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DISTRIBUTION PATTERNS OF TERRICOLOUS BRYOPHYTES AND LICHENS ALONG EDAPHIC AND LATITUDINAL GRADIENTS IN THE SUBARCTIC FOREST-TUNDRA OF THE NORTHWEST TERRITORIES

by

ANNE L. ROBINSON

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

PLANT ECOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

SPRING 1989

ISBN 0-315-53008-1

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: ANNE L. ROBINSON

TITLE OF THESIS: DISTRIBUTION PATTERNS OF TERRICOLOUS BRYOPHYTES AND LICHENS ALONG EDAPHIC AND LATITUDINAL GRADIENTS IN THE SUBARCTIC FOREST-TUNDRA OF THE NORTHWEST TERRITORIES

DEGREE FOR WHICH THESIS WAS PRESENTED: MASTER OF SCIENCE

YEAR THIS DEGREE GRANTED: 1989

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled DISTRIBUTION PATTERNS OF TERRICOLOUS BRYOPHYTES AND LICHENS ALONG EDAPHIC AND LATITUDINAL GRADIENTS IN THE SUBARCTIC FOREST-TUNDRA OF THE NORTHWEST TERRITORIES submitted by ANNE L. ROBINSON in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in PLANT ECOLOGY.

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Date 29 November 1988

ABSTRACT

Terricolous bryophyte and lichen communities in the subarctic forest-tundra of the Northwest Territories, Canada were analyzed quantitatively on the basis of community structure and species distribution with respect to environmental gradients.

Bryophytes and lichens from 95 stands were collected, stands were ordinated by species presence, and patterns of stand distribution were analyzed. Environmental gradients were overlaid on the ordinations and correlations between stand patterns and gradients examined. Soil pH indicator species (occurring on either basic or acidic soils) and non-preferential species (occurring on both basic and acidic soils) were identified and patterns of occurrence of those species studied. Correlations between edaphic gradients and community and morphological characteristics were analyzed.

Terricolous bryophyte and lichen distribution in the subarctic forest-tundra is strongly correlated with meso-environmental gradients of soil pH, texture, moisture, and with latitude. Bryophytes from basic, medium- and fine-textured soils and northern latitudes form one group; those from acidic, coarse-textured soils, and southern latitudes form another. The southern group is distributed along a moisture gradient; the moisture gradient is less well-defined for northern stands. Degree of acrocarpy and papillosity of mosses increases from wet to dry along a moisture gradient.

Lichens are distributed along a complex gradient from coarse-textured, dry to mesic, acidic soils and southern latitudes to finer-textured, mesic to wet, basic soils and northern latitudes. The

proportion of fruticose and light-coloured lichens is high in the region overall, and fruticosity is more prevalent on acidic, coarse-textured soils.

Basic, medium- to fine-textured, mesic to wet soils are characterized by a high proportion of mosses compared with lichens. Acidic, coarse-textured, drier soils have a higher proportion of lichens. Lichens may have adapted structurally and physiologically to conditions unacceptable to most bryophytes and vascular plants. Mosses may be better competitors in more favourable habitats.

The bryophyte and lichen flora of acidic soils appears to have few unique species; that of acidic areas overlaps into basic areas. Conversely, the flora of basic soils has many unique species and fewer overlapping ones. Mosses dominate the rich indicator flora of basic soils. Many lichen species occur on both acidic and basic soils.

ACKNOWLEDGEMENTS

I gratefully acknowledge financial support of this research by a grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) and from the University of Alberta. I wish to especially thank Dale H. Vitt for his valuable suggestions, patience, and encouragement for the duration of the work. In addition, his taxonomic expertise was invaluable. I am also thankful to Janet Marsh for taxonomic assistance with the difficult lichens. Discussions of many aspects of the research with fellow students were most helpful. Thanks to the University of Alberta Botany Department for computer facilities, use of the cryptogam herbarium, and financial support. In the field, Patrick O'Leary and Jim Donaldson were a great help and a pleasure to work with. Thanks also to my parents, Donald and Barbara Robinson, and to the Hall family, for their generosity during this rather lengthy period of impecunity. Finally, my husband Kevin Timoney, in addition to providing vascular species, soils, and site data (his fieldwork funded in part by grants from the Boreal Institute of Northern Studies, and from NSERC via a grant to George La Roi), has supported and encouraged my efforts, and generously shared his expertise through all phases of the research.

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1. INTRODUCTION

Studies of plant community dynamics are becoming increasingly valuable in assessing the impact of environmental disturbance. In order to be most useful, thorough descriptions of plant communities must be made before disturbance occurs. The quickening pace of environmental destruction worldwide highlights the urgent need for baseline environmental data, especially in sensitive arctic and subarctic communities (Bliss and Wein 1972; Kershaw and Kershaw 1985).

The structure of a plant community is the result of the biotic and abiotic processes acting in the community. Identification of the spatial and temporal organization of the community is a first step towards the recognition of these processes. Although the ultimate parts of a community are the individual plants, it is impracticable to describe a community in terms of the characters of each plant (Watt 1947). Instead, patterns of occurrence of characters relating to the community as a whole can be identified and used to describe the community. Once the patterns have been elucidated, hypotheses as to the causes of the patterns can be made and tested.

Recognition of bryophytes and lichens as significant components of some plant communities is increasing (e.g., arctic: Vitt and Pakarinen 1977; subarctic: Timoney 1988; boreal forest: La Roi and Stringer 1976, Vitt 1989; alpine: Flock 1978; tropical rain forest: Gradstein and Pócs 1988; and desert: Nash and Moser 1982). In recent years, beginning with Slack's (1971) study on bryophyte community structure, studies of the cryptogam component have become more numerous on both a local (e.g., Flock 1978) and a regional scale

(e.g., La Roi and Stringer 1976; Vitt 1988). Thus, information is accumulating about the processes organizing the bryophyte and lichen component of plant communities.

Vegetation studies in the subarctic forest-tundra region have shown that bryophytes and lichens are a significant component of plant communities (Hardy 1976; Ritchie 1977, 1984; Zoltai and Johnson 1978; Timoney 1988). Yet most studies of forest-tundra bryophytes and lichens have been taxonomically oriented (e.g., Scotter 1966; Scotter and Thomson 1966; Ahti et al. 1973; Steere 1977). While documentation of the flora of a region is a necessary first step, more data regarding species composition, diversity, and patterns of distribution (e.g. Slack 1977; Lee and La Roi 1979; Nimis 1984; Vitt et al. 1986) are needed in order to understand the structure and dynamics of this vegetation stratum.

Although quantitative studies of northern bryophyte- and lichen-dominated communities are still relatively few, the last ten years has seen an increase, greatly assisted by advances in computer technology (e.g., alpine communities: Jonasson 1981; forests: Oksanen 1983; mires: Vitt and Bayley 1984; streams: Slack and Glime 1985; arctic tundra: LaFarge-England 1988).

The subarctic forest-tundra of the Northwest Territories (NWT) is ideal for an ecological study of bryophytes and lichens. Not only is this vast region still relatively undisturbed, it also possesses a diverse vegetation including wetland, forest and thicket, shrub, and upland tundra communities. Surficial materials and their derived soils are diverse, and both maritime and continental climatic regions are represented.

The goals of this research were to quantitively assess patterns of terricolous bryophyte and lichen distribution in the subarctic forest-tundra region of the NWT by answering the questions:

1. How do gradients of latitude, soil pH, soil texture, and soil moisture relate to the occurrence of bryophyte and lichen species?

2. Do patterns of bryophyte distribution differ from those of lichen distribution? If so, how?

3. Do distribution patterns of bryophytes and lichens differ from those of vascular plants? If so, how?

4. Can some bryophytes and lichens be identified as indicators of soil pH and how are those indicators distributed in the region?

5. How does bryophyte and lichen community structure relate to environmental gradients of soil pH, texture, and moisture?

6. How are morphological characteristics of bryophytes and lichens distributed relative to these gradients?

Chapter 2, using the two-step ordination and indirect gradient analysis technique (e.g., Vitt and Bayley 1984; Vitt et al. 1986; Vitt 1988), examines how gradients of latitude, soil pH, soil texture, and soil moisture are related to the occurrence of bryophyte and lichen species; how patterns of bryophyte distribution differ from those of lichen distribution; and how the distribution of bryophyte and lichen species compares to that of vascular plants. In addition, soil pH indicator and non-preferential species are identified and distribution patterns of those species are analyzed. Chapter 3 assesses community structure and some morphological characteristics of bryophytes and lichens with respect to soil pH, texture, and moisture. Chapter 4 summarizes the conclusions from the previous two chapters.

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2. DISTRIBUTION PATTERNS IN RELATION TO GRADIENTS OF LATITUDE AND SOIL PH, TEXTURE, AND MOISTURE

2.1 INTRODUCTION

Bryophytes and lichens are an important component of subarctic forest-tundra plant communities (Hardy 1976; Ritchie 1977, 1984; Zoltai and Johnson 1978; Timoney 1988) and a study of their distribution and the factors affecting it would contribute to the understanding of the forest-tundra ecosystem. Quantitative bryophyte and lichen studies of the forest-tundra region are rare. The ecophysiology of lichen-dominated communities has been studied in SE Mackenzie District and northern Ontario (Kershaw and Rouse 1971, 1976; Kershaw 1975; Larson and Kershaw 1975, 1976). Relative abundances of the dominant bryophytes and lichens along a longitudinal transect in the Keewatin District were provided by Zoltai and Johnson (1978), while vegetation descriptions and cover values of the main bryophyte and lichen species were given by Ritchie for the northwestern (1984) and southeastern (1959, 1960a, 1960b) part of the forest-tundra region, west of Hudson Bay.

Distribution of lichens has been correlated with substrate characteristics (e.g., pH: Nimis 1982, 1984; nitrogen content: Nimis 1984; moisture: Lechowicz and Adams 1974) and some lichens are well-known as indicators of substrate conditions (Brodo 1973). Many studies of peatland vegetation have shown that bryophyte distribution is correlated with physical and chemical properties of the water, and that some peatland species can be used as indicators of these

properties (e.g., Vitt et al. 1975; Horton et al. 1979; Slack et al. 1980; Vitt and Bayley 1984).

The objective of this study was to assess the occurrence of terricolous bryophyte and lichen species in relation to environmental gradients within the forest-tundra ecotone of the NWT. More specifically:

1. How do soil characteristics and latitude correlate with bryophyte and lichen species distribution?
2. Do patterns of bryophyte distribution differ from those of lichens? If so, how?
3. Do patterns of bryophyte and lichen distribution differ from those of vascular plants? If so, how?
4. Which, if any, bryophytes and lichens can be used as pH indicators and how are the indicators distributed in the region?

2.2 STUDY REGION

The forest-tundra, as defined here, comprises the transition region lying north of the low subarctic open crown forest and south of the low arctic tundra; the forest-tundra is bounded on the north by the limit of trees >/= 3-4 m in height, and on the south by the limit of upland tundra; between these extremes, zonal tree and upland tundra vegetation exist in a mosaic (Timoney 1988). The fieldwork was conducted in five areas referred to as the Dubawnt, the Snare-Yellowknife, the Coppermine-Kendall, the Horton, and the Tuktoyaktuk-Inuvik areas (Fig. 2.1).

The physiography of the study region has been described by Bostock (1976) and his nomenclature for the physiographic subdivisions of Canada is followed here. The overview of soils is based on Dept. of Agriculture (1972), Clayton et al. (1977), and Canada Soil Survey Committee (1978).

The Dubawnt area is located in the Kazan Upland of the Precambrian Shield where the bedrock is primarily Archean granitic gneiss. The topography is relatively smooth with monadnocks and small ranges of hills providing local relief. Lakes and streams are numerous. The predominant surficial material is sandy loam to loamy sand, non-calcareous till with low clay content. Soils are predominantly dystric and eutric brunisols (often of cryoturbic phase), gleyed cryosols, and fibric cryosols; pH is generally acidic.

Sampling in the Snare-Yellowknife area was conducted in the vicinity of Mackay Lake (Salmita mine) and the Snare, Yellowknife, McCrea, and Beaulieu Rivers, north of Great Slave Lake. These sites

are located in the Bear-Slave Upland. The bedrock of this part of the Shield consists predominantly of Archean gneisses and schists with allied granites, granodiorites, diorites, and related rocks. Rounded, rocky hills, typically <100 m high, provide local relief. Surficial material is primarily thin and patchy loamy sand and sandy loam till. Soils are predominantly dystric brunisols (often of cryoturbic, rocky and stony phases) and fibric cryosols developed on widespread permafrost. Soil pH is generally acidic.

The Coppermine-Kendall area, located in the Bear-Slave Upland and Coronation Hills, extends from Rocknest Lake on the Coppermine River north to the mouth of the Kendall River, then west along the Kendall to the western end of the Dismal Lakes. Bedrock is variable and includes carbonates, granitic rocks, diabase dykes, sandstone, and interbedded red shales and dolomites (Timoney 1988). Local relief often exceeds 150 m. Surficial material is till, glaciofluvial, and ice contact material. Mineral soils are predominantly loamy cryosols, showing the finer texture and higher pH characteristic of the Interior Plains soils farther west (Timoney 1988).

The southern part of the Horton study area is underlain by dolomites and limestones; the northern portion by shales, siltstones, and mudstones. Lakes are small and scattered, set in gently rolling till-covered hills. Most of the soils, derived from calcareous tills, are medium- to fine-textured with high pH. In the area of the Smoking Hills near the mouth of the Horton River, most of the surficial material is clay-textured and colluvial or aeolian-like (Zoltai et al. 1979). Glaciofluvial, alluvial, and ice-contact derived soils with coarser textures also occur along the Horton River (Timoney 1988).

In the Tuktoyaktuk-Inuvik study area, soils are typically moderately calcareous loam and clay loam cryosols (Clayton et al. 1977). Organic soils are widespread.

All five study areas were glaciated during the Pleistocene (Dyke and Prest 1987) except for a portion of the lower Horton River (Zoltai et al. 1979). Retreat of the Laurentide Ice Sheet began in the northwestern part of the study region by about 14 thousand years before present (KBP) and proceeded generally west to east, reaching the central district north of Great Slave Lake by 10 KBP, and Keewatin and the southeast corner of the Mackenzie District by 8.4 KBP (Dyke and Prest 1987). Deglaciation of the study region was essentially complete by 7.8 KBP (Dyke and Prest 1987). Glacial deposits, mostly composed of till, are late Wisconsinan in age.

Climate

The climatic description that follows is based on the climatic maps of Hare and Hay (1974), and Fletcher and Young (1978), and the subarctic forest-tundra region of Timoney (1988).

The climate of the subarctic forest-tundra is continental, with long cold winters and short cool summers. July mean air temperatures range from 10-13 C, and mean annual temperatures range from -10.5 to -6.5 C. Mean daily air temperatures rise to zero C by 7 May to 31 May and fall to zero C by 25 September to 5 October. Mean July precipitation is generally 1.6-2.0 cm. Mean annual measured precipitation is light, ranging from about 25-40 cm in the southeast and about 18-30 cm in the drier northwest. Mean annual measured snowfall increases generally from northwest (90-110 cm/yr) to

southeast (80-140 cm/yr). Between these extremes, the forest-tundra receives about 100-120 cm snowfall/yr.

Plant communities

Plant communities in the forest-tundra vary not only across the width of the region but from east to west as well, as the generally acidic, coarse-textured soils of the Shield give way to the more basic, finer-textured Borderland soils to the west. Detailed studies of plant communities are found in Larsen (1965, 1971, 1972, 1980), Zoltai and Pettapiece (1973), Hardy (1976), Zoltai and Johnson (1978), Zoltai et al. (1979), Bradley et al. (1982), Fleck and Gunn (1982), Ritchie (1984), Thomson (1984), and Timoney (1988). Table 2.1 presents an overview based on those and the present study.

2.3 METHODS

Fieldwork was conducted during the summers of 1982-84. Travel was by canoe across and along the forest-tundra. Study sites averaged about 2-4 ha in area, had high internal homogeneity at the level of vegetation type, and included 25 upland tundra, 5 tall shrub, 46 forest and forest-tundra, and 19 wetland sites. No attempt was made to select bryophyte and lichen micro-habitat types. For example, a forest-tundra site consisting of tree clumps in a matrix of upland tundra would contain several bryophyte and lichen micro-habitats.

At each site, an attempt was made to collect all terricolous bryophytes and lichens, i.e., those growing on mineral soil, humus, detritus, and on other bryophytes and lichens. Those growing on trees, shrubs, and rocks were excluded. Collections from Snare-Yellowknife and Dubawnt study areas were made by K. Timoney; all others were made by the author. Where possible, field identifications were made; however, all of the material was scrutinized in the laboratory to minimize the chance of overlooking species. Approximately 5700 identifications were made (Appendices 10-13). Site and soil descriptions and species presence of vascular plants for each site were available from a study of the forest-tundra conducted by Timoney (1988 and unpublished data).

Nomenclature follows Ireland et al. (1987) for mosses (except for *Dicranum* spp. where Peterson (1979) was used), Stotler and Crandall-Stotler (1977) for hepatics, Thomson (1979, 1984) for lichens, and Porsild and Cody (1980) for vascular plants. Voucher specimens are deposited in ALTA.

Site moisture assignments were based on soil drainage properties as follows: dry = excessively-drained and/or exposed; dry-mesic = rapidly-drained; mesic = well-drained to moderately well-drained; wet-mesic = imperfectly-drained; wet = poorly-drained to submerged.

A soil pit was dug at each site and soil pH was determined using a Hellige-Truog field pH kit. Site pH assignments were based on those available from Timoney (1988 and unpublished data). For the Snare-Yellowknife area, soil pH was taken from a soil depth of about 10 cm; typically the A or B horizon. Soil pH from the Dubawnt, Coppermine-Kendall, and Horton study areas represents the B horizon. When there was no B horizon, the C was used. Using a subsurface soil pH, allowed one pH assignment to represent an entire study site without regard to microenvironmental differences.

Hand-texturing of soils was done in the field; textures here are those of the uppermost mineral horizon. Nine texture classes were used: sand, loamy sand, sandy loam, loam, silty loam, silt, clay loam, silty clay loam, and clay. Textures for the organic soils were usually not determined but were predominantly fibric.

The study sites were ordinated (Appendices 1-4 and 9), based on species presence, using DCA (detrended correspondence analysis, DECORANA: Hill 1979). Rare species (those occurring 3 or fewer times) were excluded. Four categories of species were ordinated: bryophytes only, lichens only, bryophytes and lichens, and vascular plants. All 95 sites were ordinated except for the lichens category where 86 were used (in six sites no lichens were collected; three others caused extreme distortion of the ordination and were excluded). The first

two axes accounted for most of the variability; eigenvalues for the third axis were below 0.2 in all cases.

In order to identify patterns of distribution of plant species with respect to environmental factors, correlation matrices (MINITAB: Ryan et al. 1982) based on rank (Spearman's rho; inspection of the data indicated non-normality) were calculated for the physical factors with respect to one another and to the DCA stand ordination scores for bryophytes, lichens, bryophytes and lichens, and vascular plants. Significance at $p \leq 0.001$, $p \leq 0.01$, and $p \leq 0.05$ is noted as ***, **, and *, respectively (Table 2.4 and Figs. 2.2-2.5). Moisture classes were assigned numbers 1 through 5 for dry to wet; and texture classes, numbers 1 through 9 for sand to clay. Soil pH, soil texture, soil moisture, and latitude were each superimposed upon the DCA stand ordinations for bryophytes, lichens, bryophytes and lichens, and vascular plants (Appendices 5-8).

In order to clarify relationships between physical factors and vegetation pattern, these 16 ordinations were summarized as follows. An 11x10 grid was superimposed upon the ordinations and physical factor data for all stands within each grid box were grouped together (mean = 6 stands per group). Grid boxes with fewer than 3 stands were grouped with adjacent boxes to make up the minimum of 3 stands per group. A circle was plotted for each grid box or group of boxes. The centre of the circle is the centre of the box(es); the radius represents the median value of the physical factor data for the stands within the group.

Indicator and non-preferential species were identified from species that occurred in 4 or more sites at which pH was determined.

Excluding the lowest and highest values, acidic indicators were species occurring only in sites with pH <7.0 and basic indicators were those occurring only in sites with pH >/=7.0. Non-preferential species occurred in two or more sites with pH </=5.5 and two or more with pH >/=7.5. Residual species were those that did not fit into any other group.

2.4 RESULTS AND DISCUSSION

Physical Factors

Table 2.2 gives location, soil parameters, and vegetation characteristics of each study site and Table 2.3 relates soil pH, soil moisture, soil texture, and latitude to the five study areas. Soil pH from the Dubawnt and Snare-Yellowknife study areas ranged from 4.0 to 7.0, reflecting the generally acidic parent material of the Shield. Higher values, ranging from 7.0 to 8.0, were found on the calcareous soils of the Coppermine-Kendall and Horton sites with the exception of 5.3 in the Smoking Hills of the lower Horton River. No soil analyses were done at the Tuktoyaktuk-Inuvik sites. Tarnocai (1973), however, reported a silty clay loam having a pH of 5.1 northwest of Inuvik; Zoltai and Tarnocai (1974) reported silt loam soils on the Tuktoyaktuk Peninsula with pH between 4.6 and 7.1; and Pawluk and Brewer (1975) reported four loam soils including one at Inuvik and two at Tuktoyaktuk with pH ranging from 4.5 to 7.1.

Textures of the mineral soils from the Dubawnt and Snare-Yellowknife sites were coarse, typically loamy sand or sandy loam; the modal texture was loamy sand. Farther west in the Coppermine-Kendall area, the modal texture was silty loam. In the Horton area, textures ranged widely, but most were fine. The mode was clay loam, reflecting the dominance of dolomite, limestone, and shale in the parent material.

Moisture varied substantially within each study area, although modal moistures reflect the general trends. Moistures ranged at least from dry-mesic to wet within each area.

The southernmost site, at 60°54'N, is in the Dubawnt area; the northernmost is near the mouth of the Horton River at 69°45'N, resulting in a latitudinal extent of ~1000 km for the study region. There is a significant climatic gradient within the forest-tundra from from NW to SE; e.g., mean annual net radiation ranges from 12-18 kcal cm^{-2} yr^{-1} in the northwest and from 15-25 kcal cm^{-2} yr^{-1} in the southeast; the frost-free period ranges from 50-65 days in the northwest and from 70-75 days in the southeast (Timoney 1988).

All four physical variables are significantly correlated with one another (Table 2.4). Coarse-textured acidic soils dominate the southeast; finer-textured basic soils dominate the northwest. Because moisture regime is at least partly determined by soil texture, better drainage is found more often in the southeast than in the northwest. Thus, latitude represents a complex gradient that includes the climatic factor as well as the three edaphic factors. Texture and latitude are the most highly correlated; moisture and pH the least. The correlations among pH, latitude, and texture are all more significant than those with moisture.

Bryophytes

Distribution patterns of the bryophyte component with respect to the four environmental gradients are shown in Figs 2.2a-2.5a. Stand separation based on the bryophyte component allows recognition of two stand groups: one varies along the first (x) axis towards the centre of the ordination; the other varies along the second (y) axis on the right side of the ordination. Soil pH is the most significantly correlated variable along the first axis of the bryophyte stand

ordination. Two major groups are evident: the basic group with pH above 7.0 is to the left; the acidic group with pH below 7.0, to the right. These two groups are also separable with respect to texture (Fig 2.3a) and latitude (Fig. 2.4a), with coarser textures and southern latitudes corresponding to the acidic soil group and fine textures and northern latitudes to the basic soil group.

Moisture is more strongly correlated with the second axis than the first (Fig. 2.5a), especially within the coarse texture, acidic group on the right side of the ordination where stands clearly separate along a wet-dry gradient. A moisture gradient is also evident along the first axis for the basic group; however, perhaps because fewer dry stands were sampled from that group, the moisture gradient is less well-defined.

Thus, two distinct bryophyte groups can be described (Fig. 2.6). Bryophytes from basic, medium- to fine-textured soils and northern latitudes are grouped together on the left of the ordination. The significant separation along the first axis might be attributable to a moisture gradient, but no strong correlation with any of the measured variables exists. Site S76, with *Bryoerythrophyllum recurvirostrum*, *Bryum pseudotriquetrum*, *Campylium stellatum*, *Dicranum acutifolium*, *Myurella julacea*, *Onchophorus wahlenbergii*, *Tomenthypnum nitens*, *Arnellia fennica*, *Barbilophozia kunzeana*, *Lophozia heterocolpos*, and *Scapania gymnostomophylla*, is a stand from this group.

Bryophytes from acidic, coarse-textured soils and southern latitudes are grouped together on the right and the stands separate clearly from top to bottom along a moisture gradient. At the dry end, for example, site S36 includes *Pogonatum dentatum*, *Pohlia nutans*,

Polytrichum piliferum, *Rhacomitrium lanuginosum*, *Rhytidium rugosum*, and *Cephaloziella divaricata*. Site S53, with a wet-mesic moisture regime, includes *Aulacomnium palustre*, *A. turgidum*, *Dicranum groenlandicum*, *Hylocomnium splendens*, *Sphagnum angustifolium*, *S. russowii*, *Barbilophozia binsteadii*, *Calypogeja muelleriana*, *Cephalozia lunulifolia*, *Ptilidium ciliare*, and *Tritomaria exectiformis*.

Several recent studies on bryophyte ecology show pH and/or water chemistry to be strongly correlated with species distribution. Vitt et al. (1986) showed that bryophytes of montane streams were grouped according to water chemistry, soil texture, geographic distribution, and height above or below water level. Vitt and Horton (1979) concluded that the most important factor affecting moss distribution in boreal montane and polar sites was substrate type, particularly the availability of calcareous and non-calcareous rock surfaces. Vitt et al. (1987) found that the flora of one non-calcareous study area in the Yukon was quite different from a comparable calcareous area. Important gradients of pH and height above water level were discussed with respect to distribution of peatland species in several studies (Vitt et al. 1975; Vitt and Slack 1975, 1984; Horton et al. 1979; Vitt and Bayley 1984). Shade is often found to be a third important gradient in mire systems.

Lichens

Ordinations based on the lichen component (Figs. 2.2b-2.5b) reflect a gradient from the upper left to lower right. Along the first axis of the lichen stand ordination, latitude, texture, and pH

are highly correlated. A complex gradient from coarse-textured, acidic soils and southern latitudes to fine-textured, basic soils and northern latitudes can be identified (Figs. 2.2b, 2.3b, 2.4b). Moisture is more significantly correlated with the second axis (Fig. 2.5b), with dry sites at the top varying towards wetter ones at the bottom. From the fine-textured, basic, northern sites on the right side of the ordination, site S82, with dry-mesic soil (including *Alectoria nigricans*, *A. ochroleuca*, *Cetraria islandica*, *Cladonia pocillum*, *Cornicularia aculeata*, *Dactylina arctica*, *Ochrolechia frigida*, and *Thamnolia subuliformis*) occurs near the top. Site S791, also from the right side but with wet-mesic soil (including *Cetraria cucullata*, *C. nivalis*, *Cladonia chlorophaea*, *C. cyanipes*, *C. phyllophora*, *C. pyxidata*, and *Peltigera aphthosa*) occurs near the bottom. From the acidic, coarse-textured, southern sites, site S12 (with *Alectoria ochroleuca*, *Cetraria ericetorum*, *Cladonia gracilis*, *C. mitis*, *C. rangiferina*, *Masonhalea richardsonii*, and *Stereocaulon paschale*) occurs in the upper left of the ordination. Fig. 2.7 summarizes these results.

Other studies have shown that light intensity (Moser and Nash 1978), humidity (Nimis 1984; Nimis and Losi 1984), pH (Alvin 1960; Nimis 1982), snow cover (Larson and Kershaw 1975; Jonassen 1981), and soil moisture (Kershaw and Rouse 1971) are the primary factors affecting lichen species distribution. All of these studies measured attributes of the micro- rather than meso-environment.

Bryophytes compared to lichens

The main difference between the lichen and bryophyte ordinations

is the smaller degree of stand separation based on lichens (cf. Appendices 1 and 2). For bryophytes, the first and second axes, with eigenvalues of 0.545 and 0.290 respectively, explain most of the variability; whereas, eigenvalues for the first and second axes on the lichen ordination were only 0.343 and 0.259. Lichen species assemblages vary less within the forest-tundra region than those of bryophytes.

For bryophytes, a moisture gradient clearly separates the southern, acidic, coarse-textured sites. This gradient is not as apparent with respect to the northern, basic, finer-textured sites. For lichens, stand separation in relation to moisture exists but is not as well-defined within either the northern, basic, finer-textured sites or the southern, acidic, coarse-textured sites.

