., those recorded in 1-few stands). The completed list of 150 species moisture indices (see APPENDIX B) was compared with the results of vegetation research in the study area, then discussed with and modified by several workers having experience in the locale (see ACKNOWLEDGEMENTS, p.vi).

Two methods were then used to determine the composite moisture index of a stand. In the first, the moisture indices of all vascular species in a stand were averaged, resulting in an unweighted moisture index. In the second, a weighted average was computed by multiplying each species' moisture index by its percent cover, adding these for all species and then dividing by total cover.

Indirect ordination. The Bray and Curtis (1957) technique utilizes a data matrix of species importance values which serve as stand characters in the computation of similarity indices for all stand pairs. Two different similarity measures were used in this study:

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

where CC is the coefficient of community, and where S_j and S_k are the number of species present in plots j and k, and S_c is the number of species common to both j and k (Sørensen 1948);

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

where PS is percentage similarity, P_j is the sum of the quantitative measures of the species in stand j and P_k

is the same quantity for stand k, and w is the sum of the lesser values for those species common to both j and k (Bray and Curtis 1957).

Stands were located in two dimensional space on the basis of their similarity to one another using the methodology of Cottam, Goff, and Whittaker (1973). Data transformations and internal association values were not employed in the ordinations (<u>see</u> Whittaker and Gauch 1973).

All calculations, including similarity values and stand locations along the X and Y axes, were accomplished using Cornell Ecology Programs 4 (Bray-Curtis Ordination) and 5 (Resemblance or Distance Matrix) (Gauch 1973b), and were edited for and adapted to the University of Alberta IBM 360/67 computer.

Since many pairs of the 30 stands had zero similarity values resulting from the wide variety of communities sampled, it was decided that only stands whose relationships to one another were somewhat unclear would be ordinated. The rock outcrops, montane grassland and sedge fen, as well as all alpine communities were thus eliminated from the data set to reduce heterogeneity and produce a more informative ordination. The remaining 19 stands included dry and moist forest communities, subalpine heath tundra and wooded fens.

Four ordinations were constructed, first using coefficient of community and percentage similarity on vascular plant data, then on bryophyte data. Experimentation with several pairs of end stands indicated that choice of end stands was not crucial to interpretation.

It is important to note that the data used to represent presence and cover of bryophytes in each stand were derived solely from the performance of species on the most abundant substratum in each stand. Since other substrata may have provided a different set of environmental conditions within the stand, it was thought that their exclusion from the ordinations would reduce noise in the data matrix and yield results that better portrayed general stand relationships.

Results

The ordination of stands arising from direct gradient analysis using unweighted averages of moisture indices expressed relationships among stands based on their positions along gradients of moisture and elevation (Fig. 2). Stand composite moisture index values derived from weighted averages of species moisture indices produced an ordination quite similar to that resulting from the unweighted technique. Therefore, only the results of the latter were examined in detail.

The even distribution of the 30 stands in the ordination indicated that the wide range of conditions along both gradients in the study area was well represented. There was, however, a blank area evident at 1600m in the

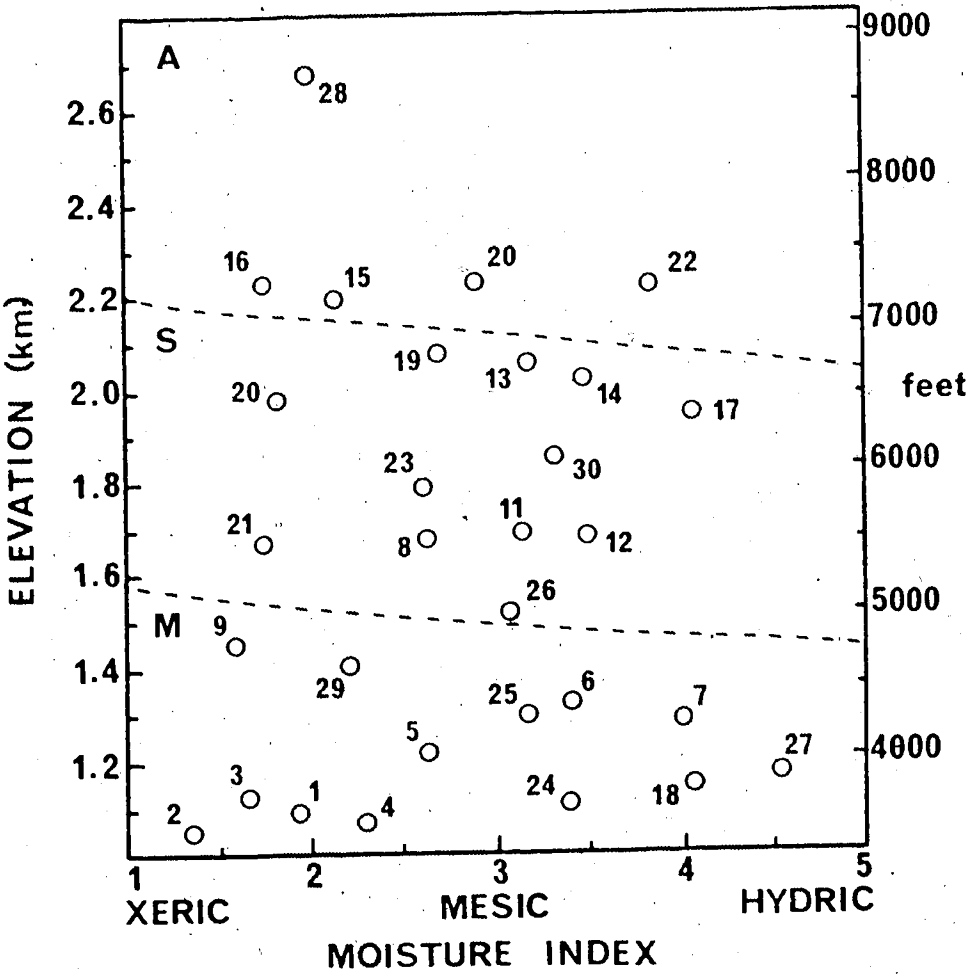

Figure 2. Direct ordination of 30 stands in relation to elevation and subjective moisture index. Dotted lines represent approximate boundaries between montane (M), subalpine (S), and alpine (A) zones.

hydric portion of the ordination. This gap was due to the unavailability of a lower subalpine wetland for sampling within the study area, and did not detract significantly from the value of the ordination.

Based on broad physiognomic and floristic similarities between stands and on my knowledge of the study area, a rough mosaic diagram of the vegetation of the study area was superimposed on the direct ordination (Fig. 3). It clarified relationships between stands in the overall vegetation mosaic.

The mosaic diagram suggested that gradients of elevation and moisture were influential in determining plant distributions. Before proceeding further, however, it was necessary to test the validity of the direct gradient analysis for both vascular plants and bryophytes.

The Bray-Curtis ordination of stands using coefficient of community on vascular plant data (Fig. 4) was utilized as an objective, visual check on the direct technique. The arrangement of stands in this two dimensional ordination was related to gradients of moisture and elevation, and appeared comparable to the direct ordination (Fig. 2). In both Figures 2 and 4 the fens (stand nos. 7, 17, 18) were located on the right side, while dry forest stands (nos. 1, 4, 29, 23 and 19) were located on the left; high altitude stands were clustered at the top and low elevation stands at the bottom.

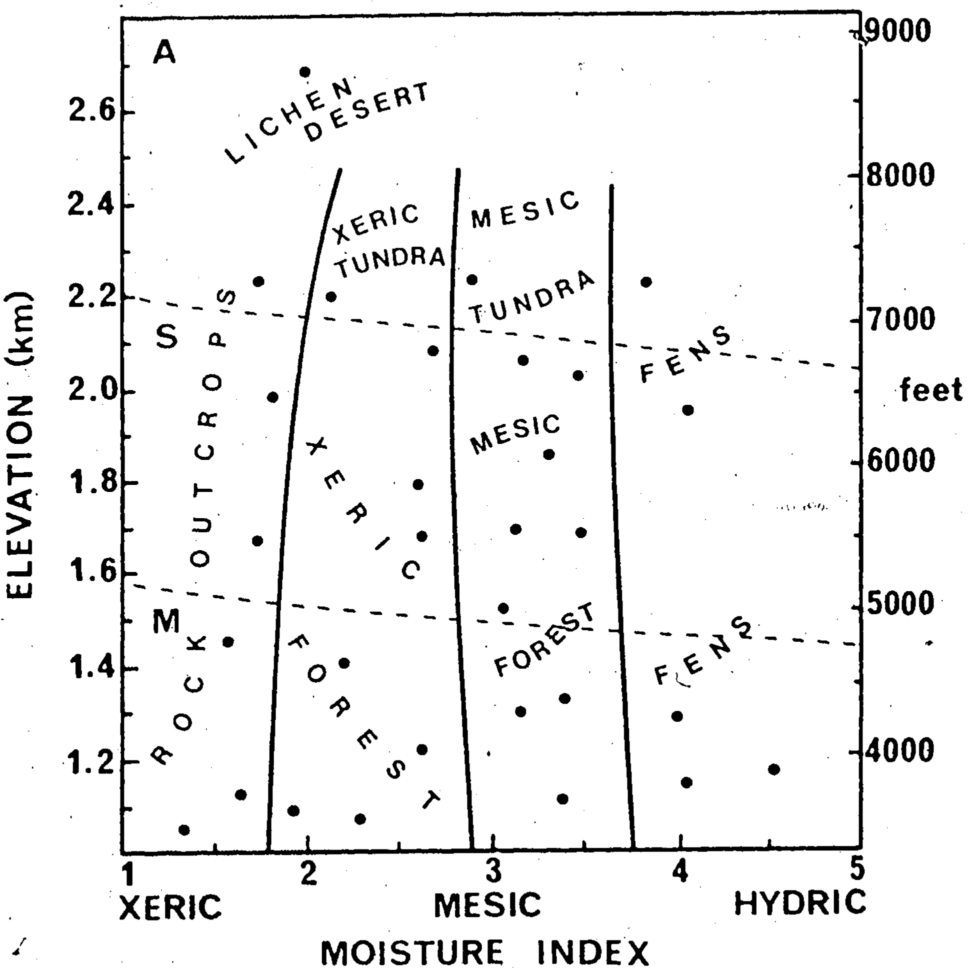

Figure 3. Mosaic diagram depicting the pattern of vegetation in response to complex gradients of elevation and moisture in the Jasper study area. • = stands, as positioned by direct gradient analysis; A, S, M = alpine, subalpine, and montane zones.

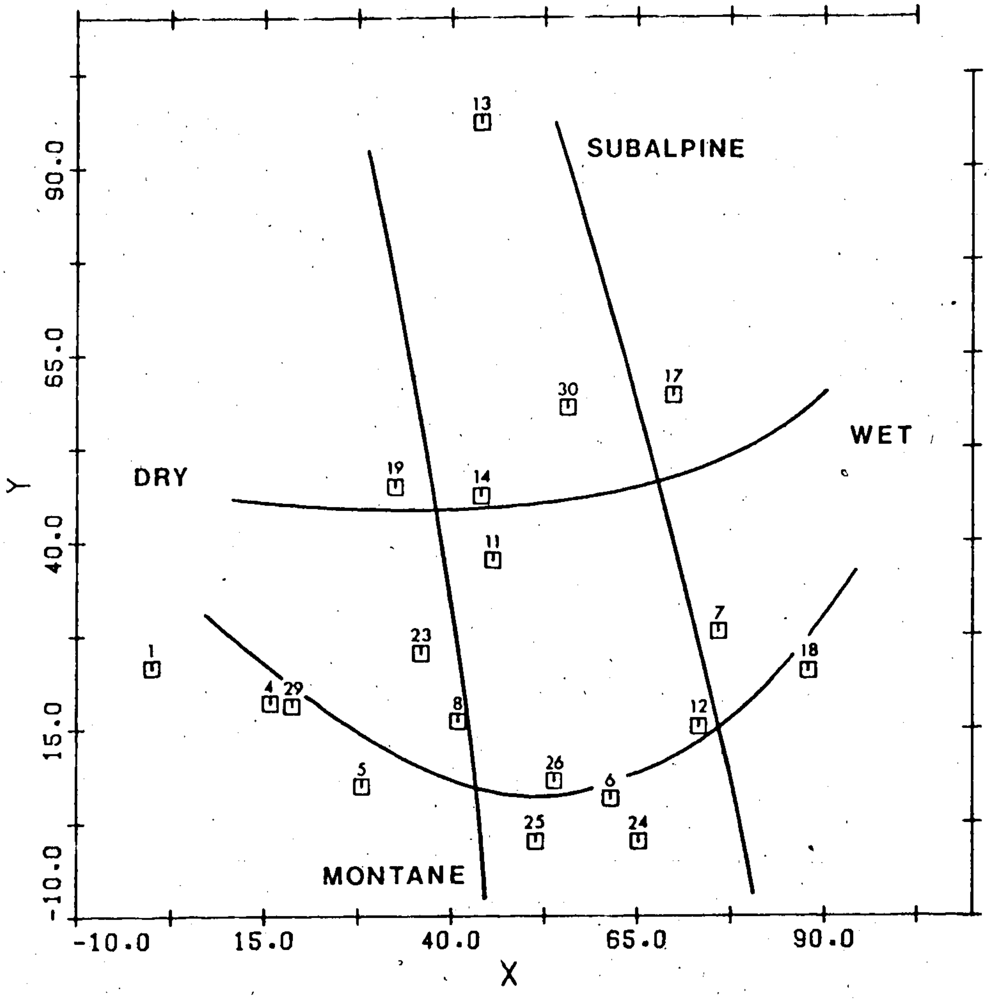

Figure 4. Indirect, Bray-Curtis ordination of 19 wooded stands using understory vascular plant data and coefficient of community (CC). X axis endpoints are stand nos. 1 and 18; Y axis endpoints are stand nos. 13 and 25. Vertical lines partition stands into groups with similar moisture index; horizontal lines partition stands into groups with similar elevation.

More objectively, the direct ordination was divided into 3 roughly horizontal rows and 3 vertical columns (see Fig. 4 and Table 4) and mean elevations and moisture indices were calculated for all stands in each of the 9 resulting cells. Significant differences in elevation corresponded to row location, and significant differences in moisture index were related to column location (Table 4).

A more rigorous check of the direct ordination was accomplished by correlating distance between 2 stands with their coefficient of community. Fifty stand pairs were chosen at random, and the product-moment correlation coefficient calculated between interstand distance and coefficient of community using vascular plant data was $r = -.76$ (significant at $p < 0.01$). The correlation between interstand distance and coefficient of community using bryophyte data was also highly significant ($r = -.65$, $p < 0.001$).

I concluded that the direct ordination provided a reasonable approximation of stand relationships for both vascular plants and bryophytes.

Table 4. Mean values of stand elevation and stand moisture index in ordination cells delineated in Figure 4.

	VERTICAL CELLS		
	TOP	MIDDLE	BOTTOM
Elevation (m)	1984*	1609	1206

	HORIZONTAL CELLS		
	LEFT	MIDDLE	RIGHT
Moisture Index (1 - 5)**	2.44*	3.28	4.03

* All values significantly different ($p < 0.01$, rank test, Steel and Torrie,1960).

** 1 = xeric, 3 = mesic, 5 = hydric.

DISTRIBUTION OF BRYOPHYTE ABUNDANCE

Results

Before investigating the performance of individual species in relation to moisture and elevation gradients, it was appropriate to describe the relationship between these gradients and the importance of bryophytes in communities. Within the study area, bryophyte abundance or importance, as measured by absolute cover, generally increased from xeric to hydric conditions along the moisture gradient (Fig. 5). This relationship was consistent for all 3 elevational zones of vegetation. Bryophyte cover ranged from approximately 1% on some rock outcrops to almost 70% in the subalpine spruce-fir forest (stand no. 12). Highest cover values were located in montane and subalpine spruce or spruce-fir forests, but the montane sedge fen (stand no. 27) also had high absolute cover. The bryophyte strata of wooded fens, however, had less cover than mesic forests. Alpine communities generally had less well developed bryophyte strata than lower elevation communities with similar moisture indices.

Discussion

The above results may help to interpret broader geographic trends in the importance of bryophytes. The

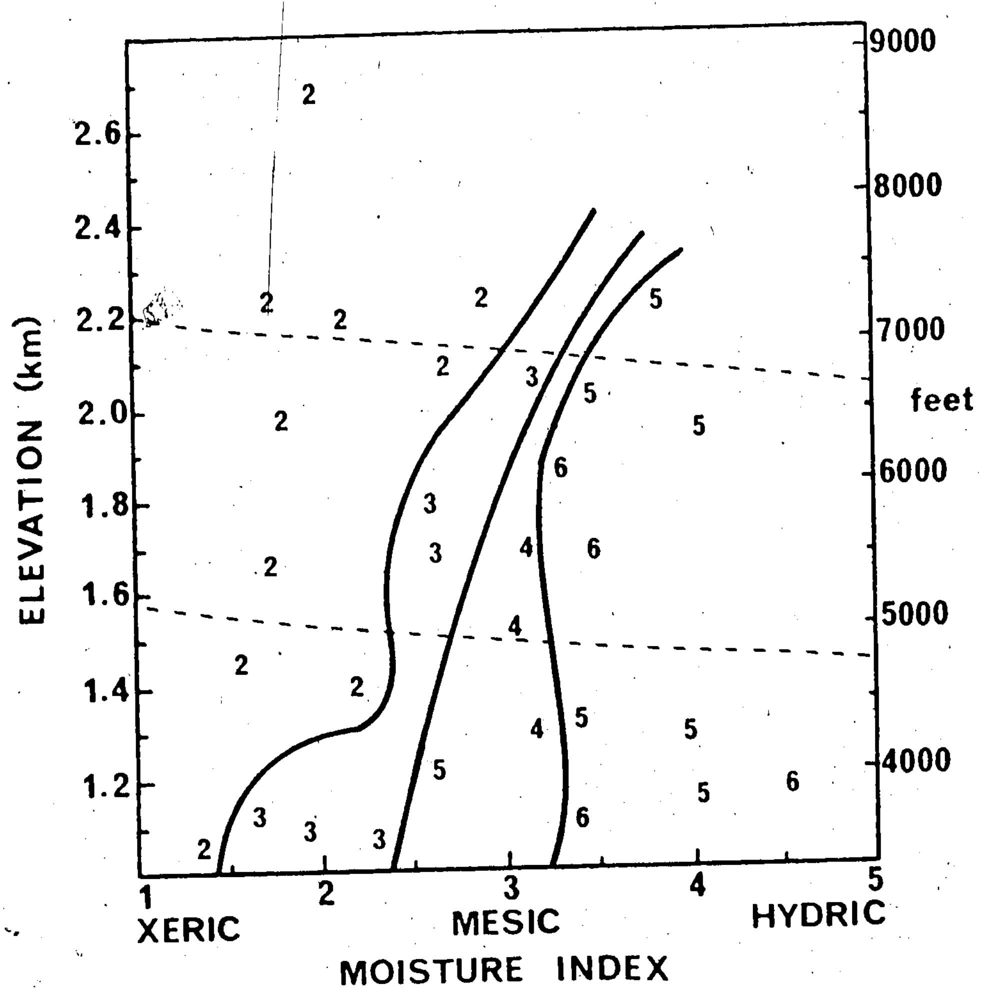

Figure 5. Absolute bryophyte cover in relation to elevation and moisture gradients. Numbers are cover classes for each of the 30 stands where 1 = less than 1%, 2 = 1-5%, 3 = 6-15%, 4 = 16-25%, 5 = 26-50%, 6 = 51-100%. Solid lines are approximate cover isolines.

Rocky Mountains and other ranges in the western cordillera provide an opportunity to examine geographical variation in bryophyte cover as it relates to latitude. All 3 vegetation zones found at Jasper are present, though at progressively higher elevations, further south in the Rockies. The alpine and subalpine zones extend far to the north of the study area. Within each of the zones along the gradient there are definite trends in bryophyte cover.

In the Douglas-fir-dominated upper montane zone of Arizona's Santa Catalina Mountains, Whittaker and Niering (1965) reported that bryophyte cover reached a maximum of 1.3%. Montane Douglas-fir forests in Waterton Lakes National Park in southwestern Alberta were found to have 1-5% moss cover (Kuchar 1973). In contrast are the findings of Stringer and La Roi (1970) for Alberta's Banff and Jasper Parks at the northern limit of Rocky Mountain montane vegetation, where bryophyte cover in Douglas-fir forests averaged 10%. In the present study, I found that north-facing mesic forests of white spruce, which are uncommon in the Jasper montane, had 50% bryophyte cover.

The subalpine spruce-fir forests of the Santa Catalina Mountains of Arizona have poorly developed bryophyte strata with cover reaching a maximum of 1.3% in the most mesic stands (Whittaker and Niering 1965). Further north, near Crested Butte, Colorado, Langenheim (1962) described Engelmann spruce-subalpine fir forests in which mosses again played a minor role. In the Medicine Bow Mountains of Wyoming, Oosting and Reed (1932) observed that moss cover averaged less than 1% in the spruce-fir forest type. Bryophytes were likewise unimportant in the red fir *(Abies magnifica)* forests of the Sierra Nevada, where Oosting and Billings (1943) have noted "mosses are rather rare except in very damp places and occasionally on rotting wood and on the bases of trees." In Waterton Lakes Park, Alberta, Kuchar (1973) noted that the feathermoss forests found farther north in the Rockies were not characteristic of the park. However, he did observe stands where absolute bryophyte cover reached 60%.

Bryophyte cover seems to increase in subalpine forests of the Pacific Northwest and in the northern Rockies. Higinbotham and Higinbotham (1954) found that bryophytes were noticeably abundant in subalpine forests of the western slopes of the Cascade Mountains in Washington, and Hämet-Ahti (1965) has reported extensive feathermoss wefts of *Pleurozium schreberi* in the Engelmann spruce - subalpine fir forests of Wells Gray Park in interior British Columbia west of Jasper. In Banff and Jasper Parks in Alberta, Beil (1966) observed that bryophytes represented the best developed subordinate stratum in subalpine spruce-fir forest, averaging 57% cover. For this reason subalpine forests in the Jasper and Banff areas more closely resemble boreal forests of white spruce and balsam fir *(Abies balsamea)*, at least physiognomically (see Beil 1966, La Roi and Stringer 1976). My results for climax forests in the subalpine zone of Jasper largely support the work of Beil. In the Alsek River region of the Yukon, the white spruce forests below timberline are boreal in character and support luxuriant bryophyte communities of up to 90% bryophyte cover on north-facing slopes (Douglas 1974).

Mosses and liverworts are usually important constituents of spruce-fir forests in the Appalachian Mountains of eastern North America. Oosting and Billings (1951) compared New England spruce-fir forests with those of North Carolina and stated that, although important components of both forests, bryophytes were apparently less extensive in the northern area.

Although bryophyte synusiae in the alpine zone rarely match the high absolute cover values they have in the subalpine, geographic trends in abundance are similar in these two zones. All plant ecologists studying alpine vegetation in the Canadian Rockies have found bryophytes to be numerous and abundant (Beder 1967, Hrapko 1970, Broad 1973, Kuchar 1975). Hrapko (1970) has observed that, concomitant with a decline in heath tundra vegetation, bryophytes have reduced importance as one travels south in the Rockies. Studies of alpine vegetation in the central Rocky Mountains conducted by Langenheim (1962) in central Colorado, and Johnson and Billings (1962) in Wyoming, both mentioned lichens as community components but conspicuously ignored bryophytes, probably because they were unimportant. Bamberg and Major (1968) listed several mosses, all xerophytes, in tundra communities of the Montana Rockies, but none of these were abundant. Bliss (1956), contrasting alpine communities in the Medicine Bow Mountains of Wyoming with arctic tundra in northern Alaska, found that "heath species, lichens and mosses were very important in the Arctic but very rare in alpine tundra." Even in the high arctic bryophytes assume considerable importance as noted by Brassard (1971) for northern Ellesmere Island and Vitt and Pakarinen (1972) for Devon Island.

Thus there is a general trend of increasing bryophyte cover from the southern end of the cordillera in the southwestern U.S. northward to southern Alberta. There is probably little further increase in bryophyte cover as one moves north from southwestern Alberta. The increase of bryophyte cover with increasing latitude is probably correlated with decreasing evapotranspiration rates, a result of decreasing temperatures and increasing cloud cover, along the gradient.

The pattern of bryophyte cover in relation to moisture in Jasper supports an interpretation of latitudinal trends in bryophyte cover based on moisture-related factors. In all 3 vegetation zones in Jasper bryophytes are most abundant in sheltered, north-facing stands where humidity is probably high. Farther south in the Rockies higher evapotranspiration rates may cause similar topographic positions to be less favorable for bryophyte growth.

RESPONSE PATTERNS AND HABITAT METRICS

Introduction

The considerable confusion in the literature concerning the terms "habitat" and "niche" has been recently clarified by Whittaker, Levin and Root (1973, 1975), whose interpretation I have adopted. To describe a species response to the full range of biotic and physical environmental variables to which it is exposed these authors have proposed the term "ecotope", which is the "ultimate evolutionary context of a species...." and has two components. The first, "niche", is the population response of a species to the n variables by which species in a community are adaptively related. In contrast, the "habitat" of a species is defined on an intercommunity level, being the population response of a species to "spatially extensive" variables such as moisture regime and elevation.

The habitats of species may be viewed using species population response patterns (Whittaker 1967, 1973) which graphically display the importance of species at sample locations along selected gradients. The range of distribution of a species along intercommunity gradients is the "habitat breadth" of the species and is roughly synonomous with "ecological amplitude", a term used almost exclusively in plant ecology (e.g. Shimwell 1971, Mueller-Dombois and Ellenberg 1974). The degree of mutual occurrence of two species along a gradient is referred to as "habitat overlap" and provides information about the similarity of species responses along the gradient.

Although the species response pattern conveys a visual representation of the location and shape of a species' habitat and allows gross comparison of habitats, quantitative measures of habitat breadth and overlap may assist in the resolution of finer differences.

Any of the proposed measures of niche breadth may be employed to estimate habitat breadth since these two entities differ only in spatial context. Levins (1968) introduced the following as possible niche or habitat metrics:

$$B_i = \frac{1}{\Sigma(P_{ij}^2)} \qquad (1)$$

$$B_i^1 = -\Sigma P_{ij} \log(P_{ij}) \qquad (2)$$

where B_i is habitat breadth, and P_{ij} is the proportion of species i in stand j. Both (1) and (2) are really measures of heterogeneity of population distribution between stands and may be regarded as indices of the probability that an individual of a given species will be encountered in a given community. Equation (2) has received more extensive use in the recent literature (Pielou 1972, Pianka 1973, Sabath and Jones 1973, Cody 1974, Heithaus *et al.* 1975).