Since bryophytes and lichens are not rooted in the soil and their absorbing surfaces are often not in contact with the soil, it is surprising that their distribution is significantly correlated with subsurface soil pH. There may be several causes for this. Windblown soil particles can collect between leaves and branches to be washed by rainwater and melting snow. Mosses with conducting systems, such as all *Polytrichum* spp., can take up soil water internally (Hébant 1977). Some lichens and bryophytes without internal conducting tissue might be able to take up soil water by capillary action within external structures (Gimingham and Smith 1971). Northern and alpine bryophytes and lichens growing below late snow patches can be influenced substantially by soil water as the melting snow percolates downslope (Kershaw 1977). Soil pH may influence the establishment of bryophyte propagules and young plants that are closer to the substrate

than the gametophytes (Anderson and Bourdeau 1955; Longton 1980). The same may be true of terricolous lichens. With their comparative lack of structural features to collect soil water, the adult plants may be less likely than juveniles to be influenced by soil pH.

These results indicate that bryophytes and lichens may be significantly influenced by soil pH. Uptake of the soil water may come about by capillary action either externally or internally, by inundation during spring runoff, or by washing of entrapped soil particles by rainwater.

Bryophytes and lichens compared to vascular plants

When bryophytes and lichens are ordinated together (Figs. 2.2c-2.5c), two groups can, again, be clearly recognized. The group on the left side of the four ordinations is distributed primarily along the second axis. The group in the centre and right is distributed in both directions. The basic, fine-textured northern group is to the right and the acidic, coarse-textured, southern group is to the left. Moisture separates both groups along the second axis and, as in the bryophyte ordination, the acidic group varies more in relation to moisture than the basic group.

Comparison of these ordinations (Figs. 2.2c - 2.5c) with the ordinations for vascular plants (Figs. 2.2d - 2.5d) indicates similar patterns. Soil pH, texture, and latitude are all highly correlated with the first axis; moisture is significantly correlated with both axes but more so with the second; and latitude, representing a complex gradient including climate and soil pH, texture, and moisture, is the factor most strongly correlated with the first axis. The bryophytes

and lichens in this data set appear to reflect the major environmental gradients as well as do vascular plants. Orbán (1987) in Hungary and Sérgio et al. (1987) in the Iberian Peninsula showed that bryophytes are as useful as indicators of environmental gradients as vascular plants. Stringer and Stringer (1974) found that in a southern boreal forest in southern Manitoba, bryophytes reflected the moisture gradient at least as well as vascular plants. Lee and La Roi (1979) showed that along a moisture gradient in the Rocky Mountains, change in species composition of understory vascular plants was similar to that of bryophytes. Distribution of lichens in prairie grassland communities corresponded well with that of vascular plants (Looman 1964a); the bryophyte and lichen associations are, however, related to the successional sequences of the vascular plants, and thus may be dependent on them (Looman 1964b). Oksanen (1983) found a larger difference in understory vascular plant species composition along a moisture macro-gradient in lichen-rich pine forests across Finland than that of bryophytes and lichens; he concluded that bryophytes and lichens may be relatively independent of moisture on a macro-environmental scale. Alpert and Oechel (1982) concluded that on a scale of kilometers, bryophyte and lichen communities may have a wider range than those of vascular plants, but on a scale of meters, they have a narrower range. In mid-range, as in this study, the community distributions appear to be about the same.

Schuster (1977) pointed out that bryophytes and lichens are independent of the macro-environment only when the macro-environment includes suitable micro-environments. In this study, soil pH and texture varied less within a stand than did moisture. That pH and

texture are more significantly correlated than moisture along the first ordination axis may reflect their consistency at the micro-site level. Moisture represents a complex of gradients. While soil moisture is governed to a certain extent by texture, it is also affected by slope, aspect, shade, wind exposure, and permafrost depth, so is more variable within a stand. As a result, moisture appears less significant at the stand (meso-environmental) level in determining species composition. Many studies have found that moisture-related factors, measured at the micro-environmental level, have the greatest effect on the distribution of bryophytes and lichens (e.g. Foote 1966; Lechowicz and Adams 1974; Busby et al. 1978; Lee and La Roi 1979; Alpert and Oechel 1982).

Indicators

Since pH appears to influence bryophyte and lichen species distribution, individual species can be examined for their preferences and identified as indicators. Table 2.5 lists the species that occurred in more than 3 sites, number of sites in which they occurred, and pH median and range. Forest-tundra species whose pH range is acidic (pH <7.0 with one exception allowed), basic (pH >/=7.0 with one exception allowed), or shows no preference (at least two occurrences </=5.5 and two occurrences >/=7.5) are listed in Table 2.6.

Two patterns emerge from these data. Only 13% of the species occurring in acidic sites are indicators, whereas 39% are indicators in basic sites (Table 2.7). Of the non-preferential species, a higher proportion occur in acidic sites than in basic sites, both of total species (57:41) and of each plant group (mosses, 52:27; hepatics,

38:26; lichens, 68:64). Thus, there appear to be more habitat specialists than generalists in the terrestrial bryophyte and lichen flora of basic soils in the forest-tundra, and more generalists than specialists in the terrestrial flora of acidic soils.

Secondly, the plant groups differ in proportion of specialist and generalist species. Mosses are the specialists: 64% of moss species are soil pH indicators compared with 48% of hepatics and only 25% of lichens. Lichens are the generalists: 61% of lichens are non-preferential species compared with only 26% of mosses and hepatics.

Since most of the specialists occur in basic areas, it is not surprising that most of the indicators in basic areas are mosses (67%), and most of the mosses in basic sites are indicators (59%) compared with only 35% of hepatics and 17% of lichens. In the acidic areas, the number of indicators of each plant type is about the same (4 mosses, 3 hepatics, 4 lichens) and the proportion of mosses, hepatics, and lichens that are indicators are all low (15%, 19%, and 10%, respectively). In contrast, the proportion of non-preferential moss species to total moss species in acidic areas is almost twice as high (52%) as in basic areas (27%). For lichens, there is a high proportion of non-preferential species in both acidic (68%) and basic (64%) areas.

The terrestrial bryophyte and lichen flora of acidic soils appears to have few unique species; the species of acidic areas overlap into the basic areas. In contrast, the terrestrial flora of basic soils has many unique species and fewer overlapping ones. Mosses are the specialists and they dominate the unique component of

basic areas; lichens are the generalists, overlapping into both areas; and hepatics lie midway between mosses and lichens in proportion of indicators and are similar to mosses in proportion of non-preferential species.

While it is not yet clear to what extent lichens absorb nutrients from the substrate, the fact that lichens numerically dominate the non-preferential group (27:20) and bryophytes, the indicator group (45:11), suggests that lichens may be less influenced by soil pH than are bryophytes. Lichens in closest contact with the substrate may be the most substrate-specific (Brodo 1973). Since the majority (75%) of terricolous lichens in this study are fruticose, the low degree of substrate specificity might be expected unless substrate affects the establishment of propagules and the survival of juvenile plants. Kershaw (1977), however, suggested that pH is of substantial importance to northern lichens, and that uptake of nutrients may occur during snowmelt when the lichens are inundated. Larson (1981) showed that there is significant variability in the mechanism of water uptake of lichen species with similar morphology: one might absorb water from the substrate surface while another relies strictly on precipitation. Autecological studies such as those of Larson using adult plants, and those of Armstrong (1981), germinating and propagating young plants on various substrates, could shed more light on the question of how much lichens depend on substrate nutrients.

Comparison of these indicators with those identified in other studies is difficult in that few quantitative studies of terricolous bryophyte and lichen pH indicators exist (e.g., Rypacek 1934; Shaw 1981; Nimis and Losi 1984; Horton 1988). Studies of bryophytes as

indicators of peatland pH conditions are more numerous (e.g., Jeglum 1971; Slack et al. 1980; Andrus 1986); however, pH for the peatland sites in this study was seldom measured. Furthermore, soil pH in other studies (if given) may be taken from a different soil horizon, often from just below the soil surface, rather than from the B horizon as was usually used in this study.

Only 4 bryophytes occurred in the acidic category and all occurred 5 or fewer times. Of the 23 hepatics that occurred in 4 or more sites where pH was measured, only 3 occurred only on acidic terrain. Hepatic species averaged 4.2/stand on acidic terrain and 5.8/stand on basic terrain. Vitt and Horton (1979) reported an increase in richness of hepatics with a change from calcareous to non-calcareous substrata in alpine areas. Schuster (1977) in Minnesota reported 63 "oxylophytic" and 43 circumneutral and "basiphilic" species. However, those studies included all, not just terricolous, species. Perhaps many of the acidophilic hepatic species are epiphytic, saxicolous, or semi-aquatic, occupying habitats where competition from other plants is not as great. In this study there were few acidic, wet-mesic and wet sites (7), and epiphytes and saxicols were exluded.

Four lichens are indicators of acidic conditions; two of these are *Cladonia* spp. Rypacek (1934) showed pH ranges for 8 *Cladonia* spp. Of the 3 in his study that would be considered acidophiles (pH < 5.5; soil sample taken from just below the plant), all occurred in this study at least once in sites with pH of 8.0. Kershaw (1977) labelled *Stereocaulon paschale* an acidophile, but in this study it was found in sites with pH as high as 8.0. A

preference for low pH is indicated, however, as 23 of the 28 occurrences (82%) were from acidic sites.

Most of the bryophyte indicators of basic conditions have been previously documented as calciphiles elsewhere. Surprisingly, *Pohlia cruda*, with 10 occurrences, is a widespread species that was expected to fall in the non-preferential group but, here, appears to prefer habitats with higher pH. *Plagiochila asplenoides* was noted by Schuster (1977) to show an exceedingly wide pH tolerance; in this study, it is clearly an indicator of basic conditions.

Some of my non-preferential species have distinct pH preferences elsewhere. For example, Steere and Inoue (1978) indicated that *Ptilidium ciliare* typically occurs on calcareous soil and humus in Alaska. In this study it was found more often on acidic terrain. In Minnesota it occurs in the circumneutral range (Schuster 1977). *Cladonia pyxidata* usually grows on acid mineral soils (Thomson 1984) but in this study it was found across the region with a pH range of 4.0 to 8.0 and a median of 7.6. Ahti (1961, in Kershaw 1977), commented that most *Cladonia* spp. avoid calcareous ground; yet in this study, all but 2 of the 21 species of *Cladonia* that occurred 4 or more times, occurred in sites with pH as high as 8.0, and 8 species occurred in the non-preferential group. *Cladonia mitis* and *Polytrichum juniperinum* were assigned to Jeglum's (1971) group with pH of 3.0 - 3.9.; however, 16 of the 47 occurrences of *Cladonia mitis* and 9 of the 31 occurrences of *Polytrichum juniperinum* were recorded in this study from study sites with pH >/= 7.0. In Jeglum's study, mean quantity and frequency of the species were used

to assign species to pH classes; in this study, assignments were based on presence.

These differences may be explained several ways. Firstly, the pH value assigned to the stand may not be the same as the pH of the micro-site. For example, *Gymnocolea inflata* occurred in a stand with pH of 8.0 but is an acidophile by other accounts (e.g. Steere and Inoue 1978; Schuster 1977), and the calciphile, *Oncophorus wahlenbergii*, occurred in a stand with pH of 5.5.

Secondly, the pH ranges of the species in these studies represent ecological not physiological measurements. Such factors as competition and lack or overabundance of water and light may alter the theoretical distribution based strictly on physiological tolerances (Zehr 1977). Several species are near the limit of their range (e.g. southern limit: *Dactylina arctica, Dicranum angustum, Aulacomnium acuminatum*; northern limit: *Cladonia multiformis, Ptilium crista-castrensis, Pleurozium schreberi*). At the limit of its range, a species showing no pH preference might be one that can tolerate less favourable conditions, e.g., a lower pH, in order to meet a physiological requirement for another condition, e.g., adequate moisture (Zehr 1977). A species with a narrower pH range than at other locations might not be able to tolerate the extremes of a physiological range if other conditions are not optimal.

Finally, pH may be gradually altered as succession proceeds within a plant community. Plants that germinated or propagated under one pH condition might persist as "relicts" during a successional stage that has a different pH condition.

This study points out the critical nature of quantitative studies in determining the substrate preference of bryophyte and lichen species. Frequently encountered statements on indicator value of particular bryophyte and lichen species need to be verified by correlations and experimental means.

2.5 CONCLUSIONS

Meso-environmental gradients of soil pH, texture, moisture, and latitude are strongly correlated with bryophyte, lichen, and vascular plant species distribution in the forest-tundra region of the NWT. Bryophyte and lichen species distributions appear to be influenced primarily by soil pH, soil texture, and latitude; latitude represents a complex gradient reflecting the climatic and edaphic differences between the northwestern and southeastern parts of the region.

Bryophytes from basic, medium- to fine-textured soils and northern latitudes are grouped together and stands within this group are widely spread along the first ordination axis. This variation in stand position is not strongly correlated with any of the measured variables, although a weak correspondence with the gradient from mesic to wet soil moisture is evident. Bryophytes from acidic, coarse-textured soils and southern latitudes are grouped together, and these stands are distributed clearly along a moisture gradient.

Lichens vary along a complex gradient from coarse-textured, acidic soils and southern latitudes to fine-textured, basic soils and northern latitudes. Lichens are also distributed on the basis of moisture.

Overall, there is less variability of lichen assemblages within the region compared to bryophytes. Bryophyte assemblages appear to be more variable towards the dry end of the moisture gradient than the wet end.

Terricolous bryophytes and lichens are useful indicators of soil pH, texture, and moisture just as are vascular plants. This is

especially apparent with respect to pH: certain bryophytes and lichens occur consistently within an acidic or a basic pH range and can be used as indicators. The terrestrial bryophyte and lichen flora of acidic areas appears to have few unique species; those of acidic areas overlap into the basic areas. Conversely, the terrestrial flora of basic areas has many unique species and fewer overlapping ones. Mosses are the specialists and they dominate the indicator species of basic soils; lichens are the generalists, overlapping into both areas; and hepatics lie midway between mosses and lichens in proportion of indicators and are similar to mosses in proportion of non-preferential species.

Table 2.1. Representative plants of the forest-tundra region, NWT.

DRY, DRY-MESIC	MESIC	WET-MESIC, WET	
Mineral Soil, Acidic, Treed			
Picea mariana	*Picea mariana*	*Picea mariana*	
Empetrum nigrum	*Betula glandulosa*(north)	*Larix laricina*	
Vaccinium vitis-idaea	*Betula papyrifera*(south)	*Alnus crispa*	
V. uliginosum	ericads*	*Salix planifolia*	
Ptilidium ciliare	*Dicranum elongatum*	*Betula glandulosa*	
Cladonia spp.	*Polytrichum juniperinum*	ericads	
Stereocaulon paschale	*Ptilidium ciliare*	*Rubus chamaemorus*	
Cetraria nivalis	*Cladonia* spp.	*Equisetum scirpoides*	
C. ericetorum	*Stereocaulon paschale*	*Sphagnum* spp.	
	Cetraria spp.	*Aulacomnium turgidum*	
	Nephroma arcticum	*Gymnocolea inflata*	
Mineral Soil, Acidic, Treeless			
Empetrum nigrum	*Betula glandulosa*	(Tall shrub)	(Low shrub)
Vaccinium vitis-idaea	*Salix arbusculoides*	*Salix planifolia*	*Betula glandulosa*
V. uliginosum	*Salix glauca*	*S. glauca*	ericads
Polytrichum piliferum	*Carex bigelowii*	*Alnus crispa*	*Salix* spp.
Alectoria ochroleuca	ericads	*Betula glandulosa*	*Cassiope tetragona*
Cornicularia aculeata	*Polytrichum juniperinum*	*Andromeda polifolia*	*Sphagnum* spp.
Cetraria nivalis	*Dicranum elongatum*	*Carex aquatilis*	*Aulacomnium palustre*
C. ericetorum	*Hylocomium splendens*	*Pedicularis labradorica*	*Barbilophozia binsteadii*
Thamnolia subuliformis	*Ptilidium ciliare*	*Sphagnum* spp.	*Drepanocladus fluitans*
	Cladonia spp.	*Aulacomnium palustre*	

*ericads = *Arctostaphylos alpina*, *Empetrum nigrum* (Empetraceae), *Ledum decumbens*, *L. groenlandicum*, *Vaccinium uliginosum*, *V. vitis-idaea*

Table 2.1 concluded.

DRY, DRY-MESIC	MESIC	WET-MESIC, WET	
Mineral Soil, Basic, Treed			
Picea glauca	*Picea glauca*	*Picea glauca*	
Dryas integrifolia	*Betula glandulosa*	*Betula glandulosa*	
Carex rupestris	*Salix* spp.	*Salix* spp.	
Oxytropis spp.	*Carex* spp.	*Carex* spp.	
Thuidium abietinum	*Lupinus arcticus*	*Lupinus arcticus*	
Ditrichum flexicaule	*Hedysarum alpinum*	*Hedysarum alpinum*	
Cetraria cucullata	*Rhytidium rugosum*	*Oxytropis* spp.	
C. tilesii	*Tomenthypnum nitens*	*Hypnum bambergeri*	
Cladonia spp.	*Hylocomium splendens*	*Drepanocladus revolvens*	
	Cladonia spp.	*Cinclidium stygium*	
Mineral Soil, Basic, Treeless			
Dryas integrifolia	*Dryas integrifolia*	(Tall shrub)	(Low shrub)
Salix niphoclada	*Arctostaphylos rubra*	*Salix lanata*	*Cassiope tetragona*
Carex spp.	*Carex* spp.	*Carex aquatilis*	*Dryas integrifolia*
Oxytropis spp.	*Oxytropis* spp.	*Equisetum arvense*	*Carex aquatilis*
Tortella fragilis	*Lupinus arcticus*	*Eriophorum* spp.	*Eriophorum* spp.
Ditrichum flexicaule	*Hedysarum alpinum*	*Salix reticulata*	*Hypnum bambergeri*
Cetraria spp.	*Rhytidium rugosum*	*Drepanocladus revolvens*	*Cinclidium stygium*
Cornicularia divergens	*Distichium capillacium*	*Campylium stellatum*	*Bryum pseudotriquetrum*
Thamnolia subuliformis	*Bryum pseudotriquetrum*	*Cinclidium stygium*	*Aulacomnium acuminatum*
Dactylina ramulosa	*Cetraria* spp.	*Orthothecium chryseum*	*Oncophorus wahlenbergii*
Ochrolechia spp.	*Cladonia pocillum*	*Lophozia (Leiocolea)* spp.	*Orthothecium strictum*
Fens: *Carex* spp., *Eriophorum* spp., *Meesia triquetra, Scorpidium turgescens, S. scorpioides, Calliergon giganteum, C. trifarium, Loeskypnum badium, Catoscopium nigritum.*			
Bogs: ericads, *Betula glandulosa, Empetrum nigrum, Sphagnum fuscum, S. capillifolium, Gymnocolea inflata, Cladonia deformis, C. mitis, C. rangiferina, Cetraria cucullata, C. nivalis.*			

Table 2.2. Location, soil parameters, and vegetation characteristics of each study site. - indicates data not available. LOSA=loamy sand, SALO= sandy loam, SILO=silty loam, CLLO=clay loam, SICL=silty clay loam; D=dry, DM=dry-mesic, M=mesic, WM=wet-mesic, W=wet; #=number of; SPP=total species, M=mosses, H=hepatics, L=lichens; UTU=upland tundra, B-F=bog-fen, F-T=forest-tundra, OCF=open crown forest, CCF=closed crown forest, STU=shrubland, WTU=wetland.

STUDY SITE	LONGITUDE °	′	"	LATITUDE °	′	"	SOIL pH	SOIL TEXTURE	SOIL MOISTURE	#SPP	#M	#H	#L	VEG TYPE
Dubawnt study area:														
S30	112	47	0	62	30	30	4.7	LOSA	DM	24	5	1	18	CCF
S31	104	43	45	61	14	0	5.3	LOSA	DM	30	7	6	17	F-T
S33	104	15	20	61	23	20	5.2	LOSA	DM	21	4	2	15	F-T
S34	104	11	10	61	25	25	5.4	LOSA	M	26	6	2	18	OCF
S35	104	2	40	61	25	40	6.0	LOSA	M	18	4	4	10	F-T
S36	103	52	40	61	22	10	6.2	SAND	DM	22	7	1	14	F-T
S37	103	41	45	61	25	20	5.4	LOSA	M	22	11	8	3	F-T
S38	103	27	45	61	29	35	5.9	LOSA	DM	20	5	3	12	F-T
S40	103	27	10	61	14	35	5.3	LOSA	DM	23	8	3	12	OCF
S41	103	39	35	61	6	30	5.9	SALO	DM	24	5	5	14	OCF
S43	103	42	55	60	54	35	6.0	SALO	WM	32	7	5	20	F-T
S45	103	44	10	61	5	50	5.7	SALO	DM	26	9	4	13	OCF
S47	103	20	20	61	28	30	6.9	LOSA	DM	39	7	12	20	F-T
S48	103	13	20	61	38	10	6.2	LOSA	DM	33	10	8	15	F-T
S49	103	13	15	61	48	15	5.7	LOSA	DM	38	10	9	19	F-T
S50	103	8	0	61	53	10	5.7	SAND	M	12	3	4	5	F-T
S51	103	8	20	61	54	20	7.0	SALO	M	45	13	8	24	F-T
S53	102	55	30	62	3	30	6.4	SALO	WM	28	14	12	2	F-T
S54	102	49	30	62	16	15	5.5	SAND	M	38	12	7	19	F-T
S55	102	55	35	62	19	45	7.0	SILO	M	31	9	6	16	F-T
S56	102	43	50	62	29	5	5.2	SALO	M	18	6	5	7	UTU
S57	103	11	30	62	28	30	6.0	LOSA	M	24	5	7	12	F-T
S58	103	31	50	62	25	20	5.7	LOSA	DM	33	6	9	18	UTU
S59	103	50	20	62	18	35	5.9	LOSA	M	39	15	10	14	F-T
T28	102	49	0	62	41	0	-	-	W	14	11	3	0	OCF

Table 2.2 continued.

STUDY SITE	LONGITUDE °	′	"	LATITUDE °	′	"	SOIL pH	SOIL TEXTURE	SOIL MOISTURE	#SPP	#M	#H	#L	VEG TYPE
Snare-Yellowknife study area:														
S01	115	59	15	63	31	45	4.2	-	DM	15	4	1	10	OCF
S04	116	10	0	63	26	0	5.0	CLLO	M	11	7	3	1	OCF
S07	115	20	15	64	3	45	5.5	LOAM	M	13	1	1	11	CCF
S12	113	20	30	64	25	30	5.4	LOSA	M	17	3	0	14	F-T
S14	113	3	0	64	33	0	4.2	SALO	M	22	5	3	14	UTU
S18	113	32	20	63	54	0	4.0	LOSA	DM	15	3	2	10	OCF
S20	113	45	20	63	34	30	4.0	SALO	DM	15	3	2	10	OCF
S21	112	17	30	63	19	10	6.0	SAND	D	15	2	1	12	F-T
S22	112	9	15	63	28	15	6.8	LOSA	M	15	1	0	14	UTU
S26	112	25	30	63	7	45	6.9	-	W	14	10	1	3	OCF
R01	111	4	0	64	4	15	5.5	-	WM	29	12	4	13	F-T
R02	111	4	15	64	4	35	5.5	-	W	21	17	4	0	FEN
R03	111	4	45	64	4	35	5.5	-	WM	26	8	7	11	B-F
R04A	111	3	30	64	4	30	5.5	-	DM	14	3	0	11	UTU
R04B	111	3	30	64	4	30	5.5	-	DM	24	5	2	17	UTU
R05A	111	3	0	64	4	25	5.5	-	DM	33	6	2	25	UTU
R05B	111	3	0	64	4	25	5.5	-	D	9	1	1	7	UTU
Coppermine-Kendall study area:														
SA1	114	16	0	65	44	20	8.0	SILO	WM	41	14	7	20	OCF
SA2	114	20	0	66	10	15	-	-	M	37	15	6	16	UTU
S61	114	17	15	65	43	50	8.0	SICL	M	61	24	7	30	F-T
S62	114	25	50	65	57	10	8.0	LOAM	WM	39	20	6	13	OCF
S64	115	9	15	66	42	35	8.0	SILO	WM	34	22	2	10	WTU
S65	115	9	5	66	42	20	7.2	SILO	W	31	15	3	13	OCF
S66A	115	45	35	66	51	10	8.0	LOAM	DM	29	10	0	19	UTU
S67	116	20	10	66	51	10	8.0	SILO	WM	35	15	4	16	OCF
S69	116	20	40	67	7	35	7.2	SILO	M	61	35	11	15	UTU
S70	116	36	35	67	14	50	8.0	SILO	DM	45	25	7	13	UTU
S72	116	59	15	67	25	20	8.0	SILO	M	48	27	2	19	UTU
S73	117	0	0	67	24	45	8.0	CLAY	W	24	16	6	2	STU
S74	117	35	0	67	27	55	7.0	SICL	WM	19	11	4	4	F-T
R11	114	38	15	66	32	55	-	-	W	39	19	13	7	F-T
R12	114	38	15	66	32	40	8.0	-	M	46	20	13	13	UTU
R13	115	9	25	66	42	40	-	-	DM	14	8	0	6	UTU
R14P	116	19	35	66	51	0	-	-	W	6	6	0	0	FEN
R14S	116	19	35	66	51	0	-	-	WM	51	23	17	11	BOG
R15	117	31	20	67	28	30	-	-	W	46	32	9	5	WTU
R16	117	31	50	67	28	20	-	-	DM	50	23	9	18	UTU

Table 2.2 concluded.

STUDY SITE	LONGITUDE °	′	″	LATITUDE °	′	″	SOIL pH	SOIL TEXTURE	SOIL MOISTURE	#SPP	#M	#H	#L	VEG TYPE
Horton study area:														
S75	122	25	0	67	35	50	8.0	LOSA	M	28	14	3	11	F-T
S76	122	53	45	67	47	40	8.0	SICL	DM	42	22	9	11	UTU
S77	123	12	15	67	59	10	8.0	SICL	M	37	16	5	16	OCF
S78	123	27	45	68	13	15	8.0	SILO	WM	84	41	22	21	F-T
S791	123	41	15	68	27	40	7.2	LOAM	WM	56	32	11	13	WTU
S792	123	41	15	68	27	40	7.2	LOAM	M	28	15	1	12	UTU
S793	123	41	15	68	27	40	7.2	SALO	D	17	6	0	11	UTU
S80	123	45	5	68	27	45	8.0	SALO	M	23	16	0	7	F-T
S81	124	35	40	68	40	50	8.0	-	M	36	18	5	13	OCF
S82	125	27	30	68	55	30	8.0	SICL	DM	50	24	7	19	UTU
S83	125	57	30	69	2	30	8.0	SAND	M	35	23	1	11	OCF
S84	125	56	15	69	2	0	8.0	CLAY	DM	40	34	0	6	UTU
S85	126	22	45	69	9	10	7.6	CLLO	WM	51	35	8	8	OCF
R17	122	24	20	67	35	30	-	-	M	30	6	2	22	UTU
R18P	122	25	40	67	36	20	-	-	W	20	17	2	1	FEN
R18S	122	25	40	67	36	20	-	-	WM	29	14	2	13	BOG
R19	123	27	0	68	13	20	-	-	W	6	6	0	0	FEN
R20	123	26	50	68	13	30	-	-	M	52	38	6	8	WTU
R21	124	7	0	68	39	0	7.4	SILT	M	43	27	7	9	STU
R22P	124	7	0	68	39	5	-	-	W	19	15	4	0	FEN
R22S	124	7	0	68	39	5	-	-	WM	53	36	9	8	BOG
R23	125	55	20	69	0	50	8.0	-	WM	29	15	8	6	STU
R24P	125	55	0	69	0	30	-	-	W	27	23	3	1	FEN
R24S	125	55	0	69	0	30	-	-	WM	41	15	8	18	BOG
R25	126	52	10	69	29	50	5.3	CLLO	WM	12	3	5	4	STU
R27	126	59	40	69	45	10	-	CLLO	DM	36	24	1	11	UTU
R28C	126	59	35	69	44	50	-	CLLO	M	26	12	5	9	UTU
R28T	126	59	35	69	44	50	-	CLLO	W	10	10	0	0	WTU
Tuktoyaktuk-Inuvik study area:														
R34	126	58	35	69	45	30	-	CLLO	WM	26	22	2	2	STU
R351	133	2	20	69	23	0	-	-	DM	36	18	5	13	UTU
R352	133	2	20	69	23	0	-	-	WM	20	8	2	10	B-F
R355	133	2	20	69	23	0	-	-	WM	25	11	10	4	B-F
T45	133	29	15	68	18	40	-	-	M	51	19	19	13	OCF

Table 2.3. Summary of physical variables for the five study areas.