Habitat overlap may be quantified using

$$\text{overlap} = 100(1-1/2\Sigma|P_{ij}-P_{hj}|)$$

where P_{ij} equals the abundance of species i in stand j (Schoener 1970). Levins (1968) has suggested treating overlap as equivalent to the coefficient of competition, α, where

$$\alpha ij = \frac{\Sigma P_{ij} P_{hj}}{\Sigma P_{ij}{}^2}.$$

The measurement of habitat breadth and overlap has been complicated by severe scaling problems that include 1) the range of the gradient sampled, 2) the spacing of sample units along the resource gradients and 3) the non-linearity of the gradient (Colwell and Futuyma 1971). In the first case, comparison of habitat breadth measurements for the same species in two different sets of gradient samples demands that an equal range of variation be sampled along each gradient. A species may have an identical habitat breadth in two areas, but if all sample units are taken within the species range on one of the gradients while some sample units fall above and below its range on the other, different values will result. Secondly, the spacing of samples along a gradient may introduce bias into habitat measurements. Certain sections of an environmental gradient may be oversampled and the habitat breadths of species common to that segment exaggerated. Consider also a third case, in which environmental gradients or the responses to those gradients are non-linear; under these circumstances even a systematic distribution of sample units along a seemingly, but not quite, uniform gradient would bias results through oversampling the segment of least variability.

Colwell and Futuyma (1971) have proposed a measurement technique that minimizes the scaling problems by estimating t[illegible]ctness of resource states (i.e. stands) in re[illegible] to the presence and abundance of the organisms [illegible]. Weighting factors are developed for the resource states based on their distinctness. Thus, a stand which is floristically very different from most other stands would be assigned a greater weight. The weighting factors are used in the modification of the habitat metrics to compensate for the 3 problems described above.

Such a weighting system has obvious utility in studies such as the present one, where equal distinctness or similarity of samples is impossible to achieve in the field and, consequently, researchers are beginning to make use of this valuable technique (e.g. Sabath and Jones 1973, Heithaus *et al.* 1975).

Methods

The method of Colwell and Futuyma (1971) was utilized to measure habitat breadth and overlap. Two kinds of habitat metrics were computed using this technique: relative measures in which breadth and overlap have the range 0-1; and absolute measures, which take into account the range of variation covered by stands along the gradients and for most situations produce breadth and overlap values smaller than the relative measures (<u>see</u> Colwell and Futuyma 1971).

Absolute stand weighting factors were defined by

$$\delta_j = M_j(X) \qquad \text{where}$$

$$M_j(X) = \frac{X_j(\log X_j - \log Z) - \sum_j N_{ij} \log (N_{ij}/Y_i)}{\sum_j X_j \log X_j - Z \log Z}$$

(Colwell and Futuyma 1971). $M_j(X)$ is the distinctness of the jth stand in the stand matrix, N_{ij} is the cover of species i in stand j, X_j is the total cover for species i in the stand matrix, and Z is the total cover, i.e., sum of all species covers in the stand matrix.

Relative stand weighting factors were defined as

$$d_j = \frac{M_j(X)}{\sum_j M_j(X)}.$$

Modifying equation (2) by including weighting factors, relative habitat breadth was measured by

$$B_i' = -\frac{K}{\log K} \sum_j d_j(P^*_{ij} \log P^*_{ij})$$

where

$$P^*_{ij} = \frac{N_{ij}}{Y^*_i} = \frac{N_{ij}}{\sum_j d_j K\, N_{ij}},$$

and K is a constant greater than the number of stands. Relative overlap between species i and h was computed using

$$\gamma_{ih} = 1 - \tfrac{1}{2} \Sigma\, d_j K |P^*_{ij} - P^*_{hj}| .$$

The expression for absolute habitat breadth is identical to that for the relative measures except δ_j is substituted for all d_j but the values of P^*_{ij} and P^*_{hj} are calculated using d_j. In addition the overlap summation must be subtracted from Σdj instead of 1.

Circularity in the technique was avoided by removing the species whose habitat breadth was being computed (or the pair of species whose overlap was being computed) from the data set, resulting in the need for a different set of weighting factors for each calculation of a habitat metric.

Relative and absolute, circular and non-circular habitat metrics were calculated for bryophytes using a variety of stand matrices as follows: all stands, rock outcrops (stand nos. 3, 9, 10, 16, 21 and 28), dry stands (stand nos. 1, 4, 5, 8, 15, 19, 23, 29), moist stands (stand nos. 6, 11, 12, 13, 14, 20, 24, 25, 26, 30), subalpine stands, and montane stands. The latter five stand groups are selected coenoclines along elevation and moisture gradients.

In all cases weighting factors for stands were derived from absolute bryophyte cover. Habitat metrics were computed first using cover data drawn from all quadrats on the most abundant substratum in the stand, which was usually humus, rock, or soil. In this case, presence and abundance of bryophyte species on other substrata were ignored in the determination of weighting factors. A second series of computations utilized total cover data for each stand.

Metrics were calculated only for species that had over 3% cover in a single stand or had a mean cover greater than 0.3% cover over all 30 stands. All calculations were performed using a FORTRAN IV algorithm, written and generously provided by R.K. Colwell,which was modified slightly for use on the University of Alberta IBM 360/67 computer.

Of equal importance to determination of habitat metrics was the graphic representation of species population response to complex gradients of moisture and elevation. Response patterns for each of the more important species were constructed by plotting the cover class values for the species on the direct ordination (<u>see</u> GRADIENT ANALYSIS, p. 30).

Due to the importance of substratum in controlling bryophyte distribution, especially in forest communities, an ordination of species based on their occurrence on humus, rock, or wood was devised (<u>see</u> La Roi and Stringer 1976) using data from forested stands only (stand nos. 1, 4, 5, 6, 8, 11, 12, 14, 19, 23, 24, 25, 26, 29, 30). Because it is a within-community phenomenon, substratum is really a niche variable, but since substratum availability varies along habitat gradients (e.g. wood is not available above tree line) it is important to consider habitats in light of available substrata. The total number of quadrats on each substratum was determined and the per cent frequency of occurrence of each species on each substratum was calculated. Then, for each species, the percent frequencies were added. The proportions of this sum contributed by humus, wood, and rock were then plotted as percentages on a triangular co-ordinate system. The results provide an assessment of bryophyte performance for an important niche dimension, substratum, generalized for all forest communities. Species on outcrops, in fens, and in the alpine also exhibited substratum restrictions but since substratum diversity was much less in these communities and since I had much less data for these communities, no computations were made.

Results

Relative habitat metrics were always higher than corresponding absolute values. Because relationships between species were identical using both techniques, and since absolute measures potentially allowed comparison of a species performance along different coenoclines, the absolute measures were selected for analysis and discussion.

I found some differences in circular and non-circular metrics for species that were present and abundant in only one stand, but since relationships among the majority of species were identical for both kinds of metrics I decided to present only the less ambiguous non-circular values (see Colwell and Futuyma 1971).

Habitat breadth and overlap values computed using data from the most abundant substratum per stand were very similar to those based on data from all substrata. This result is not surprising since the most abundant substratum almost always accounted for over 80% of the stand's ground surface, while other substrata were poorly represented. Thus, species on the less abundant substrata contributed little to stand weights.

The habitat measurements based on bryophyte data from the most abundant substrata were selected for presentation because these data reflected a narrower range of microenvironmental variation within each stand. Species on minor substrata could have been representative of different microenvironmental conditions and, since the presence or absence of additional substrata was not consistent between stands, computed stand weights would have had less precise meaning.

Overall habitat breadths for each species, as well as habitat breadths for each species along selected coenoclines, are presented in Table 5, and overall habitat

Table 5. Absolute, non-circular habitat breadth measurements (B_i') for selected species in the Jasper study area. Measurements are presented for 6 coenoclines and are based on bryophyte performance on the most abundant subatrata.

SPECIES	OVERALL[1] (30)[2]	ROCK OUTCROPS (6)	XERIC FOREST AND TUNDRA ([illegible])	MESIC FOREST AND TUNDRA (10)	MONTANE (13)	SUBALPINE (11)
HYDROPHYTES						
Bryum pseudotriquetrum	.60	-[3]	-	-	-	.47
Tomenthypnum nitens	.62	-	-	-	.64	.42
Sphagnum warnstorfii	.51	-	-	-	.37	.[illegible]2
Aulacomnium palustre	.58	-	-	-	.46	.48
MESOPHYTES						
Dicranum scoparium	.42	-	-	.23	-	.23
Barbilophozia lycopodioides	.47	-	-	.35	-	.46
Dicranum acutifolium	.46	-	.36	.32	-	.40
Dicranum fuscescens	.52	-	.62	.33	-	.36
Timmia austriaca	.49	-	.27	.27	-	.50
Ptilium crista-castrensis	.51	-	.55	.30	.47	.29
Rhytidiadelphus triquetrus	.33	-	-	.12	.34	-
Hylocomium splendens	.72	-	.74	.67	.64	.64
Pleurozium schreberi	.55	-	.32	.32	.46	.41
Drepanocladus uncinatus	.58	-	.49	.34	.57	.62
Brachythecium salebrosum	.59	-	.64	.37	.52	.44
Eurhynchium pulchellum	.51	-	.66	.28	.40	.33
Barbilophozia hatcheri	.56	-	.49	.44	-	.39
Dicranum polysetum	.50	-	.39	.13	-	-

Table 5 - Continued

SPECIES	OVERALL (30)	ROCK OUTCROPS (6)	XERIC FOREST AND TUNDRA (8)	MESIC FOREST AND TUNDRA (10)	MONTANE (13)	SUBALPINE (11)
XEROPHYTES						
Thuidium abietinum	.06	.69	.25	-	.25	-
Rhytidium rugosum	.22	-	.51	-	.08	-
Hypnum revolutum	.26	.61	-	-	-	-
Ditrichum flexicaule	.43	.56	.48	-	-	.29
Tortula ruralis	.33	.57	.39	-	.28	-
Grimmia anodon	.19	.60	-	-	.12	-
Hypnum vaucheri	.14	.53	-	-	.06	-
ALPINE SPECIES						
Pogonatum alpinum	.49	.62	.62	.28	-	-
Rhacomitrium lanuginosum	.05	.60	-	-	-	-
Polytrichum piliferum	-	.60	.62	.28	-	-

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[1] For overall values K = 200, for other coenoclines K = 50 (see METHODS, p.).

[2] Number of stands in coenocline.

[3] Insufficient data for breadth calcul[illegible]ion.

overlaps are presented in Table 6.

Examination of species response patterns (Fig. 6-8 and 10-18) revealed that no 2 species had identical habitats that exhibited varying degrees of similarity reflected by the habitat overlap values in Table 6. In the overlap matrix species were arranged to maximize overlap values along the diagonal, with the result that hydrophytes were located to the left, xerophytes to the right. Alpine species were treated separately at the far right due to their low overlap with species common at lower elevations. On the basis of the overlap matrix and the population response patterns, 4 "ecological groups" (Whittaker 1966) of species were identified. Species whose habitats or habitat centers lie in the montane or subalpine zones were grouped, according to their position along the moisture gradient, as xerophytes, mesophytes, and hydrophytes; alpine species were treated as a fourth unit. These ecological groups were further subdivided as discussed below. Several of the species mentioned in the ensuing interpretation were too rare for calculation of habitat metrics but were characterized graphically using population response patterns alone.

Xerophytic species. Xerophytic species were those found on rock outcrops, in grassland or in dry forest. They grew on bedrock, erratic boulders, soil, humus, or wood.

Table 6. Matrix of absolute overall habitat overlap values for important performance on most abundant substrata in all 30 stands in the

/6f

	HYDROPHYTES									
	Bryum pseudotriquetrum	Tomenthypnum nitens	Sphagnum warnstorfii	Aulacomnium palustre	Dicranum scoparium	Barbilophozia lycopodioides	Dicranum acutifolium	Dicranum fuscescens	Timmia austriaca	Ptilium crista-castrensis
Bryum pseudotriquetrum		.33	.19	.24	.05	.02	.02	.01	.02	.01
Tomenthypnum nitens		.	.21	.26	.01	–	–	–	–	–
Sphagnum warnstorfii		.	.	.35	.13	–	–	–	–	–
Aulacomnium palustre		.	.	.	.05	.06	.05	.04	.06	.03
Dicranum scoparium		.	.	.	.	.28	.19	.26	.10	.02
Barbilophozia lycopodioides		.	.	.	.	.	.31	.33	.21	.08
Dicranum acutifolium		.	.	.	.	.	.	.33	.22	.03
Dicranum fuscescens		.	.	.	.	.	.	.	.14	.05
Timmia austriaca		.	.	.	.	.	.	.	.	.17
Ptilium crista-castrensis		.	.	.	.	.	.	.	.	.
Rhytidiadelphus triquetrus		.	.	.	.	.	.	.	.	.
Hylocomium splendens		.	.	.	.	.	.	.	.	.
Pleurozium schreberi		.	.	.	.	.	.	.	.	.
Drepanocladus uncinatus		.	.	.	.	.	.	.	.	.
Brachythecium salebrosum		.	.	.	.	.	.	.	.	.
Eurhynchium pulchellum		.	.	.	.	.	.	.	.	.
Barbilophozia hatcheri		.	.	.	.	.	.	.	.	.
Dicranum polysetum		.	.	.	.	.	.	.	.	.
Thuidium abietinum		.	.	.	.	.	.	.	.	.
Rhytidium rugosum		.	.	.	.	.	.	.	.	.
Hypnum revolutum		.	.	.	.	.	.	.	.	.
Ditrichum flexicaule		.	.	.	.	.	.	.	.	.
Tortula ruralis		.	.	.	.	.	.	.	.	.
Grimmia anodon		.	.	.	.	.	.	.	.	.
Hypnum vaucheri		.	.	.	.	.	.	.	.	.
Pogonatum alpinum		.	.	.	.	.	.	.	.	.
Rhacomitrium lanuginosum		.	.	.	.	.	.	.	.	.

ues for important bryophyte species based on
30 stands in the Jasper study area.

acutifolium	Dicranum fuscescens	Timmia austriaca	Ptilium crista-castrensis	Rhytidiadelphus triquetrus	Hylocomium splendens	Pleurozium schreberi	Drepanocladus uncinatus	Brachythecium salebrosum	Eurhynchium pulchellum	Barbilophozia hatcheri	Dicranum polysetum	Thuidium abietinum	Rhytidium rugosum	Hypnum revolutum	Ditrichum flexicaule	Tortula ruralis	Grimmia anodon
	MESOPHYTES												XEROPHYTES				
2	.01	.02	.01	-	.01	-	.10	.03	-	.06	.05	-	-	-	-	-	-
	-	-	-	-	.03	.01	.07	.03	-	-	.10	-	-	-	.02	-	-
	-	-	-	-	.07	.02	.09	.04	-	.01	.06	-	-	-	-	-	-
5	.04	.06	.03	.01	.12	.08	.11	.08	.01	.03	.15	-	-	-	.05	-	-
9	.26	.10	.02	-	.12	.02	.14	.11	.05	.21	.05	-	-	-	.13	-	-
1	.33	.21	.08	.02	.15	.15	.23	.13	.04	.11	.03	-	-	-	.04	-	-
	.33	.22	.03	.02	.19	.13	.29	.17	.08	.24	.19	.01	.04	.07	.10	.02	-
	.	.14	.05	.03	.19	.[illegible]3	.25	.21	.12	.30	.04	.01	.06	.09	.07	.01	-
	.	.	.17	.02	.24	.22	.28	.23	.18	.16	.10	-	-	-	.10	-	-
	.	.	.	.29	.32	.28	.07	.13	.14	.07	.09	-	-	-	.03	-	-
	.	.	.	.	.18	.09	.03	.08	.09	.03	.03	-	-	-	.02	-	-
	.	.	.	.	.	.32	.22	.24	.16	.18	.17	.02	.02	.02	.08	.03	-
	.	.	.	.	.	.	.16	.19	.13	.15	.14	-	-	-	.06	-	-
	.	.	.	.	.	.	.	.28	.20	.23	.15	.01	-	.01	.12	.01	-
	.	.	.	.	.	.	.	.	.33	.25	.13	.02	.02	.01	.12	.02	-
	.	.	.	.	.	.	.	.	.	.22	.12	.01	.02	.01	.12	.01	-
	.	.	.	.	.	.	.	.	.	.	.11	-	-	.03	.08	-	-
	.	.	.	.	.	.	.	.	.	.	.	.06	.08	.03	.04	-	-
	.	.	.	.	.	.	.	.	.	.	.	.	.24	.06	.06	.24	.05
	.	.	.	.	.	.	.	.	.	.	.	.	.	.24	.06	.22	-
	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.11	.12	-
	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.12	.25
	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.15
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hyte species based on
study area.

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YTES								XEROPHYTES								
Hylocomium splendens	Pleurozium schreberi	Drepanocladus uncinatus	Brachythecium salebrosum	Eurhynchium pulchellum	Barbilophozia hatcheri	Dicranum polysetum	Thuidium abietinum	Rhytidium rugosum	Hypnum revolutum	Ditrichum flexicaule	Tortula ruralis	Grimmia anodon	Hypnum vaucheri	Pogonatum alpinum	Rhacomitrium lanuginosum
.01	-	.10	.03	-	.06	.05	-	-	-	-	-	-	-	.06	-
.03	.01	.07	.03	-	-	.10	-	-	-	.02	-	-	-	-	-
.07	.02	.09	.04	-	.01	.06	-	-	-	-	-	-	-	.11	-
.12	.08	.11	.08	.01	.03	.15	-	-	-	.05	-	-	-	.07	-
.12	.02	.14	.11	.05	.21	.05	-	-	-	.13	-	-	-	.18	-
.15	.15	.23	.13	.04	.11	.03	-	-	-	.04	-	-	-	.11	-
.19	.13	.29	.17	.08	.24	.19	.01	.04	.07	.10	.02	-	-	.08	-
.19	.13	.25	.21	.12	.30	.04	.01	.06	.09	.07	.01	-	-	.11	-
.24	.22	.28	.23	.18	.16	.10	-	-	-	.10	-	-	-	-	-
.32	.28	.07	.13	.14	.07	.09	-	-	-	.03	-	-	-	-	-
.18	.09	.03	.08	.09	.03	.03	-	-	-	.02	-	-	-	-	-
.	.32	.22	.24	.16	.18	.17	.02	.02	.02	.08	.03	-	-	.07	-
.	.	.16	.19	.13	.15	.14	-	-	-	.06	-	-	-	.02	-
.	.	.	.28	.20	.23	.15	.01	-	.01	.12	.01	-	-	.05	-
.	.	.	.	.33	.25	.13	.02	.02	.01	.12	.02	-	-	.02	-
.	.	.	.	.	.22	.12	.01	.02	.01	.12	.01	-	-	.01	-
.	.	.	.	.	.	.11	-	-	.03	.08	-	-	-	.16	.02
.	.	.	.	.	.	.	.06	.08	.03	.04	-	-	-	-	-
.	.	.	.	.	.	.	.	.24	.06	.06	.24	.05	.04	.01	-
.	.	.	.	.	.	.	.	.	.24	.06	.22	-	-	.05	.01
.	.	.	.	.	.	.	.	.	.	.11	.12	-	-	.13	.11
.	.	.	.	.	.	.	.	.	.	.	.12	.25	.22	.03	.03
.	.	.	.	.	.	.	.	.	.	.	.	.15	.14	.03	.03
.	.	.	.	.	.	.	.	.	.	.	.	.	.38	-	-
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.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Several species were restricted exclusively to rock outcrops. *Grimmia anodon* and *Hypnum vaucheri* (Fig. 6) both dominated low elevation outcrops but were not found elsewhere. This narrow habitat was reflected by low habitat breadths for both species.(Table 5). The high degree of overlap between these two species (.387) relative to other species pairs indicated strong habitat similarity. *Orthotrichum jamesianum* (Fig. 6) was also an outcrop exclusive, possessing a response pattern similar to *Grimmia* and *Hypnum*, but was less abundant (Plate 2).

Two common xerophytes, *Thuidium abietinum* and *Rhytidium rugosum* (Fig. 7), were limited to the driest forest and tundra types where they were sometimes important. Although occasional in fissures and crevices on rock outcrops, they reached cover values of 3.1% and 0.8%, respectively, in dry Douglas-fir forest. It is interesting that while *Thuidium* exhibited a continuous distribution with elevation, *Rhytidium* seemed to be bimodally distributed, with a second region of peak abundance in the cushion plant-lichen tundra of the low alpine.

The less abundant members of outcrop communities tended to be more widespread in their distribution, extending into dry forest on a variety of substrata and having

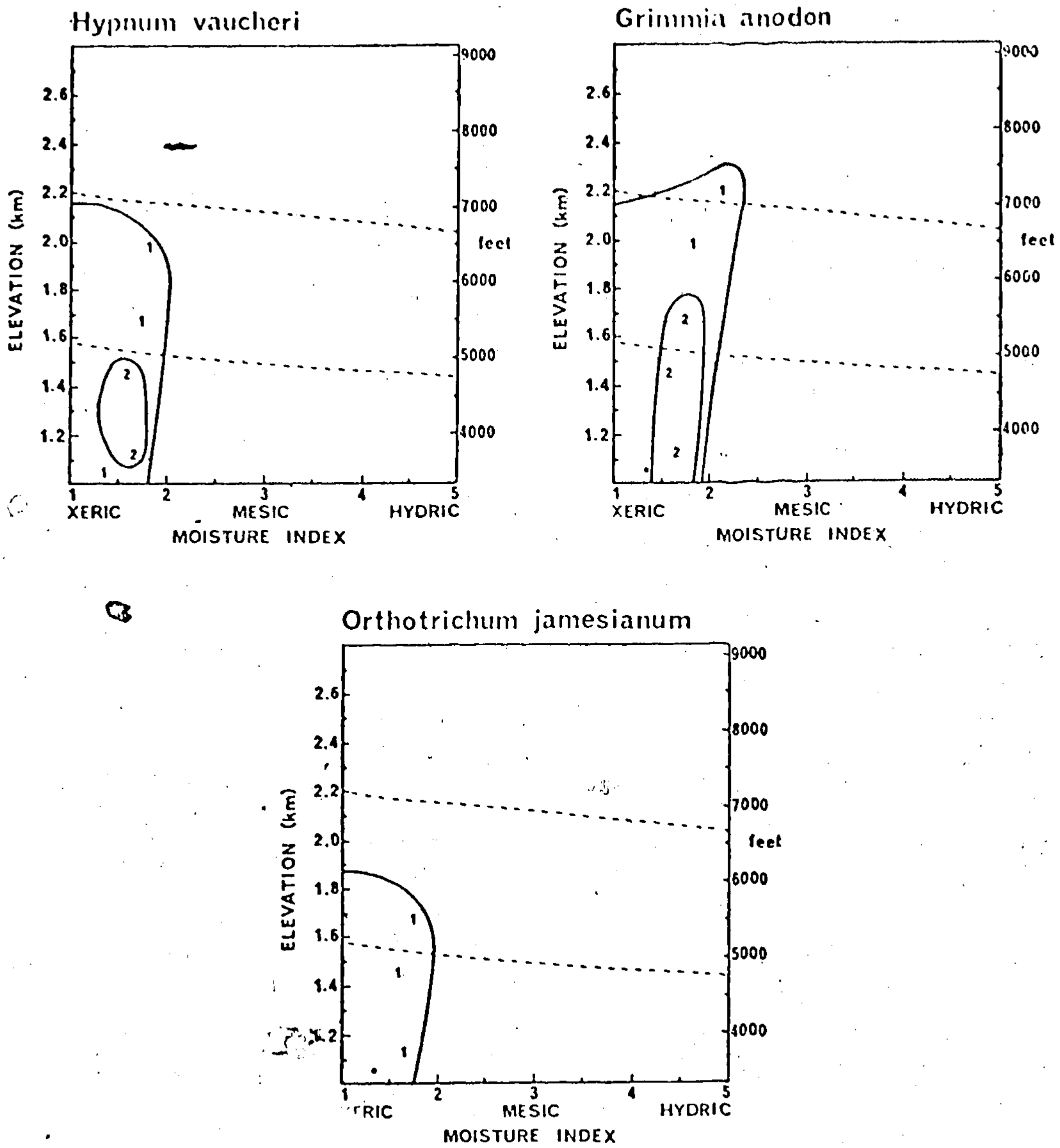


Figure 6. Habitats of *Orthotrichum jamesianum*, *Grimmia anodon*, and *Hypnum vaucheri* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 0-1.0%, 2 = 1.1-5.0%, • = stand with species absent but included in species habitat.

Plate 2. *Grimmia anodon* and *Hypnum vaucheri* on a montane rock outcrop (stand no. 3).

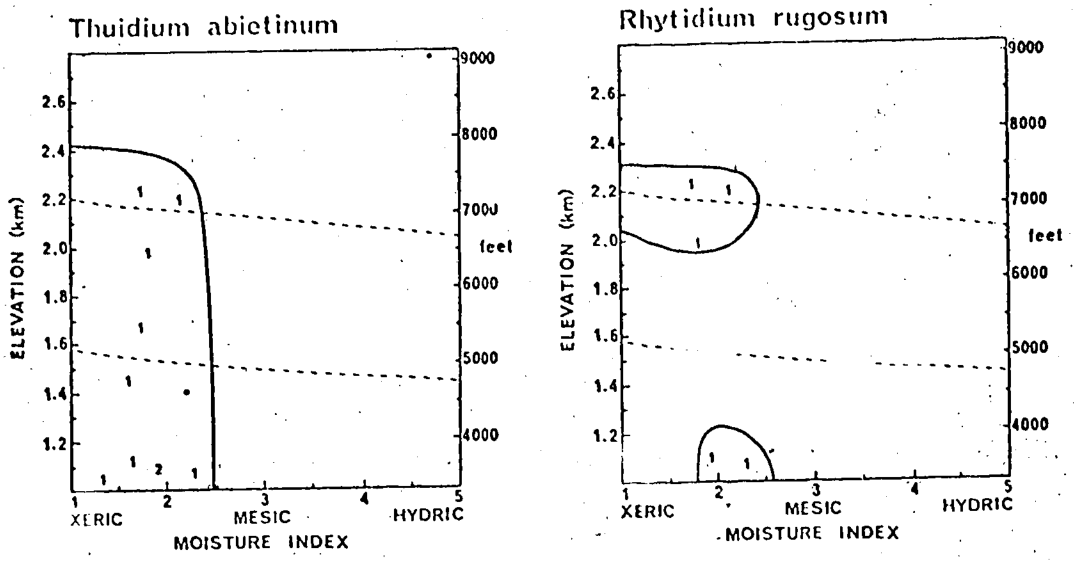


Figure 7. Habitats of *Thuidium abietinum* and *Rhytidium rugosum* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 0-1.0%, 2 = 1.1-5.0%, • = stand with species absent but included in species habitat.

generally greater habitat breadths than the 'exclusives'. *Ditrichum flexicaule, Tortula ruralis* and *Polytrichum juniperinum* (Fig. 8) were rare on rock outcrops, where they grew on soil in crevices, but were also found in xeric or even mesic forests. The extension of *Ditrichum* into more mesic stands than *Tortula* was evident from the response patterns of these species and correlated with the broader habitat (Table 5) of the former. Both species, however, were most common on rock and humus in forest stands whereas *Polytrichum* was mainly restricted to wood and humus (Fig. 9).

Three characteristic saxicoles of forest communities were *Grimmia apocarpa, Hypnum revolutum* and *Orthotrichum laevigatum* (Fig. 10), all of which were widely distributed on erratic boulders. As was typical for widespread xerophytes they were never abundant on low elevation outcrops although *Grimmia* and *Orthotrichum* were present there. *Hypnum,* however, was an important component of higher elevation rock outcrop communities. *Orthotrichum laevigatum* was one of a few species present on all rock outcrops sampled, including the high alpine lichen desert at 2676m.

Mesophytic species. Species whose response patterns or pattern centers were located within mesic forest or tundra as designated on the mosaic diagram (Fig. 3) were considered mesophytic. Since forests provided the highest substratum diversity of all sampled communities with rock, humus, soil, wood and bark often available for bryophyte

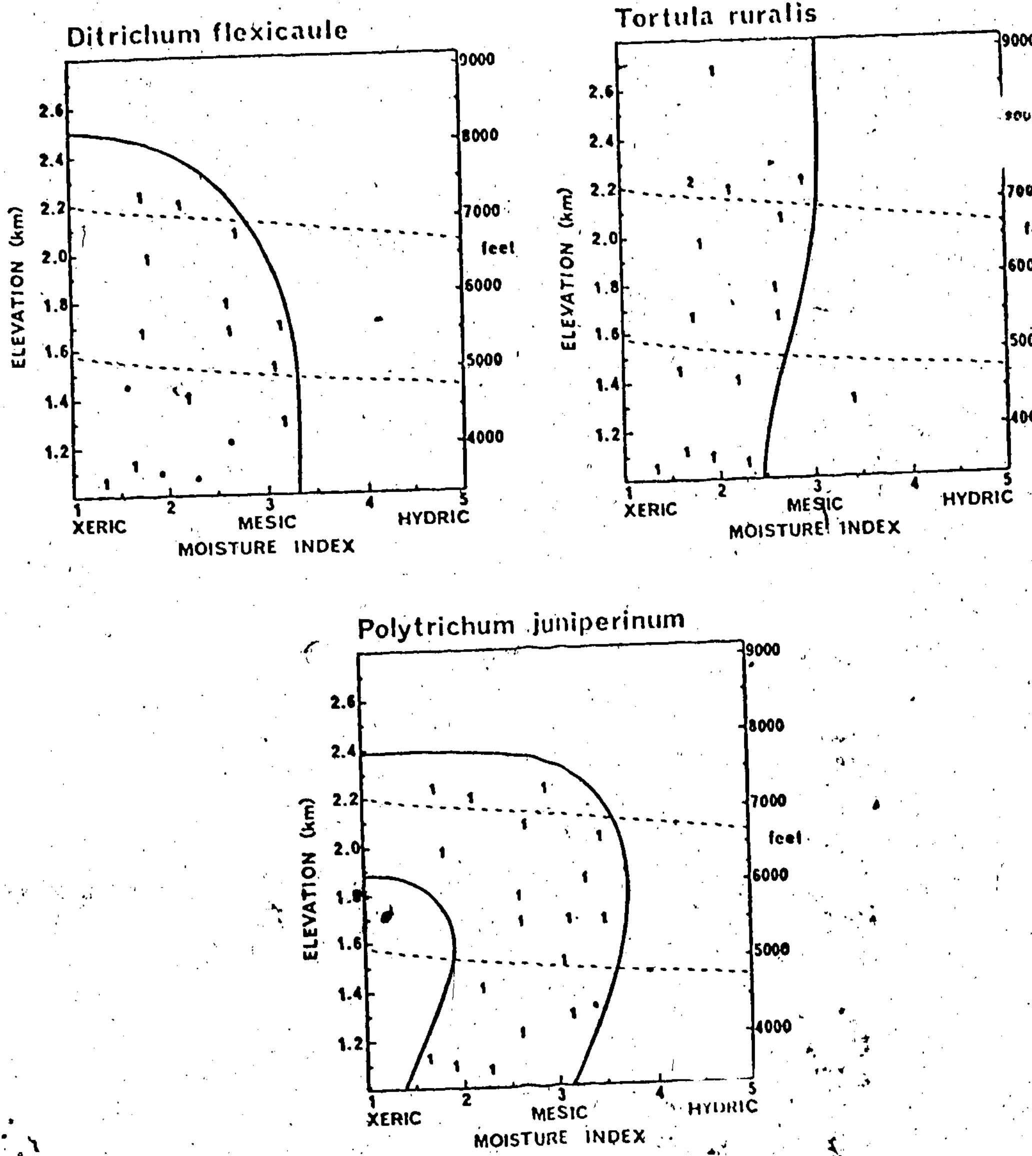
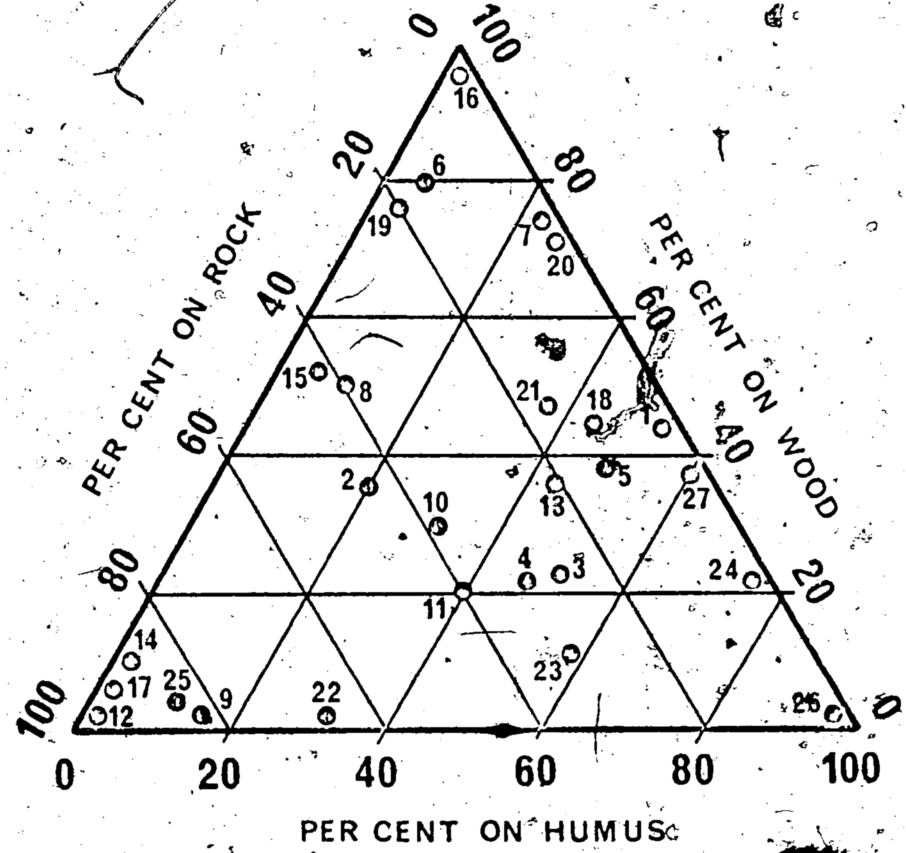


Figure 8. Habitats of *Ditrichum flexicaule*, *Tortula ruralis*, and *Polytrichum juniperinum* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 0-1.0%, 2 = 1.1-5.0%; • = stand with species absent but included within species habitat.



KEY

1. Aulacomnium palustre
2. Barbilophozia hatcheri
3. Barbilophozia lycopodioides
4. Brachythecium salebrosum
5. Dicranum acutifolium
6. Dicranum fuscescens
7. Dicranum polysetum
8. Dicranum scoparium
9. Ditrichum flexicaule
10. Drepanocladus uncinatus
11. Eurhynchium pulchellum
12. Grimmia apocarpa
13. Hylocomium splendens
14. Hypnum revolutum
15. Mnium spinulosum
16. Oncophorus wahlenbergii
17. Orthotrichum laevigatum
18. Pleurozium schreberi
19. Pohlia nutans
20. Polytrichum juniperinum
21. Ptilium crista-castrensis
22. Thuidium abietinum
23. Timmia austriaca
24. Tomenthypnum nitens
25. Tortula ruralis
26. Rhytidiadelphus triquetrus
27. Rhytidium rugosum

Figure 9. Ordination of 27 bryophyte species based on their substratum affinities in forest stands in the Jasper study area. Axes represent the per cent frequency of occurrence on humus, wood, and rock (see METHODS, p.52).

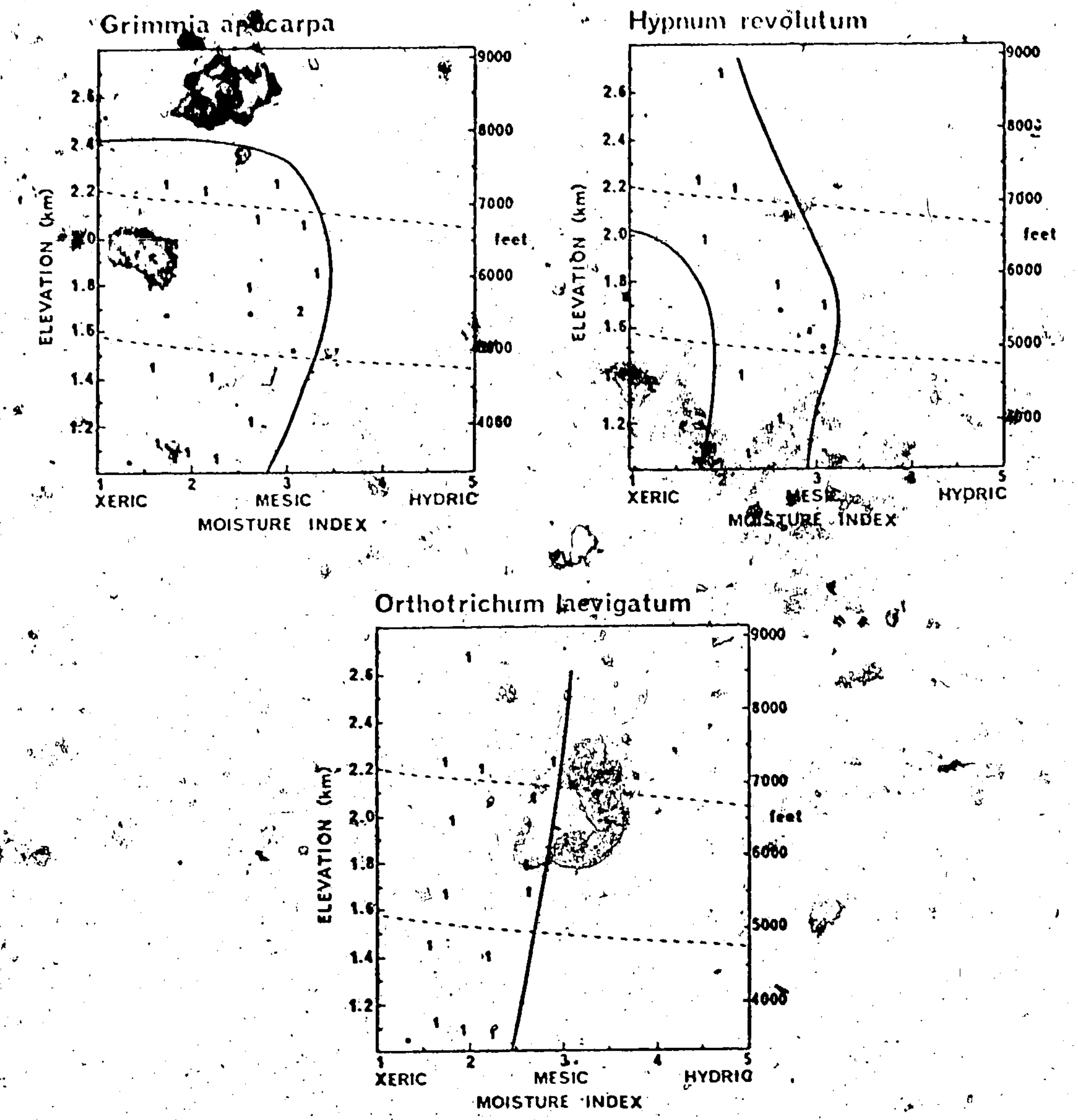


Figure 10. Habitats of *Grimmia apocarpa*, *Hypnum revolutum*, and *Orthotrichum laevigatum* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 0-1.0%, 2 = 1.1-5.0%, • = stand with species absent but included within species habitat.

colonization in the same stand, it was especially important to keep bryophyte-substratum relationships in perspective when interpreting the response patterns of mesophytes.

Within the mesophytic group, two sets of species were identified: "Ubiquists", characterized by broad habitats and large response patterns; and "specialists", that were confined to specific segments along the gradients and had narrow habitats.

The important ubiquists included the three most abundant feathermosses in the study area: *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis* (Fig. 11). All three had very broad overall habitats, but *Hylocomium* was the most widely distributed species in the study area, having an overall habitat breadth of .72. This robust weft-former was the most abundant species in the study area and was also the leading dominant in 37% of the stands sampled. Its response pattern clearly indicates that peak abundance values were attained in mesic spruce-fir forests of the subalpine and montane zones where it covered as much as 48% of the ground surface. However, it was also a major component in alpine dwarf shrub-heath (1.4%) and wet sedge tundra (6.4%). *Hylocomium* was present, although quite uncommon, in fen communities where it was usually associated with hummocks. I observed it in mixed clumps with pronounced hydrophytes like *Aulacomnium palustre* and *Sphagnum warnstorfii*. *Hylocomium* extended beyond the limits

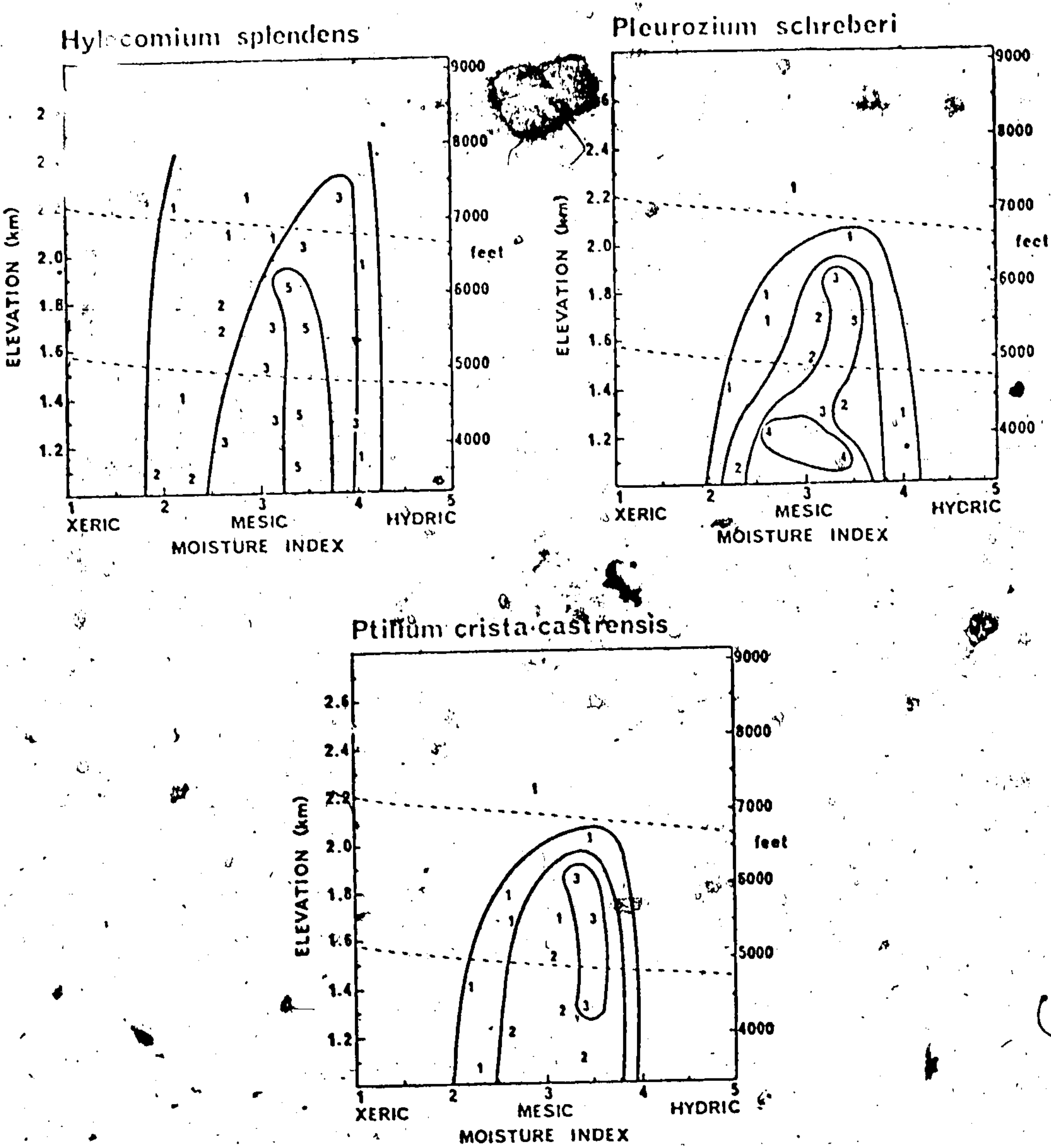


Figure 11. Habitats of *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 0-1.0%, 2 = 1.1-5.0%, 3 = 5.1-15.0%, 4 = 15.1-25.0%, 5 = 25.1-50.0%, • = stand with species absent but included within species habitat.

of *Pleurozium* and *Ptilium* not only on the wet side of the moisture gradient but on the dry side as well, being abundant in montane Douglas-fir forest and in xeric subalpine forests (e.g. stand no. 19). The broad response of this species to the moisture gradient was quantitatively demonstrated by habitat breadth measurements in subalpine and montane stands (see Table 5) which were, in both cases, greater than corresponding values for *Ptilium* and *Pleurozium*. *Hylocomium* had greater habitat breadth than the other feathermosses in relation to altitude as well. *Pleurozium schreberi*, despite its smaller overall habitat (.55), was a widespread species as exhibited by its response pattern (Fig. 11). Its greatest abundance was reached in mesic montane forests which had lower moisture indices than stands in which *Hylocomium* attained peak values. *Pleurozium* covered 17 to 21% of the ground surface in these stands.

Ptilium crista-castrensis was found in the same stands as *Pleurozium*, with one exception, but due to its concentration of abundance in a few stands *Ptilium* had smaller overall habitat breadth (.51). Although the outlines of the response patterns for these two species were nearly identical, *Ptilium* attained maximum cover of 10% (stand no. 6) and 8% (no. 12) in wet-mesic upper montane and lower subalpine forests of spruce and fir where *Hylocomium* cover was also highest. *Ptilium* was an uncommon species in the upper subalpine, even in mesic situations, and was virtually absent above timberline.

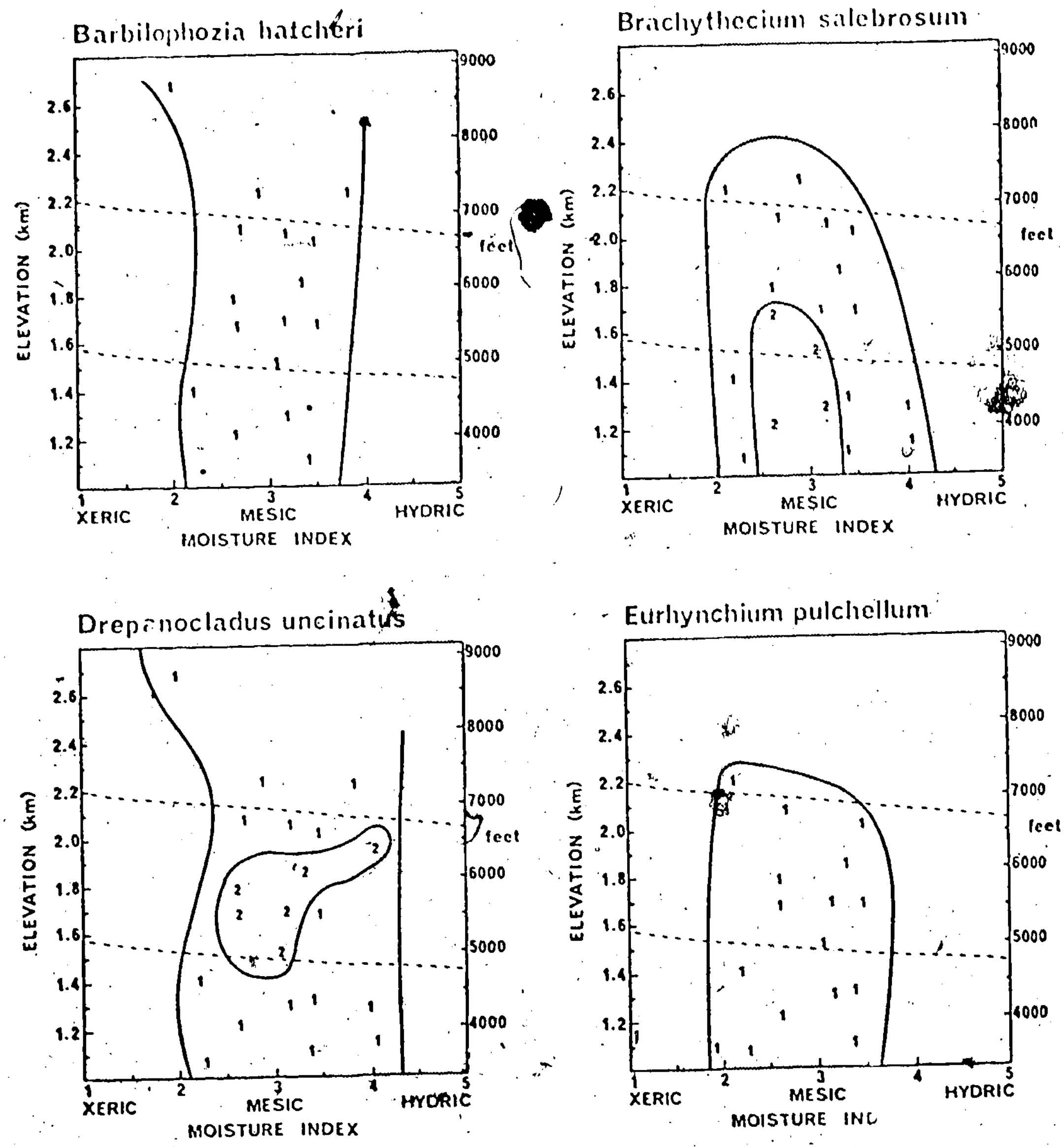
In moist forests *Hylocomium*, *Pleurozium* and *Ptilium* formed lush, continuous, undulating wefts in which individuals of all three species were intermixed (Plate 3). In 10 of the 13 stands in which all three feathermoss species occurred, *Hylocomium* was the leading dominant with *Pleurozium* second and *Ptilium* third. In two of the stands *Ptilium* replaced *Pleurozium* as the second most important species and in one stand *Pleurozium* was most abundant with *Hylocomium* second and *Ptilium* third. Within forest communities these three species were most commonly associated with humus and wood with occasional occurrences on rock (Fig. 9). However, in wet-mesic stands, rotting logs and rocks were often covered with feathermosses (Plate 4).

Unlike the important ubiquists, there were several bryophytes that never produced large populations locally, although they were widely distributed in the study area. These minor ubiquists included three pleurocarpic mosses, *Drepanocladus uncinatus*, *Brachythecium salebrosum* and *Eurhynchium pulchellum*, and one liverwort, *Barbilophozia hatcheri* (Fig. 12).

In most stands cover of *Drepanocladus uncinatus* was less than 1% but peak values of up to 5% occurred in mesic subalpine pine and spruce-fir forests. In these communities *Drepanocladus* was a component of the *Hylocomium-Pleurozium-Ptilium* weft. Despite generally small population sizes this

Plate 3. Feathermoss carpet in lower montane white spruce forest (stand no. 24). *Hylocomium splendens*, *Ptilium crista-castrensis* and *Pleurozium schreberi* are present.

Plate 4. - Erratic boulder covered by feathermosses, mainly *Hylocomium splendens*, in montane white spruce forest, (stand no. 24).


Barbilophozia hatcheri

Brachythecium salebrosum

Drepanocladus uncinatus

Eurhynchium pulchellum

Figure 12. Habitats of *Barbilophozia hatcheri*, *Brachythecium salebrosum*, *Drepanocladus uncinatus*, and *Eurhynchium pulchellum* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 0-1.0%, 2 = 1.1-5.0%, • = stand with species absent but included within species habitat.

species had the third broadest habitat of all species examined (B = .58), and the stands in which it occurred included high alpine lichen desert and montane black spruce fen.

Brachythecium salebrosum and *Eurhynchium pulchellum* had broad habitats (Table 5) and showed considerable overlap with *Drepanocladus* although both of the former were generally less abundant than the latter. In direct contrast to the robust growth form of *Drepanocladus*, both *Brachythecium* and *Eurhynchium* most often grew as threaded forms (Gimingham and Birse 1957), loosely twining through the feathermoss matrix and rarely producing a continuous, monospecific mat.

All three of these mosses were relatively important in dry stands due to the dramatic reduction of feathermoss cover with decreasing moisture index. For example, in mesic montane spruce-fir forest (stand no. 6) *Hylocomium splendens* was the most abundant species having 34% cover and *Brachythecium salebrosum* ranked sixth in abundance with 0.1% cover, whereas, in dry montane pine forest (stand no. 29) *Brachythecium* was the most important species with 1.4% cover and *Hylocomium* cover was only 0.6%.

Barbilophozia hatcheri was another species of broad habitat (B = .56) that normally occurred in small populations. When only mesic stands were considered this liverwort had a habitat breadth of .45 (Table 3) which indicated comparatively broad response to elevation within this segment of the moisture gradient. It was excluded from xeric and hydric portions of the moisture gradient at lower elevations, but was ubiquitous in the alpine zone where it occurred in wet sedge tundra and in high alpine lichen desert.

All four minor ubiquists had very similar substratum affinities and were located near the center of the ordination in Figure 9, indicating that there was an approximately equal chance of finding any of these species in a quadrat on either rock, wood or humus. This contrasts with the performance of the important ubiquists, *Hylocomium*, *Pleurozium*, and *Ptilium*, that were more restricted to humus and wood and could be considered less flexible in their substratum relationships.

Whereas both groups of the ubiquitous mesophytes thus far treated were somewhat plastic in their substratum affiliations, *Dicranum fuscescens* and *Pohlia nutans* (Fig. 13) were acrocarpic mosses that readily colonized logs in early stages of decay and were rarely found on rock (Fig. 9). Above treeline both species inhabited soil and humus in tundra communities. *Dicranum scoparium* was also common in all three vegetation zones, but spanned a narrower segment of the moisture gradient than *D. fuscescens* and *Pohlia nutans*. It was also more common than the latter 2 species on rock (Fig. 9).