	Dubawnt	Snare-Yellowknife	Coppermine-Kendall	Horton	Tuktoyaktuk-Inuvik
pH range	5.2 - 7.0	4.0 - 6.9	7.0 - 8.0	7.2 - 8.0*	-
pH median	5.7	5.5	8.0	8.0	-
modal moisture	dry-mesic	dry-mesic	wet-mesic	mesic	wet-mesic
modal texture	loamy sand	loamy sand	silty loam	clay loam	-
latitude range(°N)	60°54′ to 62°41′	62°30′ to 64°43′	65°43′ to 67°28	67°35′ to 69°45′	68°18′ to 69°23′
number of sites	24	18	20	29	4

*with the exception of pH 5.3 in the Smoking Hills (lower Horton R.)

Table 2.4. Correlation coefficients (Spearman's rho) among the physical factors and axes 1 and 2 of the DCA ordinations. B=bryophytes, L=lichens, V=vascular plants; d.f.=93 (latitude and moisture), 68 (pH), and 60 (texture); *** significant @ p</=0.001, ** @ p</=0.01, * @ p</=0.05.

	Latitude	pH	Texture	Moisture
pH	0.605***			
Texture	0.672***	0.509***		
Moisture	0.337***	0.283*	0.401**	
Axis 1: B,L	0.756***	0.725***	0.688***	0.462***
2: B,L	0.289**	0.066	0.314*	0.700***
Axis 1: B	-0.681***	-0.704***	-0.616***	-0.319**
2: B	0.351***	-0.088	0.297*	0.426***
Axis 1: L	0.741***	0.662***	0.645***	0.274**
2: L	-0.304**	-0.230	-0.264*	-0.504***
Axis 1: V	-0.777***	-0.768***	-0.635***	-0.384***
2: V	0.075	-0.465***	-0.125	0.433***

Table 2.5a. Median and range or soil pH for hepatic and moss species occurring in >/=4 study sites for which pH was determined. # = number of sites in which the species occurred.

SPECIES	#	MEDIAN	RANGE	SPECIES	#	MEDIAN	RANGE
Anastrophyllum minutum	30	6.6	4.0-8.0	*D. fuscescens*	5	5.9	5.5-6.9
Arnellia fennica	4	8.0	7.6-8.0	*D. groenlandicum*	15	7.0	5.5-8.0
Barbilophozia barbata	4	7.6	7.2-8.0	*D. muehlenbeckii*	9	7.0	4.0-8.0
B. binsteadii	10	6.7	4.2-8.0	*D. scoparium*	6	7.0	5.3-8.0
B. kunzeana	13	7.2	5.4-8.0	*D. spadiceum*	4	7.6	7.2-8.0
Blepharostoma trichophyllum	14	7.8	5.3-8.0	*D. undulatum*	4	5.3	4.2-6.0
Cephaloziella arctica	6	6.4	5.2-8.0	*Distichium capillaceum*	24	8.0	7.0-8.0
C. divaricata	6	6.1	5.3-8.0	*Ditrichum flexicaule*	27	8.0	6.9-8.0
C. hampeana	6	6.4	5.3-8.0	*Drepanocladus revolvens*	11	8.0	7.0-8.0
C. rubella	23	6.9	5.2-8.0	*D. uncinatus*	19	7.6	4.2-8.0
Gymnocolea inflata	5	5.5	5.3-8.0	*Encalypta procera*	4	8.0	7.6-8.0
Lophozia alpestris	6	5.6	5.2-8.0	*E. rhaptocarpa*	7	8.0	7.2-8.0
L. collaris	4	8.0	8.0-8.0	*Eurhynchium pulchellum*	5	8.0	7.2-8.0
L. excisa	11	7.2	5.7-8.0	*Hylocomium splendens*	35	7.2	4.7-8.0
L. longidens	5	6.9	5.5-7.0	*Hypnum bambergeri*	21	8.0	7.0-8.0
L. obtusa	5	8.0	5.0-8.0	*Isopterygium pulchellum*	10	8.0	7.2-8.0
L. ventricosa	14	6.0	5.3-8.0	*Meesia uliginosum*	8	8.0	7.2-8.0
Odontochisma macounii	4	8.0	7.6-8.0	*Myurella julacea*	16	8.0	7.0-8.0
Plagiochila asplenoides	4	8.0	7.2-8.0	*M. tenerrima*	9	8.0	7.2-8.0
Ptilidium ciliare	46	5.9	4.0-8.0	*Oncophorus wahlenbergii*	14	8.0	5.5-8.0
Scapania gymnostomophila	8	7.8	7.2-8.0	*Orthothecium chryseum*	4	7.8	7.2-8.0
Tritomaria exectiformis	8	6.0	5.2-8.0	*O. strictum*	7	8.0	7.2-8.0
T. quinquedentata	7	8.0	7.2-8.0	*Platydictya jungermannioides*	4	7.8	7.4-8.0
Aulacomnium acuminatum	12	8.0	7.2-8.0	*Pleurozium schreberi*	15	5.9	4.7-8.0
A. palustre	17	7.0	5.0-8.0	*Pohlia cruda*	10	8.0	7.2-8.0
A. turgidum	22	5.8	4.2-8.0	*P. nutans*	37	5.9	4.0-8.0

Table 2.5a concluded.

SPECIES	#	MEDIAN	RANGE	SPECIES	#	MEDIAN	RANGE
Brachythecium plumosum	4	8.0	7.4-8.0	*Polytrichum juniperinum*	31	5.7	4.0-8.0
B. turgidum	7	8.0	6.9-8.0	*P. piliferum*	27	5.9	4.2-8.0
Bryoerythrophyllum recurvirostrum	8	8.0	7.2-8.0	*Ptilium crista-castrensis*	5	6.2	5.4-8.0
Bryum pseudotriquetrum	27	8.0	6.9-8.0	*Rhacomitrium lanuginosum*	5	7.2	5.5-8.0
Campylium stellatum	19	8.0	7.0-8.0	*Rhytidium rugosum*	26	8.0	5.3-8.0
Catoscopium nigritum	5	8.0	7.2-8.0	*Scorpidium turgescens*	10	8.0	7.0-8.0
Ceratodon purpureus	19	6.2	5.2-8.0	*Sphagnum russowii*	5	6.4	5.5-7.0
Cirriphyllum cirrosum	5	7.6	7.2-8.0	*Thuidium abietinum*	15	8.0	7.2-8.0
Dicranum acutifolium	32	6.4	4.7-8.0	*Tomenthypnum nitens*	28	8.0	5.5-8.0
D. amannii	5	5.7	5.2-7.2	*Tortella fragilis*	13	8.0	7.2-8.0
D. angustum	11	6.4	5.4-8.0	*Tortella tortuosa*	16	8.0	7.2-8.0
D. elongatum	21	5.5	4.0-8.0	*Tortula ruralis*	6	8.0	8.0-8.0

Table 2.5b. Median and range of soil pH for lichen species occurring in >/=4 study sites for which pH was determined. # = number of sites in which the species occurred.

SPECIES	#	MEDIAN	RANGE	SPECIES	#	MEDIAN	RANGE
Alectoria nigricans	7	7.0	5.5-8.0	*Cladonia pocillum*	11	8.0	7.0-8.0
A. ochroleuca	22	5.9	4.2-8.0	*C. pyxidata*	19	7.6	4.0-8.0
Bryoria nitidula	13	5.9	5.2-8.0	*C. rangeriferina*	44	5.8	4.0-8.0
Cetraria andrejevii	8	5.6	5.3-8.0	*C. stellaris*	17	6.2	4.7-8.0
C. cucullata	45	7.2	5.2-8.0	*C. subfurcata*	4	7.5	5.5-8.0
C. ericetorum	28	5.6	4.0-8.0	*C. uncialis*	23	5.9	5.2-8.0
C. islandica	24	7.2	5.4-8.0	*Cornicularia aculeata*	12	5.9	4.2-8.0
C. laevigata	23	7.2	5.3-8.0	*C. divergens*	28	6.0	4.2-8.0
C. nivalis	57	6.9	4.0-8.0	*Dactylina arctica*	13	7.2	5.5-8.0
C. tilesii	12	8.0	7.0-8.0	*Hypogymnia physodes*	6	8.0	5.2-8.0
Cladonia amaurocraea	26	5.9	4.0-8.0	*Masonhalea richardsonii*	14	8.0	4.2-8.0
C. cenotea	6	6.2	5.2-8.0	*Nephroma arcticum*	4	5.8	5.7-7.0
C. chlorophaea	20	7.2	4.0-8.0	*Ochrolechia upsaliensis*	4	8.0	8.0-8.0
C. coccifera	11	6.0	5.4-8.0	*Peltigera aphthosa*	25	7.2	4.2-8.0
C. cornuta	13	6.9	4.7-8.0	*P. canina*	17	8.0	5.5-8.0
C. crispata	12	5.5	4.0-6.9	*P. malacea*	20	6.0	4.0-8.0
C. deformis	9	6.9	4.7-8.0	*P. polydactyla*	4	6.1	4.2-8.0
C. gracilis	39	5.9	4.0-8.0	*Physconia muscigena*	5	7.4	7.2-8.0
C. mitis	47	6.0	4.0-8.0	*Stereocaulon paschale*	28	5.8	4.2-8.0
C. multiformis	5	5.5	4.7-6.9	*S. tomentosum*	6	7.1	4.0-8.0
C. phyllophora	11	6.0	4.0-8.0	*Thamnolia subuliformis*	16	8.0	4.2-8.0
C. pleurota	12	5.7	4.0-8.0	*Xanthoparmelia separata*	9	5.7	4.2-8.0

Table 2.6. Forest-tundra hepatic, moss, and lichen indicators of soil pH. Excluding the lowest and highest values, acidic = pH <7.0, basic = pH >/=7.0, non-preferential = two or more of pH </=5.5 and two or more of pH >/=7.5. All species occurred in 4 or more sites at which pH was determined.

ACIDIC	BASIC	
Cephaloziella divaricata	*Arnellia fennica*	*Hypnum bambergeri*
Lophozia alpestris	*Barbilophozia barbata*	*Isopterygium pulchellum*
Tritomaria exectiformis	*Lophozia collaris*	*Meesia uliginosum*
Dicranum amannii	*L. obtusa*	*Myurella julacea*
D. fuscescens	*Odontochisma macounii*	*M. tenerrima*
D. undulatum	*Plagiochila asplenoides*	*Onchophorus wahlenbergii*
Ptilium crista-castrensis	*Scapania gymnostomophila*	*Orthothecium chryseum*
Cetraria andrejevii	*Tritomaria quinquedentata*	*O. strictum*
Cladonia crispata	*Aulacomnium acuminatum*	*Platydictya jungermannioides*
C. multiformis	*Brachythecium plumosum*	*Pohlia cruda*
Nephroma arcticum	*B. turgidum*	*Scorpidium turgescens*
	Bryoerythrophyllum recurvirostrum	*Thuidium abietinum*
	Bryum pseudotriquetrum	*Tortella fragilis*
	Campylium stellatum	*T. tortuosa*
	Catoscopium nigritum	*Tortula ruralis*
	Cirriphyllum cirrosum	*Cetraria tilesii*
	Dicranum spadiceum	*Cladonia pocillum*
	Distichium capillaceum	*C. subfurcata*
	Ditrichum flexicaule	*Hypogymnia physodes*
	Drepanocladus revolvens	*Ochrolechia upsaliensis*
	Encalypta procera	*Peltigera canina*
	E. rhaptocarpa	*Physconia muscigena*
	Eurhynchium pulchellum	

NON-PREFERENTIAL		
Anastrophyllum minutum	*Pohlia nutans*	*Cladonia gracilis*
Cephaloziella rubella	*Polytrichum juniperinum*	*C. mitis*
Barbilophozia kunzeana	*P. piliferum*	*C. phyllophora*
B. binsteadii	*Rhytidium rugosum*	*C. pleurota*
Lophozia ventricosa	*Alectoria ochroleuca*	*C. pyxidata*
Ptilidium ciliare	*Bryoria nitidula*	*C. rangiferina*
Aulacomnium palustre	*Cetraria cucullata*	*C. stellaris*
A. turgidum	*C. ericetorum*	*C. uncialis*
Ceratodon purpureus	*C. islandica*	*Cornicularia aculeata*
Dicranum acutifolium	*C. laevigata*	*C. divergens*
D. elongatum	*C. nivalis*	*Masonhalea richardsonii*
D. groenlandicum	*Cladonia amaurocraea*	*Peltigera aphthosa*
D. muehlenbeckii	*C. cenotea*	*P. malacea*
Drepanocladus uncinatus	*C. chlorophaea*	*Stereocaulon paschale*
Hylocomium splendens	*C. cornuta*	*Thamnolia subuliformis*
Pleurozium schreberi	*C. deformis*	

Table 2.7. Comparison of number (#) and proportion of indicator, non-preferential, and residual species in acidic and basic sites for each plant group and for total species.

	Mosses	Hepatics	Lichens	Total
# indicator species	34	11	11	56
% of indicator species to total species	64	48	25	47
# acidic indicators	4	3	4	11
% of acidic indicators to species in acidic sites	15	19	10	13
# basic indicators	30	8	7	45
% of basic indicators to species in basic sites	59	35	17	39
# non-preferential species	14	6	27	47
% of non-preferential species to total species	26	26	61	39
% of non-preferentials to species in acidic sites	52	38	68	57
% of non-preferentials to species in basic sites	27	26	64	41
# residual species	5	6	6	17
% of residual species to total species	11	26	14	14
total # of species	53	23	44	120
# species occurring in acidic sites	27	16	40	83
# species occurring in basic sites	51	23	42	116

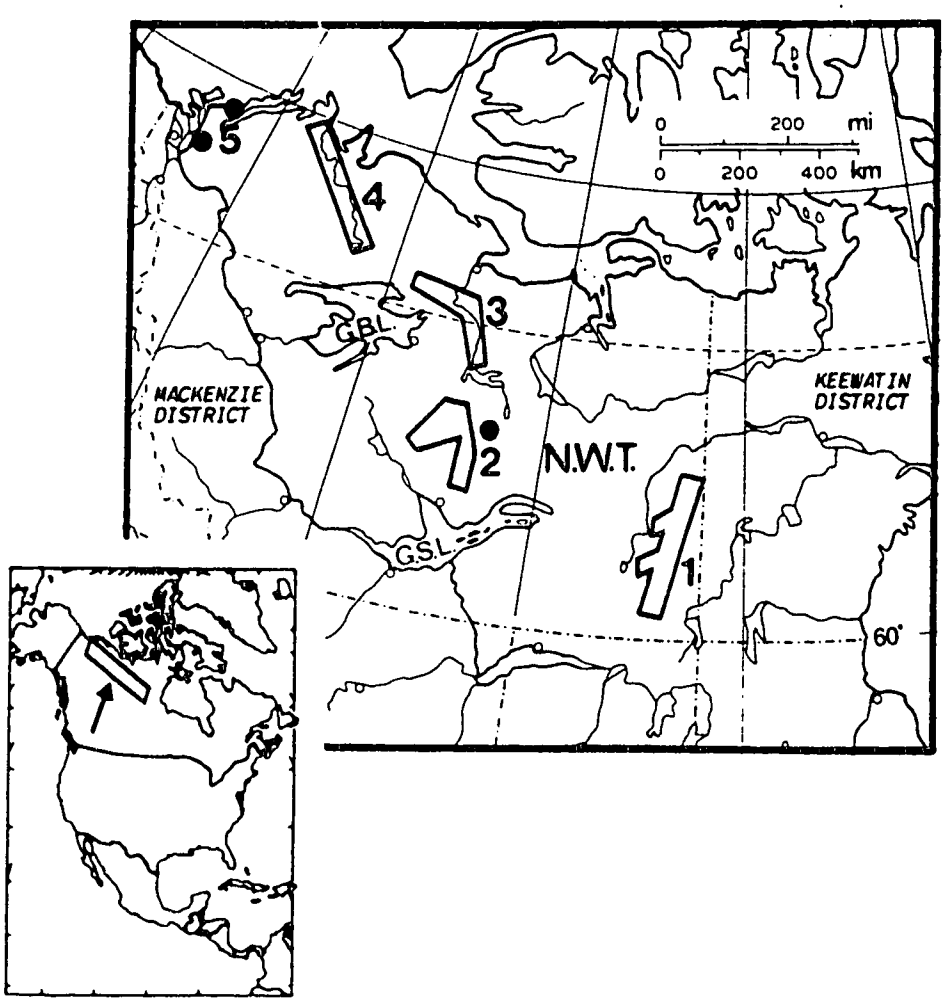

Fig. 2.1. Location of each study area: 1 = Dubawnt; 2 = Snare-Yellowknife, with Salmita area indicated to east; 3 = Coppermine-Kendall; 4 = Horton; 5 = Tuktoyaktuk-Inuvik.

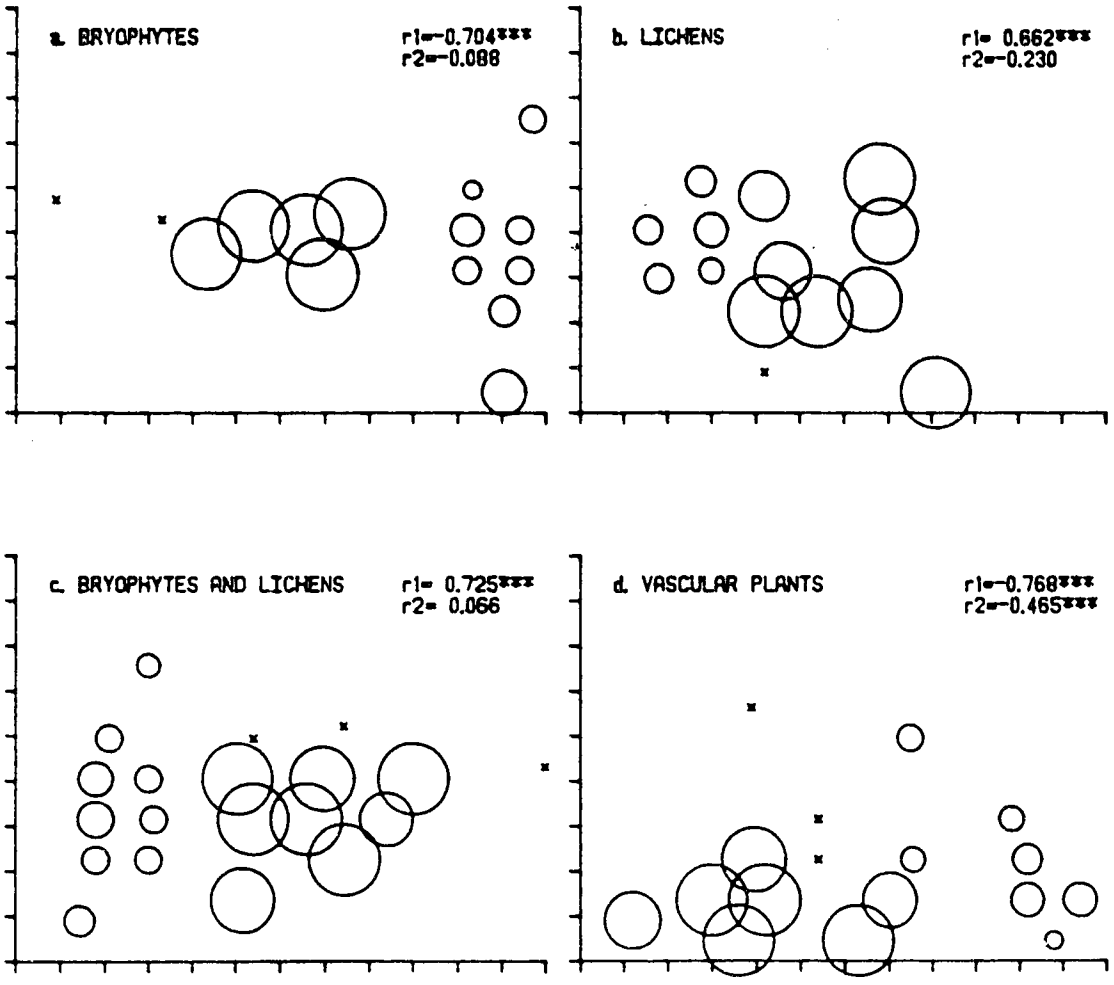

Fig. 2.2. Summary depictions of soil pH plotted over stand position on the DECORANA ordinations. Circle size increases with increasing pH; r1 (1st axis) and r2 (2nd axis) = rank correlation coefficient (Spearman's rho), d.f.= 68, *** significant @ p</=0.001, ** @ p</=0.01, * @ p</=0.05.

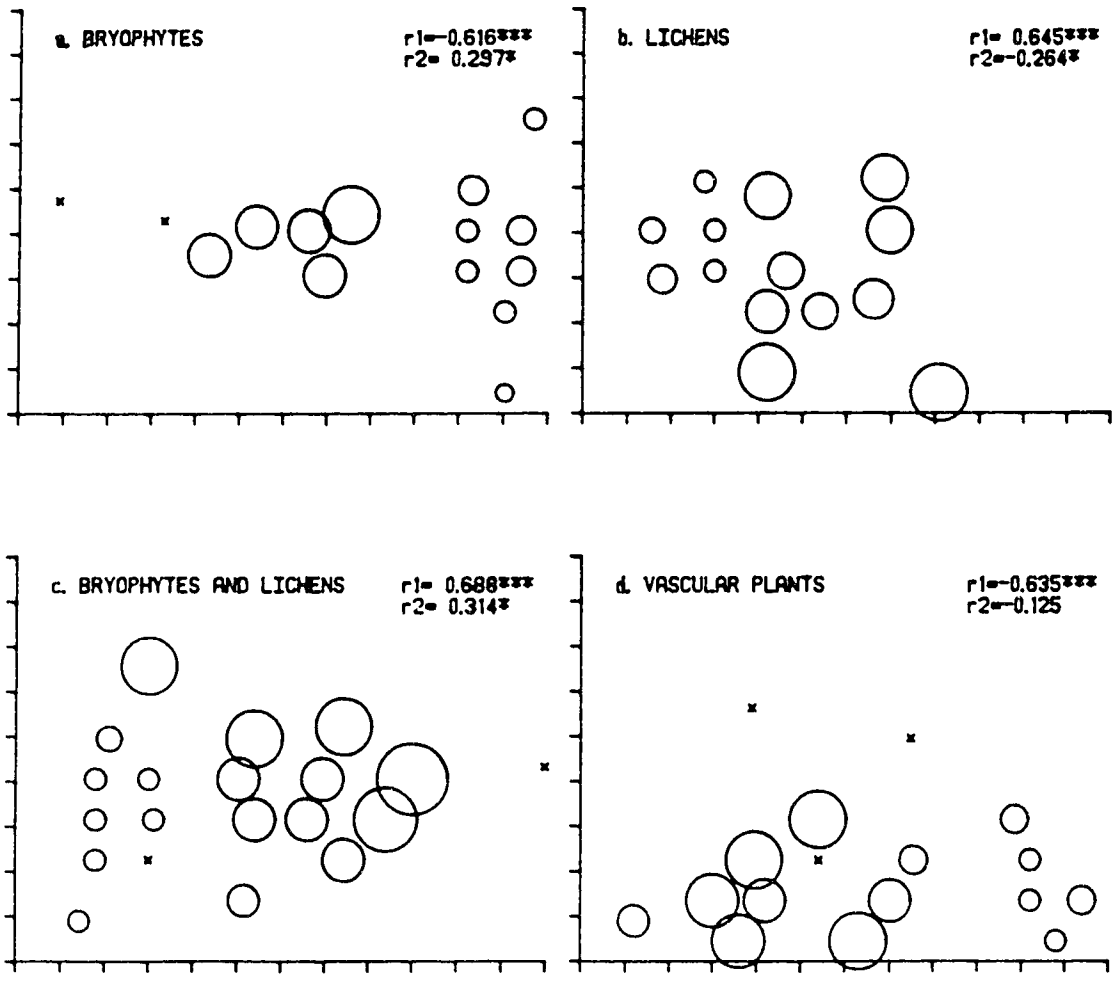

Fig. 2.3. Summary depictions of soil texture plotted over stand position on the DECORANA ordinations. Circle size increases from coarse to fine; r1 (1st axis) and r2 (2nd axis) = rank correlation coefficient (Spearman's rho), d.f.= 61, *** significant @ p</=0.001, ** @ p</=0.01, * @ p</=0.05.

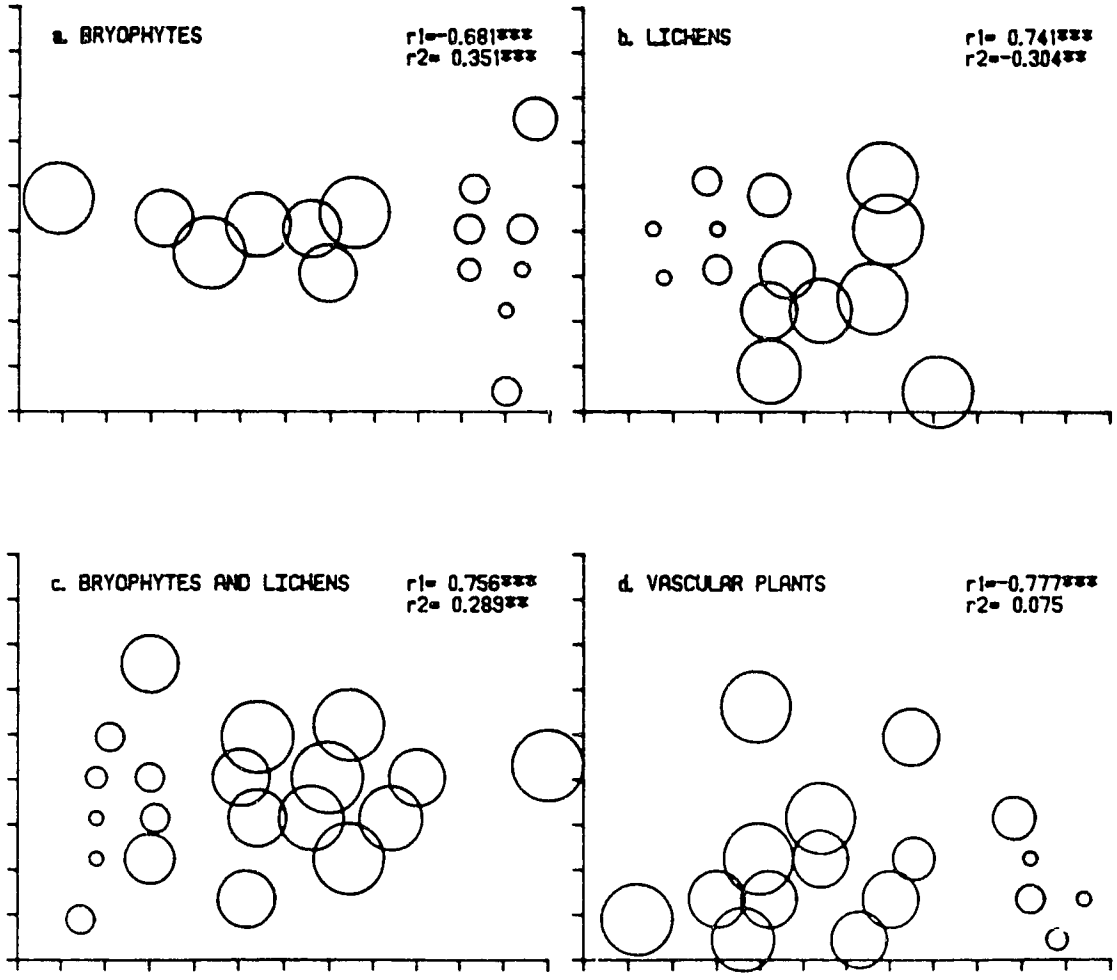

Fig. 2.4. Summary depictions of latitude plotted over stand position on the DECORANA ordinations. Circle size increases from south to north; r1 (1st axis) and r2 (2nd axis) = rank correlation coefficient (Spearman's rho), d.f.= 93 except 84 for LICHENS, *** significant @ p</=0.001, ** @ p</=0.01, * @ p</=0.05.

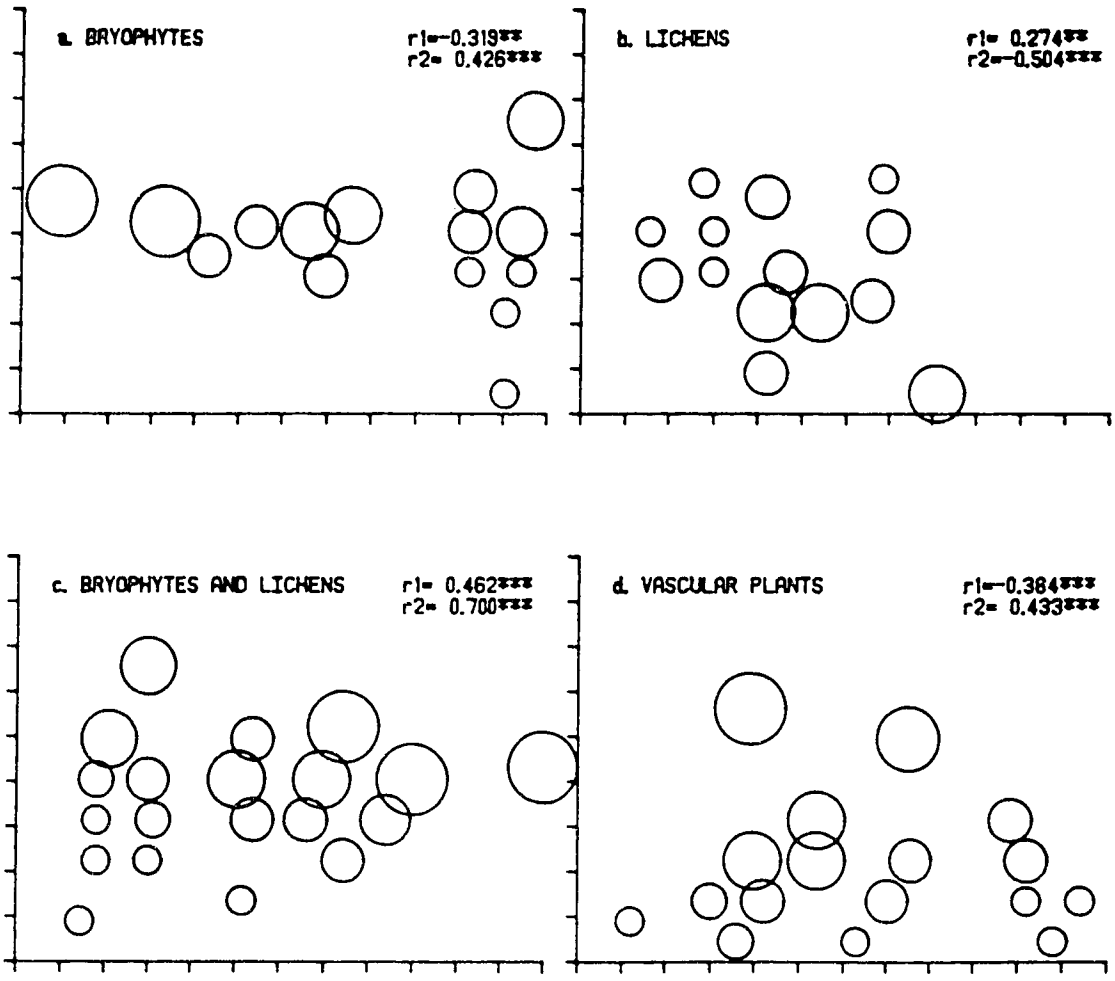

Fig. 2.5. Summary depictions of soil moisture plotted over stand position on the DECORANA ordinations. Circle size increases with increasing moisture; r1 (1st axis) and r2 (2nd axis) = rank correlation coefficient (Spearman's rho), d.f.= 93 except 84 for LICHENS, *** significant @ p</=0.001, ** @ p</=0.01, * @ p</=0.05.

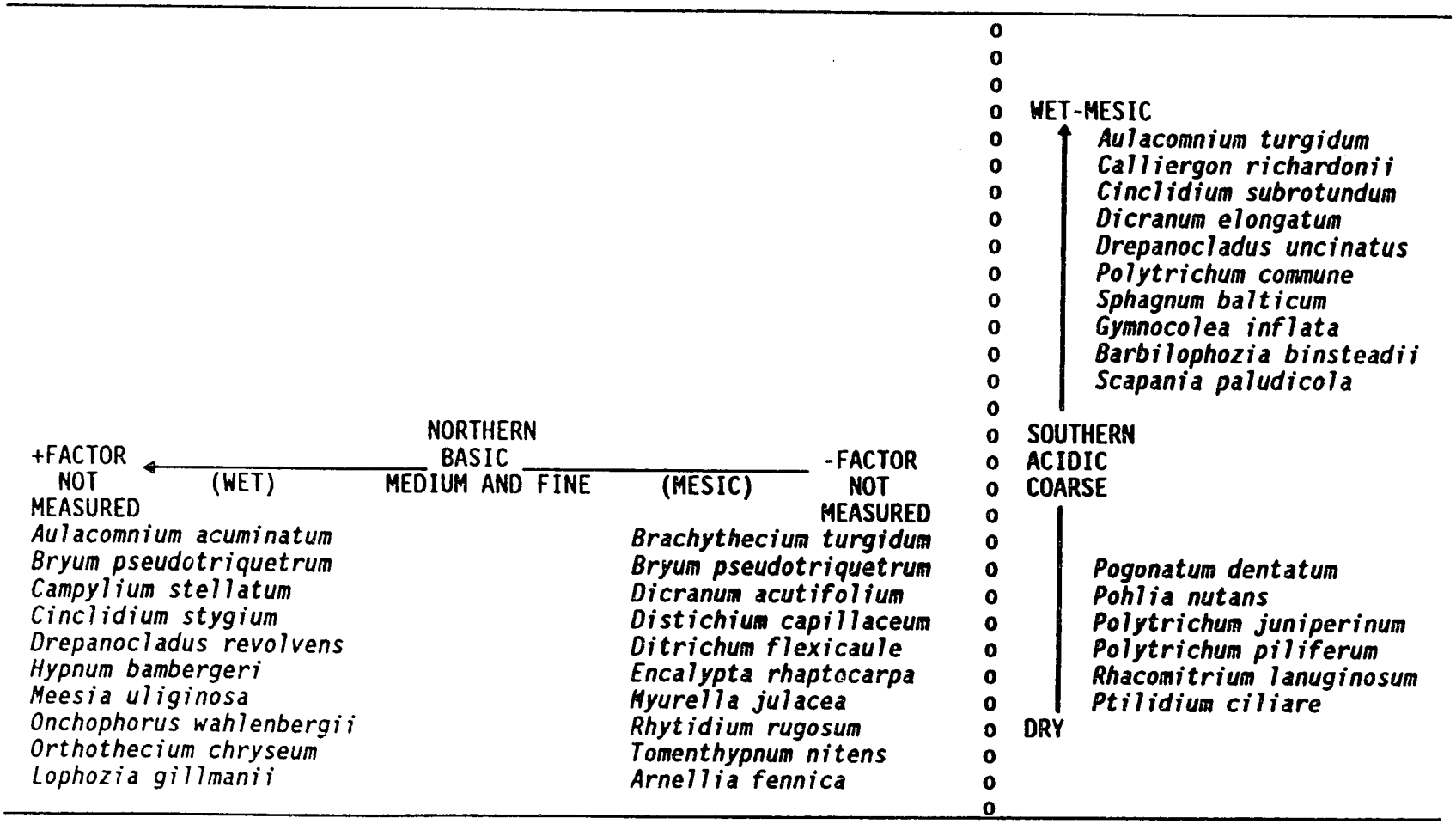

Fig. 2.6. Summary diagram for bryophytes in relation to gradients of soil pH, texture, moisture, and latitude. Typical species representing the four major habitats are listed.

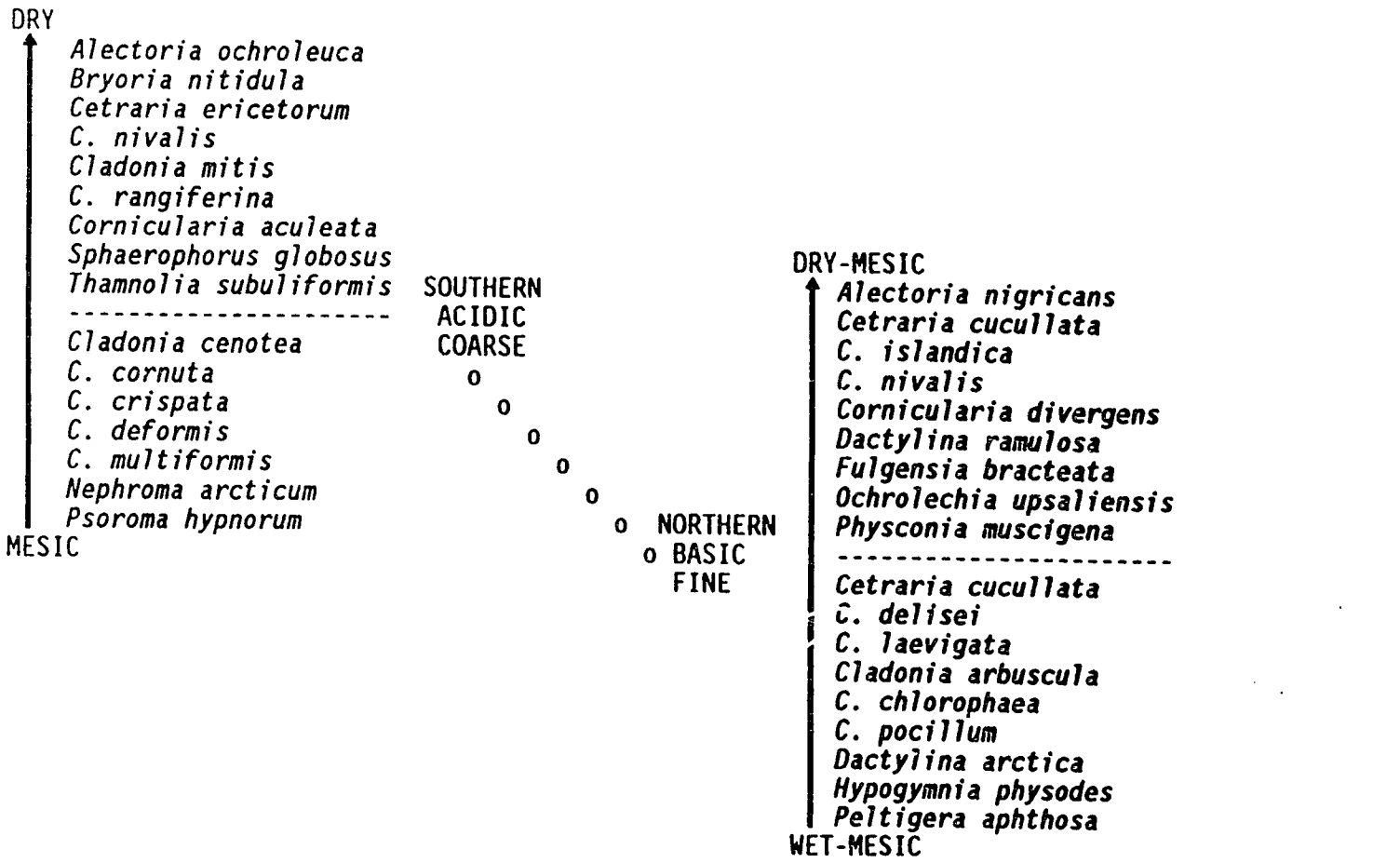

Fig. 2.7. Summary diagram for lichens in relation to gradients of soil pH, texture, moisture, and latitude. Typical species representing the four major habitats are listed.

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3. PATTERNS OF COMMUNITY STRUCTURE AND DISTRIBUTION OF MORPHOLOGICAL CHARACTERS IN RELATION TO EDAPHIC GRADIENTS

3.1 INTRODUCTION

An important goal of plant ecology is to identify the environmental factors that influence species distribution and the function of the structures that differentiate the species. Plants exist along certain parts of environmental gradients because of adaptations that allow them to tolerate the conditions there. In order to discover which adaptations are critical at certain parts of a gradient, we might look for patterns of characters along the gradient. Clarification of these patterns can give clues about the processes that are organizing the plant community. It can also lead to hypotheses about how the adaptations relate to evolutionary change.

In this study, patterns of community structure and the distribution of acrocarpy and papillosity in mosses and fruticosity and light colour in lichens were examined with respect to three edaphic gradients in the subarctic forest-tundra region of the NWT.

Two categories have long been used to classify mosses as to growth form. Acrocarpous mosses are those in which perichaetia differentiate at the growing tips; thus, subsequent growth of the gametophyte cannot continue unless branching occurs below the apical cell. Pleurocarpous mosses are those in which the perichaetia develop laterally on branches and growth can continue during and after initiation of sexual reproduction. The evolution of pleurocarpy is deemed by many to have been a significant advancement for mosses (Vitt

1981; Buck and Vitt 1986). The adaptive significance of pleurocarpy is that vegetative growth is separate from sex organ production. That allows for continuous growth and amplification of the stature of the plant. Thus, pleurocarpy enhances competitive ability in stable, mesic environments where pleurocarpous mosses can assume a life strategy of long-lived perennials (Vitt 1984). Conversely, the acrocarpous growth strategy is often more appropriate when stress tolerance and avoidance are more important than competition.

Papillosity, the presence of ornamented leaf cells, is an adaptation for rapid capillary uptake and distribution of water in leaves, and it may also enhance gas exhange (Proctor 1979). The adaptive significance of this character is that mosses with papillose leaves may have an improved degree of hydration, thus, of growth, because of the increased rate by which and the area over which water is distributed on the leaf. Papillosity may be viewed as an adaptation for drought-tolerance in xerophytic, unstable, or unpredictable habitats.

Lichens can be categorized by growth form. Crustose and foliose forms give lichens a two-dimensional relationship with the environment. They range from being tightly to loosely connected to the substrate and have one or two exposed sides. Fruticose lichens extend away from the substrate and present three dimensions to the environment. The adaptive significance of fruticosity in terricolous lichens is that the thallus and propagules can be raised above the level of the substrate, the boundary layer, the litter layer, and plants of low stature. As well, groups of strands or podetia may benefit individual ones by forming a protective canopy for reduction

of evaporative stress (Larson 1981) or perhaps by providing reflectance into the lower canopy (Gauslaa 1984). Finally, the fruticose growth form often provides a high surface area:weight ratio beneficial for rapid uptake of water and rapid cooling when dry (Kershaw 1985).

The adaptive significance of particular lichen colours has been investigated by several lichen ecologists, however no general conclusions have been made (Kershaw 1985). The lichens of the forest-tundra region are conspicuously light-coloured. The light colour of some lichens may provide reflectance for protection against overheating (Kershaw 1975a), absorption of ultra-violet radiation by usnic acid (Rundel 1969), or reflection of light into lower thallus parts beneath the lichen canopy (Gauslaa 1984). Thus, light colour may be a successful strategy where light and heat during times of active growth are overabundant.

The objectives of this study were to use terricolous bryophytes and lichens of forest-tundra plant communities in the subarctic NWT to assess 1) how bryophyte and lichen community structure is correlated with environmental gradients, and 2) how morphological characteristics of bryophytes and lichens are distributed relative to environmental factors. Environmental gradients used were soil pH, soil texture, and soil moisture. Three attributes of community structure and four species attributes were evaluated with respect to those gradients: ratio of moss (1), hepatic (2), and lichen (3) species to total bryophyte and lichen species; ratio of acrocarpous (4) and papillose (5) mosses to total moss species; and the ratio of light-coloured (6) and fruticose (7) lichens to total lichen species.

3.2 STUDY REGION

The study region is the same as described in the previous chapter (see 2.2 STUDY REGION); a summary is presented here.

Five study areas were sampled in or adjacent to the subarctic forest-tundra region of the NWT (sensu Timoney 1988). Physical parameters for each study area are summarized in Table 3.1. The Dubawnt and Snare-Yellowknife areas are located on the Precambrian Shield and are characterized by numerous lakes and streams and generally coarse-textured, acidic soils. The Dubawnt area included the southernmost study site at latitude 60°54'N. The Coppermine-Kendall area is underlain by a variety of typically sedimentary bedrock types; soils are loamy-textured and basic in pH. The Horton area, containing the northernmost site at latitude 69°45'N, is underlain by dolomites and limestones in the south, and shales, siltstones, and mudstones to the north. Soils are medium- to fine-textured and basic in pH. In the Tuktoyaktuk-Inuvik area, mineral soils are typically moderately calcareous loam and clay loam.

All five study areas were glaciated during the Pleistocene (Dyke and Prest 1987) except for a portion of the lower Horton River (Zoltai et al. 1979). The climate of the subarctic forest-tundra is continental, with long cold winters and short cool summers. An overview of the representative plants is presented in Table 2.1.

3.3 METHODS

The bryophyte and lichen collections and soils data for the 95 study sites used in this chapter are the same as those described in the previous chapter (see 2.3 METHODS). A summary is presented here.

Site moisture assignments were based on soil drainage properties as follows: dry = excessively-drained and/or exposed; dry-mesic = rapidly-drained; mesic = well-drained to moderately well-drained; wet-mesic = imperfectly-drained; wet = poorly-drained to submerged. Mineral soil pH was determined with a Hellige-Truog field pH kit and site pH assignments were based on the B horizon where possible. Hand-texturing of soils was done in the field; textures are those of the uppermost mineral horizon. Textures for the organic soils were usually not determined but were predominantly fibric.

Site and soil descriptions, species presence of vascular plants, and cover percent (%) of vascular plants, total bryophytes, and total lichens for each site were available from a study of the forest-tundra conducted by Timoney (1988 and unpublished data).

Mosses were categorized as being acrocarpous or pleurocarpous, and papillose or non-papillose. An acrocarpous moss is one in which perichaetia differentiate at the growing tips; thus, subsequent growth of the gametophyte cannot continue unless branching occurs below the apical cell. Perichaetia in pleurocarpous mosses develop laterally on branches and growth can continue during and after initiation of sexual reproduction.

Moss leaf papillae are thickenings or ornamentations of the exposed surfaces of the cells; they give a textured or dull appearance

to the leaf. If the majority of leaf cells of a species usually have papillae, then the species was categorized as papillose. Species from the Polytrichaceae were included in this category.

Lichens were categorized as fruticose or non-fruticose, and light- or dark-coloured. The fruticose category includes lichens that are anchored at the base of round to flattened branches or podetia, and that show little difference between the upper and lower thallus surfaces. All species of *Cladonia* were included in this category, and *Masonhalea richardsonii* (unattached) was also considered to be fruticose. *Ochrolechia frigida* and *Pertusaria dactylina*, though sometimes found with threadlike or fingerlike projections, were considered to be non-fruticose.

The assignment of light- and dark-coloured as a morphological characteristic of lichens was subjective. If white, yellow, orange, light gray, light green, or light brown was the usual and conspicuous thallus colour in the field, the lichen was categorized as light-coloured. If most of the thallus was medium or dark brown, dark gray or black, or medium or dark green, the lichen was put in the dark-coloured category.

The relationships between the seven plant characteristics (ratio of moss (1), hepatic (2), and lichen (3) species to total bryophyte and lichen species; ratio of acrocarpous (4) and papillose (5) mosses to total moss species; and the ratio of light-coloured (6) and fruticose (7) lichens to total lichen species) and the environmental gradients of soil pH, texture, and moisture were determined as follows. A correlation matrix based on rank (Spearman's rho; inspection of the data indicated non-normality) was calculated between

the three environmental gradients and the seven categories of plant characteristics using MINITAB (Ryan et al. 1982) (*** significant @ p </= 0.001; ** @ p </= 0.01; * @ p </= 0.05). The 21 pairs of environmental factors and plant characteristics were graphed. The ordinate of the graphs is the mean percent of species with the given attribute. The lichen graphs are nearly mirror images of the moss graphs; the difference is made up by the proportion of hepatics to total species, which was not significantly correlated with any of the gradients. Graphs for pleurocarpous and non-papillose mosses would be mirror images of those for acrocarpous and papillose mosses, respectively. Similarly, graphs for dark-coloured lichens, and crustose and foliose lichens would be mirror images of those for light-coloured and fruticose lichens, respectively.

3.4 RESULTS AND DISCUSSION

Table 3.1 relates soil pH, soil moisture, soil texture, and latitude to the five study areas and Table 3.2 lists the location, soil parameters, and vegetation characteristics for each study site. Appendices 10-12 list the mosses, hepatics, and lichens along with the morphological characteristics for each moss and lichen species. Table 3.3 shows correlation coefficients between the soil parameters and vegetation characteristics.

Environmental Factors

Important correlations exist among the physical factors. Soil pH and texture are highly correlated (r=+0.509***) in the region because the fine-textured soils of the northwest are primarily derived from calcareous Paleozoic marine sediments. Texture and moisture are correlated (r=+0.401**) because, on sites with similar topography, fine-textured soils retain more water than coarse-textured soils. Thus, soil pH and moisture are also correlated (r=+0.283*), though less significantly. The Dubawnt and Snare-Yellowknife areas in the eastern part of the region (Fig. 3.1) are characterized by coarse-textured, dry-mesic, acidic soils while the Coppermine-Kendall and Horton areas farther west have generally fine-textured, mesic to wet-mesic, basic soils (Table 3.1).

Vascular plant species richness may also affect bryophyte and lichen distribution patterns by increasing habitat diversity (Lee and La Roi 1979; Vitt 1979; Vitt and Horton 1979). Species richness of both mosses and hepatics was highly correlated with that of vascular

plants (mosses: r=+0.658***; hepatics: r=+0.344***), but that of lichens was not (r=+0.155). Vascular plant species richness is much higher in the northwest than in the southeast: the basic, fine-textured soils of the northwest support twice as many vascular species as the acidic, coarse-textured soils of the southeast (Table 3.4).

Soil pH

Soil pH affects the solubility, availability, and toxic state of various soil substances; it may also directly affect the activity of enzyme systems of the plant (Brodo 1973). Basic soils have more of the essential nutrients available than do acidic soils (Black 1968). The macronutrient requirements of bryophytes are thought to be similar to those of vascular plants (Longton 1980), while those of lichens are relatively unknown (Kershaw 1985). Wielgolaski et al. (1975) found low macronutrient contents in lichens when compared with bryophytes and vascular plants.

Acidic soils of the forest-tundra are characterized by a high proportion of lichen species compared to bryophyte species (Figs. 3.2-3.4). On basic soils, the proportions are reversed. Of the bryophytes, it is primarily the mosses that respond to pH differences (Fig. 3.2); the proportion of hepatics does not change significantly along the gradient (Fig. 3.3). Acrocarpy is prevalent throughout the region although the proportion of acrocarpous moss species decreases along the gradient from acidic to basic pH (Fig. 3.5). No significant correlation exists between papillosity and pH (Fig. 3.6). Morphological characteristics of lichens reflect differences in pH

only slightly: a decrease in proportion of fruticosity and an increase in proportion of light-coloured lichens occurs from acidic to basic soils (Figs. 3.7, 3.8).

Soil texture

Soil texture affects soil properties such as drainage and susceptibility to deflation and cryoturbation. Well-drained, sandy soils with a sparse vegetation cover are exposed and easily deflated. In this study region, the finer-textured soils have high vascular plant cover and species richness relative to the coarse-textured soils (Tables 3.4 and 3.6) and are less stable with respect to cryoturbation, but the resulting hummocky ground provides a greater diversity of microsites for bryophytes and lichens.

The graphs showing soil pH and texture gradients exhibit similar patterns. Moss species are more numerous than lichen species on fine-textured soils (Figs. 3.2, 3.4); lichen species are more numerous on coarse-textured soils. A decrease in acrocarpous mosses (Fig. 3.5) and fruticose lichens (Fig. 3.7) (and corresponding increase in pleurocarpous mosses and non-fruticose lichens) is evident along a gradient from coarse- to fine-textured soils.

Soil moisture

The great importance of moisture in influencing both species composition and abundance of bryophytes and lichens is well-documented. Kershaw (1985:30) summarized for lichens: "The ecology of a lichen is controlled by a large number of parameters but certainly the water relations are of central importance". The same could be

said of bryophytes (Steere 1976; Busby et al. 1978). Because both plant types are poikilohydric (unable to control water potential), and since photosynthesis does not occur unless the plant is hydrated, many morphological characteristics of lichens and bryophytes relate to the availability, absorption, and retention of water and the reduction of evaporative and thermal stress (Busby et al. 1978; Schofield 1981).

Dry and dry-mesic soils in the study region are characterized by a high proportion of lichen species compared to bryophytes (Figs. 3.2-3.4). Though most mosses are non-papillose, more are papillose on dry to mesic soils than on wet soils (Fig. 3.6). At the wet end of the gradient, moss species overwhelmingly outnumber lichen species, most mosses are non-papillose, and the ratio of acrocarpy to pleurocarpy is about 1:1 (Fig. 3.5). Fig 3.3 shows that the highest proportion of hepatic species occurs on wet-mesic soils, although hepatics and moisture are significantly correlated at only $p<0.1$.

Bryophyte and Lichen Community and Structural Characteristics in the Study Region

Mosses

A total of 161 moss species were identified, from 66 genera (Appendix 10). Moss species outnumber both hepatic and lichen species. The majority of mosses are acrocarpous (62%) and non-papillose (77%). Although these data represent only the terricolous component of the moss flora, Vitt (1988) found similar values of 67% acrocarpous and 77% non-papillose moss species in the flora of a high subantarctic site. In temperate North America the ratio of acrocarpous to pleurocarpous mosses is about 1:1 while in

polar regions it is 3:1 (Vitt 1979). In this high subarctic study region the ratio for the terricolous mosses is about 3:2.

Percent papillosity is positively correlated with % acrocarpy in mosses (r=+0.436***). Whereas 19% of the mosses are both acrocarpous and papillose, only 4% are pleurocarpous and papillose (Table 3.7). Even though the overall percentage of acrocarpous and non-papillose mosses (43%) exceeds that of pleurocarpous and non-papillose mosses (34%), 83% of the papillose mosses are acrocarpous compared with 17% pleurocarpous. This is in contrast to a tropical region where papillosity was positively correlated with pleurocarpy (Vitt 1988). The structure of the moss component of plant communities of this study region is similar to that of the poles and it differs from that of tropical areas with respect to degree of papillosity and pleurocarpy. If acrocarpy and non-papillosity can be considered to be ancestral character states, i.e., plesiomorphous (Vitt 1988) then these data suggest that the terricolous moss flora of this high subarctic region exhibits an early evolutionary status. This lends support to the hypothesis that apomorphy (derived character states) in mosses decreases poleward (Vitt 1979).

Hepatics

Seventy-four hepatic species from 24 genera were collected (Appendix 11). The proportion of hepatic species to total bryophyte and lichen species was not significantly correlated with the environmental gradients (pH: r=-0.077, texture: r=-0.023, moisture: r=+0.194). Factors other than those examined here, such as shade or

temperature, may control the distribution of terricolous hepatic species in the forest-tundra region.

Lichens

A total of 111 lichen species in 33 genera were identified (Appendix 12). Most of the lichens are fruticose (75%) and light-coloured (62%). Almost half of the lichens are both fruticose and light-coloured (Table 3.7). For example, species of *Cladonia*, *Cetraria*, *Thamnolia*, *Dactylina*, and *Stereocaulon* are characteristic of the region.

Bryophyte and Lichen Community and Structural Characteristics in Relation to Environmental Factors

Mosses compared with lichens

Mosses and lichens comprise the same vegetation stratum, and have the common trait of being poikilohydric. However, there are major ecological differences between these two groups:

1. Mosses require water for fertilization; lichens do not have motile gametes.

2. Some mosses are aquatic; many others are semi-aquatic. In contrast, few lichens are found in wet places; indeed, the lichen symbiosis may break down when the thallus has been saturated for too long (Kappen 1973).

3. The lichen phycobiont is buffered from environmental extremes by the mycobiont.

4. Mosses possess a more complex morphology, thus have greater potential for adaptations that allow for water storage, such as

concave, overlapping leaves and porose hyaline cells. These allow mosses to extend the period of hydration, hence, the period of metabolism, beyond that of lichens and may contribute to faster growth rates.

5. Lichens contain less chlorophyll per living biomass than mosses; hence, they have a lower growth potential.

The increase in proportion of mosses (and corresponding decrease in that of lichens) to total number of bryophyte and lichen species is highly correlated with increasing pH and moisture, and with finer soil textures (Figs. 3.2, 3.4). The proportion of mosses may increase by an increase in the number of moss species and/or a decrease in the number of lichen species. On mesic acidic soils, mean number of moss species was half that of mesic basic sites (Table 3.5). Similarly, number of species of vascular plants of mesic acidic sites was half that of mesic basic sites. In contrast, mean number of lichen species showed little difference between mesic acidic and mesic basic sites.