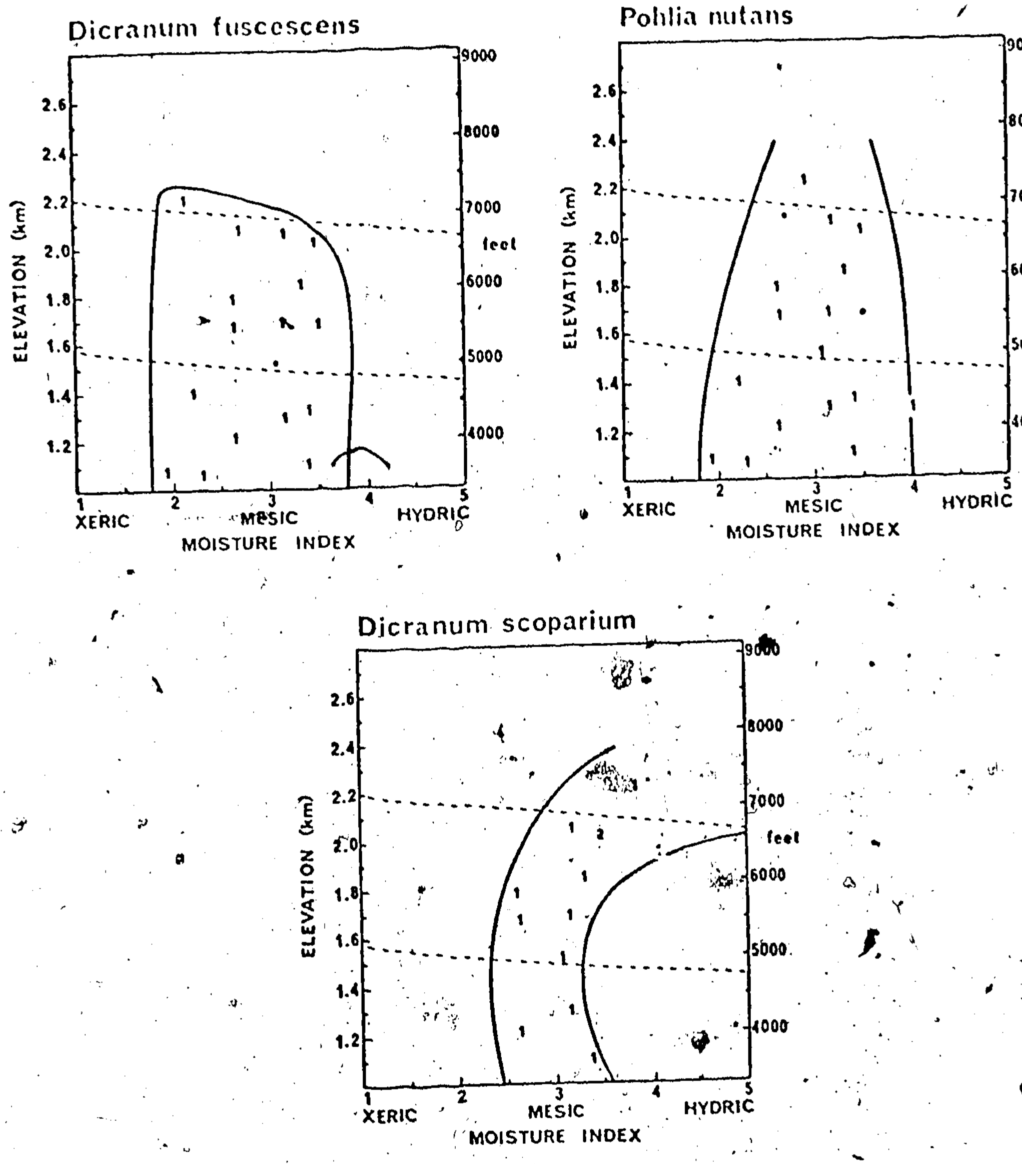


Figure 13. Habitats of *Dicranum fuscescens*, *Pohlia nutans*, and *Dicranum scoparium* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 0-1.0%, 2 = 1.1-5.0%, • = stand with species absent but included within species habitat.

Most of the species previously described in this section were not strongly restricted by elevation. Several mesophytes did have response patterns strongly tied to one segment of the elevational gradient. Four of these had their pattern centers in the upper montane or lower subalpine zones while three others were strongly associated with the middle and upper subalpine zone.

Rhytidiadelphus triquetrus (Fig. 14), a humicolous, robust feathermoss, reached cover maxima in upper montane spruce-fir forest (2.5%) where it was a conspicuous component of the bryophyte weft. It was less abundant in other stands and was completely excluded from dry forest communities or hydric fens. This restriction in relation to moisture regime was reflected by the narrow habitat of *Rhytidiadelphus* in the montane zone (Bm = .34). When habitat breadth was measured for mesic stands, implying elevation as the controlling variable, *Rhytidiadelphus* again had low habitat breadth. The narrow range of response for this species for both elevation and moisture regime was reflected by low overall habitat breadth (.33).

While *Rhytidiadelphus triquetrus* was predominantly humicolous (Fig. 9), *Mnium spinulosum*, *Oncophorus wahlenbergii* and *Dicranum polysetum* (Fig. 14) were chiefly xylicolous and like many other pioneers on rotting wood all three were turfs (Gimingham and Birse 1957). *Mnium* and *Oncophorus* maintained population sizes too small for calculation of

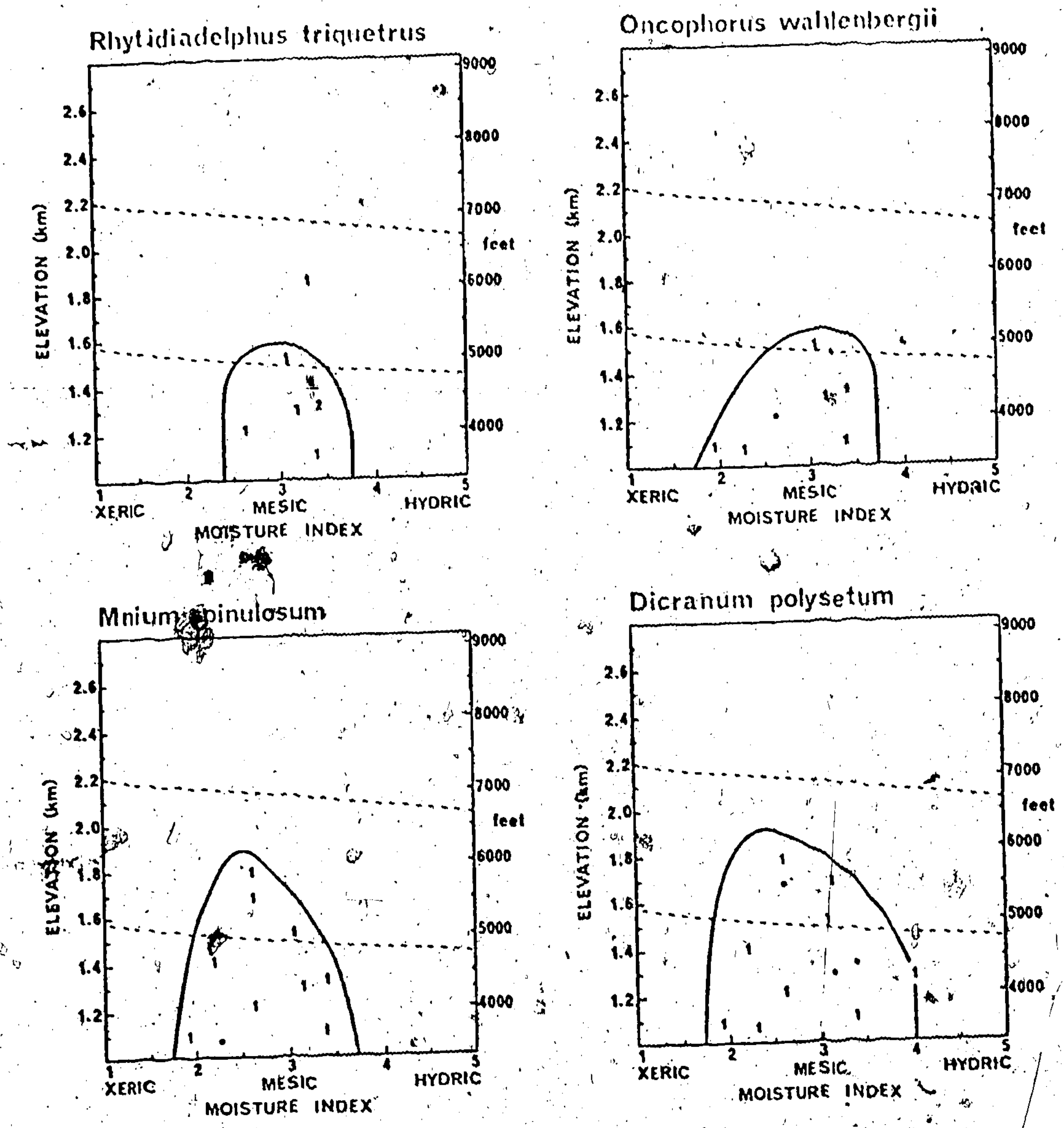


Figure 14. Habitats of *Rhytidiadelphus triquetrus*, *Oncophorus wahlenbergii*, *Mnium spinulosum*, and *Dicranum polysetum* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 0-1.0%, 2 = 1.1-5.0%, • = stand with species absent but included within species habitat.

habitat metrics, but from their response patterns it was evident that *Mnium* had a slightly broader habitat with elevation since it was present in some subalpine stands where *Oncophorus* was not. *Dicranum polysetum* reached the middle subalpine zone but was more conspicuous in montane pine forests on partly decomposed wood.

The distribution centers of the second group of elevational specialists were located in the subalpine zone. Included were 1 leafy liverwort, *Barbilophozia lycopodioides*, and 2 acrocarpic mosses, *Dicranum acutifolium* and *Timmia austriaca* (Fig. 15). All three species were humicolous (Fig. 9), had high overlap values with each other (Table 6), and had overall habitat breadth values in the range .46-.48. In wet-mesic forests the 3 species were mixed with one another and the feathermosses in a continuous carpet over the forest floor.

Barbilophozia lycopodioides was most successful in wet, upper subalpine forests under Engelmann spruce and subalpine fir where it sometimes covered over 8% of the ground surface. It was also an important component of the bryoid stratum in subalpine heath tundra (3.6% cover). As well as being the largest leafy liverwort in the study area it was the only hepatic to attain real significance in any of the stands sampled.

One of the more characteristic bryophytes of the subalpine zone was *Timmia austriaca* which, although occasionally present at lower elevations, became an important

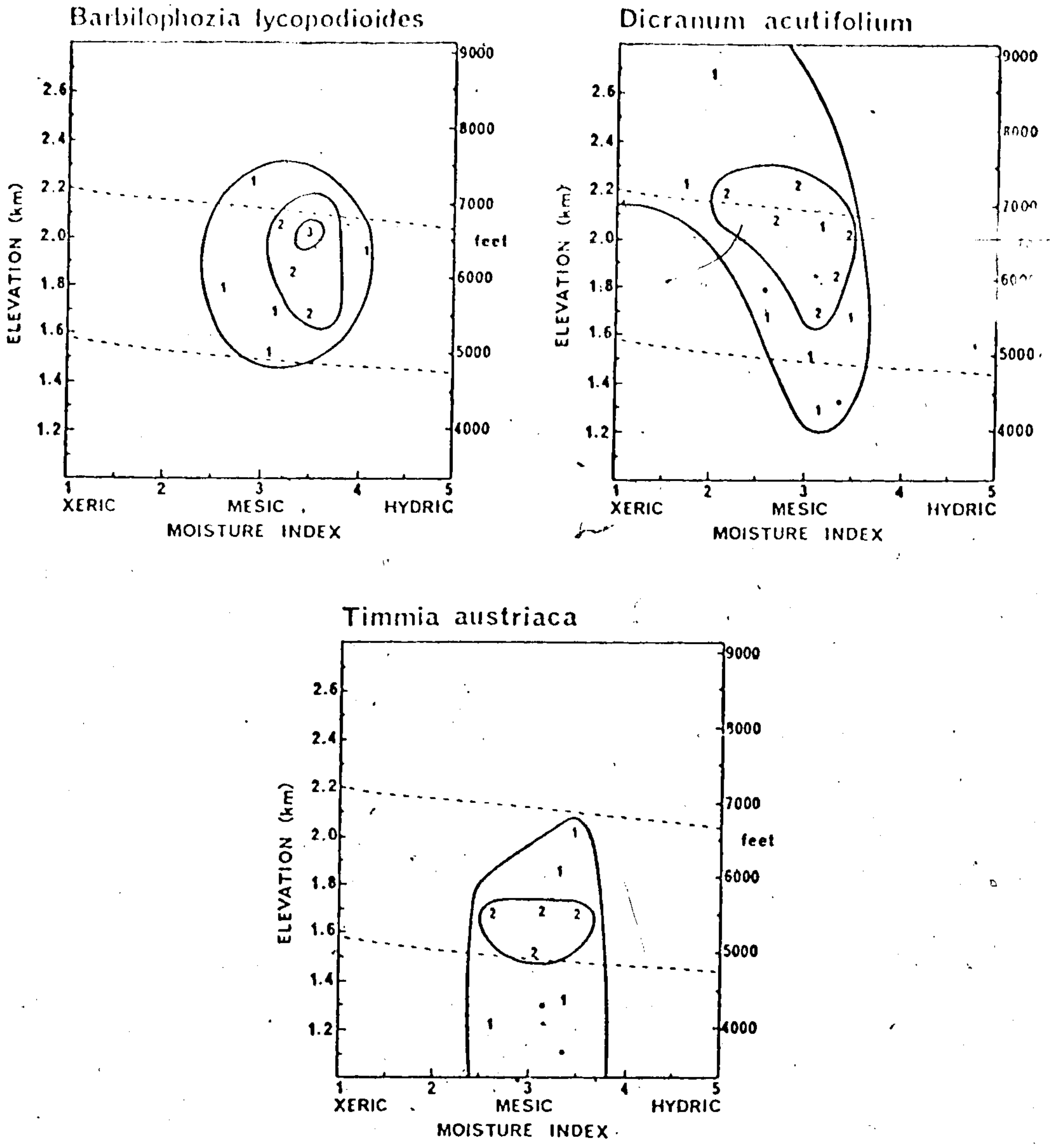


Figure 15. Habitats of *Barbilophozia lycopodioides*, *Dicranum acutifolium*, and *Timmia austriaca* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 0-1.0%, 2 = 1.1-5.0%, 3 = 5.1-15.0%, • = stand with species absent but included within species habitat.

member of bryophyte synusiae at elevations between 1530m and timberline. In middle subalpine, mesic lodgepole pine forests, *Timmia* reached 4.2% cover and although often less abundant, it was extremely widespread within the subalpine zone and had a broader habitat in this zone than either *Barbilophozia lycopodioides* or *Dicranum acutifolium* (Table 5).

Dicranum acutifolium was found at higher elevations than either of the preceding species but achieved maximum cover of 4% in middle to upper subalpine spruce-fir forests. It was a minor component of the bryophyte communities in these forests, relative to other species, and this contrasts with its performance as leading dominant in dwarf shrub-heath tundra and in upper subalpine dry forests (i.e. stand no. 19). Its cover in these latter communities, however, was only 1-2%.

Hydrophytic species. Only 4 bryophytes reaching peak cover in the fen communities were abundant enough to permit discussion of their habitat relationships. All four responded minimally to elevation and were present in all wooded fens as well as in wet sedge tundra, but they were differentially successful in drier stands. *Sphagnum warnstorfii*, *Aulacomnium palustre* and *Tomenthypnum nitens* (Fig. 16, Plate 5) shared dominance in the montane and subalpine wetlands, although the latter two had less cover in wet sedge tundra. They were also the dominant bryophytes in

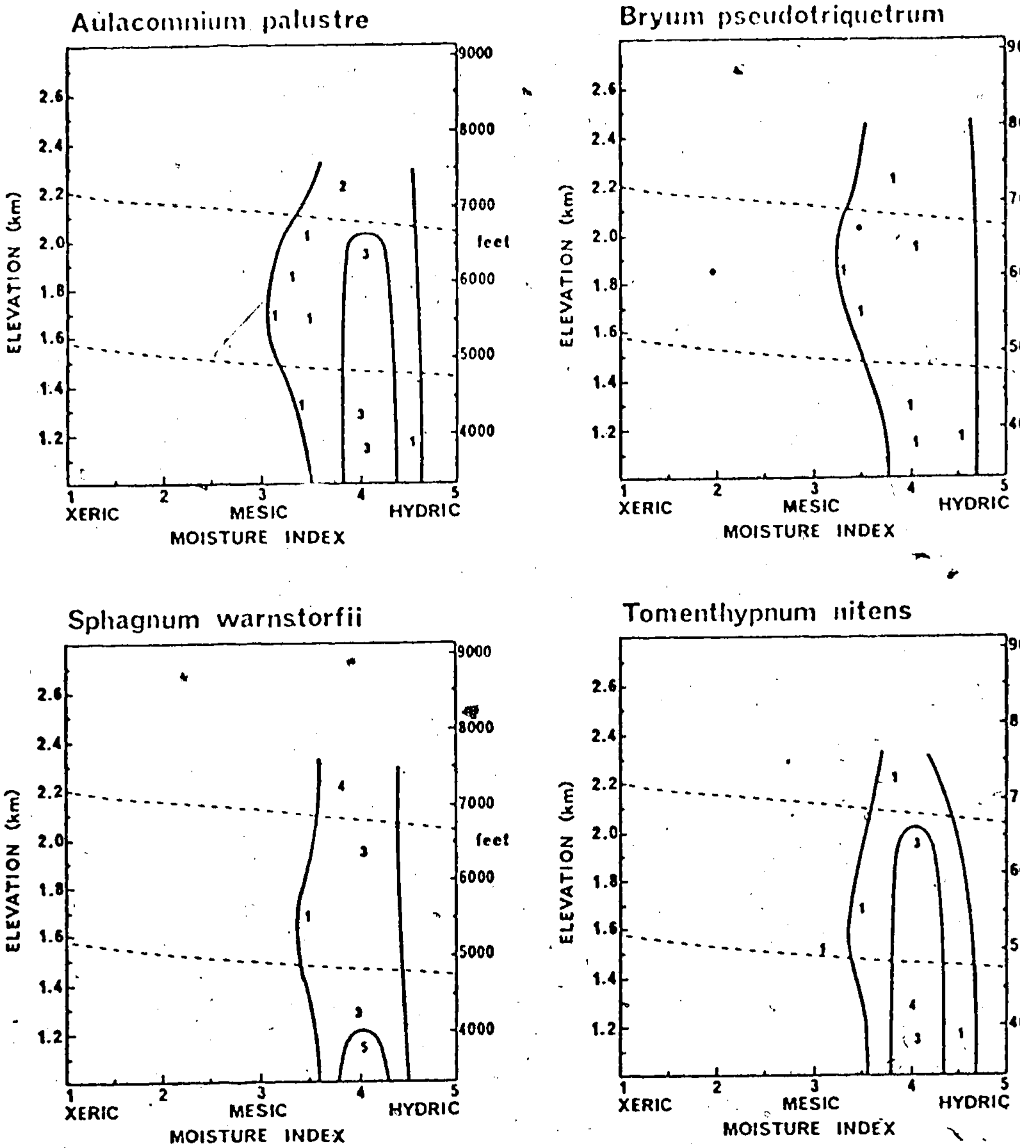


Figure 16. Habitats of *Aulacomnium palustre*, *Bryum pseudotriquetrum*, *Sphagnum warnstorfii*, and *Tomenthypnum nitens* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 0-1.0%, 2 = 1.1-5.0%, 3 = 5.1-15.0%, 4 = 15.1-25.0%, 5 = 25.1-50.0%, • = stand with species absent but included within species habitat.

Plate 5. *Sphagnum warnstorfii* in wet sedge tundra (stand no. 22) near summit of Signal Mountain.

hydric communities. The fourth widely distributed hydrophyte, *Bryum pseudotriquetrum* (Fig. 16), never exceeded 1% cover and was typically scattered throughout fens in small clumps or as individual stems.

The habitat breadth values for these species were revealing. *Sphagnum warnstorfii* was strongly restricted to wetlands and had the lowest overall habitat breadth of the 4 (.51). The divergent turf, *Tomenthypnum nitens*, however, was abundant in the open montane sedge fen and present in some mesic forests. It thus had the second broadest habitat of any species in the study (.61) largely because it was present in the montane sedge fen (stand no. 27) which was consistently weighted as the most distinct stand by the Colwell and Futuyma (1971) technique. It is interesting that in the montane zone, where the sedge fen was included in the computation of weighting factors, *Tomenthypnum* had a very high habitat breadth (Bm = .64) exceeding that of *Aulacomnium palustre* (see Table 5). In the subalpine zone *Aulacomnium* had a broader habitat due to its more extensive invasion of mesic forests and to the lack of an open fen that heavily weighted *Tomenthypnum*. In both zones *Aulacomnium* exhibited greater success in upland forests than *Tomenthypnum*, but the latter was more successful in the environment provided by the open sedge fen, indicating greater tolerance or competitive ability in extreme hydric situations.

All of the hydric species presented above were usually found growing directly on partially decomposed, organic peat.

Alpine species. A small group of species showed strong restriction to the alpine zone. But since only five truly alpine communities were sampled, response patterns and habitat measurements for alpine species were less certain than for lower-elevation species.

Pogonatum alpinum (Fig. 17) was certainly the most widespread bryophyte in this group and was collected in high alpine lichen desert, low alpine rock outcrop, and wet sedge tundra communities apparently spanning the entire moisture gradient. Like many, but not all, widespread species it was never abundant and was typically scattered throughout a stand growing as individual stems on humus or soil.

Two other important species, *Grimmia calyptrata* and *Rhacomitrium lanuginosum*, were primarily alpine in distribution (Fig. 17). *G. calyptrata* was common on rock outcrops and also on erratic boulders in subalpine forest and alpine tundra communities, whereas *Rhacomitrium* was a boulder-field specialist that dominated the high alpine lichen desert (Plate 6).

Desmatodon latifolius, *Polytrichum piliferum*, and *Rhacomitrium canescens* (Fig. 18), grew on humus or mineral soil in dry to mesic tundra communities and dry, upper subalpine

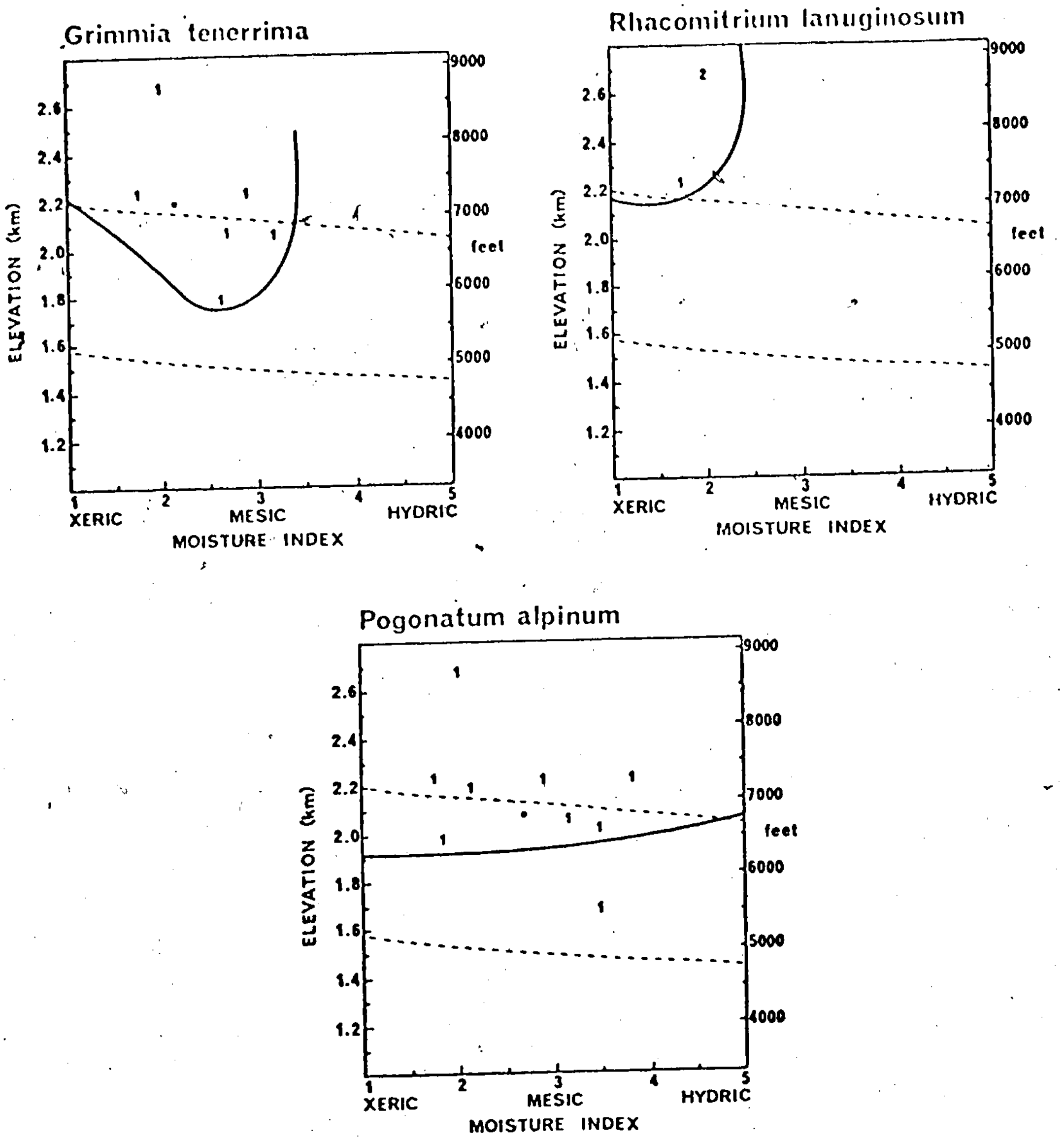


Figure 17. Habitats of *Grimmia calyptrata*, *Rhacomitrium lanuginosum*, and *Pogonatum alpinum* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 0-1.0%, 2 = 1.1-5.0%, • = stand with species absent but included within species habitat.

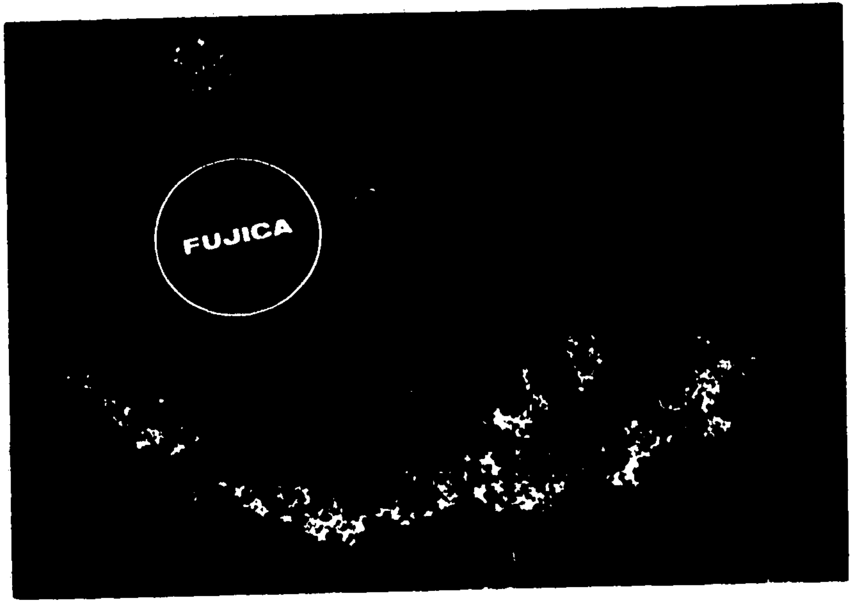


Plate 6. *Rhacomitrium lanuginosum*, a dominant species of upper alpine boulder fields, is shown here on Mount Tekarra (stand no. 28).

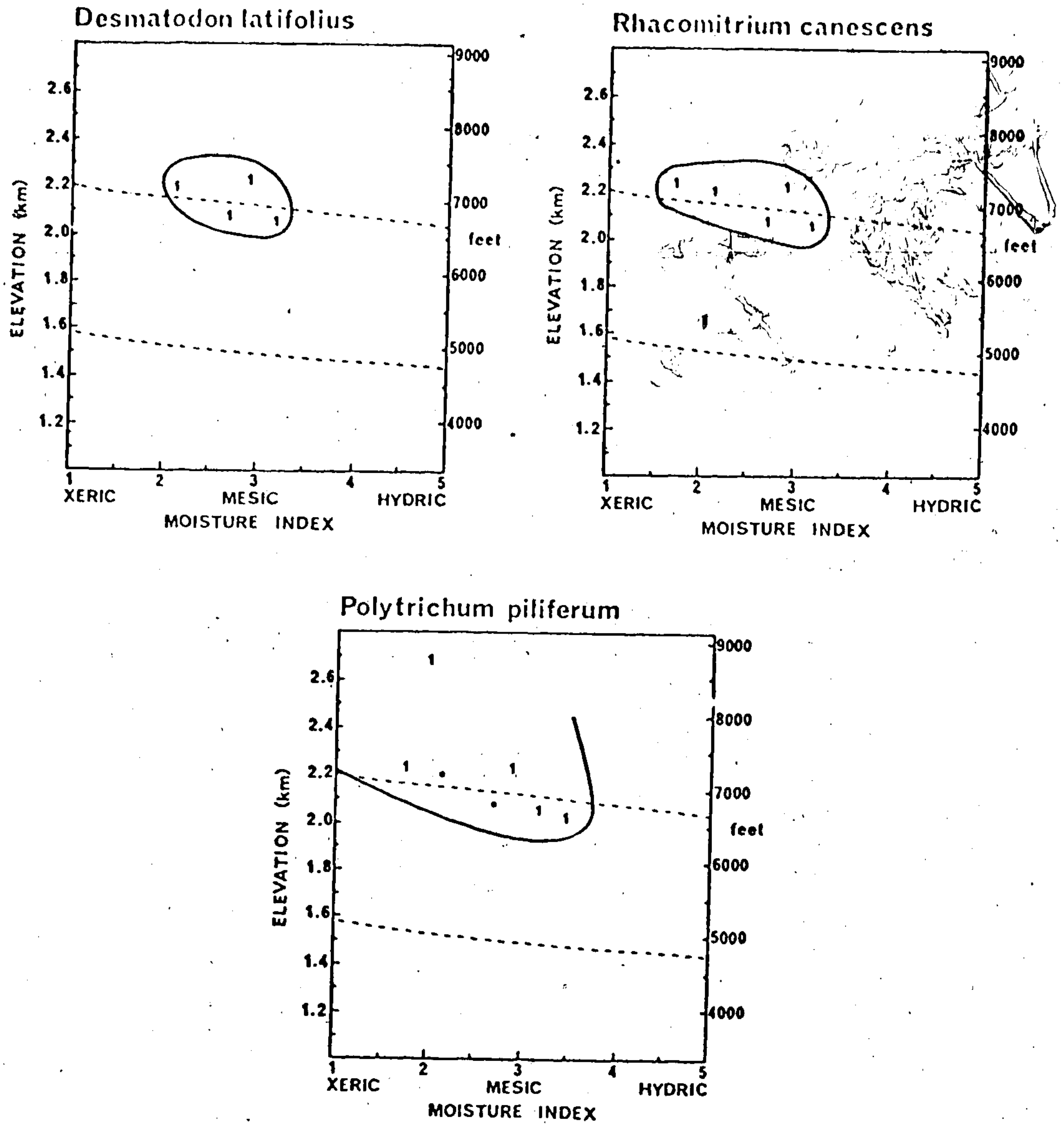


Figure 18. Habitats of *Desmatodon latifolius*, *Rhacomitrium canescens* and *Polytrichum piliferum* in relation to complex moisture and elevation gradients. Cover classes are: 1 = 1-1.0%, 2 = 1.1-5.0%, • = stand with species absent but included within the species habitat.

forests. *Polytrichum* was the most wide-ranging of the 3 and was found on alpine and subalpine rock outcrops and in lichen desert at higher elevations.

Discussion

Consistency of species habitats. Although little quantitative information is available on bryophyte population response patterns in other regions, it is worthwhile to compare the performance of bryophytes in Jasper with their performance in community studies undertaken elsewhere. Such a comparison serves to test my results and also provides information for potential studies on ecological bryophyte geography and, perhaps, ecotypic differentiation.

Four important hydrophytes, *Sphagnum warnstorfii*, *Tomenthypnum nitens*, *Aulacomnium palustre* and *Bryum pseudotriquetrum*, are associated with wetlands throughout their ranges. The first three of these are very important in the *Picea mariana* wetlands of Jasper described by Laidlaw (1971). Because of the high correlation between the abundance of *Sphagnum warnstorfii* and *Tomenthypnum nitens* and the nutrient levels in wetland communities, both European and North American phytosociologists have come to regard these two species as indicators of "rich fen" conditions (Mårtensson 1956, Perrson and Sjörs 1960, Sjörs 1963, Crum 1973, Vitt and Hamilton 1975). Using soil analyses Laidlaw (1971) demonstrated that *Picea mariana* fens in the Jasper vicinity are indeed eutrophic, and the presence of *Sphagnum warnstorfii* and *Tomenthypnum nitens* in wetlands sampled in the present study suggests that these peatlands are also nutrient-rich.

The response pattern of the hydrophyte *Aulacomnium palustre* in the study area correlates well with its performance in northern Michigan (Crum 1973) and northern Europe (Mårtensson 1956). *Aulacomnium* seems less tied to eutrophic conditions than *Sphagnum warnstorfii* or *Tomenthypnun nitens* (Jeglum 1971) and this fact may account for its ability to invade less hydric and perhaps more oligotrophic upland communities.

The feathermoss, *Hylocomium splendens, Pleurozium schreberi* and *Ptilium crista-castrensis,* are important constituents of mesic forest communities throughout boreal North America and Eurasia, although their abundance relative to one another varies geographically (La Roi and Stringer 1976). My habitat breadth results for these three species are in agreement with the work of other researchers in the study area (Beil 1966, Stringer and La Roi 1970, Hnatiuk 1969, Hrapko 1970, Laidlaw 1971). However, in contrast to the present findings, both Beil (1966) and Hnatiuk (1969) suggested that *Pleurozium* reached peak abundance in more mesic stands than did *Hylocomium.* Beder (1967), working in eastern Banff, and Hrapko (1970), on Signal Mountain in Jasper, both reported *Hylocomium splendens* as abundant in alpine dwarf shrub-heath communities. Brassard (1971) has described a *Hylocomium splendens* community associated with dwarf shrub-heath vegetation on Ellesmere Island in the Canadian high arctic. Mårtensson (1956) said *Hylocomium* also ranges above timberline in Swedish Lappland while *Pleurozium* and *Ptilium* are largely restricted to forested zones. It is noteworthy that *Hylocomium* is absent above timberline in Wells Gray Park in interior British Columbia (Ahti and Fagersten 1967). Further, in eastern North American alpine areas, *Pleurozium* is common in dwarf shrub-heath communities (Bliss 1963, Slack 1971) while *Hylocomium* is rare and *Ptilium* absent above timberline. Geographically, the ability of the feathermosses to invade alpine communities seems to correlate with their performance in subalpine forests. For example, *Pleurozium* dominates spruce-fir forests in the Adirondack Mountains (Heimburger 1934, Slack 1971) and in the White Mountains of New Hampshire (Forman 1969) where it also crosses timberline, while *Hylocomium* is most important in the spruce-fir forests of the Alberta Rocky Mountains where it is common in the alpine zone.

Geographic patterns in the relative dominance of the 3 feathermosses may be related to climatic or edaphic factors. Research in boreal forest communities indicates that *Pleurozium* dominates feathermoss wefts in humid, maritime climates (Heimburger 1934, Davis 1964, McIntosh and Hurley 1964, Hamet-Ahti 1965) while *Hylocomium* is more abundant in the forests of dry, continental regions (e.g. Douglas 1974, La Roi and Stringer 1976). *Ptilium* seems to be most successful in areas of extremely high precipitation and cool temperatures, such as the higher elevation forests of the Swan Hills (Achuff 1973) and parts of the eastern boreal forest (La Roi and Stringer 1976).

However, La Roi (pers. comm.) has suggested that the various abundance patterns of the feathermosses, particularly *Pleurozium* and *Hylocomium*, are likely not controlled by climate alone, but may be strongly influenced by the mineralogy of the substratum. For example, in eastern Canada *Hylocomium* dominates on nutrient-rich sites while *Pleurozium* is more abundant on nutrient-poor sites. Nagano (1969), however, has demonstrated that although very different saxicolous bryophyte communities develop on different rock types, communities developing on humus over these rock types are very similar. Nagano's results are not surprising since it is difficult to understand how substratum mineralogy would affect plants whose living parts are no longer in contact with the substratum. Unfortunately, since acidic rock types are mostly coincident with maritime climates in northern North America, climatic and edaphic variables cannot be separated by examining only geographic patterns in feathermoss abundance.

Since the feathermosses are responding to microenvironmental, rather than macroenvironmental factors, broad geographic correlation does not permit cause-effect statements to be made. However, large scale patterns in species abundance may give better direction to future studies. An experimental approach to the feathermoss question will undoubtedly prove rewarding.

The mesophytic species reported herein as minor ubiquists, i.e. *Drepanocladus uncinatus, Brachythecium salebrosum* and *Eurhynchium pulchellum,* perform similarly elsewhere. La Roi and Stringer (1976) described these species as minor components of *Picea glauca-Abies balsamea* and *Picea mariana* forests in the boreal zone and noted their great plasticity regarding substratum affinities. Kil'dyushevskii (1965) stated that although *Drepanocladus* is never dominant in subarctic Siberia it is very common there and has wide "ecological amplitude".

Two ubiquitous mesophytes that are restricted to rotting wood in the Jasper region, *Dicranum fuscescens* and *Pohlia nutans,* have been reported as successional on wood in the Bow River drainage, Alberta (Lacusta 1970). The former is also common on wood in subalpine forests of Wells Gray Park in interior British Columbia where it extends beyond timberline on humus or mineral soil (Ahti and Fagersten 1967) just as it does on the Maligne Range in Jasper Park.

Many of the species showing restricted elevational ranges in this study are similarly limited in other regions. *Barbilophozia lycopodioides*, for example, reaches peak abundance in the upper subalpine zone of the Bow River watershed (Bird and Hong 1969) and in subalpine communities in Wells Gray Park, British Columbia (Hämet-Ahti 1965).

Although much has been published concerning the ecology of wetland and forest bryophytes in North America, xeric habitats such as rock outcrops are poorly known. Most of the research on outcrop communities has been done by British ecologists (Balme 1953, Yarranton 1962, Bunce 1967, Yarranton 1967a, 1967b, 1967c, Bates 1975) in maritime regions. Both the flora and communities described in these studies as well as those studies completed in North America by Oosting and Anderson (1937), Redfearn (1960) and Foote (1966) are quite dissimilar from the rock outcrops I sampled. However, results obtained in grassland and dry forest communities in Saskatchewan (Looman 1964) and in the grasslands of Jasper and Banff National Parks, Alberta (Stringer 1971) indicate that *Thuidium abietinum*, *Tortula ruralis* and *Polytrichum juniperinum* are strongly xerophytic in other parts of their ranges. Stringer (1966) found that *Rhytidium rugosum* was abundant in dry montane *Pseudotsuga menziesii* forests in the Alberta Rockies and Beder (1967) and Hrapko (1970) demonstrated that *Rhytidium*, as well as *Thuidium* and *Tortula ruralis* are associated with dry tundra communities in these same mountains.

Pogonatum alpinum and *Polytrichum piliferum* are alpine species in the White Mountains of New Hampshire (Bliss 1963) and in New York's Adirondacks (Slack 1971), and both are reported from the high arctic (Brassard 1971). Another alpine species in the study area, *Rhacomitrium lanuginosum*, is apparently a rock-field specialist in many regions (Mårtensson 1956, Brassard 1971) while closely related *R. canescens* is restricted to less exposed tundra communities. *Hypnum revolutum* is widespread in high arctic plant communities on northern Ellesmere Island (Brassard 1971) much as it is above timberline on Signal Mountain (see Figure 9).

Although most species seem to maintain similar substratum relationships over their ranges, *Dicranum polysetum* appears to be a strong exception. La Roi and Stringer (1976) reported that this robust turf was most commonly found on humus in *Picea glauca-Abies balsamea* and *Picea mariana* forests in the boreal taiga of North America. In the Jasper area this species showed pronounced affinity for wood.

Summarizing, it is evident that on the northern end of the Maligne Range in Jasper National Park most of the more common and important bryophytes respond to moisture and elevation gradients in a way that is quite similar to their performance elsewhere in the world. Although much of the literature surveyed presented only scant qualitative data, no major contradictions with the habitats and response patterns of species described in the results of this study could be found.

Shapes, sizes and distribution of habitats. Since its inception, the technique of gradient analysis has been used to demonstrate that populations of vascular plant species distributed along two continuous environmental gradients usually form binomial solids "any transection of which cuts a binomial curve" (Whittaker 1967). As expected, the population response patterns of bryophyte species in the present study are binomial solids but these are generally elliptic in shape. In most cases, the longer axis of the ellipse is aligned parallel tothe elevational gradient while the short axis corresponds to a segment of the moisture gradient. Given the ranges of elevational and moisture gradients within the study area, this orientation of most species habitats implies that bryophytes are less responsive to elevation related factors than to factors associated with the complex moisture gradient. Further elaboration on this point will be presented in the section on beta diversity.

Another tenet of gradient analysis is the principle of species individuality which concerns the distribution of species habitats in hyperspace and is based largely on the theoretical arguments of Gleason (1926, 1939). It states that along complex gradients species have different rather than coincident population maxima, with no two species having identical response patterns (Whittaker 1973b). Whittaker (1967) has observed that plant species evolve toward habitat differentiation through occupation of different positions in the "environmental hyperspace, so that plant species are, in general, not competing with one another in their population centers". Also, since many of the species which occur together in the same community are separated within it by niche characteristics, populations tend not to form distinct boundaries but overlap broadly. Thus the observed pattern of species habitats is a result of species evolution toward niche and habitat differences.

The principle of species individuality has been substantiated by recent research (Curtis and McIntosh 1951, Whittaker 1956, 1960, Whittaker and Niering 1965, Beals 1969) and is supported by the results of this study as well. The more important Jasper bryophytes exhibit the expected separation of habitat centers and broadly overlapping distributions in a complex population continuum. In general, species with very similar habitats do not share the same substratum in a community, and thus separate on niche-related variables. For example, *Rhytidiadelphus triquetrus* and *Oncophorus wahlenbergii* have very similar response patterns (Fig. 13) but very different substratum relationships. However, there are species with nearly identical habitat centers that also grow on the same substrata such as *Hylocomium splendens* and *Ptilium crista-castrensis*, or *Sphagnum warnstorfii* and *Tomenthypnum nitens*.

Several hypotheses may be advanced to account for such anomalous, i.e., coincident response patterns. First, it could be argued that the communities in which species with similar habitats co-occur may not be at competitive equilibrium, especially if space and resources are not yet limiting. This situation is conceivable in early successional communities such as recently burned forests, fallen logs or perhaps erratic boulders, but in stable, climax co communities, such as the ones sampled, where bryophytes often provide continuous cover, a non-competitive condition is unlikely. A second explanation is that species are separated in communities by niche variables that I did not measure. Subtle, patchy changes in microclimate or nutrient regime might permit species to gain or lose competitive advantage over short distances within the stand or even within a quadrat.

An important question arising from this line of thought involves the role of competition in bryophyte communities. For example, how is it that *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilium crista-castrensis* form mixed wefts under what appear to be very homogeneous conditions? What role does competition play in determining the species structure of this feathermoss guild? What life history strategies are associated with species growing under such packed conditions as opposed to those more commonly found on ephemeral, patchy substrata? These kinds of questions open doors to experimental studies that are the logical consequence of the present research.

One of the earliest ideas in the development of niche theory was that some species utilize broader segments of resource or environmental gradients than do other species (MacArthur 1965, Levins 1968, Cody 1974). Cody (1974) has observed that "species with broad niches in a particular dimension have come to be known as 'generalists' in that dimension, whereas species with narrower utilization curves are termed 'specialists.'" The same concept may be applied to utilization patterns along habitat dimensions.

The results of the present study show that *Hylocomium splendens* qualifies as a habitat generalist since it is widely distributed along both gradients. In contrast, *Rhytidiadelphus triquetrus* is relatively more specialized in its response to both elevation and moisture and their associated variables. Likewise, *Aulacomnium palustre* is a generalist in response to moisture regime when compared to *Sphagnum warnstorfii* although both respond similarly to elevation. Within some genera there is a tendency for some species to be marked habitat specialists and others to be more generalized. *Grimmia anodon* is a specialist on low elevation rock outcrops while *G. apocarpa* is widely distributed on erratic boulders in forests and on rock outcrops. Similarly, *Orthotrichum jamesianum* and *Hypnum vaucheri* are low outcrop specialists whereas their congeners *O. laevigatum* and *H. revolutum* are more widespread. Two liverworts, *Barbilophozia hatcheri* and *B. lycopodioides* provide another example of this phenomenon; the former is present in all three vegetation zones in a variety of community types while the latter is limited to mesic subalpine forests.

The concept of 'generalist versus specialist' has been discussed, usually in terms of niche variables, by MacArthur and Levins (1964, 1967), MacArthur (1965), Pianka (1974), Cody (1974). Pianka (1974) observed that although generalists are usually more widespread and have more flexible habitat requirements, "more specialized individuals are more efficient on their own ground than generalists." One might expect, therefore, that bryophyte habitat specialists would reach greater abundance in communities than do the generalists.

The *Barbilophozia* species seem to follow this prediction since *B. hatcheri*, the most widespread species, is never very abundant in communities (usually less than 1% cover), despite the fact that it occurs on a wide variety of substrata, while *B. lycopodioides* reaches over 8% cover on humus under most favorable conditions. Specialists *Grimmia anodon* and *Hypnum vaucheri* are the most abundant species on the low elevation rock outcrops where their generalist congeners are not common. *Grimmia apocarpa* and *Hypnum revolutum* are relatively unimportant in most communities although *Hypnum revolutum* attains some prominence in high alpine stands. No clear abundance patterns can be discerned for the other congeneric species pair, *Orthotrichum laevigatum* and *O. jamesianum*.

SPECIES DIVERSITY

Introduction

Species diversity may be examined within communities as a function of the number of species in the community and the way in which they divide available niche space, or between communities as a function of changing species composition and abundance along habitat gradients (MacArthur 1965). Whittaker (1965, 1969, 1972) refers to within-community diversity as "alpha diversity" and between community diversity as "beta diversity", and further suggests that alpha and beta diversities combined for a given geographic unit be called "gamma diversity".

Although the concept of alpha diversity is theoretically stimulating, its measurement has proven difficult and, as a result, researchers have taken divergent approaches reflective of varied objectives and the wide array of ecological systems under study. Peet (1974) has reviewed the measurement of alpha diversity and, although he has offered no panacea, he has clarified relationships between diversity indices by explicitly defining three concepts of diversity. The first, "species richness", is simply the number of species in a community sample and is the "least-ambiguous of all diversity terminology". Species richness is inherently dependent on sample size

(Gleason 1922). "Equitability" refers to the evenness of distribution of species abundance within a community and is independent of species richness. Heterogeneity, however, measures the functional or apparent number of species in a sample and is thus a composite index of richness and equitability. Heterogeneity indices include what have become known as "diversity" indices, such as the information theory formula ($H^1 = -\Sigma p_i \log[p_i]$, where H^1 is heterogeneity and p_i is the proportional abundance of the ith species [Shannon and Weaver 1949]) and the inverse of Simpson's (1949) index of dominance ($c = \Sigma[p_i]^2$, where c is a dominance index). Peet (1974) has used the term "heterogeneity" to describe these indices, freeing the term "diversity" for more general denotation.

Although heterogeneity measures have been most popular in diversity studies, many ecologists such as Whittaker (1969), Addicott (1974) and Nicholson and Monk (1974) have preferred to utilize separate indices for richness and evenness since these concepts are, as Peet has observed, independent. However, Hill (1973) has demonstrated that richness, Simpson's index and the Shannon-Weaver information formula are related by a common function, and has defined measures of evenness based on this function. Since Hill's approach provides a clear relationship between indices of richness, evenness, and heterogeneity, it has been viewed favorably by Peet (1974) and has been adopted for use in the present study.

Patterns of alpha diversity have been identified for many groups of organisms and their explanation has been the cause of much speculation. Plant species diversity has been related to a variety of factors among which are environmental rigor (Whittaker 1965, Monk 1967, Nash 1975), predation (Harper 1969), disturbance (Platt 1975), island or patch size and degree of isolation (Johnson and Raven 1970, Terborgh 1973), succession (Monk 1967, Nicholson and Monk 1975, Mellinger and McNaughton 1975, Tramer 1975, Bazzaz 1975) and others. In most of these studies the diversity of vascular plants has been the subject under study, while bryophytes and lichens have been largely ignored. Slack (1971), however, completed a study of bryophyte species diversity in northern New York State in which the relationship between alpha diversity and elevation was examined.

In this part of the study I chose to investigate patterns of bryophyte alpha diversity in relation to moisture and elevation gradients.

As Bratton (1975) has observed, beta diversity, the change in species composition per unit gradient, may be expressed as a single number or as a function. A single index of beta diversity has been suggested by Whittaker (1972):

$$BD = Sc/\bar{S}$$

where Sc is the number of species in a composite sample and $\bar{S}$ is the mean number of species per sample. An alternative beta index is the number of "half changes" which is a complex measure of the dissimilarity between the 2 end samples on a gradient (see Gauch 1973a for details.) Treating beta diversity as a function, however, permits examination of non-linear changes in, and the influence of specific gradient segments on, species composition (Bratton 1975). To view beta diversity as a function, Whittaker (1972) and Bratton (1975) have suggested the use of similarity indices such as coefficient of community and percentage similarity (see GRADIENT ANALYSIS, p.30) which may be computed and then plotted for stand pairs along any habitat gradient.

In plant ecology much attention has been focused on the influence of beta diversity on various ordination techniques (Austin and Noy-Meir 1971, Gauch 1973a, Gauch and Whittaker 1972) but only a few researchers have attempted to examine other implications. Bratton's (1975) study, for example, indicates that different strata or synusiae may respond differentially to environmental gradients, a suggestion that has theoretical and practical importance.

Three specific questions concerning beta diversity were asked in this study: (i) what are the patterns of bryophyte beta diversity along moisture and elevation gradients? (ii) what differences in bryophyte beta diversity exist between these 2 gradients? and (iii) are there important differences between bryophyte and understory vascular plant beta diversity along moisture and elevation gradients?

Methods

Alpha diversity. Alpha diversity and evenness were examined using the diversity numbers and equitability measures presented by Hill (1973). Diversity numbers for each stand are defined by:

$$N_a = (P_1^a + P_2^a + \ldots\ldots P_n^a)^{1/(1-a)},$$

where P_n is the ratio of the cover of the nth species to total cover in the sample and a, which may be any number, is the order of diversity number N_a (Hill 1973). Thus defined, N_0 is simply the richness of a stand, N_1 is [illegible] $(-\Sigma P_n \log(P_n))$ and N_2 is $1/(\Sigma P_n^2)$; the latter two are [illegible]s related to Shannon's and Simpson's indices respectively.

Evenness, as redefined by Hill is:

$$E_{a,b} = N_a/N_b,$$

where a and b are any order of diversity numbers.

I calculated diversity numbers for a = 0, 1, 2, 3, 4 and evenness values E_{10}, E_{21}, E_{32}, E_{43} for bryophytes in all 30 stands. Since the number of substratum types per stand was found to be positively correlated with richness (see RESULTS, p.112), it was thought that richness, evenness and heterogeneity should be examined on the single most important substratum in each stand. Cover estimates used in the diversity indices were derived from 40 quadrats on the dominant substratum of each stand. All species collected on the dominant substratum in the stand were included in the computation, with species not found in the quadrats being assigned a cover value of .01 percent.

Beta diversity. Based on elevation and subjective moisture index, stands were grouped into coenoclines; stands of similar moisture regime were classed as elevation-related coenoclines; stands of similar elevation were called moisture-related coenoclines. These arbitrary classes and their constituent stand numbers are listed below.

COENOCLINES RELATED TO COMPLEX ELEVATION GRADIENTS

rock outcrops - 3, 9, 10, 16, 21, 28

xeric forest and tundra - 1, 4, 5, 8, 15, 19, 23, 29

mesic forest and tundra - 6, 11, 12, 13, 14, 20, 24, 25, 26, 30

mesic spruce - fir and heath - 6, 12, 14, 20, 30

fens - 7, 17, 18, 22

COENOCLINES RELATED TO COMPLEX MOISTURE GRADIENTS

montane - 1, 2, 3, 4, 5, 6, 7, 9, 18, 24, 25, 27, 29
subalpine-0 8, 10, 11, 12, 13, 14, 17, 19, 23, 26, 30
alpine - 15, 16, 20, 22, 28

For each coenocline a single index of beta diversity, BD (see above) was calculated.

To examine beta diversity as a function, I measured the total change in similarity along a given coenocline using an index of similarity between stands. A reference stand was chosen for each coenocline and, for all other stands, similarity to the reference stand was plotted along an axis representing the variable in question, i.e. moisture or elevation. Two similarity curves were drawn for each coenocline, one based on bryophyte similarity, the other on understory vascular plant similarity. For elevation-related coenoclines reference stands were those of lowest elevation but for moisture-related coenoclines, which tended to have greater beta diversity (at least for bryophytes), a reference stand of intermediate moisture regime was chosen. Had an end stand been utilized for moisture coenoclines, beta functions for both vascular plants and bryophytes would have reached 0 only a short distance along the gradient, due to the great floristic dissimilarity between extreme stands and mesic stands. For each coenocline bryophyte and vascular plant curves were determined for 2 similarity measures, coefficient of community (CC), which computes similarity treating each species equally, regardless of abundance, and percentage similarity (PS) which results in an index weighted by the more common species (see GRADIENT ANALYSIS, p. 30).

The change in similarity per unit elevation was determined for all stand pairs in the 4 elevational coenoclines by subtracting the CC or PS value for a stand pair from 1.00, then dividing by the elevation difference between stands. These values were then plotted along the gradients.

Results

Alpha diversity. The total number of bryophyte species per stand, irrespective of substratum, ranged from 8 in the montane sedge fen to 33 in subalpine *Pinus contorta* forests (Table 7) and averaged 23.5. Forest communities seemed to maintain greater richness than either rock outcrops or fens. This phenomenon was largely attributable to the greater structural heterogeneity of forests which, in turn, was primarily due to the large number of substrata available for bryophyte colonization. In fact, the product-moment correlation coefficient between bryophyte richness and the number of substratum types stand was + .45 (d.f. = 28, significant at $p < .05$). Since my intent was to view patterns of diversity regarding elevation and moisture gradients it was necessary to eliminate the influence of substratum number by examining diversity on

Table 7. Total richness, diversity numbers and evenness measures for bryophytes in all stands. Diversity numbers and evenness values are based on species abundance on the dominant substratum in stands.