These data show that moss species of the region are more numerous on mesic to wet, basic, finer-textured soils. In contrast, lichens, perhaps because of their ability to withstand drought and exposure, combined with their inability to compete with faster-growing plants, show little change in number of species along these soil gradients.

Acrocarpy compared to pleurocarpy

The distinction between acrocarpous and pleurocarpous mosses is related to branching and sexual reproduction. The ability of pleurocarpous mosses to continue growing during and after initiation of sexual reproduction and to form extensive mats or wefts enhances

their ability to compete with forest floor vascular plants (Vitt 1984). Vitt (1988) suggested that pleurocarpous species are adapted to mesic, relatively stable habitats as long-lived perennials; acrocarpous species, many of which rarely branch, have limited life spans, and generally smaller stature, are adapted to more open, disturbed habitats. Thus, pleurocarpy can be associated with the "K-selected" species described by Gadgil and Solbrig (1972), "equilibrium" species as discussed by Slack (1977), the "competitive" species of Grime (1977), and During's (1979) "perennial stayers" category. Conversely, "r-selected" species, "opportunistic" species, "ruderal and stress-tolerant" species, and the species in During's other categories, would be predominantly acrocarpous. That acrocarps produce sexual and vegetative diaspores more often than do pleurocarps (Schofield 1981) is further evidence for their adaptation to exposed areas, where successful dispersal of diaspores is more likely than in moist protected sites and more important for non-perennial life strategies.

Acrocarpy may be an adaptation to water stress. The tight turf and cushion growth forms of many acrocarpous mosses allow for better uptake and retention of moisture and reduced air movement close to leaf surfaces than the weft and mat forms of most pleurocarpous mosses (Gimingham and Birse 1957; Schofield 1972, 1981; Longton 1980). As well, conducting tissue in acrocarps is apparently more prevalent than in pleurocarps (Frey 1971, in Hébant 1977), although Hébant (1977) cautioned against an ecological interpretation of this condition because of the variability of its occurrence within both groups, and the lack of supporting quantitative data.

A number of studies have compared acrocarpy and pleurocarpy with respect to moisture. La Roi and Stringer (1976) showed a significant correlation between bryophyte growth form and moisture availability on a macro-climatic scale and suggested that species with the short turf growth form may be better competitors under xeric conditions than mat species. Conversely, Stringer and Stringer (1974) stated that dry-area dominants include a much higher proportion of pleurocarps than wet-area dominants; however, study of their data indicates a ratio of 5:2 pleurocarps to acrocarps in their driest stand, and 3:1 in their wettest stand. Flock (1978) showed that acrocarpous moss species at an alpine site were more numerous in dry and moist sites than in wet sites (36:7); pleurocarpous mosses were more numerous in moist and wet than dry sites (12:2); and, as in the present study, acrocarpous moss species were more numerous in all three site types. Longton (1979), in his classification of Antarctic vegetation based on growth form, concluded that water supply was the major factor determining the distribution of the major subformations.

In this study region, acrocarpy is floristically more prevalent than pleurocarpy overall (62%). It is more common in sites of low to circumneutral pH but percent acrocarpy is above 50% for all but pH 7.5 where it falls to 47% (Fig. 3.5). Acrocarpy decreases towards habitats characterized by 1) mesic to wet soils, 2) medium to fine-textured soils, and 3) high vascular plant diversity (Tables 3.4 and 3.6). These data support the view that the acrocarpous growth form is an adaptive strategy to open, droughty, or less stable environments.

Papillosity compared to non-papillosity in mosses

Many morphological characteristics of mosses are thought to enhance absorption, conduction, and retention of water, including leaf plicae, sheathing leaf bases, porous hyaline cells, overlapping concave leaves, rhizoids, and papillae (Proctor 1979). Interstitial grooves between papillae can allow for capillary uptake and redistribution of water to the leaf cells (Proctor 1979). That papillosity is related to moisture availability is evident from Loeske's observation that many mosses are strongly papillose in dry sites but have reduced papillae when growing in wet sites (Loeske 1926, in Schofield 1981).

Thus, a large proportion of papillose mosses might be expected at the dry end of the moisture gradient in this study. Although a decrease in papillosity was significantly correlated with an increase in moisture (Fig. 3.6), the range along the gradient was only 17% (dry-mesic 32% to wet 15%). In comparison, Vitt (1988) found that papillosity was related to a latitudinal gradient on South Pacific Islands, which appears to be largely an evolutionary gradient with apomorphic characters increasing northward. Papillosity ranged from 21% on the subantarctic island to 52% on the tropical island. Papillosity was not, however, related to an elevational gradient, which is largely one of precipitation.

Two explanations might account for the relatively small decrease in papillosity from dry to wet soil conditions. The plesiomorphous status of many forest-tundra moss species may outweigh the prevalence of papillosity at the dry end of the moisture gradient even though papillosity is an adaptation for xeromorphy. Other physiological and

morphological adaptations in addition to papillosity may allow these mosses to tolerate dry soil conditions.

A second possible explanation is that many of the papillose species in the study region were excluded because they are epiphytic or saxicolous. There is considerable bryophyte diversity in those habitats and many of the species would be papillose (Vitt and Horton 1979, Vitt et al. 1987). This possibility could be easily tested.

Fruticosity compared to non-fruticosity in lichens

Slight but significant decreases in fruticosity occur from low to high pH and from coarse to fine texture (Fig. 3.4). Acidic soils support fewer vascular and bryophyte species (Tables 3.4 and 3.5) and a lower vascular plant and bryophyte cover (Table 3.6) compared with basic soils. Coarse-textured soils, particularly those with low plant cover, are less cohesive than finer-textured soils. Since fruticose forms are typically attached to the substrate only at the base, only a small substrate area is required to support a relatively large thallus surface area. In contrast, crustose and foliose forms typically require a larger area for attachment. Thus, fruticose forms may have a greater ability to colonize loose, sandy soils. A parallel exists for mosses. The very loose colonies or single stems of *Polytrichum piliferum* and *P. juniperinum* are the common mosses of sandy soils rather than tighter mat or turf colonies.

Fruticose forms may be better able to tolerate the drying winds and solar radiation of exposed conditions, compared with foliose and crustose forms. Fruticose lichens, having a relatively high surface area:weight ratio, can quickly absorb moisture when it becomes

available and resume photosynthesis (Kershaw 1985). However, a high surface area:weight ratio also leads to rapid drying, with potentially damaging evaporative and thermal stress. The fruticose growth form can reduce this stress in several ways:

1. Photosynthetic activity is greatest in the tips of fruticose lichens, with almost none occurring at the base (Moser and Nash 1978). The growing tips of sturdy, erect podetia are above the warm, humid, still air layer at the soil surface, where convective cooling can reduce high thallus temperatures (Coxson and Kershaw 1983); e.g., *Dactylina arctica*, *Cladonia* spp.

2. Filamentous forms with large surface areas grow in exposed areas where wind reduces the thickness of the boundary layer allowing for convective cooling of a hydrated thallus and sensible heat transfer of a dry thallus (Kershaw 1975a); e.g., *Bryoria nitidula*, *Alectoria ochroleuca*.

3. Erect, finely branched forms grow in clumps where the rate of evaporation is reduced (Larson 1981); e.g., *Cladonia stellaris*, *Stereocaulon paschale*.

The data from this study suggest that in the forest-tundra, fruticosity may be a successful strategy for tolerating more exposed and erosionally unstable areas where both vascular plant and bryophyte cover and species richness are lower.

The degree to which successional processes among lichen growth forms influence lichen distribution patterns in the forest-tundra region remains to be studied. John (1988) noted that crustose lichens on some rocks in the Canadian Rocky Mountains were generally not amenable to colonization by foliose lichens, and that cyclic

successional processes among the species were likely occurring. There was little evidence of succession to a more mature sere, however. Grime (1977) suggested that lichens are, as a group, "stress-tolerators", with the ability to survive extremes of temperature, moisture supply, and low mineral nutrition. In this study, a slightly higher proportion of fruticose lichens occurred in dry, exposed, areas with acidic soils, where stress tolerance seems to be a critical adaptive strategy.

Light-coloured compared to dark-coloured lichens

Thallus colour appears to modify thallus temperature, although few quantitative studies have been published (Kershaw 1985). Kershaw (1975b) noticed that areas of thin snow cover, (e.g., beach ridge tops), often support dark-coloured lichens such as *Bryoria nitidula* and *Cornicularia divergens*. Under a thin covering of snow or in protected melt pockets, these dark, ridge-top lichens in still air conditions may absorb enough incoming radiation to raise the temperature above 0 C, permitting photosynthesis and low respiration rates in early winter and spring. In summer, thallus temperatures may be sufficiently lowered by wind to compensate for temperature increases resulting from the dark thallus (Coxson and Kershaw 1983).

Gaussla (1984) tested reflectance for various arctic and/or alpine lichen species. He speculated that the intense reflectance within the canopy of dense, light-coloured fruticose lichens (e.g., *Cladonia stellaris*) allows for net photosynthesis in the lower, protected parts of the canopy. Dark-coloured, fruticose forms with low reflectance rarely grow in large mats since light must enter the

canopy from both top and sides in order to reach the inner canopy. *Bryoria nitidula* and *Cornicularia divergens*, for example, grow in loose mats often together with light-coloured, highly reflectant lichens such as *Alectoria ochroleuca* and *Thamnolia subuliformis*. Conversely, lichens such as *Cetraria nivalis* and *Stereocaulon paschale* can grow in extensive, dense mats.

Thallus pigmentation may also screen the algal component against high levels of incident radiation (e.g., *Peltigera aphthosa* is darker in unshaded habitats than in shaded habitats); however, data are insufficient to support a general conclusion (Kershaw 1985). Rundel (1969) found a strong correlation between usnic acid and absorption of ultra-violet radiation; thus, the algae of (often light-coloured) usnic acid-containing lichens may be protected from UV radiation in exposed conditions.

Thallus colour in this study was not markedly associated with any of the environmental gradients, although there was a slight and inexplicable increase in number of light-coloured lichen species along the pH gradient (Fig 3.8). The mean proportion of light-coloured lichens of acidic sites (pH <7.0) was 60.0 (sd=17.9); that of basic sites was 67.3 (sd=17.2).

If the adaptive strategy of light colour in lichens is one of absorbance of UV light and reflectance of visible light, then we could expect a pattern of increasing proportion of light-coloured lichens along a light intensity gradient. Preliminary results comparing proportion of light-coloured lichens from treed (open and closed crown forest), to partially treed (forest-tundra), to treeless (upland,

shrub, and wetland) sites in this study indicate a positive but insignificant correlation ($r=+0.055$, $p>0.1$). A finer scale along the gradient is required for a more thorough evaluation of this character.

3.5 CONCLUSIONS

Community structure and distribution of several morphological characteristics of terricolous bryophytes and lichens in the subarctic forest-tundra of the NWT are correlated with soil pH, moisture, and texture. The proportion of moss species to total bryophyte and lichen species increases with increasing soil pH and moisture, and with finer soil texture; the proportion of lichens correspondingly decreases. The proportion of hepatics is not significantly correlated with any of the gradients. The ability of lichens to tolerate growing conditions unacceptable to bryophytes and vascular plants may allow them to be relatively successful in areas of low pH and dry, exposed soils.

Acrocarpous moss species are more numerous than pleurocarpous species throughout the region; acrocarps reach their greatest prominence on acidic, coarse-textured, dry soils, and in sites with low vascular plant species richness. This may be a reflection of the adaptation of acrocarpous mosses to droughty, open, less stable environments where stress tolerance is more important than competition. The more stable, moister habitats favour a higher proportion of pleurocarpous moss species which can be viewed as better competitors and largely K-selected species.

Non-papillose moss species numerically dominate in the study region. There is no significant correlation of papillosity with either soil pH or texture. Although a significant decrease in papillosity occurs from dry to wet along the moisture gradient, it reaches a high of only 32% (dry-mesic). The plesiomorphous status of many forest-tundra mosses may preclude papillosity from being a major

adaptation of forest-tundra mosses to dry soil conditions. As well, xerophytic habitats on rocks, trees, and shrubs were excluded.

Most of the terricolous lichens in the region are light-coloured and fruticose; these characteristics vary little with respect to pH, texture, and moisture. Fruticosity generally decreases with increasing soil pH and finer texture. The higher proportion of fruticose lichens in the study region as a whole and particularly on exposed, sandy, acidic soils may be attributable to the greater ability of fruticose forms to colonize erosionally unstable soils and to reduce evaporative and thermal stress, compared with crustose and foliose forms. The significance of light colour in lichens appears not to be related to the gradients investigated here.

The structure of the terricolous bryophyte and lichen component of forest-tundra plant communities may be summarized:

1. The region is characterized by a higher proportion of a) bryophytes compared with lichens, b) acrocarpous compared with pleurocarpous mosses, c) non-papillose compared with papillose mosses, d) fruticose compared with crustose and foliose lichens, and e) light-coloured compared with dark-coloured lichens.

2. From acidic to basic soil pH, from coarse to fine soil texture, and from dry to wet soil moisture, the proportion of mosses increases while that of lichens decreases, acrocarpy decreases, and fruticosity decreases slightly. In addition, from dry to wet along the moisture gradient, papillosity in mosses decreases.

As a result of this study, some aspects of the structure of the bryoid flora of this subarctic forest-tundra study region are

quantitatively described with respect to three edaphic gradients and the region as a whole, and the adaptive significance of two moss and two lichen characters are analyzed.

Table 3.1. Summary of physical variables for the five study areas.

	Dubawnt	Snare-Yellowknife	Coppermine-Kendall	Horton	Tuktoyaktuk-Inuvik
pH range	5.2 - 7.0	4.0 - 6.9	7.0 - 8.0	7.2 - 8.0*	-
pH median	5.7	5.5	8.0	8.0	-
modal moisture	dry-mesic	dry-mesic	wet-mesic	mesic	wet-mesic
modal texture	loamy sand	loamy sand	silty loam	clay loam	-
latitude range(°N)	60°54′ to 62°41′	62°30′ to 64°43′	65°43′ to 67°28	67°35′ to 69°45′	68°18′ to 69°23′
number of sites	24	18	20	29	4

*with the exception of pH 5.3 in the Smoking Hills (lower Horton R.)

Table 3.2. Location, soil parameters, and vegetation characteristics of each study site. LOSA=loamy sand, SALO=sandy loam, SILO=silty loam, CLLO=clay loam, SICL=silty clay loam; D=dry, DM=dry-mesic, M=mesic, WM=wet-mesic, W=wet; #=number of; SPP=total species, M=mosses, H=hepatics, L=lichens; %ACRO=%acrocarpous; %PAPI=%papillose; %FRUT=%fruticose; UTU=upland tundra, B-F=bog-fen, F-T=forest-tundra, OCF=open crown forest, CCF=closed crown forest, STU=shrubland, WTU=wetland.

STUDY SITE	LONGITUDE ° ′ ″	LATITUDE ° ′ ″	SOIL pH	SOIL TEXTURE	SOIL MOISTURE	#SPP	#M	#H	#L	%ACRO MOSSES	%PAPI MOSSES	%FRUT LICHENS	%LIGHT LICHENS	VEG TYPE
Dubawnt study area:														
S30	112 47 0	62 30 30	4.7	LOSA	DM	24	5	1	18	60	20	71	76	CCF
S31	104 43 45	61 14 0	5.3	LOSA	DM	30	7	6	17	71	29	94	59	F-T
S33	104 15 20	61 23 20	5.2	LOSA	DM	21	4	2	15	100	33	87	67	F-T
S34	104 11 10	61 25 25	5.4	LOSA	M	26	6	2	18	67	17	94	59	OCF
S35	104 2 40	61 25 40	6.0	LOSA	M	18	4	4	10	100	50	90	50	F-T
S36	103 52 40	61 22 10	6.2	SAND	DM	22	7	1	14	57	43	100	62	F-T
S37	103 41 45	61 25 20	5.4	LOSA	M	22	11	8	3	100	30	67	33	F-T
S38	103 27 45	61 29 35	5.9	LOSA	DM	20	5	3	12	100	20	75	58	F-T
S40	103 27 10	61 14 35	5.3	LOSA	DM	23	8	3	12	71	29	83	58	OCF
S41	103 39 35	61 6 30	5.9	SALO	DM	24	5	5	14	80	40	93	64	OCF
S43	103 42 55	60 54 35	6.0	SALO	WM	32	7	5	20	83	33	95	60	F-T
S45	103 44 10	61 5 50	5.7	SALO	DM	26	9	4	13	71	29	85	77	OCF
S47	103 20 20	61 28 30	6.9	LOSA	DM	39	7	12	20	100	17	89	63	F-T
S48	103 13 20	61 38 10	6.2	LOSA	DM	33	10	8	15	56	11	87	67	F-T
S49	103 13 15	61 48 15	5.7	LOSA	DM	38	10	9	19	78	44	84	58	F-T
S50	103 8 0	61 53 10	5.7	SAND	M	12	3	4	5	100	33	100	80	F-T
S51	103 8 20	61 54 20	7.0	SALO	M	45	13	8	24	92	25	86	64	F-T
S53	102 55 30	62 3 30	6.4	SALO	WM	28	14	12	2	62	15	100	50	F-T
S54	102 49 30	62 16 15	5.5	SAND	M	38	12	7	19	67	17	94	59	F-T
S55	102 55 35	62 19 45	7.0	SILO	M	31	9	6	16	75	25	88	75	F-T
S56	102 43 50	62 29 5	5.2	SALO	M	18	6	5	7	83	17	100	50	UTU
S57	103 11 30	62 28 30	6.0	LOSA	M	24	5	7	12	80	20	92	67	F-T
S58	103 31 50	62 25 20	5.7	LOSA	DM	33	6	9	18	100	20	93	67	UTU
S59	103 50 20	62 18 35	5.9	LOSA	M	39	15	10	14	75	25	93	50	F-T
T28	102 49 0	62 41 0	-	-	W	14	11	3	0	50	0	-	-	OCF

Table 3.2 continued.

STUDY SITE	LONGITUDE ° ′ ″	LATITUDE ° ′ ″	SOIL pH	SOIL TEXTURE	SOIL MOISTURE	#SPP	#M	#H	#L	%ACRO MOSSES	%PAPI MOSSES	%FRUT LICHENS	%LIGHT LICHENS	VEG TYPE
Snare-Yellowknife study area:														
S01	115 59 15	63 31 45	4.2	-	DM	15	4	1	10	100	50	78	56	OCF
S04	116 10 0	63 26 0	5.0	CLLO	M	11	7	3	1	71	43	0	0	OCF
S07	115 20 15	64 3 45	5.5	LOAM	M	13	1	1	11	100	100	91	55	CCF
S12	113 20 30	64 25 30	5.4	LOSA	M	17	3	0	14	100	33	100	54	F-T
S14	113 3 0	64 33 0	4.2	SALO	M	22	5	3	14	80	40	93	64	UTU
S18	113 32 20	63 54 0	4.0	LOSA	DM	15	3	2	10	100	0	100	80	OCF
S20	113 45 20	63 34 30	4.0	SALO	DM	15	3	2	10	100	50	80	60	OCF
S21	112 17 30	63 19 10	6.0	SAND	D	15	2	1	12	100	50	91	64	F-T
S22	112 9 15	63 28 15	6.8	LOSA	M	15	1	0	14	100	100	83	67	UTU
S26	112 25 30	63 7 45	6.9	-	W	14	10	1	3	70	30	67	67	OCF
R01	111 4 0	64 4 15	5.5	-	WM	29	12	4	13	73	18	91	64	F-T
R02	111 4 15	64 4 35	5.5	-	W	21	17	4	0	93	36	-	-	FEN
R03	111 4 45	64 4 35	5.5	-	WM	26	8	7	11	88	25	100	64	B-F
R04A	111 3 30	64 4 30	5.5	-	DM	14	3	0	11	67	33	86	57	UTU
R04B	111 3 30	64 4 30	5.5	-	DM	24	5	2	17	100	40	93	67	UTU
R05A	111 3 0	64 4 25	5.5	-	DM	33	6	2	25	100	50	92	63	UTU
R05B	111 3 0	64 4 25	5.5	-	D	9	1	1	7	100	0	100	100	UTU

Table 3.2 continued.

STUDY SITE	LONGITUDE ° ′ ″	LATITUDE ° ′ ″	SOIL pH	SOIL TEXTURE	SOIL MOISTURE	#SPP	#M	#H	#L	%ACRO MOSSES	%PAPI MOSSES	%FRUT LICHENS	%LIGHT LICHENS	VEG TYPE
Coppermine-Kendall study area:														
SA1	114 16 0	65 44 20	8.0	SILO	WM	41	14	7	20	64	21	88	65	OCF
SA2	114 20 0	66 10 15	-	-	M	37	15	6	16	53	40	81	69	UTU
S61	114 17 15	65 43 50	8.0	SICL	M	61	24	7	30	65	35	85	52	F-T
S62	114 25 50	65 57 10	8.0	LOAM	WM	39	20	6	13	74	32	85	77	OCF
S64	115 9 15	66 42 35	8.0	SILO	WM	34	22	2	10	62	33	70	60	WTU
S65	115 9 5	66 42 20	7.2	SILO	W	31	15	3	13	57	29	77	69	OCF
S66A	115 45 35	66 51 10	8.0	LOAM	DM	29	10	0	19	89	67	65	59	UTU
S67	116 20 10	66 51 10	8.0	SILO	WM	35	15	4	16	57	7	100	69	OCF
S69	116 20 40	67 7 35	7.2	SILO	M	61	35	11	15	52	29	77	46	UTU
S70	116 36 35	67 14 50	8.0	SILO	DM	45	25	7	13	52	14	75	83	UTU
S72	116 59 15	67 25 20	8.0	SILO	M	48	27	2	19	64	40	76	71	UTU
S73	117 0 0	67 24 45	8.0	CLAY	W	24	16	6	2	43	7	50	0	STU
S74	117 35 0	67 27 55	7.0	SICL	WM	19	11	4	4	36	18	67	100	F-T
R11	114 38 15	66 32 55	-	-	W	39	19	13	7	47	21	100	86	F-T
R12	114 38 15	66 32 40	8.0	-	M	46	20	13	13	59	29	85	85	UTU
R13	115 9 25	66 42 40	-	-	DM	14	8	0	6	100	50	100	75	UTU
R14P	116 19 35	66 51 0	-	-	W	6	6	0	0	33	0	-	-	FEN
R14S	116 19 35	66 51 0	-	-	WM	51	23	17	11	78	17	91	73	BOG
R15	117 31 20	67 28 30	-	-	W	46	32	9	5	55	19	75	75	WTU
R16	117 31 50	67 28 20	-	-	DM	50	23	9	18	57	29	82	71	UTU
Tuktoyaktuk-Inuvik study area:														
R351	133 2 20	69 23 0	-	-	DM	36	18	5	13	59	18	75	58	UTU
R352	133 2 20	69 23 0	-	-	WM	20	8	2	10	71	14	80	90	B-F
R355	133 2 20	69 23 0	-	-	WM	25	11	10	4	70	20	25	75	B-F
T45	133 29 15	68 18 40	-	-	M	51	19	19	13	71	18	77	62	OCF

Table 3.2 concluded.

STUDY SITE	LONGITUDE ° ′ ″	LATITUDE ° ′ ″	SOIL pH	SOIL TEXTURE	SOIL MOISTURE	#SPP	#M	#H	#L	%ACRO MOSSES	%PAPI MOSSES	%FRUT LICHENS	%LIGHT LICHENS	VEG TYPE
Horton study area:														
S75	122 25 0	67 35 50	8.0	LOSA	M	28	14	3	11	43	7	91	73	F-T
S76	122 53 45	67 47 40	8.0	SICL	DM	42	22	9	11	65	40	63	63	UTU
S77	123 12 15	67 59 10	8.0	SICL	M	37	16	5	16	67	7	80	67	OCF
S78	123 27 45	68 13 15	8.0	SILO	WM	84	41	22	21	50	18	83	78	F-T
S791	123 41 15	68 27 40	7.2	LOAM	WM	56	32	11	13	68	19	73	64	WTU
S792	123 41 15	68 27 40	7.2	LOAM	M	28	15	1	12	50	21	83	50	UTU
S793	123 41 15	68 27 40	7.2	SALO	D	17	6	0	11	67	17	80	80	UTU
S80	123 45 5	68 27 45	8.0	SALO	M	23	16	0	7	33	40	83	50	F-T
S81	124 35 40	68 40 50	8.0	-	M	36	18	5	13	44	17	69	69	OCF
S82	125 27 30	68 55 30	8.0	SICL	DM	50	24	7	19	43	26	81	81	UTU
S83	125 57 30	69 2 30	8.0	SAND	M	35	23	1	11	41	23	73	73	OCF
S84	125 56 15	69 2 0	8.0	CLAY	DM	40	34	0	6	41	31	60	80	UTU
S85	126 22 45	69 9 10	7.6	CLLO	WM	51	35	8	8	47	23	71	71	OCF
R17	122 24 20	67 35 30	-	-	M	30	6	2	22	100	33	90	67	UTU
R18P	122 25 40	67 36 20	-	-	W	20	17	2	1	53	7	100	100	FEN
R18S	122 25 40	67 36 20	-	-	WM	29	14	2	13	71	14	100	77	BOG
R19	123 27 0	68 13 20	-	-	W	6	6	0	0	20	0	-	-	FEN
R20	123 26 50	68 13 30	-	-	M	52	38	6	8	56	26	50	67	WTU
R21	124 7 0	68 39 0	7.4	SILT	M	43	27	7	9	59	26	78	78	STU
R22P	124 7 0	68 39 5	-	-	W	19	15	4	0	54	8	-	-	FEN
R22S	124 7 0	68 39 5	-	-	WM	53	36	9	8	60	20	67	67	BOG
R23	125 55 20	69 0 50	8.0	-	WM	29	15	8	6	71	21	50	67	STU
R24P	125 55 0	69 0 30	-	-	W	27	23	3	1	52	24	-	-	FEN
R24S	125 55 0	69 0 30	-	-	WM	41	15	8	18	80	33	89	72	BOG
R25	126 52 10	69 29 50	5.3	CLLO	WM	12	3	5	4	100	33	100	0	STU
R27	126 59 40	69 45 10	-	CLLO	DM	36	24	1	11	57	33	63	88	UTU
R28C	126 59 35	69 44 50	-	CLLO	M	26	12	5	9	33	17	67	50	UTU
R28T	126 59 35	69 44 50	-	CLLO	W	10	10	0	0	56	11	-	-	WTU
R34	126 58 35	69 45 30	-	CLLO	WM	26	22	2	2	60	20	100	100	STU

Table 3.3. Correlation coefficients (Spearman's rho) for study site characteristics; d.f. in parentheses; *** significant @ p</=0.001, ** @ p</=0.01, * @ p</=0.05.

	pH	Texture	Moisture
%Mosses	0.600*** (68)	0.624*** (60)	0.562*** (93)
%Hepatics	-0.077 (68)	-0.023 (60)	0.194 (93)
%Lichens	-0.463*** (68)	-0.586*** (60)	-0.646*** (93)
%Acrocarpous mosses	-0.659*** (68)	-0.490*** (60)	-0.351*** (93)
%Papillose mosses	-0.195 (68)	-0.082 (60)	-0.345*** (93)
%Fruticose lichens	-0.444*** (67)	-0.481*** (59)	-0.016 (86)
%Light-coloured lichens	0.321** (67)	0.147 (59)	0.079 (86)

Table 3.4. Number of vascular plant species in sites with acidic soils (pH <7.0) compared to those with basic soils (pH >/=7.0). p(Mann-Whitney)<0.0001.

	n	mean	median	sd
Acidic	44	17.1	17.0	5.4
Basic	51	36.8	38.0	15.7

Table 3.5. Number of species per site in mesic, acidic sites (pH <7.0) and mesic, basic sites (pH >/=7.0)

		Mosses			Lichens			Vasculars		
	n	mean	median	sd	mean	median	sd	mean	median	sd
Acidic	8	7.8	6.0	4.3	11.0	11.0	5.9	20.9	21.0	3.8
Basic	10	16.8	16.0	4.6	12.3	12.5	3.0	43.7	44.5	13.3

Table 3.6. Percent cover of vascular plants, bryophytes, and lichens (including saxicols) from five mesic, acidic sites (pH <7.0) and five mesic, basic sites (pH >/=7.0). n = number of quadrats. (Unpublished data from Timoney.)

	Vasculars				Bryophytes				Vasculars and Bryophytes				Lichens			
	n	mean	median	sd	n	mean	median	sd	n	mean	median	sd	n	mean	median	sd
Acidic	241	38	33	24	241	6	1	16	241	44	39	30	241	45	45	29
Basic	158	42	42	19	158	55	55	25	316	97	101	28	158	15	15	14
Acidic vs. Basic p(Mann-Whitney)			0.0082				<0.0001				<0.0001				<0.0001	

Table 3.7. Comparison of papillosity with acrocarpy in mosses and, fruticosity with light colour in lichens.