STAND AND NUMBER	TOTAL RICHNESS	N_0*	N_1	N_2	N_3	N_4	E_{10}	E_{21}	E_{32}	E_{43}
MONTANE ZONE										
grassland (2)	12	7	1.47	1.18	1.13	1.12	.210	.800	.961	.990
outcrop (3)	18	18	5.48	3.64	3.14	2.92	.305	.667	.862	.934
outcrop (9)	16	16	2.58	1.72	1.54	1.47	.161	.671	.892	.952
Douglas-fir forest (1)	26	17	3.66	2.86	2.65	2.56	.215	.781	.935	.970
lodgepole pine forest (4)	28	16	5.69	3.81	3.19	2.90	.357	.671	.840	.917
lodgepole pine forest (29)	24	16	4.11	2.83	2.47	2.30	.257	.689	.877	.934
lodgepole pine forest (5)	26	18	3.14	2.26	2.04	1.93	.174	.724	.909	.952
white spruce forest (24)	21	11	2.13	1.75	1.62	1.56	.193	.826	.925	.961
lodgepole pine forest (25)	21	11	3.34	2.72	2.54	2.45	.304	.819	.935	.970
white spruce forest (6)	23	11	2.28	1.75	1.59	1.52	.208	.769	.909	.961
black spruce fen (18)	15	12	3.06	2.44	2.21	2.09	.256	.800	.909	.952
black spruce fen (7)	20	17	4.24	3.50	3.20	3.00	.250	.826	.917	.943
sedge fen (27)	8	8	3.28	2.88	2.69	2.57	.411	.885	.943	.961
SUBALPINE ZONE										
outcrop (21)	14	14	6.35	3.62	2.86	2.57	.452	.571	.793	.900
outcrop (10)	26	26	12.98	8.00	6.46	5.79	.500	.617	.813	.900
lodgepole pine forest (8)	27	17	5.36	4.59	4.33	4.20	.318	.862	.952	.970
lodgepole pine forest (23)	33	18	6.84	5.20	4.50	4.09	.384	.763	.869	.917
spruce-pine forest (19)	25	20	5.88	4.21	3.77	3.54	.294	.719	.900	.943
lodgepole pine forest (26)	26	21	3.41	2.05	1.76	1.65	.162	.602	.862	.943
lodgepole pine forest (11)	33	24	6.02	3.95	3.33	3.04	.251	.658	.847	.917
heath tundra (13)	25	19	4.11	2.83	2.50	2.34	.217	.689	.884	.943
spruce-fir forest (30)	29	23	3.51	2.17	1.86	1.74	.152	.621	.862	.943
spruce-fir forest (14)	25	19	5.24	3.80	3.35	3.12	.276	.729	.884	.934
spruce-fir forest (12)	28	21	2.99	2.09	1.84	1.73	.142	.699	.884	.943
Engelmann spruce fen (17)	24	23	5.72	4.36	3.99	3.83	.249	.763	.917	.961
ALPINE ZONE										
outcrop (16)	23	21	2.86	1.66	1.48	1.42	.136	.584	.892	.961
lichen desert (28)	25	25	6.44	3.71	3.02	2.74	.258	.578	.819	.909
cushion plant tundra (15)	31	29	10.15	6.61	5.44	4.87	.350	.653	.826	.900
heath tundra (20)	27	26	4.69	3.01	2.64	2.47	.180	.645	.877	.943
sedge tundra (22)	31	28	3.98	2.37	2.01	1.88	.142	.598	.854	.934

*N_0 = richness on the most abundant substratum in stand.

only the most important, dominant substratum in each stand. Fortunately the choice of dominant substratum in all cases was easy; in every stand humus or rock and mineral soil covered over 80% of the macroplot.

Richness, heterogeneity and evenness on dominant substrata exhibited definite trends with elevation but seemed less influenced by moisture regime (Tables 7, 8). Richness varied from 7 on mineral soil in the montane grassland to 29 on humus and soil in the alpine cushion plant-lichen tundra, and showed a very strong, positive correlation with elevation (Table 8). This relationship was visually demonstrated by plotting richness values on the direct ordination of stands (see GRADIENT ANALYSIS, p.30 and Fig. 19). Maximum richness occurred in lower Alpine communities including *Dryas octopetala*-dominated cushion plant-lichen tundra (stand no. 15) having 29 species, *Cassiope tetragona*-*Dryas*-dominated dwarf shrub-heath (stand no. 20) with 26 species, and wet sedge tundra (stand no. 22) with 28 bryophytes. Even the lichen desert at 2676m could be considered species-rich since 25 bryophyte species were present there. Environments at the extreme end of the moisture gradient had lowest richness with 7 species found in montane grassland (stand no. 2) and 8 species in the montane sedge fen. The positive correlation between richness and elevation should be viewed only in the context of the range of elevation sampled.

Table 8. Results of Spearman's Rank Correlation (r_s; Sokal and Rohlf, 1969) between alpha diversity measures and selected variables. Diversity measures are calculated using only bryophyte abundance on the dominant substratum in each stand. For all cases degrees of freedom = 28.

	SELECTED VARIABLES				
DIVERSITY	ELEVATION	SUBJECTIVE MOISTURE INDEX	DEPARTURE FROM MESIC (SMI − 3.0)	ABSOLUTE BRYOPHYTE COVER	UNDERSTORY VASCULAR PLANT COVER
BRYOPHYTE RICHNESS	+.83 $p < .01$	+.14 NS	−.21 NS	+.05 NS	−.16 NS
BRYOPHYTE HETEROGENEITY (N_1)	+.54 $p < .01$	−.17 NS	.00 NS	+.31 NS	−.10 NS
BRYOPHYTE EVENNESS (E_{12})	−.58 $p < .01$	+.42 $p < .05$	−.02 NS	+.54 $p < .01$	+.29 NS

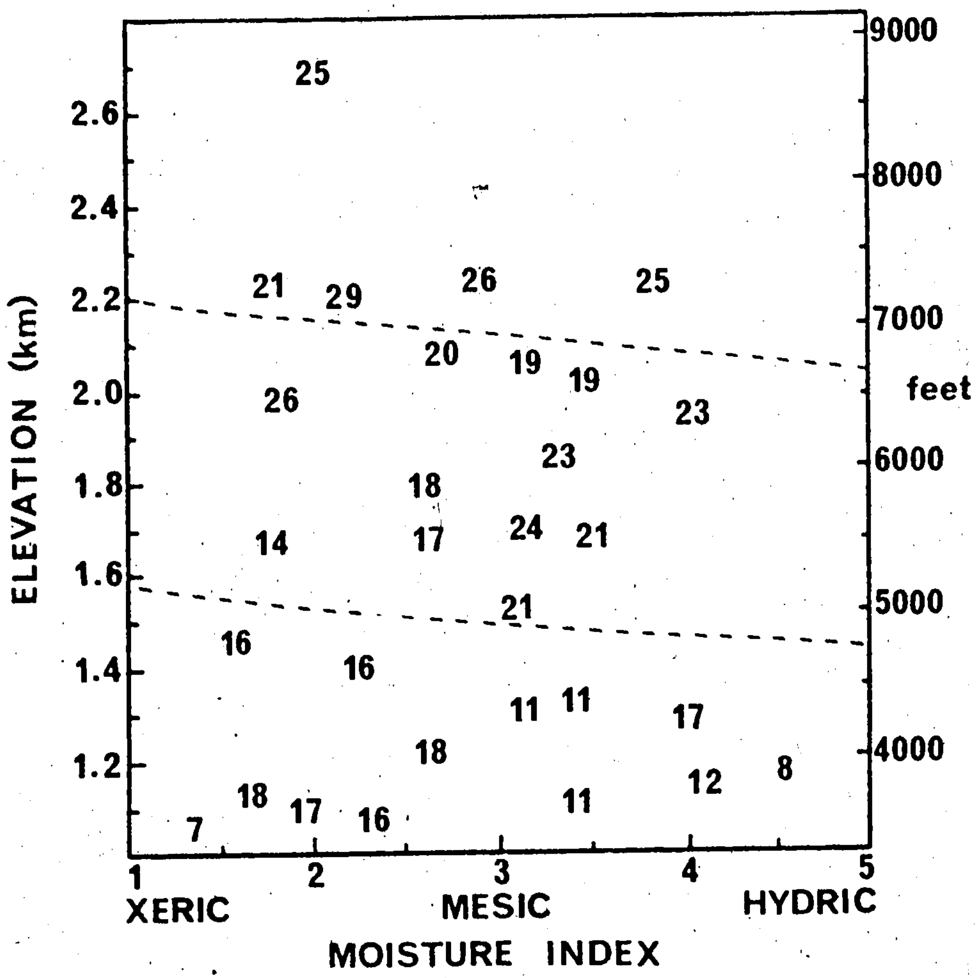


Figure 19. Bryophyte species richness on the dominant substratum in each stand, plotted with elevation and subjective moisture index on the direct ordination.

For example, one would not expect the correlation to hold at elevations much above 3000m because rock and boulder fields eventually give way to snow fields and glaciers. Observations I made in Jasper Park indicated that bryophytes were few and inconspicuous above 3300m, even in rocky areas.

Richness was not significantly correlated with subjective moisture index nor was it associated with the deviation of subjective moisture index from the mesic state of S.M.I. = 3.0 (Table 8). Correlations of richness with bryophyte and understory vascular plant cover (cover of vascular plants under 1.5m in height) were also examined (Table 8). These cover values were thought to provide an index of the degree of interference or competition for space by bryophytes or vascular plants and thus relationships between cover and richness were believed possible. The results indicated, though, that for richness no strong correlation existed with either understory vascular plant or bryophyte cover.

Heterogeneity, as measured using Hill's first order diversity number (N_1), was positively correlated with elevation (r_s = + .54, d.f. = 28, $p < .01$) although not as strongly as was richness (Table 8). Neither subjective moisture index nor deviation from mesic was correlated with heterogeneity, nor was there any obvious relationship with vascular plant cover.

Hill's E_{21} measure of evenness followed both richness and evenness in being correlated with elevation (r_s = −.58, d.f. = 28, $p < .01$) and showing no relationship with vascular plant cover. In contrast to the other diversity measures, however, evenness was positively correlated with subjective moisture index (r_s = +.42, $p < .05$) and bryophyte cover (r_s = +.54, $p < .01$).

Beta diversity. From the results of the single index measure of beta diversity, BD (Fig. 20), it is evident that bryophyte BD values were generally greater for the moisture-related coenoclines in the montane, subalpine, and alpine zones where they ranged from 3.3 to 5.5, than for the elevation-related coenoclines of rock outcrops, xeric stands, mesic stands, and fens, where values were between 2.4 and 3.3. BD values for understory vascular plants were similar to those of the bryophytes along moisture gradients, but were slightly higher along elevation gradients.

Highest BD for both bryophytes and understory vascular plants occurred in the montane zone and may have been due to the greater variety of communities sampled therein. Specifically, grassland (stand no. 2) and sedge fen (stand no. 27) were communities sampled only in the montane zone since they were rare or absent at higher elevations. The additional species present in these stands and the lack of other species common elsewhere in the zone may have been

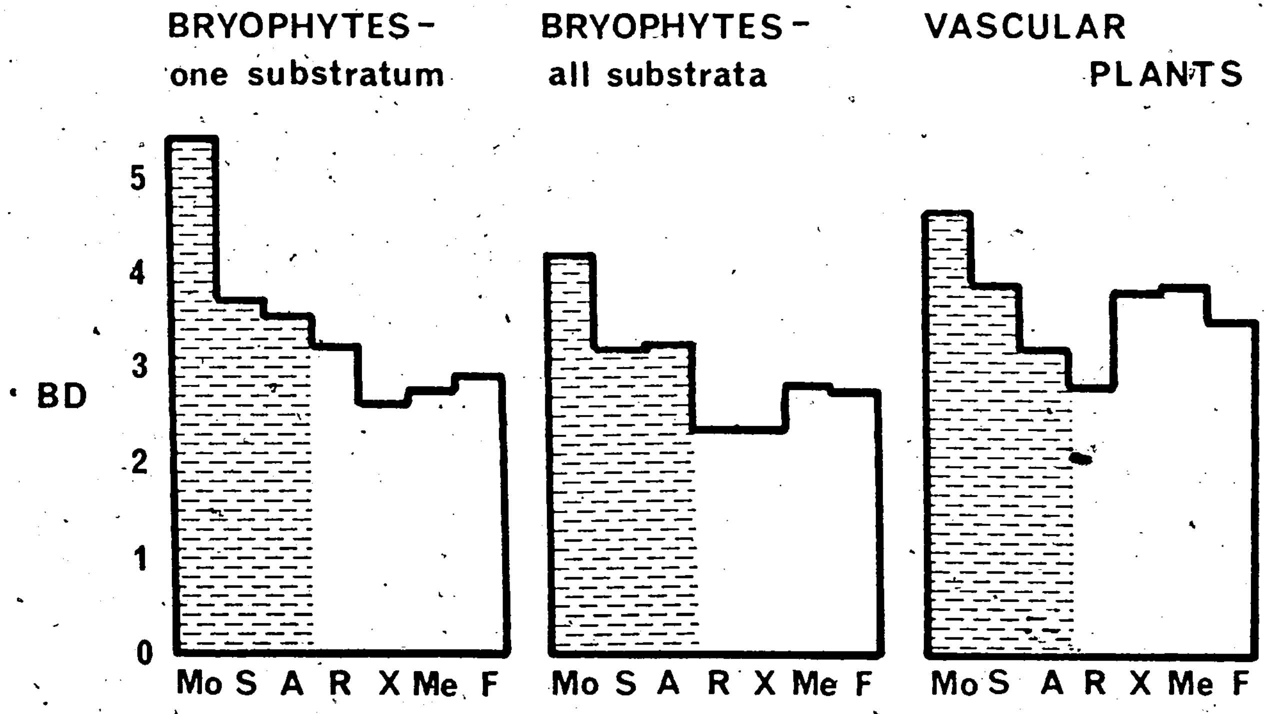


Figure 20. Single index values of beta diversity for bryophytes and vascular plants along 7 coenoclines. BD = Sc/$\overline{S}$, where Sc is the number of species in a composite sample and $\overline{S}$ is the mean number of species per sample. BD values for moisture-related coenoclines are shaded; values for elevation-related coenoclines are open. Mo = montane, S = subalpine, A = alpine, R = rock outcrop, X = xeric forest and tundra, Me = mesic forest and tundra, F = fens. BD was computed for bryophytes on dominant substrata and all substrata.

responsible for high montane BD values. This explanation emphasizes the fact that beta diversity should be interpreted in view of the ranges of the gradients sampled and, consequently, absolute statements about the relative influence of different gradients on beta diversity must be viewed with some caution.

The results of the single index measurement of beta diversity were supported by the analysis of beta functions. However, the latter conveyed more information. Since beta functions computed using coefficient of community (CC) and percentage similarity (PS) gave similar results, only findings based on CC are presented here.

Along moisture gradients the similarity change from a reference stand was very similar for bryophytes and vascular plants (Fig. 21, 22). Beta functions for these 2 plant groups tracked each other closely in both the montane and subalpine zones. In both zones beta functions dropped sharply as the gradient extremes were approached.

While bryophyte and vascular plant similarities were similar for moisture coenoclines, they were often divergent along elevation gradients (Fig. 23-26). For this reason the beta functions for elevation-related coenoclines received more thorough scrutiny.

One way of more closely examining elevation-related beta diversity to measure change in similarity per unit elevation. The results of this analysis for 4 elevational

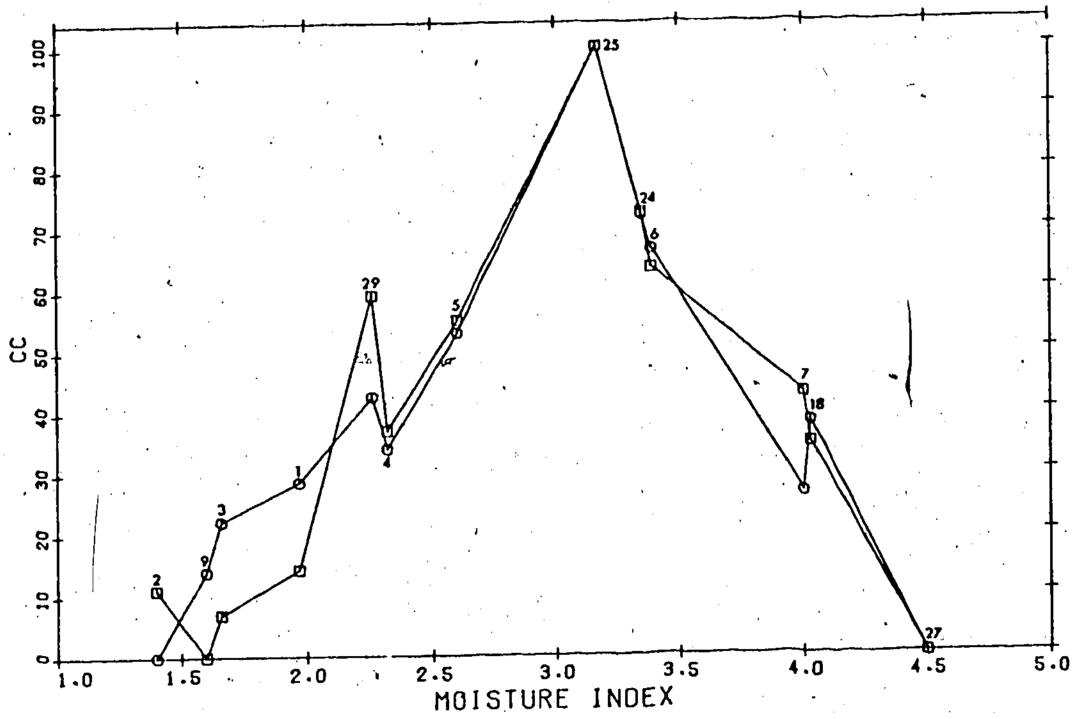


Figure 21. Similarity of stands to a reference stand (no. 25) along a moisture gradient in the montane zone. CC = coefficient of community; squares = bryophyte similarity, circles = vascular plant similarity.

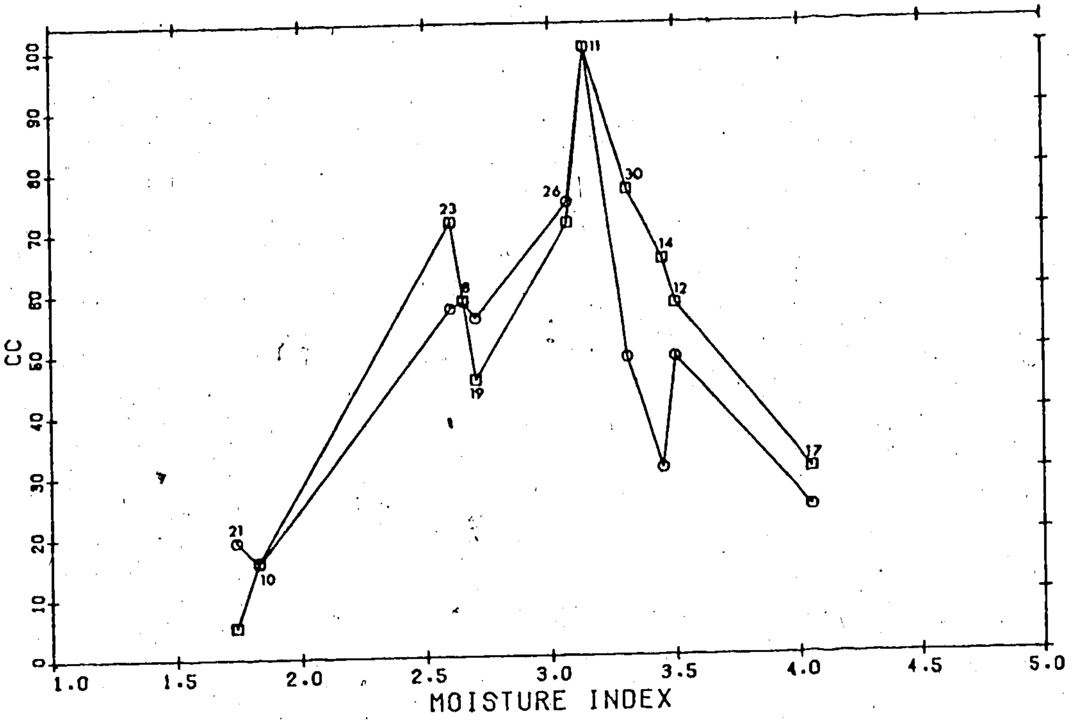


Figure 22. Similarity of stands to a reference stand (no. 11) along a moisture gradient in the subalpine zone. CC = coefficient of community; squares = bryophyte similarity, circles = vascular plant similarity.

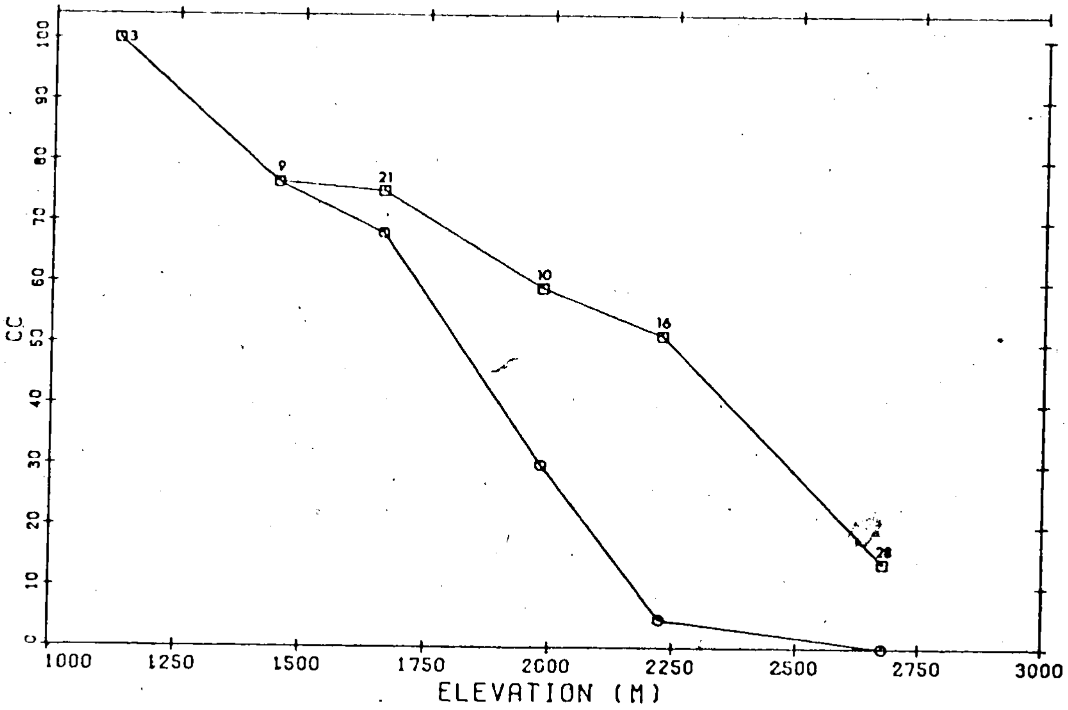


Figure 23. Similarity of rock outcrop stands to a reference stand (no. 3) along an elevation gradient. CC = coefficient of community; squares = bryophyte similarity, circles = vascular plant similarity.

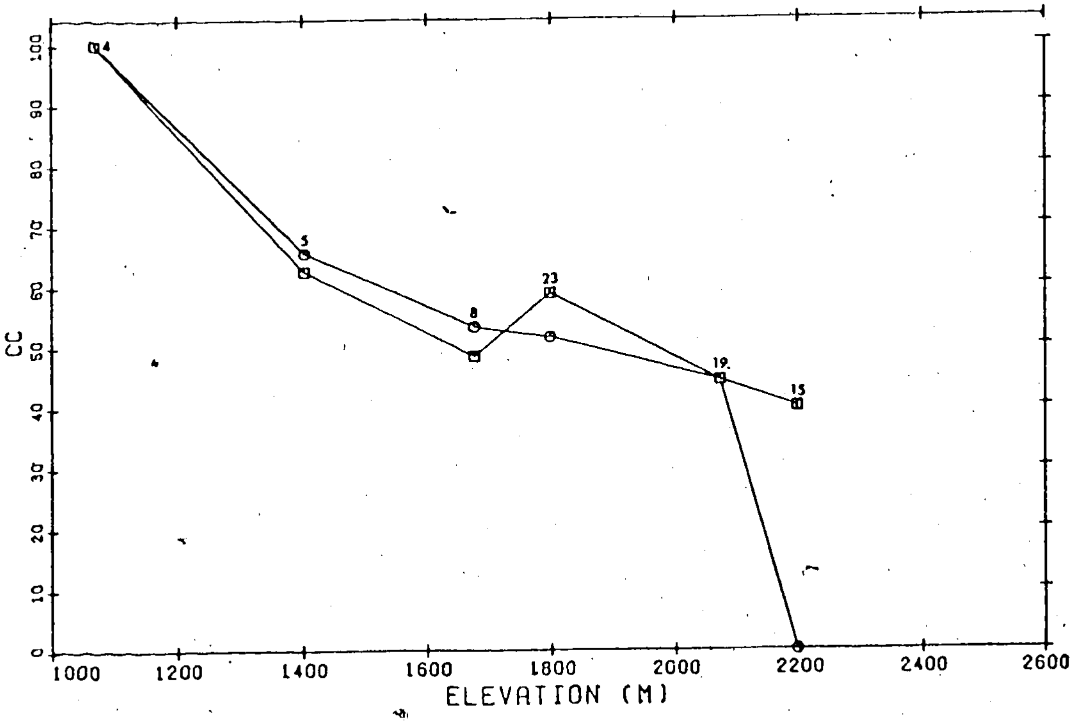


Figure 24. Similarity of xeric forest and tundra stands to a reference stand (no. 4) along an elevation gradient. CC = coefficient of community, squares = bryophyte similarity, circles = vascular plant similarity.