Mosses:	Acrocarpous	Pleurocarpous	Total
Papillose	19%	4%	23%
Non-papillose	43%	34%	77%
Total	62%	38%	100%

Lichens:	Fruticose	Non-fruticose	Total
Light-coloured	48%	14%	62%
Dark-coloured	27%	11%	38%
Total	75%	25%	100%

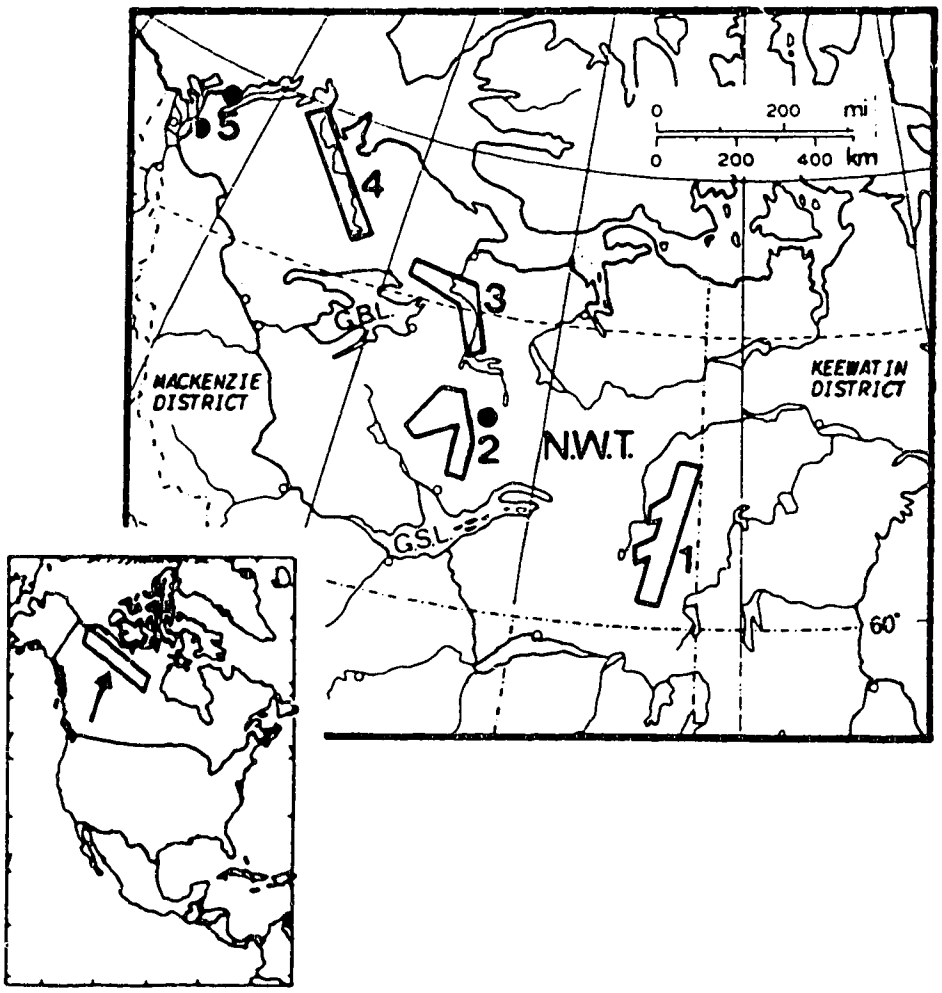

Fig. 3.1. Location of each study area: 1 = Dubawnt; 2 = Snare-Yellowknife, with Salmita area indicated to east; 3 = Coppermine-Kendall; 4 = Horton; 5 = Tuktoyaktuk-Inuvik.

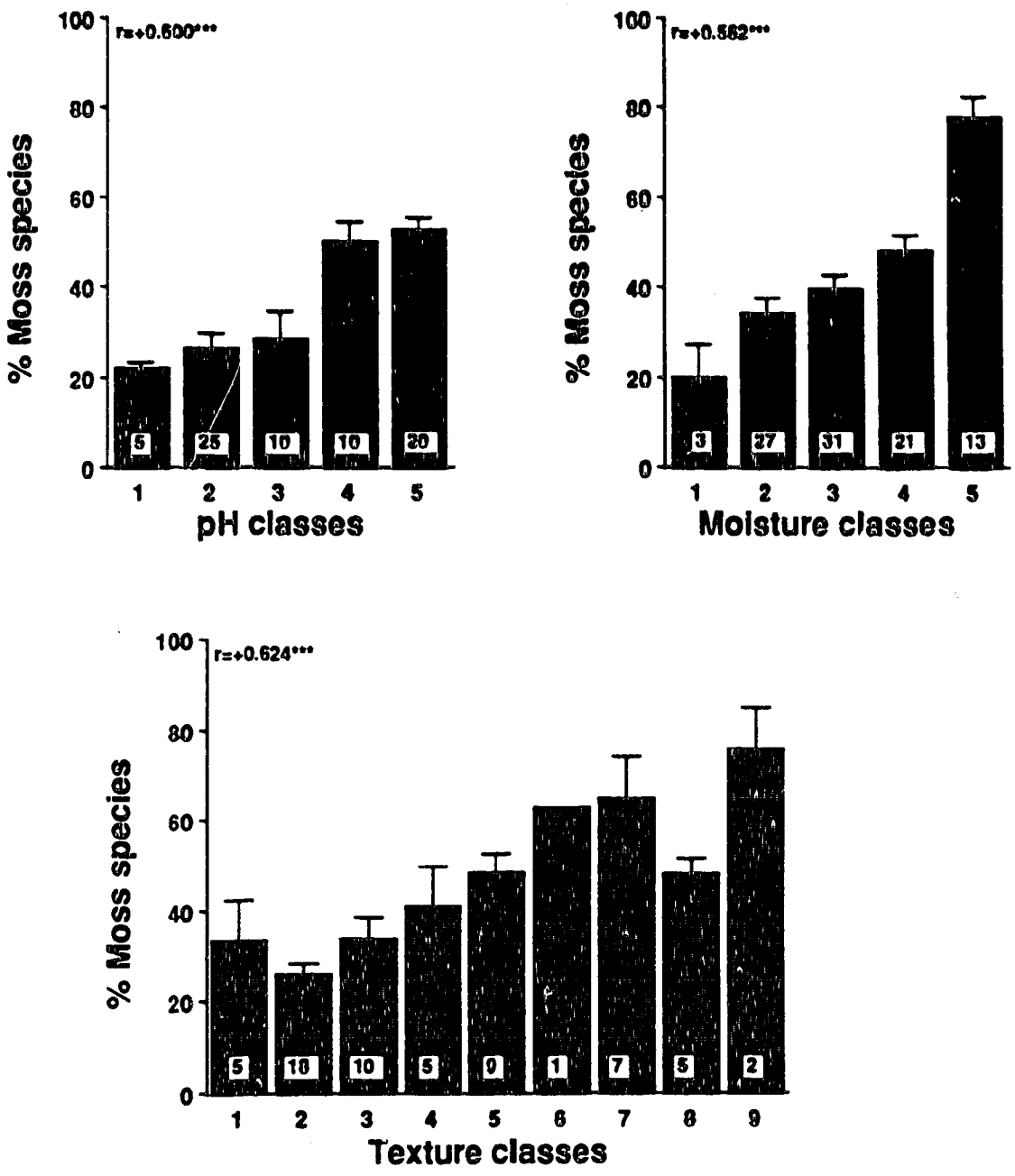

Fig. 3.2. Mean percent moss species per stand relative to soil pH, moisture, and texture. pH classes: 1=4.0-4.9, 2=5.0-5.9, 3=6.0-6.9, 4=7.0-7.9, 5=8.0; moisture classes: 1=dry, 2=dry-mesic, 3=mesic, 4=wet-mesic, 5=wet; texture classes: 1=sand, 2=loamy sand, 3=sandy loam, 4=loam, 5=silty loam, 6=silt, 7=clay loam, 8=silty clay loam, 9=clay; r=Spearman's rank correlation coefficient; *** significant @ p</=0.001, ** @ p</=0.01, * @ p</=0.05; number of stands and standard error are shown on bars.

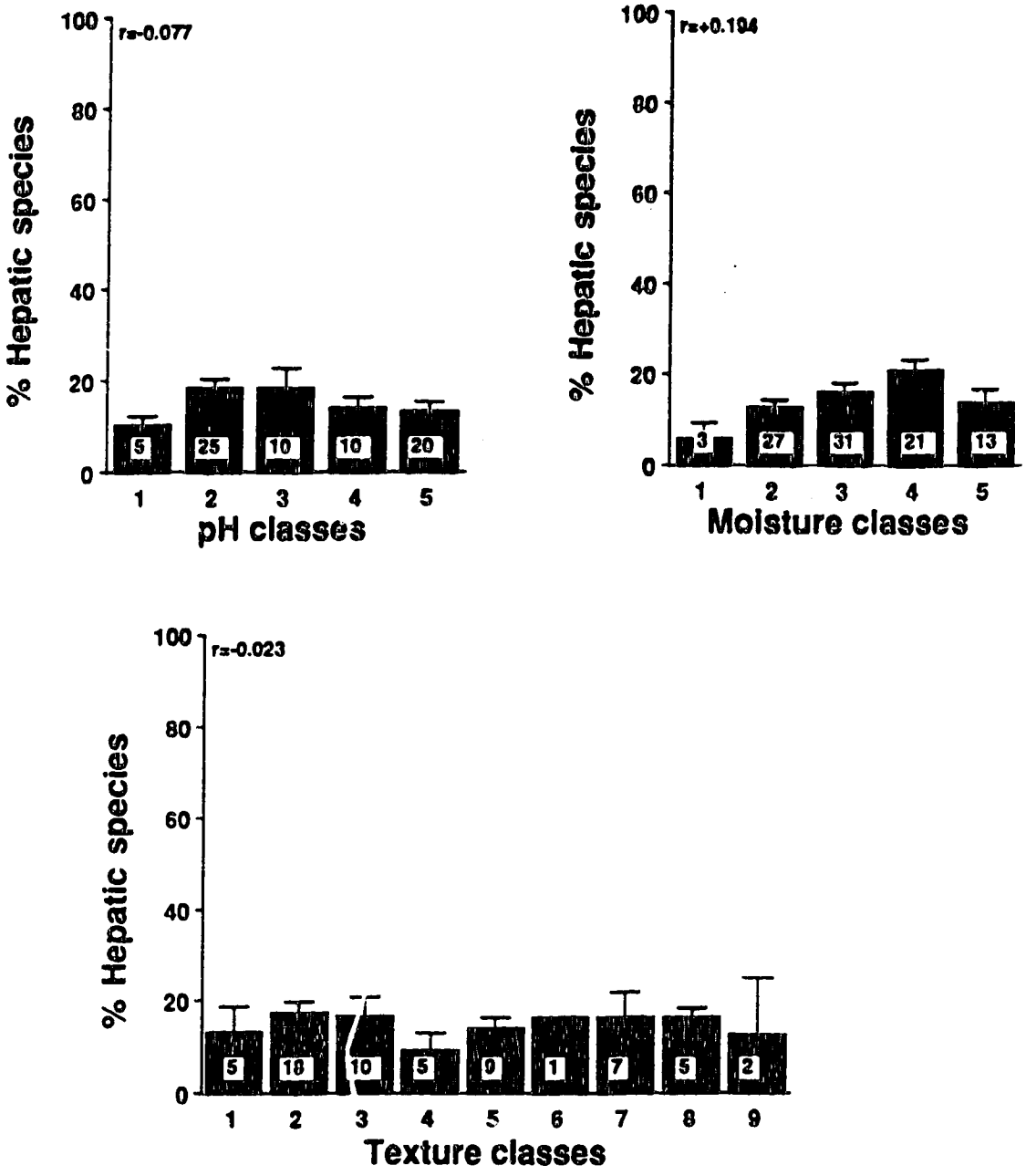

Fig. 3.3. Mean percent hepatic species per stand relative to soil pH, moisture, and texture. See Fig. 3.2 for definitions.

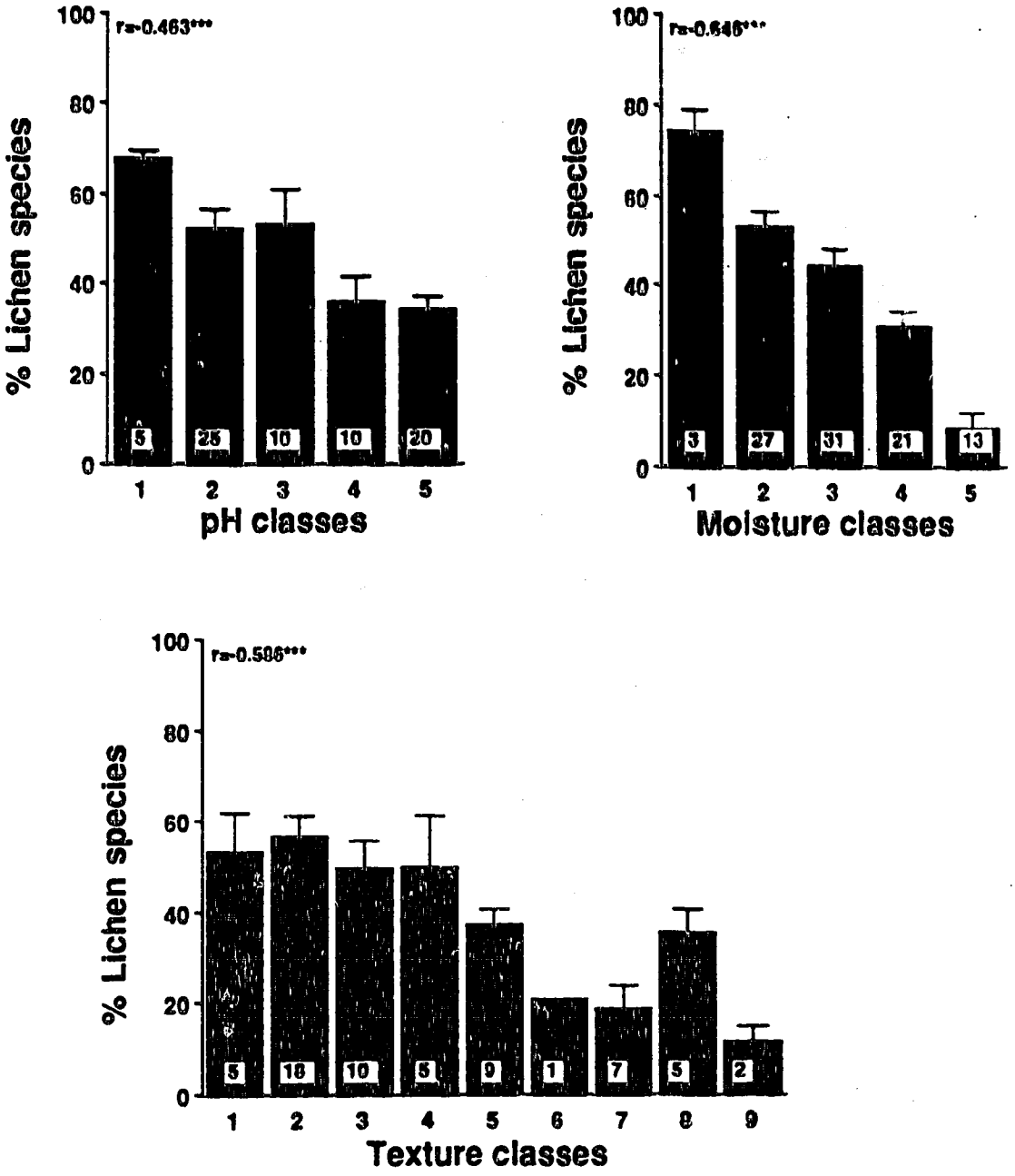

Fig. 3.4. Mean percent lichen species per stand relative to soil pH, moisture, and texture. See Fig. 3.2 for definitions.

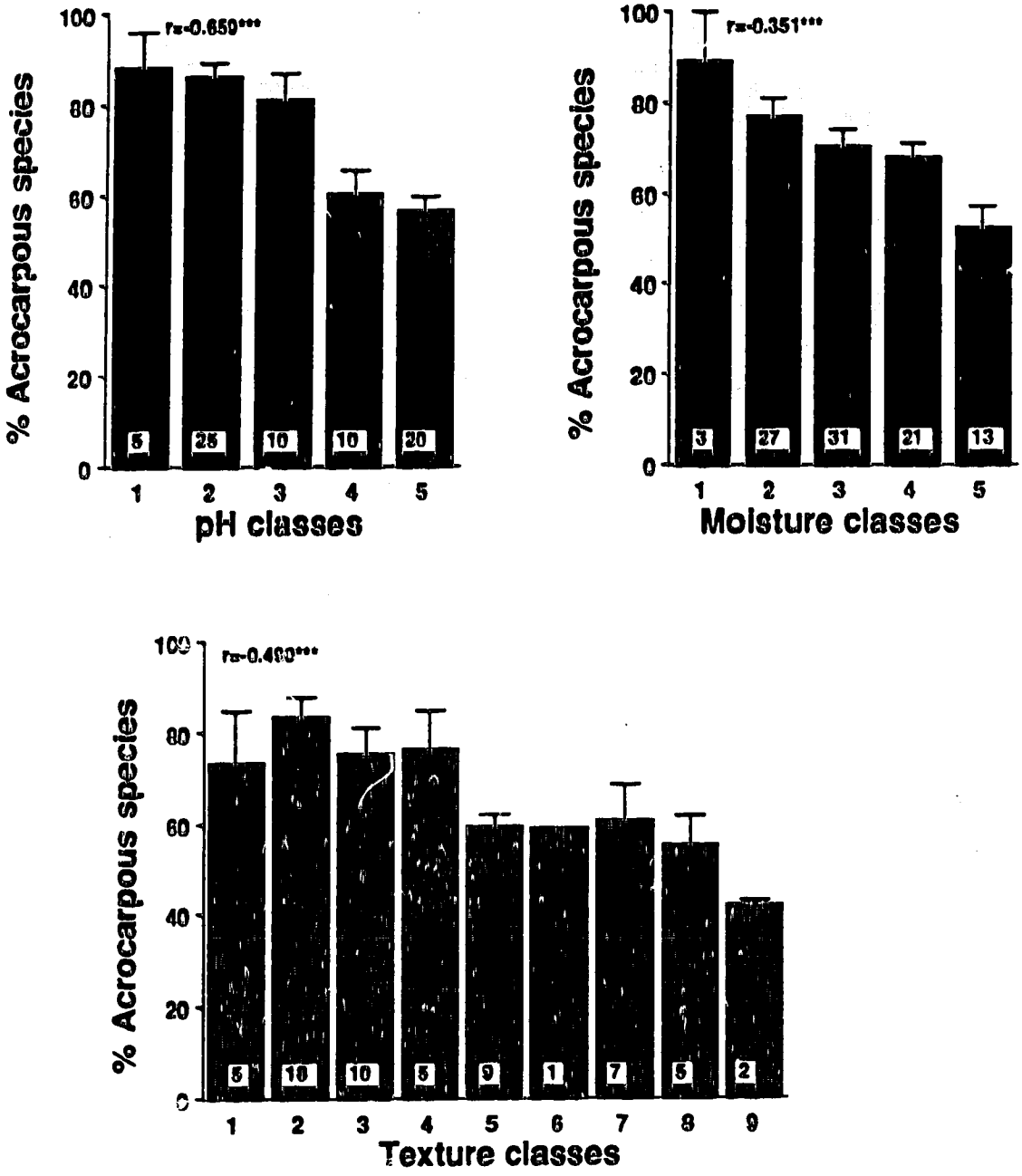

Fig. 3.5. Mean percent acrocarpous moss species per stand relative to soil pH, moisture, and texture. See Fig. 3.2 for definitions.

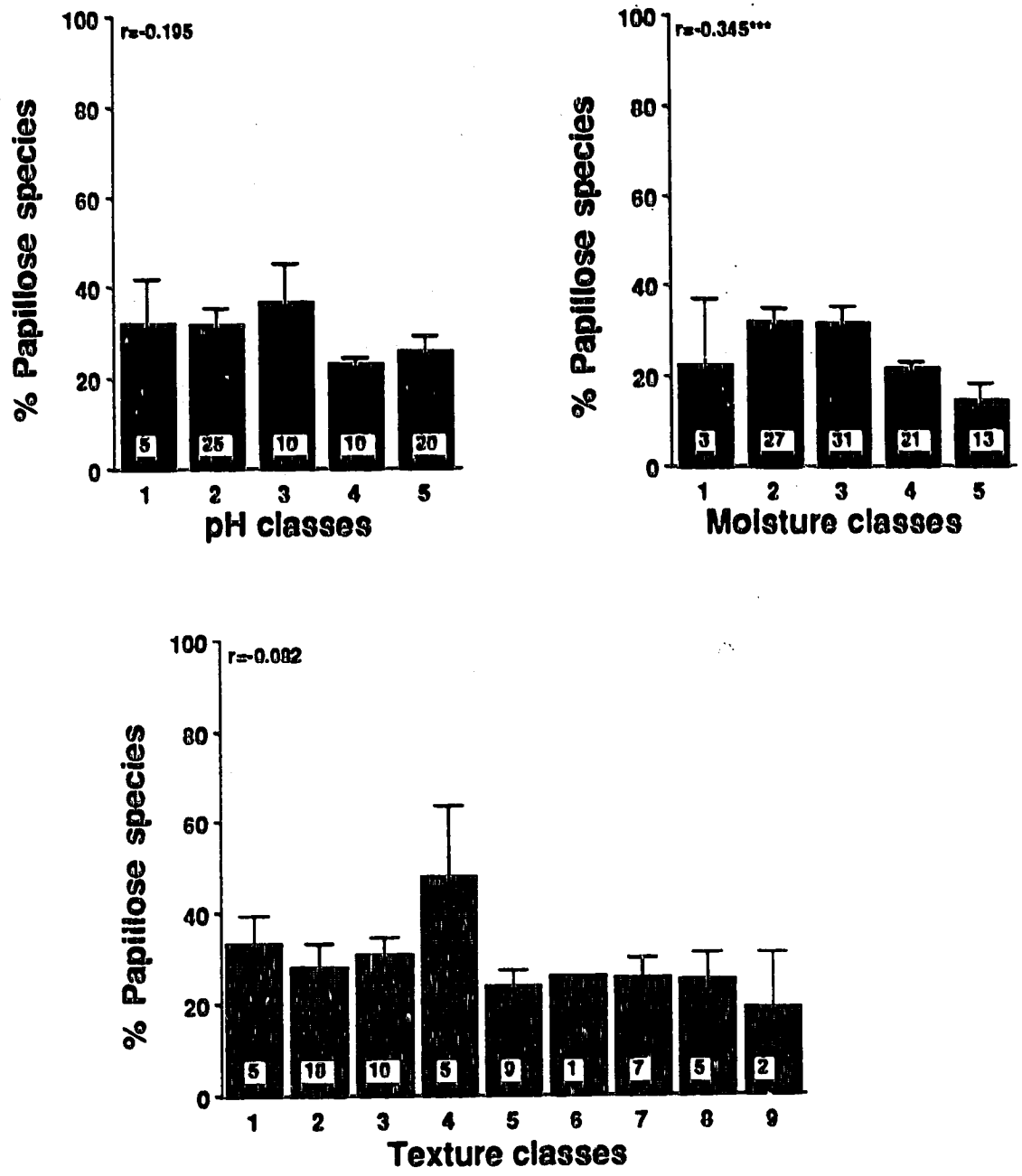

Fig. 3.6. Mean percent papillose moss species per stand relative to soil pH, moisture, and texture. See Fig. 3.2 for definitions.

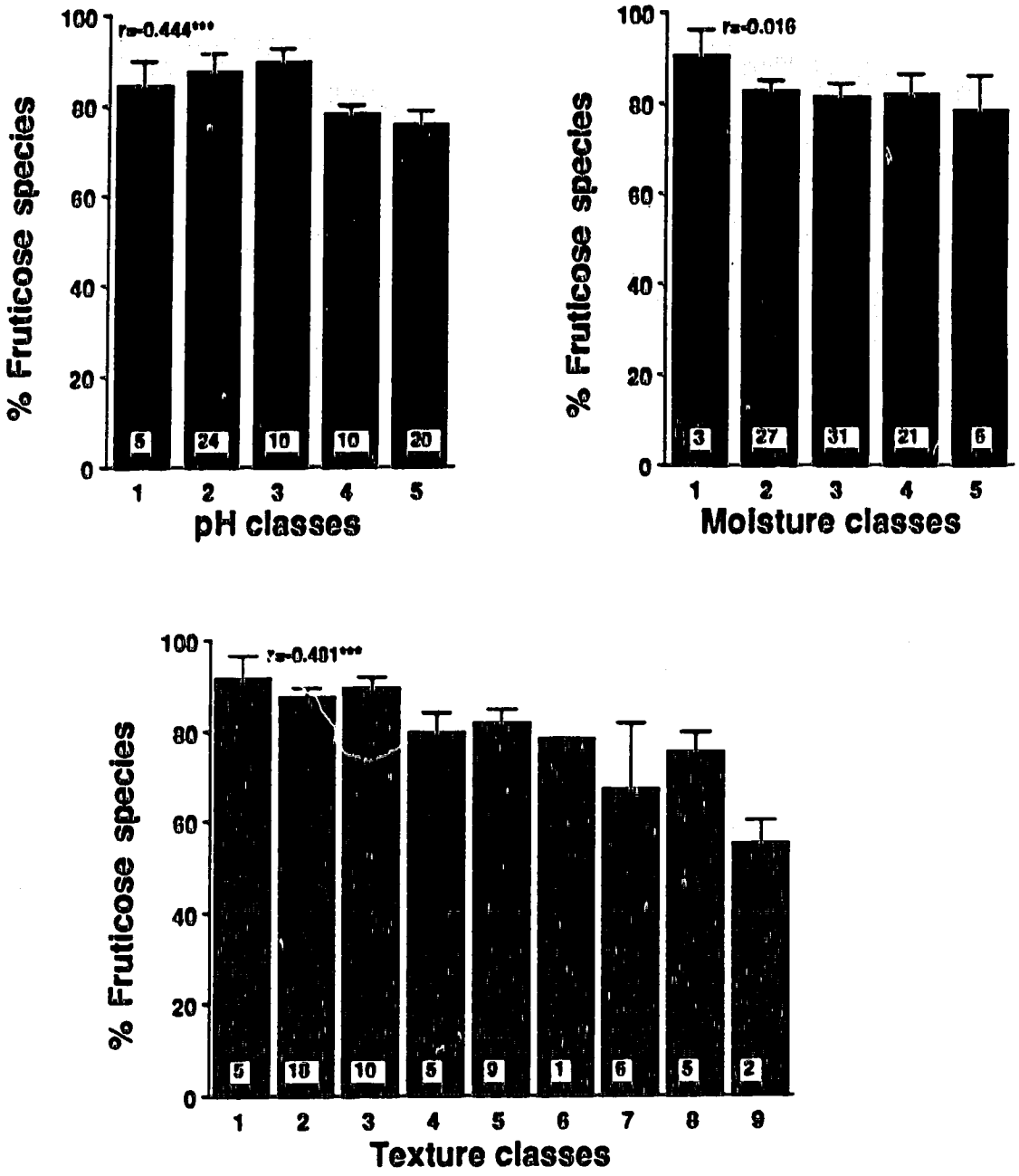

Fig. 3.7. Mean percent fruticose lichen species per stand relative to soil pH, moisture, and texture. See Fig. 3.2 for definitions.