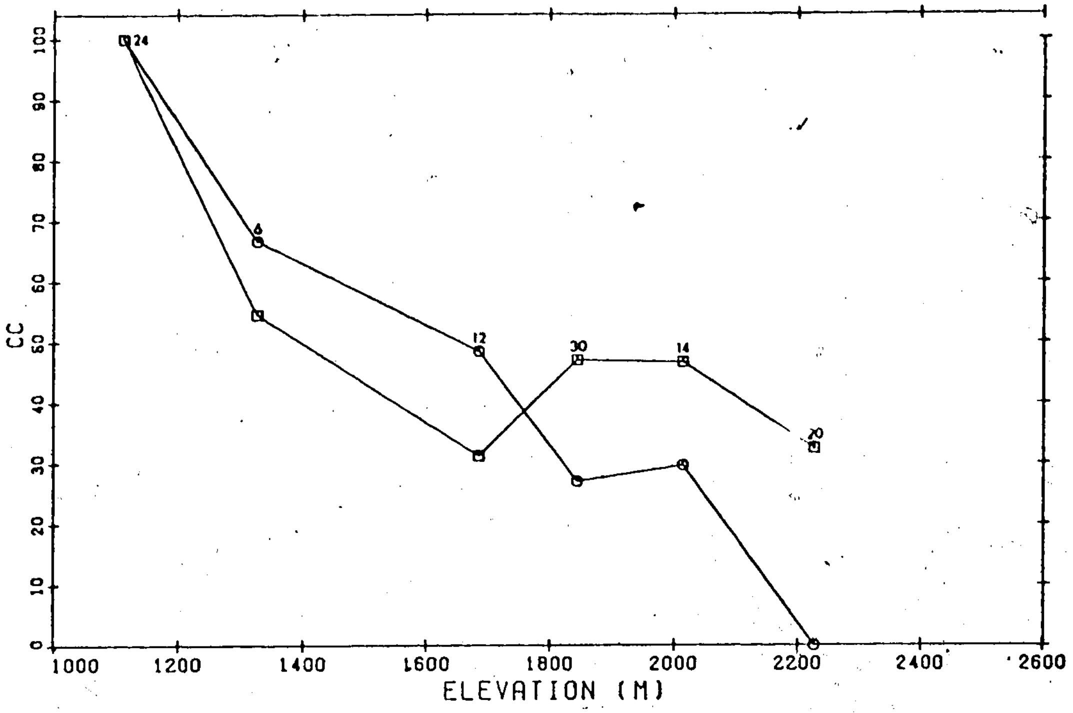


Figure 25. Similarity of mesic forest and tundra stands to a reference stand (no. 24) along an elevation gradient. CC = coefficient of community; squares = bryophyte similarity; circles = vascular plant similarity.

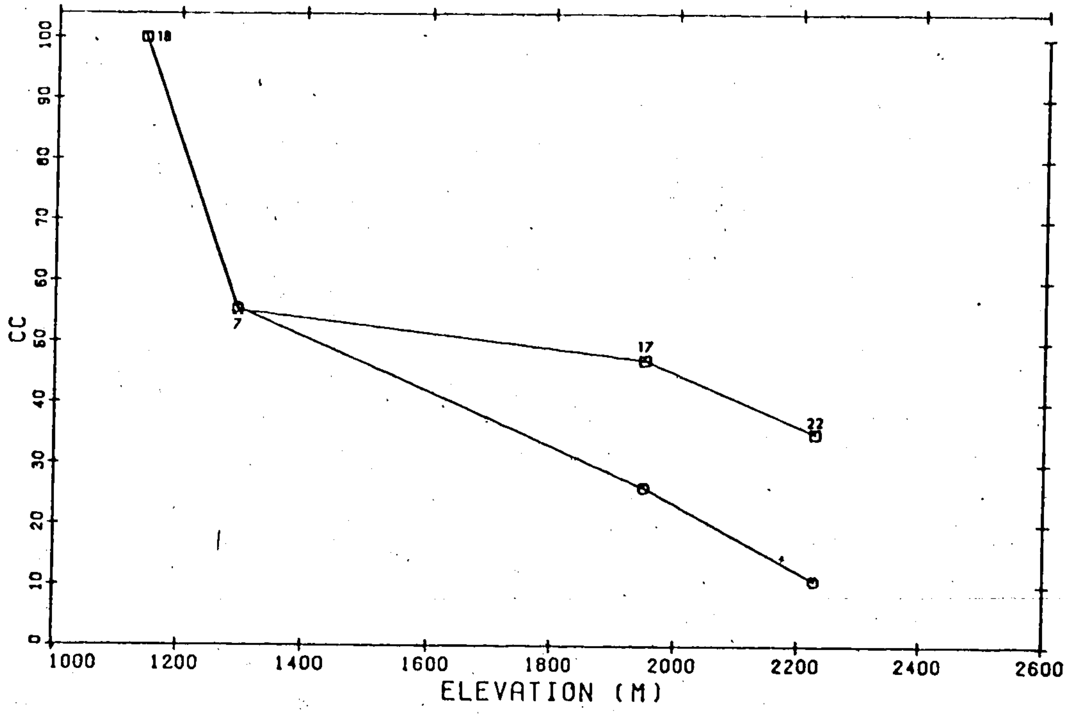


Figure 26. Similarity of fen stands to a reference stand (no. 18) along an elevation gradient. CC = coefficient of community; squares = bryophyte similarity; circles = vascular plant similarity.

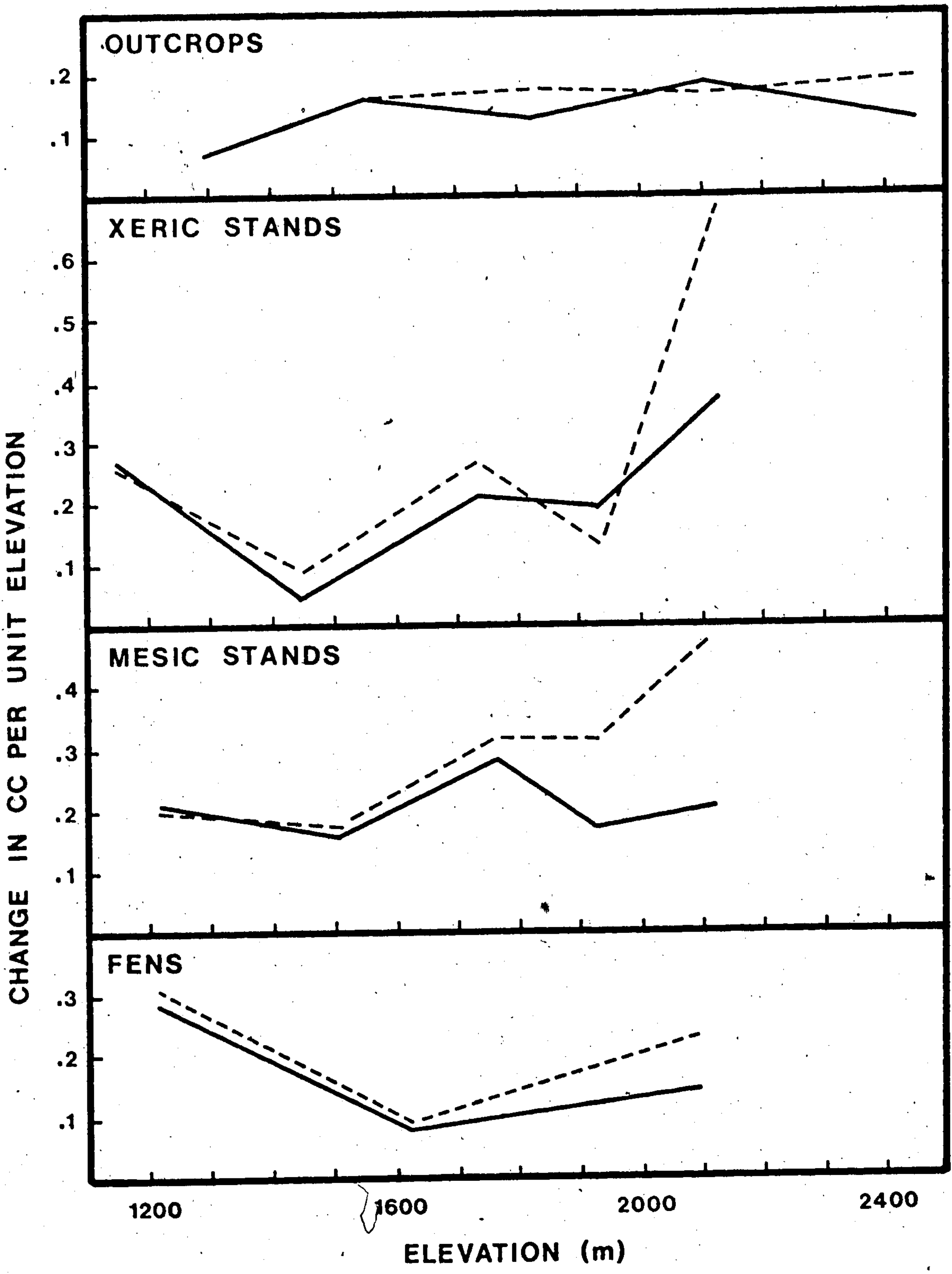
coenoclines complemented the information generated using the total change technique (Fig. 27).

For rock outcrops the curve of total change for bryophyte CC had markedly less slope than the vascular plant curve (Fig. 23). While the highest elevation stand had almost 13% bryophyte similarity with the low-elevation reference stand, these stands shared no vascular plant species. Change per unit elevation for the rock outcrop coenocline was quite similar for bryophytes and vascular plants (Fig. 27), but bryophytes showed slightly greater change at higher elevations.

In xeric forest and tundra communities, total change in CC was very similar for bryophytes and vascular plants until timberline was reached, at which point vascular plant similarity to the reference stand dropped to 0, while bryophyte similarity remained very high at 45% (Fig. 24). This phenomenon was reflected by sharp upward change in vascular plant CC per unit elevation at higher elevations (Fig. 27).

For mesic stands dominated by spruce or spruce-fir below timberline, and by heaths above timberline, there was greater total change in similarity for vascular plants (Fig. 25). Bryophytes showed a sharper rate of decrease than vascular plants at lower elevations but had greater similarity to the reference stand at higher elevations. The change in CC per unit elevation for both plant groups

Figure 27. Change in similarity (coefficient of community) per unit elevation for bryophytes (solid lines) and vascular plants (broken lines) along 4 elevation gradients. Change per unit gradient is computed for all pairs of adjacent stands by subtracting CC from 1.0, then dividing by the difference in elevation.


OUTCROPS
.2
.1
XERIC STANDS
.6
.5
.4
.3
.2
.1
MESIC STANDS
.4
.3
.2
.1
FENS
.3
.2
.1
CHANGE IN CC PER UNIT ELEVATION
1200
1600
2000
2400
ELEVATION (m)

correlated nicely with these trends (Fig. 27).

In the 4 fen communities analyzed, bryophyte similarity to the reference stand decreased more slowly than vascular plant similarity (Fig. 26). The change per unit gradient was slightly greater for vascular plants than for bryophytes throughout this coenocline (Fig. 27).

The differences in bryophyte and vascular plant similarity for a number of stands composing a coenocline were tested statistically using the non-parametric Sign Test (Sokal and Rohlf 1969). The results of the Sign Test for 7 coenoclines are presented in Table 9. Differences in bryophyte and vascular plant similarity on rock outcrops were significant when CC was used but not when PS was utilized. In the xeric forest and tundra coenocline these differences were statistically insignificant for both similarity measures but in mesic stands and in fens these differences were highly significant for both similarity indices. For moisture-related coenoclines differences in bryophyte and vacular plant similarity were not significant except in subalpine stands measured by CC where significant differences did occur. In all cases of significant difference, bryophyte similarity greater than vascular plant similarity, indicating less bryophyte beta diversity.

Thus there appeared to be a trend for bryophyte communities to have less total change in species composition and less change per unit elevation than understory

Table 9. Results of Sign Test (Sokal and Rohlf, 1969) on differences between similarity of stands based on bryophyte versus vascular plant data for 6 coenoclines.

COENOCLINE	COEFFICIENT OF COMMUNITY	PERCENTAGE SIMILARITY
rock outcrops	$\chi^2 = 6.67$ $p < .01$	$\chi^2 = 2.40$ NS
xeric forest and tundra	$\chi^2 = .17$ NS	$\chi^2 = .03$ NS
mesic forest and tundra	$\chi^2 = 15.02$ $p < .005$	$\chi^2 = 22.75$ $p < .005$
fens	$\chi^2 = 4.00$ $p < .05$	$\chi^2 = 4.90$ $p < .05$
Montane	$\chi^2 = .14$ NS	$\chi^2 = .37$ NS
Subalpine	$\chi^2 = 15.00$ $p < .005$	$\chi^2 = .39$ NS

vascular plant strata along elevation gradients. This difference, which was most evident at higher elevations, suggested that elevation and related factors played a more important regulatory role for understory vascular species composition than they did for bryophyte species composition. Furthermore, for the range of elevation and moisture regime sampled in the study, moisture and related factors appeared to exert greater influence over bryophyte species composition than did elevation and related variables.

Discussion

Alpha diversity. The correlation of total species richness per stand with the number of substratum types is not unexpected since many researchers have reported a strong relationship between alpha diversity and environmental heterogeneity. MacArthur and MacArthur (1961) and subsequent workers (MacArthur 1964, Recher 1969, Tomoff 1974) have confirmed that bird species diversity can be predicted from the structural complexity of the plant community. Abele (1974) found that the number of substrata in benthic marine communities is the most important factor regulating decapod crustacean richness.

That the kind of substratum is crucial for bryophytes is a generalization well documented in the bryoecological literature (Nagano 1966, Scott 1971, Crum 1973, La Roi and Stringer 1976). Not only do various substrata provide different textural surfaces of colonization as well as different nutrient regimes, but their shape and size may dramatically influence microclimate. The presence of rock, rotting wood, or bark in a stand dominated by humus increases the range of resources and conditions in the stand and permits coexistence of species that use these differentially.

Less common substrata (e.g. rock and wood in forest) form islands whose species richness may be regulated by dispersal and extinction rates which are, in turn, related to distance to sources of colonists and island size (MacArthur and Wilson 1967). Furthermore, rotting wood is not only discontinuous in space but is temporally impermanent as well, providing a location for a successional microsere within what might be a climax stand (McCullough 1948, Lacusta 1970). Environments such as these would likely select for "r-strategists", i.e. species with high reproductive effort (Pianka 1970, Gadgil and Solbrig 1972). Thus we may expect many substrata to provide favorable environments for species with different reproductive strategies as well as species with different environmental tolerances and competitive abilities.

In the present study the strongest correlation of species richness, heterogeneity and evenness on dominant substrata is with elevation, not with moisture. This relationship, like so many in community ecology, is open to multiple interpretation. It is tempting to speculate that reduced vascular plant competition at higher elevations, particularly in the alpine zone, may release niche space for utilization by bryophytes. With less litterfall, less competition for space and establishment sites, bryophyte richness might be expected to increase with reduced vascular plant cover. However, there is no correlation of bryophyte richness with understory vascular plant cover and it is not at all clear that vascular plant cover decreases continuously with elevation, except within the alpine zone. Furthermore, many alpine plants are more similar to bryophytes in stature and growth form than are the larger, more robust herbs and shrubs of lower zones. Thus, interference between bryophytes and vascular plants may be more, not less, intense in lower alpine tundra communities.

Undoubtedly one of the reasons for high species richness in the alpine zone is increased heterogeneity and micropatterning of the ground surface (see Hrapko 1970 for description). Although I selected only the most homogeneous stands for sampling, some of these exhibited small-scale pattern and disturbance which my plots were too large to resolve. For example, in *Dryas*-dominated tundra (stand no. 15) frost heaving and solifluction had created a pattern of bare and vegetated areas and, although I separated these on the basis of substratum as soil vs. humus, bits of soil were inevitably included in humus samples and vice-versa. High richness and heterogeneity in the alpine is undoubtedly attributable, at least in part, to the nature of this micro-pattern and the increased heterogeneity that results from it.

However, the richness increase from mesic montane stands to mesic subalpine stands cannot be attributed to heterogeneity. White spruce forests of the montane zone (stand nos. 6, 24) support only 11 species each on humus, while subalpine Engelmann spruce-subalpine fir forests (stand nos. 12, 14, 30), which are virtually identical to the montane stands in physiognomy, support between 19 and 23 species. This dramatic change in richness is difficult to explain and data are insufficient to properly analyze environmental differences between these stands. Based on meteorological datafrom La Roi (unpublished) it is evident that the subalpine zone receives more precipitation and has lower mean temperatures than the montane. It is doubtful, however, that the magnitude, per se, of environmental factors should influence richness (see Terborgh 1973). Slobodkin and Sanders (1969) and Colwell (pers. comm.) have suggested that environmental predictability may play a role in the regulation of niche breadth and species diversity. Under more predictable circumstances species could, theoretically, evolve greater resource specificity although it is not exactly clear how this would be accomplished in bryophytes. One must assume that communities similar to those presently found in Jasper have existed long enough to permit evolution of such finely-tuned relationships. Measurement of climatic predictability is not possible presently since only a few years of climatic data are available from the Pyramid-Signal environmental transect. Even if such measurement was possible meteorological data collected 2m above the ground would not have direct relevance for bryophytes.

Very few studies have examined plant species diversity along elevational gradients. Whittaker (1966) has shown that, in general, tree species richness decreases with elevation in the Great Smoky Mountains. Whittaker and Niering (1975) have observed a complex pattern of vascular plant species diversity related to elevation and associated changes in precipitation in the Santa Catalina Mountains of Arizona. Total vascular plant species diversity is maximal in the desert grassland of the Santa Catalinas, but diversity patterns for herbs, shrubs and trees are quite different.

On Secretary Island in the temperate Southern Hemisphere, Scott (1970) has sampled the ground vegetation at several elevations and their data indicate that bryophyte richness is high at middle elevations below timberline with 26-39 species per stand, and drops above timberline to 19 and 23 species per stand. Slack (1971), using 5 by 8m quadrats, found a fairly constant number of bryophytes, about 20, in stands below timberline but also observed a drop in richness in alpine quadrats.

The results of Scott (1970) and Slack (1971) contrast with my data, since richness is strongly associated with elevation in the Jasper area. One might speculate that an island effect is responsible for low richness in the Adirondack alpine. Alpine conditions and vegetation are limited to only a few of the highest Adirondack summits and the nearest source of colonists is the White Mountain Range of New Hampshire, over 240km away. The low migration rates and high extinction rates hypothesized for small, isolated islands might be in effect in the high Adirondacks , and it may be that many specialized arctic-alpine bryophytes have either not reached these mountains or have become extinct there. In the Canadian Rocky Mountains the alpine zone is extensive and virtually continuous with the arctic, and there is a large number of arctic-alpine species in the flora (see Table 2). It is possible, then, that low richness in the Adirondack alpine is a result of insular biogeography.

The positive correlation between evenness (E_{21}) and bryophyte cover is a second relationship of interest. Since bryophyte cover is generally greater in stands with high subjective moisture index, it is not surprising that evenness is also positively correlated with moisture regime. The high evenness of stands having high bryophyte cover and high moisture indices results from the shared dominance of several species. For example, in spruce or spruce-fir forests, where cover and evenness are high, the dominant species are *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilium crista-castrensis*. In contrast, communities with low evenness have dominance concentrated in one or two species (e.g. *Rhacomitrium lanuginosum*-dominated lichen desert).

Whittaker (1965) has implied that communities existing under rigorous or severe conditions exhibit low evenness, while those under more "favorable" conditions have greater equitability. Although Whittaker's rationale for this trend is not clear, many studies have indicated that communities in which resources are limiting show greater dominance than those in which species populations are not intensely competing for resources. For example, predation by starfish on sessile crustacean communities maintains high species diversity by preventing dominance by one species (Paine 1969, 1971). The evenness of protozoan communities within pitcher plants is increased through predation by mosquito larvae (Addicott 1974). Predation on pasture plants by herbivores increases the richness and evenness of pasture communities (Harper 1969), and Platt (1975) has shown that equitability is increased by disturbance of grasslands by gophers. Corns and La Roi 197[illegible] have described forest communities that showed increased evenness after removal of the tree canopy by clearcutting. In all the above cases, perturbation maintains high evenness by preventing the achievement of competitive equilibrium. Data collected by La Roi (pers. comm.)

indicate that boreal spruce-fir stands in stressed or resource-limited situations exhibit low evenness compared to other stands. Nash (1975) has shown that under extreme pollution stress lichen communities exhibit reduced evenness compared to natural situations. In the only other study of bryophyte community structure besides the present one, Slack (1971) has also reported strong dominance associated with low bryophyte cover in stands at Kenrose Preserve, near Albany, New York.

One hypothesis to account for greater dominance in severe environments or under intense competition is that dominance is best expressed where one or a few factors are strongly limiting, allowing only one or a few species to gain a strong competitive advantage. In communities where many factors play a limiting role or where recurrent disturbance is a factor, evenness may be higher.

The actual mechanisms controlling bryophyte species structure have not yet been examined. In dry stands, small locations that collect moisture or are less exposed to dessication may serve as establishment microsites for bryophytes. Intense competition for such microsites may result in strong dominance by one species. Once establishment is achieved, however, competition would be reduced. In mesic stands competition for establishment sites might be important but competition for space after establishment might also be critical. Species that were successful in getting established might lose ground to species better adapted to growth in crowded conditions.

Harper (1969) has noted that many factors interact to influence species structure and, without doubt, factors other than the ones mentioned above affect the species structure of bryophyte communities. For example, competition with lichens may also shape bryophyte evenness. Since bryophytes and lichens have similar stature, water relations, and substratum affinities, it could be argued that both groups belong to the same guild and, hence, species structure should be examined for both groups together.

I have not commented extensively on the relationship of heterogeneity to moisture and elevation gradients, primarily because this measure of diversity (N_1) showed no special or unusual response or trend of its own when correlated with the investigated variables. Rather it seemed to behave in a manner intermediate between richness and evenness, indicating that as a single index it is less informative than the other two. This conclusion supports the views of Whittaker (1965), Addicott (1974), and Nicholson and Monk (1974) who preferred to utilize separate indices for richness and evenness.

Beta diversity. The only other study of bryophyte beta diversity of which I am aware is that of Slack (1971). By analyzing the distribution of the bryoflora of New York State using multiple regression, she found that range of elevation within equal-sized quadrants of the state accounted for much of the variability in flora size between quadrants. Analysis of data collected along transects in the Adirondack Mountains and at Kenrose Preserve near Albany, N.Y., demonstrated that elevation exerts influence over the distribution of bryophyte species and, therefore, beta diversity.

The present study also shows that mosses and liverworts respond to elevation, with some species quite restricted in their distribution along the gradient. However, I have shown that bryophytes in the study area are even more sensitive to complex moisture gradients which support coenoclines of higher beta diversity than elevational gradients, at least over the range of environmental variation sampled. Thus, one is more likely to find floristically similar communities at the far ends of an elevational gradient than at the far ends of a moisture gradient. Slack (1971) did not examine bryophyte distribution along a topographical or moisture gradient, so it is not possible to compare the influence of moisture in the Adirondacks with the Rocky Mountains. It is probable, though, that the high richness Slack reported for mountainous areas in New York is not only a function of beta diversity along elevational gradients, but also of beta diversity along complex moisture gradients which are more pronounced in mountainous country than in lowland terrain, due to slope and aspect effects.

Plant strata may respond differentially to habitat gradients. For example, Bratton (1975) found that beta diversity in the overstory of Smoky Mountain beech forests differed in magnitude with, and did not parallel, understory beta diversity. Cajander (1926) and Heimburger (19 (1934) have described situations in which several kinds of understory types are associated with a single overstory type, implying that understory species are sensitive to factors which do not seriously influence overstory composition. Since trees and understory species within the same stand have such different environments the results of these studies are not surprising. In comparing beta diversity of understory vascular plant species and bryophytes, however, one might expect these two groups to have similar patterns since both inhabit the same overstory-modified environment. In the present study, it has been shown that these two components have similar beta functions for complex moisture gradients, although there are differences that a smaller scale study might better elucidate. There are significant differences, however, between bryophyte and understory vascular plant beta diversity along elevation gradients. Several explanations may be invoked to account for the differential response of bryophytes and vascular plants to elevation.

A first hypothesis is that microenvironmental variation along the gradient is responsible. Although herbs, shrubs, and bryophytes share the same moderated environment in forests at lower elevations the subordinate vascular strate become exposed to direct solar radiation and dessicating winds above timberline, while bryophytes remain somewhat protected under the mantle of dwarf shrubs, herbs and cushion plants. For bryophytes the microenvironments of a heath or cushion plant tundra community may not differ greatly from those of a subalpine forest, and many moss species are common to both stands. In contrast, rapid changes in environment across treeline might be correlated with significant changes in shrub and herb species composition. In support of this hypothesis, the coenoclines for mesic and xeric forest and tundra show highest rate of change in vascular plant species composition per unit gradient at higher elevations (Fig. 27). Beta diversity on rock outcrops, where bryophytes and vascular plants are both exposed to the full rigors of the environment, is similar for both plant groups (Fig. 27). This comparison suggests that, when subjected to the same magnitude of environmental change, species composition changes in these groups are similar.

The above hypothesis, however, does not account for all the observed differences between bryophyte and vascular plant beta diversity. For 3 of the 4 elevational coenoclines studied, bryophyte beta diversity is lower than vascular plant beta diversity at lower elevations where canopy cover is continuous (Fig. 24-26, 27).

One may hypothesize that bryophytes, in general, have broader tolerances to elevational gradients than do vascular plants. Thus, bryophytes would not divide elevational habitat space as finely as vascular plants. Broad tolerance to elevation-related factors could result from either phenotypic plasticity or from ecotypic differentiation, but little is known of bryophyte population biology or population genetics. Most bryologists seem convinced that mosses are a static, slowly evolving group in which genotypes are well established (Crum 1966). Others, such as Longton (1974), have suggested that ecotypic differentiation does occur. Bazzaz, Paolillo and Jagels (1970) have demonstrated differences in light saturation, apparent photosynthesis and CO_2 response for alpine and forest populations of *Polytrichum juniperinum.* Boerner and Forman (1975), however, found that populations of several species from salt spray and dune habitats showed insignificant differences in salt spray tolerance, indicating that little ecotypic differentiation had taken place. Whether or not elevationally wide-ranging species in the Jasper area, such as *Hylocomium splendens, Tortula ruralis, Drepanocladus uncinatus* or *Orthotrichum laevigatum,* have undergone genecological differentiation is a fascinating question that needs attention.

Setting aside this question, there are some considerations that lend support to the notion that mosses do, in fact, have broad tolerances to elevation-related factors. Dilks and Proctor (1975) found that many mosses maintain net photosynthesis over a wide range of temperatures and that northern and montane species do not differ substantially from temperate species in net assimilation in response to temperature. They also observed that bryophytes are protected from intracellular freezing by the withdrawal of water to form extracellular ice. In addition to what seems to be inherent cold-hardiness, bryophytes have not evolved a dormancy mechanism in which life processes are reduced periodically for protracted periods. Bryophytes photosynthesize whenever environmental conditions permit. Thus, "growing season", which we view as decreasing with elevation, may have less meaning for them than for vascular plants.

The differential patterns of bryophyte and vascular plant beta diversity with elevation may arise from both microclimate modification by vascular plant strata and broader tolerance of bryophytes to certain variables. The former explanation is almost certainly true while the latter awaits further critical testing.

Comparison of Alpha and Beta Diversity Trends

While bryophyte beta diversity is greatest along moisture gradients in the study area, species richness on dominant substrata is most strongly related to elevation. A closer relationship between richness and beta diversity might have been expected since factors that influence species composition should also be capable of altering the number of species in a community. Species richness does not change significantly in response to moisture regime, except at the extremes, but beta diversity is quite high along the moisture gradient. In contrast, richness increases with elevation where beta diversity is low.

Apparently there is a "core" of ubiquitous species such as *Hylocomium splendens*, *Polytrichum juniperinum*, and *Drepanocladus uncinatus*, that have wide habitats with elevation. In the subalpine and alpine zones additional species of more limited distribution, like *Barbilophozia lycopodioides* and *Dicranum acutifolium*, are added, increasing richness. Thus, while species composition exhibits only small change, richness increases with elevation.