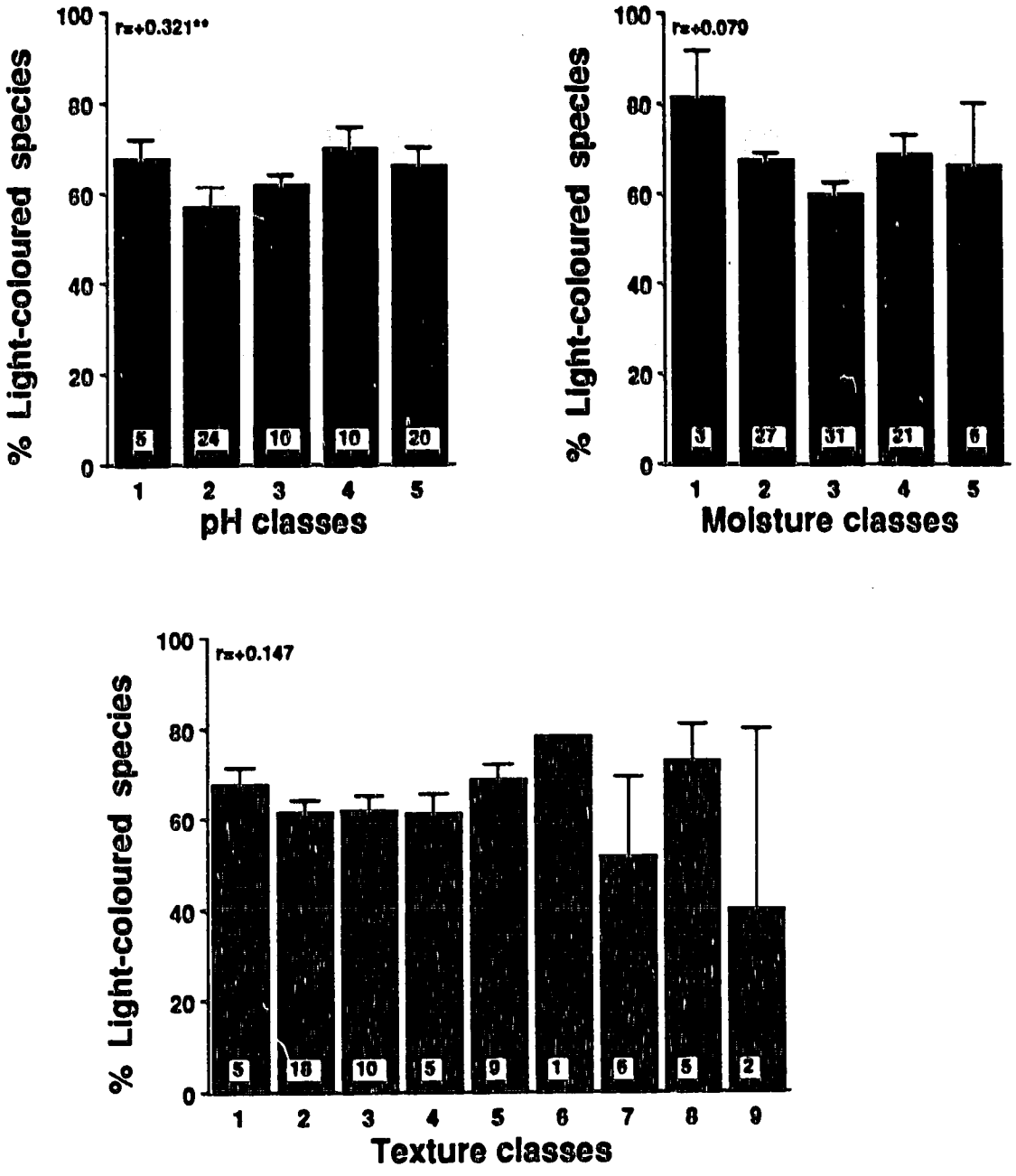

Fig. 3.8. Mean percent light-coloured lichen species per stand relative to soil pH, moisture, and texture. See Fig. 3.2 for definitions.

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4. CONCLUDING DISCUSSION

An understanding of pattern is a first step towards identifying the processes responsible for plant community organization. This study has elucidated several aspects of the structure of subarctic forest-tundra plant communities, particularly with regard to the terricolous bryophyte and lichen component. The salient aspects of the discussion are presented as follows.

The distributions of terricolous bryophytes, lichens, and vascular plants in the subarctic forest-tundra region, NWT are related to latitude and soil pH, texture, and moisture. The forest-tundra is oriented obliquely from northwest to southeast (see inset, Fig. 3.1). The northwest is characterized by medium- to fine-textured, mesic to wet, often basic soils; the southeast by coarse-textured, dry to mesic, typically acidic soils. Latitude represents a complex gradient that includes, among others, climatic and edaphic gradients.

Moss species outnumber lichens and hepatics (mosses: 47%; lichens: 32%; hepatics: 21%) and the majority of the mosses are acrocarpous and non-papillose. The numerical prevalence of acrocarpous and non-papillose species suggests an early evolutionary status of the mosses, but may also indicate that stress tolerance, which seems to favour acrocarpy, is more important than competition. Lichens are mostly fruticose and light-coloured. Most soil pH indicator species are mosses and most non-preferential species are lichens. Perhaps the inability of lichens to compete with faster-growing plants has led to the evolution of many species with the ability to tolerate a wide range of conditions.

Lichen species assemblages show less intra-site variability within the region compared to bryophytes. A large percentage of non-preferential lichen species occur in both acidic and basic areas. Bryophytes, particularly the mosses, dominate the indicator species. Understandably, bryophytes show a distinct separation between species assemblages from the northwestern and southeastern parts of the region.

Two distinct groups of bryophytes and lichens can be delineated. The northwestern group can be compared to the southeastern group as having:

1. a higher proportion of mosses to total bryophyte and lichen species;
2. a higher proportion of pleurocarpous mosses, indicating a more mesic, stable environment in the northwest;
3. a higher proportion of non-papillose mosses, indicating mesic to wet rather than dry soils;
4. a lower proportion of fruticose lichens, which may indicate a greater ability of fruticose forms colonize exposed, sandy soils and to reduce evaporative and thermal stress;
5. a greater number of indicator species, most of which are mosses;
6. fewer non-preferential (overlapping) bryophyte species but a similar number of non-preferential lichen species.

In this study, quantitative identification of pattern has allowed previously tendered hypotheses regarding the adaptive significance of several morphological characters of mosses and lichens to be corroborated, such as:

- pleurocarpy is an adaptation for a competitive life strategy in mesic, stable habitats;

- acrocarpy increases towards the poles;

- papillosity is associated with the most xerophytic habitats and as a result appears to be an adaptation for drought-tolerance;

- fruticosity of terricolous lichens is an adaptation for reduction of evaporative and thermal stress.

Testing of these hypotheses by experimental means is a next step.

The study has also posed some questions for future consideration. For example:

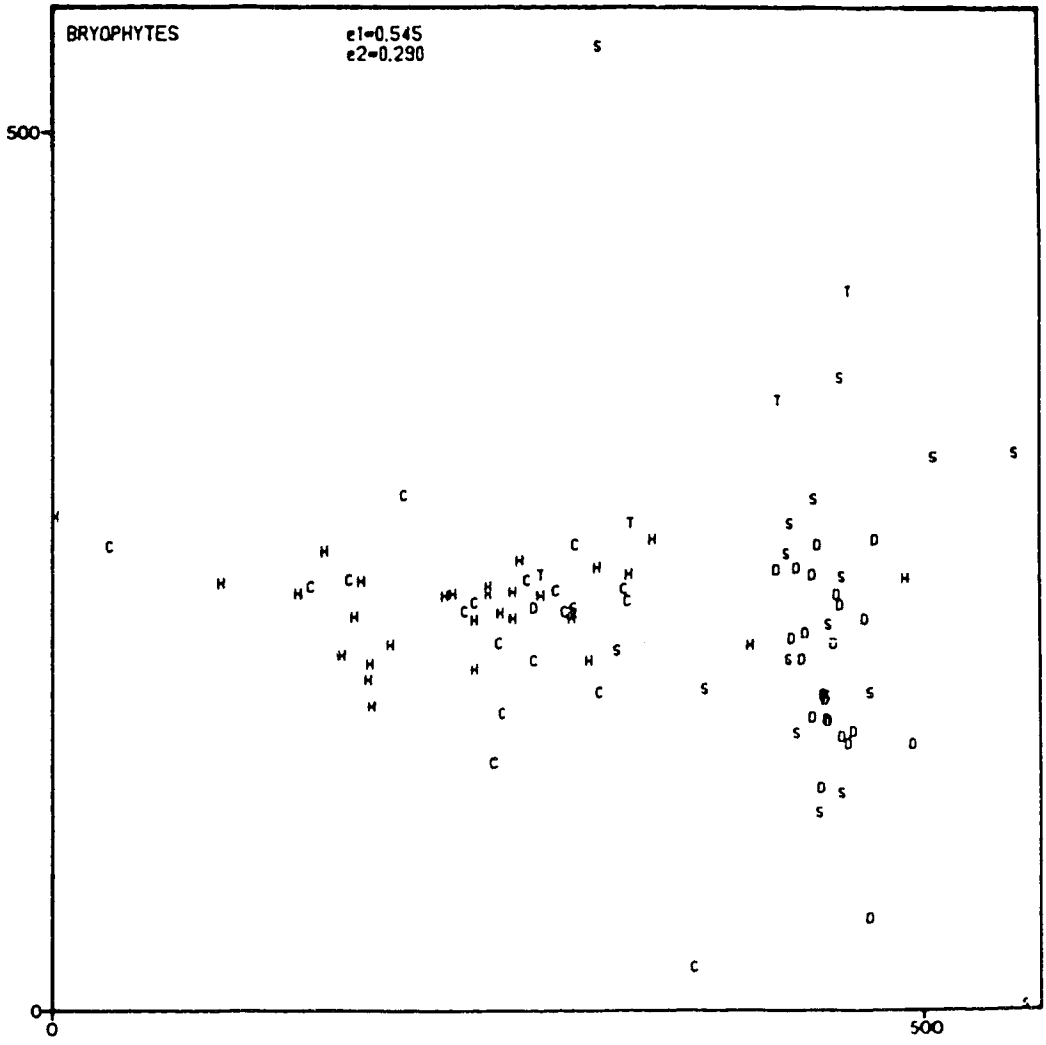
1. Terricolous hepatics in the study region represent 21% of the terricolous bryophyte and lichen flora. They appear to be responding to factors other than those analyzed in the present study. What controls the distribution of hepatics in the region?

2. Bryophytes from northern, basic, fine-textured, mesic to wet soils are significantly separated along the first DCA ordination axis in this study. While a weak moisture gradient is evident, what other factor(s) are responsible for this stand separation?

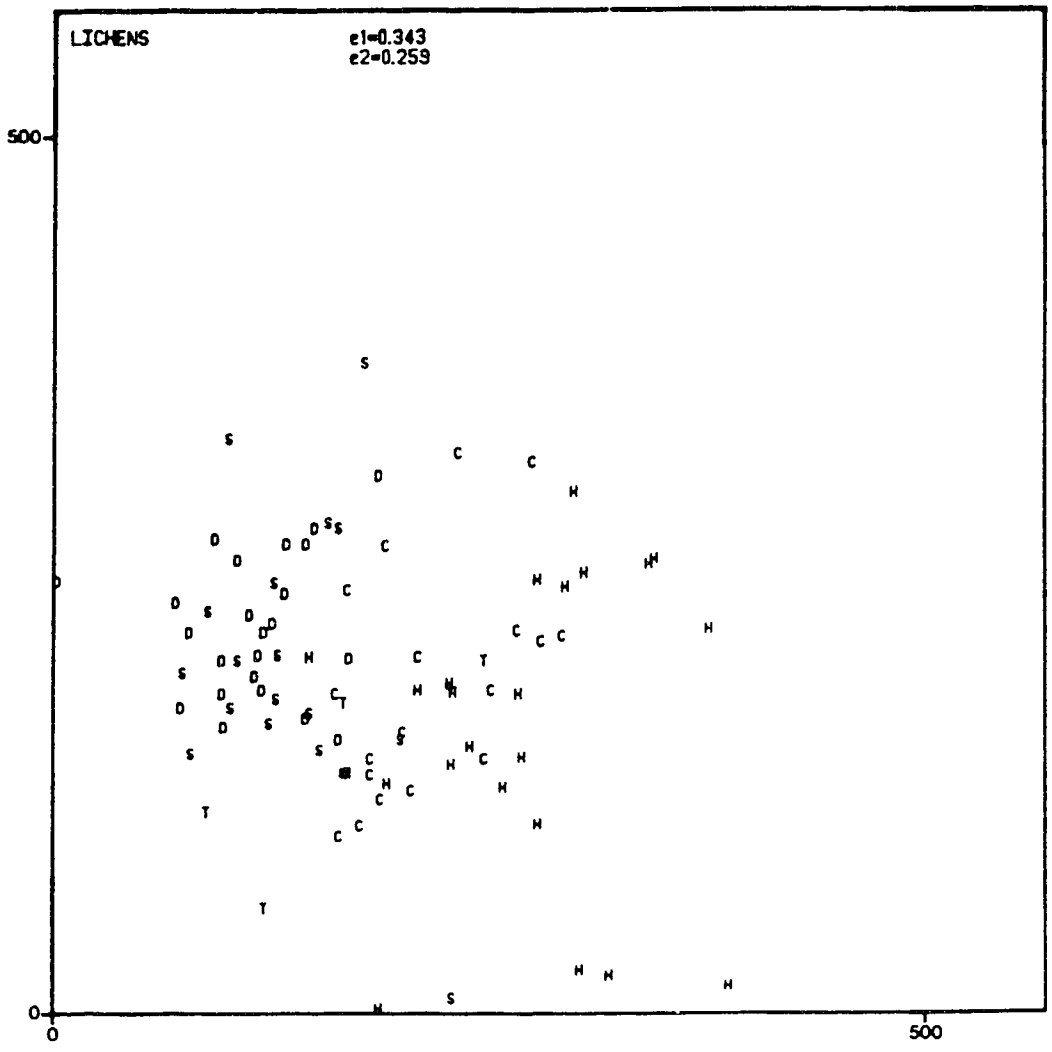
3. Why does the terricolous bryophyte and lichen flora of basic soils consist of so many specialists and that of acidic soils, so many generalists?

4. Why are lichen species so much more numerous than bryophyte species on acidic soils?

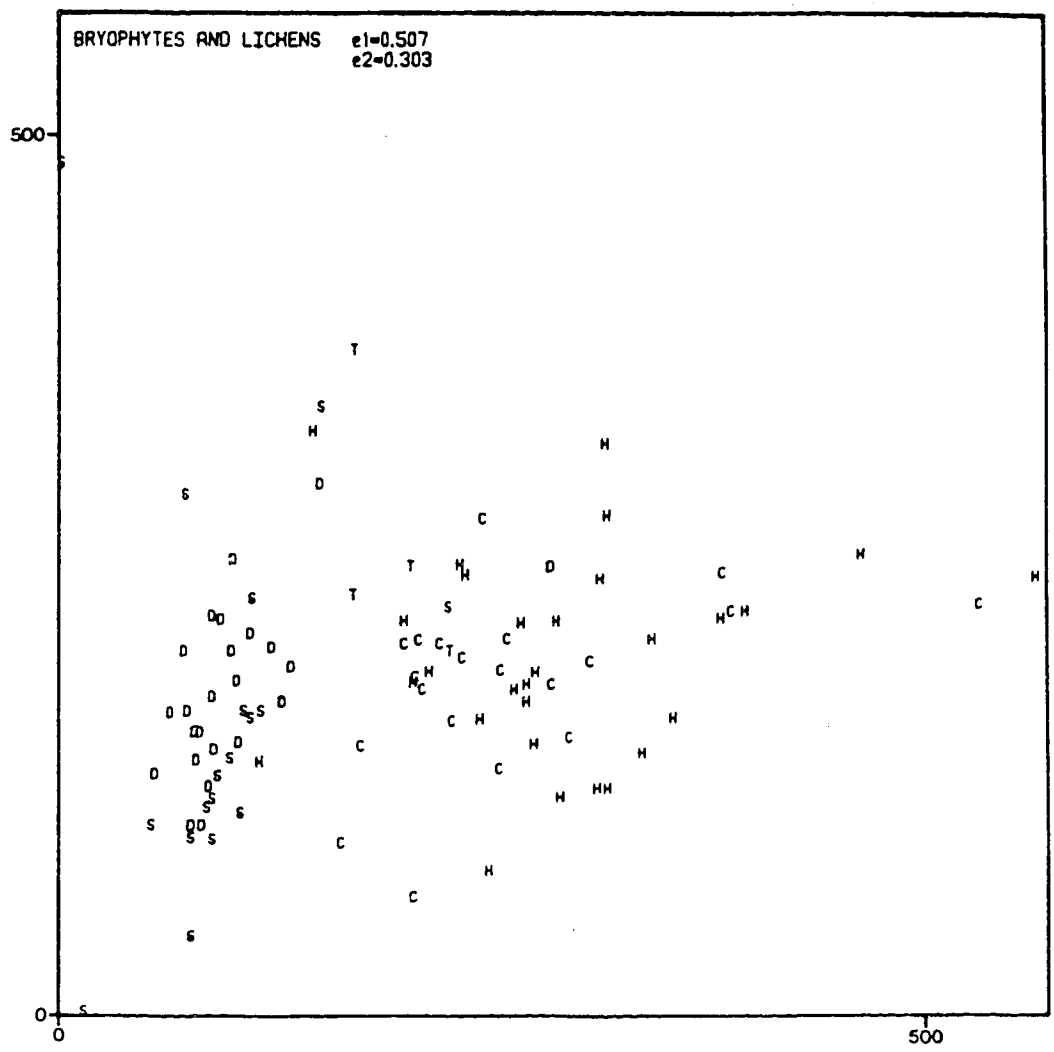
Appendix 1. Study area overlaid upon bryophyte stand ordination. S = Snare-Yellowknife, D = Dubawnt, C = Coppermine-Kendall, H = Horton, T = Tuktoyaktuk-Inuvik. e1, e2 = eigenvalues for 1st and 2nd axes, respectively. Study area significantly correlated with 1st ($r=-0.671^{***}$) and 2nd ($r=0.300^{**}$) axes.



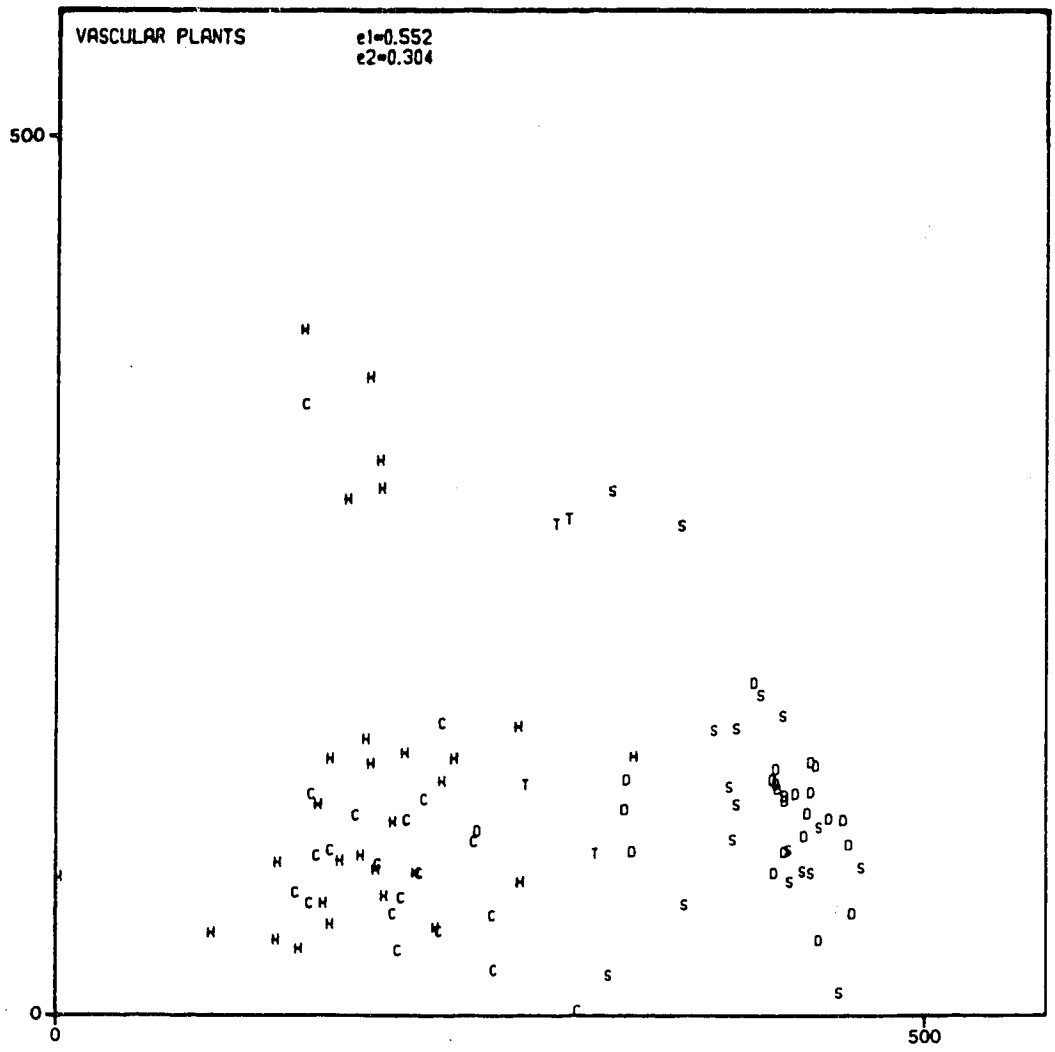
Appendix 2. Study area overlaid upon lichen stand ordination. S = Snare-Yellowknife, D = Dubawnt, C = Coppermine-Kendall, H = Horton, T = Tuktoyaktuk-Inuvik. e1, e2 = eigenvalues for 1st and 2nd axes, respectively. Study area significantly correlated with 1st (r=0.685***) and 2nd (r=-0.356***) axes.



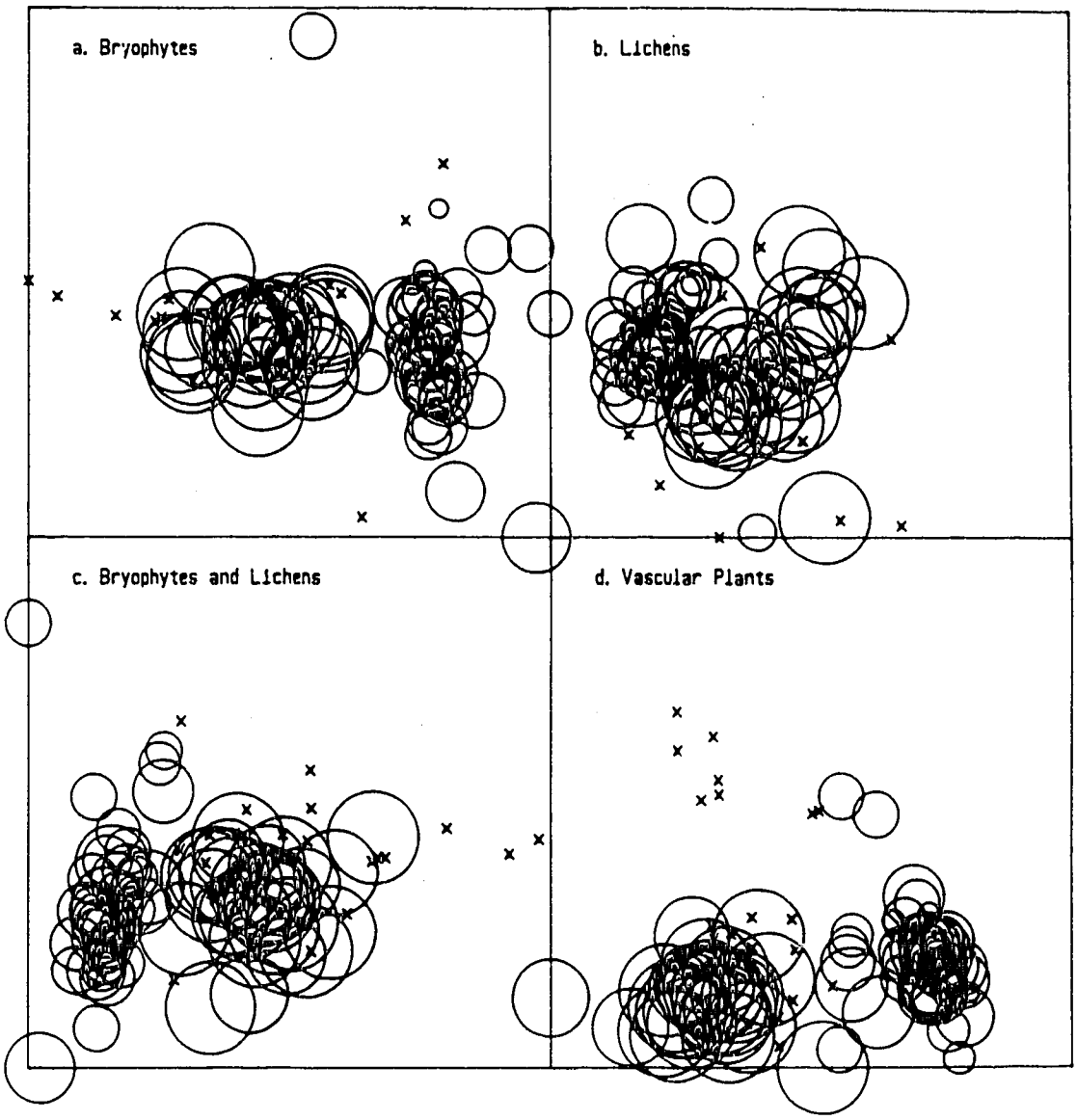
Appendix 3. Study area overlaid upon bryophyte and lichen stand ordination. S = Snare-Yellowknife, D = Dubawnt, C = Coppermine-Kendall, H = Horton, T = Tuktoyaktuk-Inuvik. e1, e2 = eigenvalues for 1st and 2nd axes, respectively. Study area significantly correlated with 1st (r=0.724***) and 2nd (r=0.228*) axes.



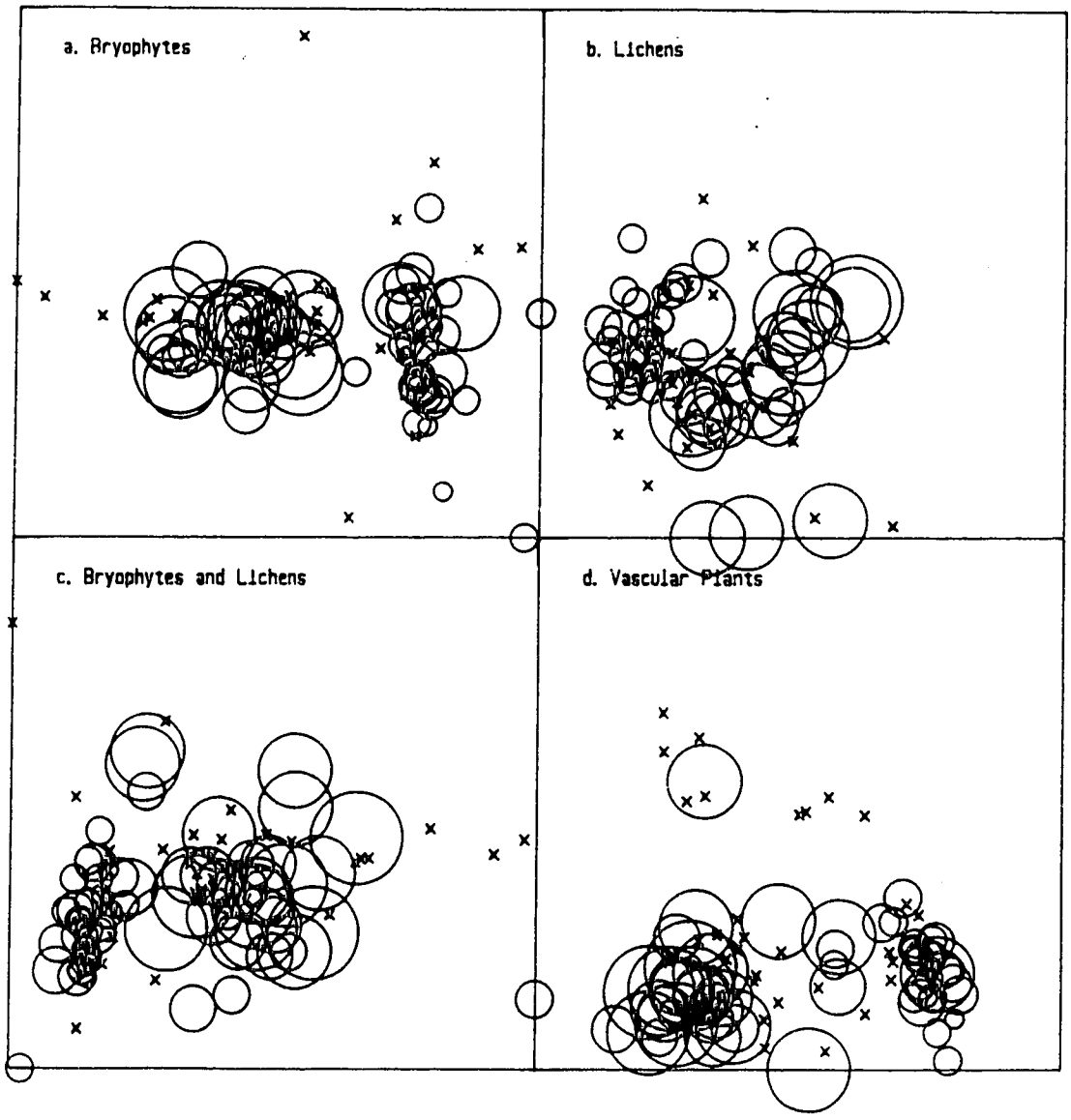
Appendix 4. Study area overlaid upon vascular plant stand ordination. S = Sneare-Yellowknife, D = Dubawnt, C = Coppermine-Kendall, H = Horton, T = Tuktoyaktuk-Inuvik. e1, e2 = eigenvalues for 1st and 2nd axes, respectively. Study area significantly correlated with 1st axis (r=-0.752***) but not 2nd.