INTEGRATION

The role of descriptive ecology is to organize, quantify, and synthesize field observations and present the results as specific questions or hypotheses in need of solution or testing. [illegible] of his intimate familiarity with the organisms he [illegible] the descriptive ecologist often has the ab[illegible]int out specific ecological systems and species that may be specially valuable in testing certain hypotheses. For these reasons the descriptive ecologist serves as a link between purely descriptive natural history and experimental ecology. In this section I will describe broad areas of bryophyte ecology that requite future research, and identify specific ecological questions that have arisen directly from the present study.

There is a need for more descriptive work in bryophyte ecology, but such research should be oriented toward specific problems. In the western cordillera, for example, the latitudinal trends in bryophyte importance and flora size merit further study. Is the trend in bryophyte importance closely tied to moisture related factors, as I have suggested?

More studies like the present one are needed to examine the relative roles of moisture and elevation in regulating beta diversity. Specifically, do moisture gradients affect bryophyte beta diversity in maritime climates as dramatically as they do in the continental Jasper area? Although Slack (1971) presented no data on bryophyte-moisture relationships, she implied that elevation was a more important factor in controlling the number of species in an area. The fact that she was working in a sub-maritime climate may be significant. In such a wet, humid area, conditions as dry as those found at Jasper probably do not exist. Thus we might expect reduced beta diversity in maritime areas.

Future bryophyte-oriented, descriptive research should examine patterns of species richness with elevation. Is the increase in richness with elevation consistent in other areas of the western cordillera? If so, why does the pattern contrast with the Slack's (1971) results in eastern North America?

High priority should be given to experimental studies in bryophyte ecology. My study has shown that moss species respond to complex gradients of moisture and elevation. In essence, each bryophyte's habitat, as described in Figures 5-17, represents an hypothesis. The species response patterns can act as a guide to experimental work aimed at determining the direct factors influencing bryophyte distribution. Both physical and biotic factors, including competition, require scrutiny. The hypothesis that broad bryophyte habitats in relation to elevation may result from broad tolerance, with or without ecotypic differentiation, to elevation-related factors, rather than microenvironmental modification by vascular plants, presents a difficult eco-physiological problem.

An area of current interest in population biology involves reproductive strategies, and mosses may provide a good system for studying resource allocation to reproductive and non-reproductive functions. Bryophytes grow in a variety of environments including ephemeral or patchy habitats like rotting wood and erratic boulders where density-dependent mortality would be low; and packed, stable habitats like forst humus, where density-dependent morality might be higher. Thus an "r-K selection continuum" (Pianka 1966) could be identified for bryophytes. Resource allocation might be more easily studied in bryophytes than in vascular plants, since the former lack roots. Species pairs in the genera *Dicranum, Mnium, Grimmia, Orthotrichum,* and *Barbilophozia* (see RESPONSE PATTERNS AND HABITAT METRICS, p. 49) would provide excellent systems for comparative studies of reproductive strategies.

The coexistence of bryophytes under apparently homogeneous conditions is a situation somewhat analogous to Hutchinson's (1961) "paradox of the plankton." The ability of *Hylocomium splendens, Pleurozium schreberi,* and *Ptilium crista-castrensis* to inhabit the same communities over much of their ranges defies simple explanation. In Jasper, the humus guild at higher elevations packs more species than at lower elevations. Why is there a difference? What role does competition play in these moss communities? Is small-scale environmental heterogeneity involved, or do niche dimensions I did not measure enable species to avoid competitive exclusion?

This study has shown that a descriptive analysis of bryophyte distribution patterns in relation to complex gradients can provide information on species habitats and elucidate patterns of community variables, including species diversity. Many question and ideas have arisen from the study and some of these have been outlined above. Research on these tantalizing questions and hypotheses is one natural consequence of this study.

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APPENDIX A. List of bryophyte species and their approximate percent cover values in 30 stands in Jasper National Park. + = less than 1% cover.

	COENOCLINES AND STANDS																													
	GRASSLAND, OUTCROPS							XERIC FOREST AND TUNDRA								MESIC FOREST AND TUNDRA										FENS				
SPECIES	2	3	9	21	10	16	28	1	4	5	29	8	23	19	15	24	6	25	26	12	11	30	14	13	20	27	18	7	17	22
HEPATICOPSIDA*																														
Barbilophozia hatcheri	-	-	-	-	-	-	+	-	-	+	+	+	+	+	-	+	-	+	+	+	[illegible]	[illegible]	+	+	+	-	-	-	-	+
B. lycopodioides	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	[illegible]	-	-	+	1	[illegible]	4	8	4	+	-	-	-	+	-
Lophozia excisa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	[illegible]	[illegible]	[illegible]	-	-	-
L. longidens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-
L. porphyroleuca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	[illegible]	[illegible]	[illegible]	-	-	-	-
L. ventricosa	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	+	-	-	[illegible]	-	-	-	-
Orthocaulis quadrilobus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Tritomaria quinquedentata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	1
Gymnomitrion coralloides	-	-	-	-	-	-	+	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	-
Jamesoniella autumnalis	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Scapania paludosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-
Plagiochila asplenioides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Ptilidium ciliare	-	-	-	-	-	-	-	-	+	-	+	-	-	[illegible]	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
P. pulcherrimum	-	-	-	-	-	-	-	+	-	+	+	+	+	-	-	+	+	+	+	+	-	+	+	-	+	[illegible]	-	-	-	-
Blepharostoma trichophyllum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	[illegible]	+	+	+	-	-	-	-	-	+	-	-
BRYOPSIDA**																														
Sphagnum warnstorfii	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	+	-	-	-	-	-	-	26	11	9	23
Andreaea rupestris	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fissidens osmundioides	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Ceratodon purpureus	+	-	-	-	-	-	[illegible]	+	+	+	+	+	+	-	-	-	+	[illegible]	-	-	-	-	-	-	-	-	-	-	-	+
Distichium capillaceum	-	+	-	+	+	+	-	-	+	-	-	+	+	-	+	+	[illegible]	-	+	-	+	-	-	-	-	-	-	-	-	-
Ditrichum flexicaule	+	+	-	+	+	+	-	-	-	-	+	+	+	+	+	-	-	+	+	-	+	+	-	-	-	-	-	+	-	-
Saelania glaucescens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	[illegible]	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Cynodontium strumiferum	-	[illegible]	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dichodontium pellucidum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Dicranoweisia crispula	-	-	-	-	-	-	+	-	-	+	-	+	+	+	-	[illegible]	-	-	-	-	+	+	+	+	-	-	-	-	-	-
Dicranum acutifolium	-	-	-	-	-	+	+	-	-	-	-	+	-	1	1	-	-	+	+	+	1	4	2	+	+	-	-	-	-	-
D. angustum	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	+	-	-	-	-	[illegible]	-	+	+	-	-	-	-	-	-	-	-
D. elongatum	-	-	-	[illegible]	+	-	+	-	-	-	-	[illegible]	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
D. fragilifolium	-	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	[illegible]	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-

APPENDIX A - Continued.

SPECIES	COENOCLINES AND STANDS																													
	GRASSLAND, OUTCROPS							XERIC FOREST AND TUNDRA								MESIC FOREST AND TUNDRA										FENS				
	2	3	9	21	10	16	28	1	4	5	29	8	23	19	15	24	6	25	26	12	11	30	14	13	20	27	18	7	17	22
Dicranum fuscescens	-	-	-	-	-	-	-	+	[illegible]	+	+	+	+	+	+	+	[illegible]	+	+	+	+	+	+	+	-	-	-	-	-	-
D. muhlenbeckii	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
D. polysetum	-	-	-	-	-	-	-	+	+	+	+	-	+	-	-	+	-	+	+	-	+	+	-	-	-	-	-	+	+	-
D. scoparium	-	-	-	-	-	-	-	+	-	+	-	+	+	[illegible]	-	+	-	+	+	-	+	+	4	+	-	-	-	-	+	+
Kiaeria starkei	-	-	[illegible]	-	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Oncophorus virens	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
O. wahlenbergii	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-
Paraleucobryum enerve	-	-	-	-	+	-	+	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Encalypta mutica	-	+	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E. procera	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
E. rhaptocarpa	-	-	-	-	+	+	-	-	-	[illegible]	-	-	+	+	+	[illegible]	-	-	-	-	-	-	-	-	+	-	-	-	-	-
E. vulgaris	+	+	+	+	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-
Barbula convoluta	+	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bryoerythrophyllum recurvirostrum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-
Desmatodon latifolius	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-
Tortella fragilis	-	+	+	+	+	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	+
T. tortuosa	-	+	+	+	+	+	-	-	-	+	-	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tortula mucronifolia	-	+	-	-	-	-	-	+	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
T. norvegica	-	-	-	-	-	-	+	-	-	-	-	-	-	[illegible]	-	-	[illegible]	-	-	-	+	+	+	+	+	-	-	-	-	-
T. ruralis	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	-	[illegible]	[illegible]	-	-	-	-	-	-	+	-	-	-	-	-
Grimmia affinis	-	-	-	-	[illegible]	-	-	-	+	-	-	-	-	-	-	-	[illegible]	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-
G. alpicola	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	[illegible]	-	[illegible]	-	[illegible]	-	-	-	-	-	-	-	-	-
G. anodon	-	2	2	+	[illegible]	-	-	-	-	-	-	-	-	-	+	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-
G. apocarpa	-	+	+	-	[illegible]	+	-	+	+	+	+	-	+	+	+	-	[illegible]	[illegible]	-	-	+	+	-	+	+	-	-	-	-	-
G. calyptrata	-	-	+	+	-	[illegible]	+	-	-	-	+	-	+	+	-	-	[illegible]	[illegible]	-	-	-	-	-	+	+	-	-	-	-	-
G. incurva	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	[illegible]	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-
G. sp.	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhacomitrium canescens	-	-	-	-	-	+	-	-	-	-	-	-	-	+	+	-	-	[illegible]	-	-	-	-	-	+	+	-	-	-	-	-
R. heterostichum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
R. lanuginosum	-	-	-	-	-	+	2	-	-	[illegible]	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tayloria lingulata	-	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Tetraplodon angustatus	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
T. mnioides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Splachnum sphaericum	-	-	[illegible]	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	+	-
S. vasculosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+

APPENDIX A - Continued

SPECIES	COENOCLINES AND STANDS																													
	GRASSLAND, OUTCROPS							XERIC FOREST AND TUNDRA								MESIC FOREST AND TUNDRA										FENS				
	2	3	9	21	10	16	28	1	4	5	29	8	23	19	15	24	6	25	26	12	11	30	14	13	20	27	18	7	17	22
Bryum angustirete	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B. argenteum	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B. caespiticium	2	-	-	-	-	-	-	[illegible]	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
B. capillare var. flaccidum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B. creberrimum	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B. pallescens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-				-	-	-
B. pseudotriquetrum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-		-	+	+
B. weigelii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				+	-
B sp.	-	-	-	-	+	+	-	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-		
Leptobryum pyriforme	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+	+	-	-
Plagiobryum zierii	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pohlia cruda	-	+	-	-	+	-	-	-	-	-	-	+	+	+	+	+	-	-	-	+	+	-	-	-	+	-	-	-	-	-
P. nutans	-	-	-	-	-	-	+	+	+	+	+	+	+	-	-	+	+	+	+	-	+	+	+	+	+	-	-	+	-	-
Mnium arizonicum	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
M. blyttii	-	-	-	+	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-
M. marginatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
M. thomsonii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+
M. spinulosum	-	-	-	-	-	-	-	+	-	+	+	+	+	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-
Plagiomnium ciliare	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
P. drummondii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
P. medium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-
P. ellipticum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	-	-	+	-	-	-	-	-	3	+	-	-	-
Rhizomnium gracile	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+
R. pseudopunctatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-
Aulacomnium palustre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+	+	1	+	-	-	-	[illegible]	8	13	1
A. turgidum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	-	[illegible]	-	2
Meesia uliginosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	[illegible]	-	+
Paludella squarrosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	[illegible]	+	+
Catoscopium nigritum	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	+	-	-
Bartramia ithyphylla	-	-	-	-	-	-	+	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-
Philonotis fontana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	+
Timmia austriaca	-	-	-	-	-	-	-	-	-	+	-	2	+	-	-	-	+	-	1	2	4	1	+	-	-	-	-	-	-	-
Orthotrichum alpestre	-	-	-	-	-	-	-	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
O. anomalum	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
O. jamesianum	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

APPENDIX A - Continued

SPECIES	COENOCLINES AND STANDS																													
	GRASSLAND, OUTCROPS							XERIC FOREST AND TUNDRA								MESIC FOREST AND TUNDRA										FENS				
	2	3	9	21	10	16	28	1	4	5	29	8	23	19	15	24	6	25	26	12	11	30	14	13	20	27	18	7	17	22
Orthotrichum laevigatum	-	+	+	+	+	+	+	+	+	-	+	+	+	+	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
O. obtusifolium	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
O. rupestre	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-
O. speciosum	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	+	+	-	-	-	-	-	-	-	-	-
Hedwigia ciliata	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myurella julacea	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leskeella nervosa	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pseudoleskea radicosa	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	5	-	-	-	-	-	-
Pseudoleskeella tectorum	-	+	+	+	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pterigynandrum filiforme	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Helodium blandowii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-
Thuidium abietinum	+	+	+	+	+	+	-	3	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
T. recognitum	-	-	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Amblystegium juratzkanum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Calliergon giganteum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13	+	-	-	-
C. sarmentosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
C. stramineum	-	-	-	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Campylium chrysophyllum	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
C. stellatum	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	+	+	5	-
Drepanocladus aduncus	-	-	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	+	-	-	+
D. badius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	+
D. revolvens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+
D. uncinatus	-	-	-	-	-	-	+	-	[illegible]	+	+	4	1	1	-	+	+	+	2	+	5	5	1	+	+	-	+	+	1	+
Brachythecium curtum	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	+	-
B. collinum	-	-	+	-	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B. salebrosum	+	-	-	-	-	-	-	-	+	1	1	3	-	1	+	+	+	1	2	+	+	+	+	+	+	-	+	+	-	-
B. velutinum	+	-	-	-	-	-	-	[illegible]	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B. turgidum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Eurhynchium pulchellum	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-
Tomenthypnum nitens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	14	12	21	9	+
Pleurozium schreberi	-	-	-	-	-	-	-	-	1	21	+	+	+	-	-	17	1	8	1	12	1	7	+	-	+	-	-	+	-	-
Plagiothecium laetum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-
Hypnum cupressiforme	-	-	-	+	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
H. revolutum	+	-	-	-	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-
H. vaucheri	+	3	1	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

APPENDIX A --Continued

SPECIES	COENOCLINES AND STANDS																													
	GRASSLAND, OUTCROPS							XERIC FOREST AND TUNDRA								MESIC FOREST AND TUNDRA										FENS				
	2	3	9	21	10	16	28	1	4	5	29	8	23	19	15	24	6	25	26	12	11	30	14	13	20	27	18	7	17	22
Isopterygium pulchellum	-	-	-	-	+	-	-	-	+	-	-	-	+	-	+	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-
Ptilium crista-castrensis	-	-	-	-	-	-	-	-	+	1	+	+	+	-	-	3	10	1	1	8	-	+	+	-	+	-	-	-	-	-
Pylaisiella polyantha	-	-	-	-	-	-	-	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhytidiadelphus triquetrus	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	3	+	+	-	-	+	-	-	-	-	-	-	-	-
Rhytidium rugosum	-	-	-	-	+	+	-	1	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hylocomium splendens	-	-	-	-	+	-	-	4	3	10	+	4	2	+	1	37	34	11	14	48	9	40	14	+	1	-	-	6	2	6
Pogonatum alpinum	-	-	-	-	+	+	+	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	+	+	+	-	-	-	-	+
P. dentatum	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polytrichum juniperinum	-	+	-	-	+	+	-	+	+	+	+	+	+	+	+	[illegible]	-	+	+	+	+	+	+	-	+	-	-	-	-	-
P. piliferum	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-
P. strictum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

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* Nomenclature follows Bird and Hong (1975).

** Nomenclature follows Crum, Steere, and Anderson (1973) for all groups except Mniaceae, for which Koponen (1974) is followed, and <u>Sphagnum</u>, for which Isoviita (1966) is followed. Voucher specimens of all liverwort and moss species are deposited in the University of Alberta Herbarium (ALTA).

APPENDIX B. List of vascular plant species and their subjective moisture indices for 30 stands in Jasper National Park*.

Polypodiaceae

Cystopteris fragilis (L.) Bernh.	1.0

Equisetaceae

Equisetum arvense L.	3.0
E. pratense Ehrl.	4.0
E. scirpoides Mich.	4.0
E. sylvaticum L.	4.0

L[illegible]eae

[illegible]*um annotinum* L.	3.5
L. [illegible]*o* L.	3.0
L. [illegible]*chense* Rupr.	3.0

Sellaginellaceae

Selaginella densa Rydb.	1.0

Pinaceae

Abies lasiocarpa (Hook.) Nutt.	3.5
Juniperus communis L.	2.0
J. horizontalis Moench	1.0
Picea engelmannii Parry	3.0
P. glauca (Moench)Voss	2.5
P. mariana (Mill.) BSP.	4.0
Pinus albicaulis Engelm.	2.5
P. contorta Loundon var. *latifolia* Engelm.	3.0
Pseudotsuga menziesii (Mirb.) Franco	2.0

Gramineae

Agropyron dasytachyum (Hook.) Scribn.	1.0
A. latiglume (Scribn. & Smith) Rydb.	4.5
Arctagrostis arundinacea (Trin.) Beal	4.5
Calamagrostis canadensis (Mich.) Beauv.	4.0
C. montanensis Scribn.	1.0
C. purpurescens R.Br.	1.0
Deschampsia caespitosa (L.) Beauv.	3.5
Elymus innovatus Beal	2.0

Festuca baffinensis Polunin	1.5
F. brachyphylla Schultes	1.5
Glyceria striata (Lam.) Hitchc.	5.0
Hierochloe alpina (Sw.) R.&[illegible]	3.0
Koeleria cristata (L.) Pers.	1.0
Phleum alpinum L.	3.0
Poa alpina L.	2.5
P. arctica R. Br.	2.0
P. glaucifolia Scribn. & Will.	3.0
P. interior Rydb.	1.5
Trisetum spicatum (L.) Richt.	1.5

Cyperaceae

Carex aquatilis Wahlenb.	5.0
C. atrosquama Mack.	4.5
C. brunnescens (Pers.) Poir.	5.0
C. concinna R.Br.	1.0
C. diandra Schrank	4.5
C. disperma Dewey	4.5
C. drummondiana Dewey	2.0
C. gynocrates Wormsk.	4.5
C. nigricans C.A.Meyer	3.0
C. phaeocephala Piper	5.0
C. rostrata Stokes	5.0
C. scirpoidea Michx.	1.0
C. spectabilis Dewey	3.0
Eriophorum angustifolium Honckeny	4.5
E. brachyantherum Trautr.	4.5
E. scheuchzeri Hoppe	4.5

Juncaceae

Juncus castaneus Sm.	5.0
J. mertensianus Bong.	5.0
Luzula spicata (L.) D.C.	1.5
L. wahlenbergii Rupr.	3.0

Liliaceae

Allium cernuum Roth	1.0
Smilacina trifolia (L.) Desf.	5.0
Streptopus amplexifolius (L.) DC.	4.0
Tofieldia pusilla (Michx.) Pers.	4.5
Zygadenus elegans Pursh.	1.5

Orchidaceae

Calypso bulbosa (L.) Oakes	2.5
Corallorhiza trifida Chatelain	3.0
Goodyera repens (L.) R.Br.	3.5
Habenaria hyperborea (L.) R.Br.	4.0

Habenaria obtusata (Pursh.) Richards	3.0
Orchis rotundifolia Banks	3.5
Salicaceae	
Populus balsamifera L.	4.0
P. tremuloides Michx.	3.0
Salix arctica Pall.	3.0
S. barklayi Anderss.	3.5
S. barrattiana Hook.	4.5
S. bebbiana Sarg.	3.0
S. glauca L.	3.0
S. maccalliana Rowlee	3.5
S. myrtillifolia Anderss.	4.5
S. nivalis Hook.	2.0
S. vestita Pursh.	3.0
Betulaceae	
Alnus crispa (Ait.) Pursh.	2.0
A. tenuifolia Nutt.	4.5
Betula papyrifera Marsh.	3.0
B. glandulifera (Regel) Butler	5.0
Santalaceae	
Geocaulon lividum (Richards.) Fern.	3.0
Loranthaceae	
Arceuthobium americanum Nutt.	-
Polygonaceae	
Polygonum viviparum L.	3.5
Portulacaceae	
Claytonia lanceolata Pursh.	3.0
Caryophyllaceae	
Silene acaulis L. var. *exscapa* (All.) DC.	1.5
Stellaria longipes Goldie	1.5
S. monantha Hulten	1.5
Ranunculaceae	
Actaea rubra (Ait.) Willd.	4.0
Anemone drummondii S. Wats.	1.0
A. multifida Poir.	1.5
A. occidentalis S. Wats.	3.0

Anemone parviflora Michx.	5.0
A. patens L. var. *wolfgangiana* (Bess.) Koch.	1.0
Aquilegia flavescens S. Wats.	3.0
Clematis verticellaris DC. var. *columbiana* (Nutt.) A.Gray	2.0
Ranunculus eschscholtzii Schlect.	4.0
Trollius albiflorus (A.Gray) Rydb.	3.5
Cruciferae	
Arabis holboelii Hornem.	1.5
Cardamine bellidifolia L.	1.5
Draba spp.	1.5
Crassulaceae	
Sedum stenopetalum Pursh.	1.0
Saxifragaceae	
Mitella nuda L.	4.0
Parnassia fimbriata Konig	4.0
P. palustris L. var. *neogaea* Fern.	5.0
Ribes lacustre (Pers.) Poir.	4.0
R. oxyacanthoides L.	2.0
R. triste Pall.	3.5
Saxifraga aestivalis Fisch. & May.	2.0
S. bronchialis L.	1.0
S. cernua L.	1.0
S. lyallii Engler	1.0
S. punctata L.	4.5
S. rivularis L.	1.0
S. oppositifolia L.	1.0
Rosaceae	
Amelanchier alnifolia Nutt.	2.0
Chamaerhodos erecta (L.) Bunge ssp. *nuttallii* Hulten	1.0
Dryas octopetala L.	2.5
Fragaria virginiana Duchesne var. *glauca* S. Wats.	2.0
Potentilla diversifolia Lehm.	2.5
P. fruticosa L.	3.0
P. gracilis Dougl.	1.0
P. nivea L.	1.0
P. pensylvanica L.	1.0
Rosa acicularis Lindl.	2.5
Rubus acaulis Michx.	5.0
R. pubescens Raf.	3.5
R. strigosus Michx.	3.5
Sibbaldia procumbens L.	3.0
Sorbus scopulina Greene	3.5
Spirea lucida Dougl.	2.0

Leguminosae	
Astragalus striatus Nutt.	1.0
A. aboriginum Richards	1.0
Hedysarum alpinum L.	2.0
Lathyrus ochroleucus Hook.	3.0
Oxytropis podocarpa A. Gray	2.0
O. sericea Nutt. var. *spicata* (Hook) Barneby	1.0
O. splendens Dougl.	1.0
Vicia americana Muhl.	3.0
Linaceae	
Linum lewisii Pursh.	1.0
Empetraceae	
Empetrum nigrum L.	3.5
Violaceae	
Viola renifolia A. Gray	3.5
Elaeagnaceae	
Shepherdia canadensis (L.) Nutt.	2.0
Onagraceae	
Epilobium angustifolium L.	3.0
E. palustre L.	5.0
Umbelliferae	
Osmorhiza sp.	
Cornaceae	
Cornus canadensis L.	3.5
C. stolonifera Michx.	4.0
Pyrolaceae	
Chimaphila umbellata (L.) Bart.	2.5
Moneses uniflora (L.) A. Gray	3.5
Pyrola asarifolia Michx.	3.5
P. secunda L.	3.0
P. virens Schweigg.	2.5

Ericaceae

Arctostaphylos rubra (Rehder&Wils.) Fern.	5.0
A. uva-ursi (L.) Spreng.	1.5
Cassiope mertensiana (Bong.) D.Don.	3.5
C. tetragona (L.) D.Don. ssp. *saximontana* (Small)Pors.	3.0
Kalmia polifolia Wang. var. *microphylla* (Hook.) Rehd.	5.0
Ledum groenlandicum Oeder	4.0
Menziesia glabella A. Gray	3.5
Oxycoccus microcarpus Turcz.	5.0
Phyllodoce empetriformis (Smith) D.Don.	4.0
P. glanduliflora (Hook.) Coville	3.0
Vaccinium caespitosum Michx.	2.5
V. membranaceum Dougl.	3.5
V. scoparium Leiberg	3.0
V. vitis-idaea (L.)var.*minus*	3.0

Primulaceae

Androsace septentrionalis L.	1.0

Gentianaceae

Gentiana glauca Pallas	3.5
Gentianella amarella (L.) Borner ssp. *acuta* (Michx.) J.M.Gillett	2.5
G. propinqua (Richards.) J.M.Gillett	2.5

Boraginaceae

Mertensia paniculata (Ait.) G.Don.	3.5
Myosotis alpestris Schmidt	2.5

Scrophulariaceae

Castelleja miniata Dougl.	2.5
C. occidentalis Torr.	2.0
Pedicularis bracteosa Benth.	3.0
P. capitata Adams	2.5
P. lanata Cham. & Schlect	4.0
Veronica alpina L. var. *unalaschensis* C.& S.	3.0

Rubiaceae

Galium boreale L.	2.0
G. triflorum Michx.	3.5

Caprifoliaceae

Symphoricarpos albus (L.) Blake	2.0
Linnaea borealis L. var. *americana* (Forbes) Rehd.	3.5
Lonicera involucrata (Richards.)Banks	4.0
Viburnum edule (Michx.) Raf.	3.5

Valerianaceae	
Valeriana sitchensis Bong.	3.5
Campanulaceae	
Campanula lasiocarpa Cham.	3.5
C. rotundifolia L.	2.0
Compositae	
Achillea millefolium L.	2.0
Antennaria alpina (L.) Gaertn.	2.0
A. lanata (Hook.) Greene	3.5
A. nitida Greene	1.0
A. racemosa Hook.	2.5
A. rosea Greene	1.0
Arnica alpina (L.) Olin	2.0
A. cordifolia Hook.	3.0
A. gracilis Rydb.	1.5
A. latifolia Bong.	3.0
A. mollis Hook.	4.5
Artemisia campestris L.	1.0
A. frigida Willd.	[illegible].0
A. norvegica Fries	2.0
Aster ciliolatus Lindl.	2.0
A. conspicuus Lindl.	2.5
Erigeron caespitosus Nutt.	1.0
E. compositus Pursh.	1.0
E. peregrinus (Pursh.) Greene ssp. *callianthemus* (Greene) Cronq.	3.0
Hieracium gracile Hook.	3.5
Petasites palmatus (Ait.) A.Gray	4.0
P. vitifolius Greene	4.5
Senecio cymbalarioides Nutt.	1.0
S. pauciflorus Pursh.	3.5
[illegible]*ngularis* Hook.	4.0
[illegible] *decumbens* Greene	2.0
[illegible]*radiata* Ait.	1.5
[illegible]*m* sp.	2.0

*Nomenclature and sequence of Families from Moss (1959) and Packer (1974).