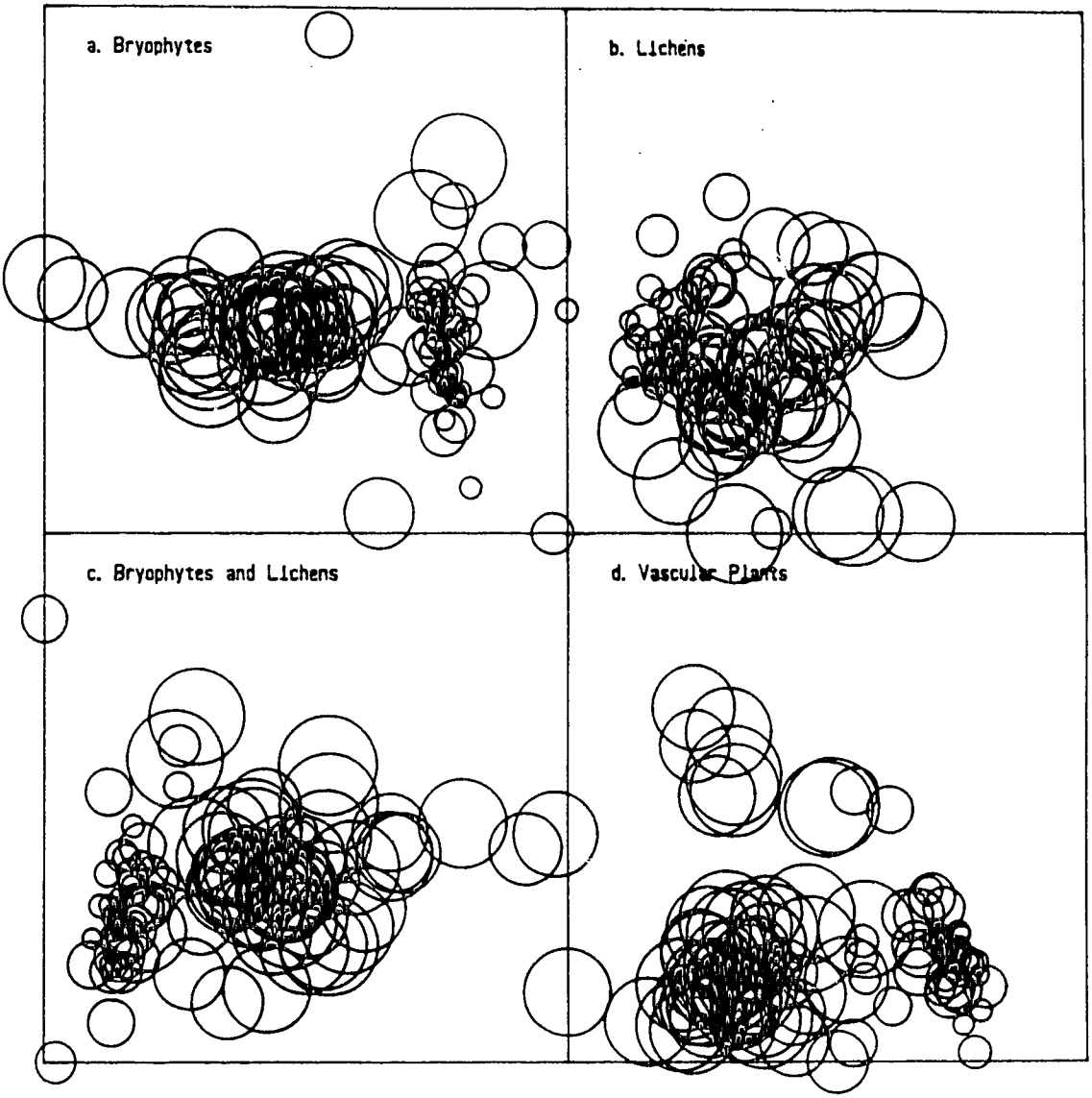
Appendix 5. Soil pH overlaid upon stand ordinations. Circle size increases with increasing pH, from 4.0 to 8.0.



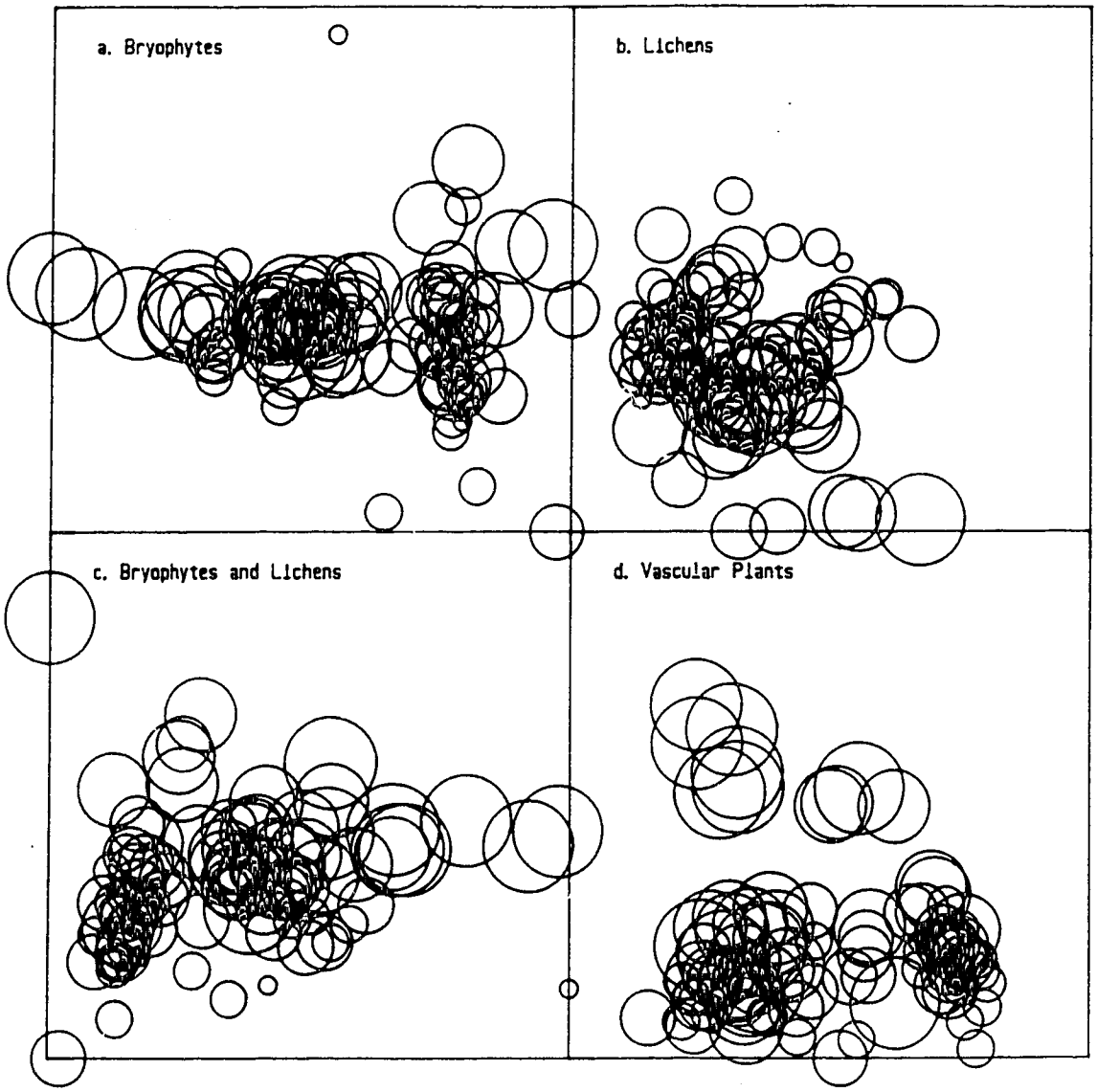
Appendix 6. Soil texture overlaid upon stand ordinations. Circle size increases from coarse to fine.



Appendix 7. Latitude overlaid upon stand ordinations. Circle size increases from south (60°54'N) to north (69°45'N).



Appendix 8. Moisture overlaid upon stand ordinations. Circle size increases with increasing moisture.



Appendix 9. DCA stand ordination scores (axes 1 and 2 as depicted in Appendices 1-4). - = stand not used for ordination.

STAND	BRYOPHYTES		LICHENS		BRYOPHYTES AND LICHENS		VASCULAR PLANTS	
	1	2	1	2	1	2	1	2
Dubawnt study area:								
S31	432	212	105	255	77	159	430	99
S33	453	153	132	236	81	106	434	141
S34	436	164	96	179	85	128	419	119
S35	494	149	112	224	63	170	414	137
S36	470	50	133	264	75	106	458	55
S37	452	228	0	243	99	257	434	124
S38	445	162	120	214	88	149	453	108
S40	441	124	144	165	102	153	439	40
S41	460	156	69	231	54	135	456	94
S43	444	163	96	198	78	143	437	139
S45	457	149	72	171	73	171	445	109
S47	443	174	97	160	87	179	414	129
S48	442	177	77	214	80	159	419	90
S49	450	234	92	267	71	205	419	122
S50	439	262	125	219	109	215	432	112
S51	467	220	115	189	92	223	425	123
S53	415	248	117	201	149	300	401	186
S54	430	197	119	181	101	188	415	126
S55	436	245	163	153	132	196	331	90
S56	427	249	186	303	121	207	328	131
S57	424	209	169	199	127	176	327	114
S58	473	265	149	273	87	225	412	131
S59	448	206	144	264	98	205	413	78
T28	277	226	-	-	281	253	242	102
Snare-Yellowknife study area:								
S01	427	155	127	176	105	171	418	167
S04	421	257	228	6	150	344	439	104
S07	470	178	73	191	52	106	422	73
S12	374	180	105	198	84	116	391	160
S14	437	288	157	276	97	144	378	159
S18	452	357	123	162	109	167	434	78
S20	423	274	88	226	75	99	463	81
S21	453	121	128	201	87	98	429	79
S22	559	0	100	324	13	0	421	91
S26	324	202	199	153	222	230	361	60
S30	444	176	101	171	87	121	451	10
R01	453	244	152	147	110	235	405	179
R02	553	314	-	-	0	482	320	295
R03	506	312	163	273	72	294	359	275
R04A	440	110	178	367	75	43	318	20
R04B	445	217	146	168	115	171	389	97
R05A	422	197	126	242	90	134	391	117
R05B	314	545	78	145	103	113	387	127

Appendix 9 continued.

STAND	BRYOPHYTES		LICHENS		BRYOPHYTES AND LICHENS		VASCULAR PLANTS	
	1	2	1	2	1	2	1	2
Coppermine-Kendall study area:								
S61	314	178	168	238	172	151	300	0
SA1	328	237	181	133	197	209	196	34
S62	289	236	205	124	230	201	193	55
SA2	299	223	187	119	207	183	251	54
R11	273	242	161	179	256	212	211	120
R12	330	230	209	200	205	211	240	96
S64	257	206	181	142	252	194	184	83
R13	368	22	232	316	161	96	252	23
S65	277	196	200	157	224	165	208	78
S66A	254	138	275	311	202	65	220	45
S67	294	224	175	104	217	209	198	64
R14S	300	262	163	98	242	280	222	163
R14P	32	261	-	-	529	232	141	344
S69	237	224	251	181	281	186	156	91
S70	201	290	266	215	291	156	136	67
S72	259	166	280	209	251	138	144	61
S73	169	242	-	-	380	250	171	111
S74	243	229	292	212	303	199	148	88
R15	147	238	247	142	385	228	145	123
R16	299	226	190	263	203	190	201	108
Horton study area:								
S75	258	223	209	181	240	166	152	61
R17	400	205	146	200	114	142	267	73
R18P	155	258	387	13	393	228	166	290
R18S	298	220	168	134	211	193	222	130
S76	265	220	267	179	267	176	156	49
S77	308	196	166	134	202	187	174	88
R19	0	278	-	-	562	248	140	386
R20	176	241	376	216	351	167	149	117
S78	230	234	191	128	284	222	183	80
S791	281	233	258	126	264	221	156	143
S792	193	205	305	248	286	122	88	44
S793	165	199	299	294	245	80	0	76
S80	181	194	269	143	307	127	138	35
R21	265	235	294	240	272	193	162	85
R22S	140	234	278	105	379	224	180	140
R22P	96	240	-	-	460	260	179	359
S81	243	219	227	185	260	183	206	78
S82	225	233	278	244	271	152	125	40
S83	243	191	228	139	267	186	188	65
S84	180	185	345	256	333	147	126	84
R23	331	245	302	22	232	248	229	143
R24P	251	234	229	180	309	246	186	296
R24S	345	265	-	-	197	222	200	146
R25	490	243	-	-	145	330	332	144

Appendix 9 concluded.

STAND	BRYOPHYTES		LICHENS		BRYOPHYTES AND LICHENS		VASCULAR PLANTS	
	1	2	1	2	1	2	1	2
R27	182	170	342	253	313	127	218	47
S85	172	221	239	149	339	212	193	107
R28C	313	249	186	0	229	254	266	161
R28T	269	253	-	-	312	323	185	312
R34	251	238	319	19	313	282	177	154
Tuktoyaktuk-Inuvik study area:								
R351	281	245	166	174	223	205	270	128
R352	457	406	247	198	168	237	295	279
R355	416	344	87	112	169	376	288	276
T45	332	274	120	57	201	253	310	89

Appendic 10. A list of mosses collected. * = not used for ordinations or analysis of morphological characters; # = number of collections.

SPECIES	#	ACROCARPOUS/ PLEUROCARPOUS	PAPILLOSE/ NON-PAPILLOSE
*AMBLYSTEGIUM SERPENS	3	P	N
AULACOMNIUM ACUMINATUM	41	A	P
AULACOMNIUM PALUSTRE	53	A	P
AULACOMNIUM TURGIDUM	75	A	P
BRACHYTHECIUM ERYTHRORRHIZON	4	P	N
*BRACHYTHECIUM MILDEANUM	1	P	N
BRACHYTHECIUM PLUMOSUM	9	P	N
BRACHYTHECIUM SALEBROSUM	9	P	N
*BRACHYTHECIUM SP.	1	P	N
BRACHYTHECIUM TURGIDUM	23	P	N
BRYOERYTHROPHYLLUM RECURVIROSTRUM	20	A	P
*BRYUM ACUTIFORME	1	A	N
BRYUM CAESPITICIUM	5	A	N
*BRYUM CAPILLARE	3	A	N
BRYUM LISAE	6	A	N
BRYUM PSEUDOTRIQUETRUM	174	A	N
*BRYUM SP.	24	A	N
BRYUM WRIGHTII	4	A	N
*CALLIERGON CORDIFOLIUM	1	P	N
CALLIERGON GIGANTEUM	12	P	N
CALLIERGON RICHARDSONII	6	P	N
*CALLIERGON STRAMINEUM	3	P	N
CALLIERGON TRIFARIUM	5	P	N
CAMPYLIUM CHRYSOPHYLLUM	5	P	N
*CAMPYLIUM HISPIDULUM	1	P	N
CAMPYLIUM POLYGAMUM	5	P	N
*CAMPYLIUM SP.	1	P	N
CAMPYLIUM STELLATUM	114	P	N
CATOSCOPIUM NIGRITUM	18	A	N
CERATODON PURPUREUS	37	A	N
CINCLIDIUM ARCTICUM	7	A	N
CINCLIDIUM LATIFOLIUM	3	A	N
CINCLIDIUM STYGIUM	17	A	N
CINCLIDIUM SUBROTUNDUM	10	A	N
CIRRIPHYLLUM CIRROSUM	14	P	N
*CLIMACIUM DENDROIDES	1	P	N
*CONOSTOMUM TETRAGONUM	1	A	P
*CRATONEURON FILICINUM	2	P	N
*CYNODONTIUM STRUMIFERUM	3	A	N
*CYNODONTIUM TENELLUM	1	A	N
CYRTOMNIUM HYMENOPHYLLOIDES	11	A	N
*CYRTOMNIUM HYMENOPHYLLUM	1	A	N

Appendix 10 continued.

SPECIES	#	ACROCARPOUS/ PLEUROCARPOUS	PAPILLOSE/ NON-PAPILLOSE
*DESMATODON HEIMII	1	A	P
*DICRANELLA GREVILLEANA	1	A	N
*DICRANELLA SP.	3	A	N
DICRANUM ACUTIFOLIUM	111	A	N
DICRANUM AMANNII	14	A	N
DICRANUM ANGUSTUM	24	A	N
*DICRANUM BREVIFOLIUM	1	A	N
DICRANUM ELONGATUM	58	A	N
DICRANUM FUSCESCENS	7	A	N
DICRANUM GROENLANDICUM	23	A	N
*DICRANUM MAJUS	1	A	N
DICRANUM MUEHLENBECKII	15	A	N
DICRANUM SCOPARIUM	6	A	N
*DICRANUM SP.	5	A	N
DICRANUM SPADICEUM	7	A	N
DICRANUM UNDULATUM	9	A	N
*DIDYMODON FALLAX	1	A	P
*DIDYMODON RIGIDULUS	1	A	N
DISTICHIUM CAPILLACEUM	152	A	N
DISTICHIUM INCLINATUM	7	A	N
DITRICHUM FLEXICAULE	233	A	N
DREPANOCLADUS ADUNCUS	8	P	N
DREPANOCLADUS EXANNULATUS	2	P	N
DREPANOCLADUS FLUITANS	3	P	N
*DREPANOCLADUS LYCOPODIOIDES	1	P	N
*DREPANOCLADUS PSEUDOSTRAMINEUS	1	P	N
DREPANOCLADUS REVOLVENS	63	P	N
DREPANOCLADUS UNCINATUS	74	P	N
*DREPANOCLADUS VERNICOSUS	2	P	N
*ENCALYPTA AFFINIS	1	A	P
ENCALYPTA ALPINA	6	A	P
ENCALYPTA PROCERA	9	A	P
ENCALYPTA RHAPTOCARPA	18	A	P
*ENCALYPTA SP.	2	A	P
EURHYNCHIUM PULCHELLUM	18	P	N
FISSIDENS ADIANTHOIDES	10	P	N
FISSIDENS OSMUNDOIDES	10	A	N
*GYMNOSTOMUM AERUGINOSUM	3	A	P
HYLOCOMIUM SPLENDENS	103	P	N
HYPNUM BAMBERGERI	126	P	N
HYPNUM CUPRESSIFORME	6	P	N
HYPNUM HAMULOSUM	8	P	N
HYPNUM LINDBERGII	10	P	N
HYPNUM REVOLUTUM	7	P	N
*HYPNUM SP.	2	P	N
HYPNUM VAUCHERI	4	P	N
ISOPTERYGIUM PULCHELLUM	39	P	N

Appendix 10 continued.

SPECIES	#	ACROCARPOUS/ PLEUROCARPOUS	PAPILLOSE/ NON-PAPILLOSE
KIAERIA GLACIALIS	2	A	N
*LEPTOBRYUM PYRIFORME	3	A	N
LOESKYPNUM BADIUM	5	P	N
MEESIA TRIQUETRA	10	A	N
MEESIA ULIGINOSA	20	A	N
MNIUM BLYTTII	4	A	N
*MNIUM THOMSONII	1	A	N
MYURELLA JULACEA	53	P	P
MYURELLA TENERRIMA	21	P	P
*ONCOPHORUS VIRENS	2	A	N
ONCOPHORUS WAHLENBERGII	36	A	N
ORTHOTHECIUM CHRYSEUM	24	P	N
*ORTHOTHECIUM INTRICATUM	3	P	N
ORTHOTHECIUM STRICTUM	17	P	N
*OXYSTEGUS TENUIROSTRIS	1	A	P
PHILONOTIS FONTANA	8	A	P
PLAGIOMNIUM ELLIPTICUM	18	A	N
*PLAGIOMNIUM MEDIUM	3	A	N
*PLAGIOPUS OEDERIANA	3	A	N
PLATYDICTYA JUNGERMANNIOIDES	10	P	N
PLEUROZIUM SCHREBERI	36	P	N
POGONATUM DENTATUM	4	A	P
POHLIA CRUDA	30	A	N
POHLIA NUTANS	97	A	N
POLYTRICHUM ALPINUM	2	A	P
POLYTRICHUM COMMUNE	11	A	P
POLYTRICHUM JUNIPERINUM	68	A	P
POLYTRICHUM PILIFERUM	66	A	P
*PSEUDOBRYUM CINCLIDIOIDES	1	A	N
*PSEUDOLESKEELA PAPILLOSA	1	P	P
PTILIUM CRISTA-CASTRENSIS	5	P	N
RHACOMITRIUM LANUGINOSUM	14	A	P
RHIZOMNIUM ANDREWSIANUM	3	A	N
RHYTIDIUM RUGOSUM	63	P	N
SCORPIDIUM SCORPIOIDES	16	P	N
SCORPIDIUM TURGESCENS	30	P	N
SPHAGNUM ANGUSTIFOLIUM	6	A	N
SPHAGNUM AONGSTROEMII	3	A	N
SPHAGNUM BALTICUM	8	A	N
*SPHAGNUM CAPILLIFOLIUM	1	A	N
*SPHAGNUM CONTORTUM	1	A	N
SPHAGNUM FIMBRIATUM	5	A	N
SPHAGNUM FUSCUM	6	A	N
*SPHAGNUM GIRGENSOHNII	2	A	N
SPHAGNUM MAGELLANICUM	4	A	N
*SPHAGNUM OBTUSUM	1	A	N
SPHAGNUM RUSSOWII	6	A	N

Appendix 10 concluded.

SPECIES	#	ACROCARPOUS/ PLEUROCARPOUS	PAPILLOSE/ NON-PAPILLOSE
*SPHAGNUM SP.	4	A	N
*SPHAGNUM SQUARROSUM	2	A	N
SPHAGNUM TERES	7	A	N
SPHAGNUM WARNSTORFII	6	A	N
*SPLACHNACEAE SP.	1	A	N
STEGONIA LATIFOLIA	2	A	N
*TAYLORIA ACUMINATA	1	A	N
*TAYLORIA FROELICHIANA	2	A	N
*TAYLORIA SP.	4	A	N
TETRAPLODON MNIOIDES	4	A	N
*TETRAPLODON PALLIDUS	1	A	N
*TETRAPLODON PARADOXUS	3	A	N
THUIDIUM ABIETINUM	22	P	P
THUIDIUM RECOGNITUM	4	P	P
TIMMIA AUSTRIACA	5	A	P
TIMMIA MEGAPOLITANA	4	A	P
TIMMIA NORVEGICA	3	A	P
TOMENTHYPNUM NITENS	163	P	N
TORTELLA FRAGILIS	51	A	P
TORTELLA TORTUOSA	45	A	P
*TORTULA NORVEGICA	1	A	P
TORTULA RURALIS	12	A	P
*TRICHODON CYLINDRICUS	1	A	N
*WEISSIA CONTROVERSA	1	A	P
*WEISSIA SP.	2	A	P

Appendix 11. A list of hepatics collected. # = number of collections.

Species	#
ANASTROPHYLLUM MINUTUM	99
ANEURA PINGUIS	3
ARNELLIA FENNICA	11
BARBILOPHOZIA ATLANTICA	2
BARBILOPHOZIA ATTENUATA	1
BARBILOPHOZIA BARBATA	10
BARBILOPHOZIA BINSTEADII	26
BARBILOPHOZIA HATCHERI	1
BARBILOPHOZIA KUNZEANA	40
BARBILOPHOZIA LYCOPODIOIDES	3
BARBILOPHOZIA QUADRILOBA	1
BLEPHAROSTOMA TRICHOPHYLLUM	47
CALYPOGEJA MUELLERIANA	9
CALYPOGEJA SPHAGNICOLA	5
CEPHALOZIA BICUSPIDATA	2
CEPHALOZIA CONNIVENS	1
CEPHALOZIA LUNULIFOLIA	5
CEPHALOZIA PLENICEPS	2
CEPHALOZIA SP.	2
CEPHALOZIELLA ARCTICA	12
CEPHALOZIELLA DIVARICATA	11
CEPHALOZIELLA ELACHISTA	5
CEPHALOZIELLA HAMPEANA	13
CEPHALOZIELLA RUBELLA	44
CEPHALOZIELLA SP.	9
CEPHALOZIELLA SUBDENTATA	3
CHANDONANTHUS SETIFORMIS	1
CLADOPODIELLA FLUITANS	5
GYMNOCOLEA INFLATA	18
GYMNOMITRION CONCINNATUM	1
LOPHOCOLEA MINOR	1
LOPHOZIA ALPESTRIS	10
LOPHOZIA ASCENDENS	2
LOPHOZIA BADENSIS	1
LOPHOZIA COLLARIS	11
LOPHOZIA EXCISA	24
LOPHOZIA GILLMANII	15
LOPHOZIA GRANDIRETIS	5
LOPHOZIA GUTTULATA	4
LOPHOZIA HETEROCOLPOS	10
LOPHOZIA HETEROMORPHA	1
LOPHOZIA (LEIOCOLEA) SP.	4
LOPHOZIA LONGIDENS	4
LOPHOZIA (LOPHOZIA) SP.	7
LOPHOZIA OBTUSA	10
LOPHOZIA OPACIFOLIA	1
LOPHOZIA (ORTHOCAULIS) SP.	1

Appendix 11 concluded.

SPECIES	#
LOPHOZIA RUBRIGEMMA	1
LOPHOZIA RUTHEANA	10
LOPHOZIA SP.	23
LOPHOZIA SUDETICA	5
LOPHOZIA VENTRICOSA	19
LOPHOZIA WENZELII	1
MARCHANTIA POLYMORPHA	4
MESOPTYCHIA SAHLBERGII	10
MYLIA ANOMOLA	5
ODONTOCHISMA MACOUNII	10
PELLIA ENDIVIIFOLIA	2
PLAGIOCHILA ASPLENOIDES	20
PREISSA QUADRATA	2
PTILIDIUM CILIARE	138
RADULA PROLIFERA	6
SCAPANIA DEGENII	2
SCAPANIA GYMNOSTOMOPHILA	15
SCAPANIA IRRIGUA	4
SCAPANIA MUCRONATA	2
SCAPANIA PALUDICOLA	7
SCAPANIA PALUDOSA	5
SCAPANIA SIMMONSII	1
SCAPANIA SP.	4
TRITOMARIA EXECTIFORMIS	9
TRITOMARIA POLITA	1
TRITOMARIA QUINQUEDENTATA	17
TRITOMARIA SCITULA	4

Appendix 12. A list of lichens collected. * = not used for ordinations or analysis of morphological characters; # = number of collections.

SPECIES	#	FRUTICOSE/ NON-FRUTICOSE	LIGHT/ DARK
ALECTORIA NIGRICANS	11	F	L
ALECTORIA OCHROLEUCA	46	F	L
*ASAHINEA CHRYSANTHA	2	N	L
BRYORIA CHALYBEIFORMIS	4	F	D
BRYORIA NITIDULA	32	F	D
*CALOPLACA JUNGERMANNIAE	3	N	D
*CALOPLACA STILLICIDIORUM	1	N	D
CETRARIA ANDREJEVII	12	F	D
CETRARIA CUCULLATA	121	F	L
CETRARIA DELISEI	7	F	D
CETRARIA ERICETORUM	50	F	D
*CETRARIA HEPATIZON	1	F	D
CETRARIA ISLANDICA	60	F	D
CETRARIA LAEVIGATA	36	F	D
*CETRARIA NIGRICANS	3	N	D
CETRARIA NIVALIS	135	F	L
*CETRARIA PLATYPHYLLA	1	N	D
CETRARIA TILESII	15	N	L
*CLADONIA ABERRANS	1	F	L
CLADONIA AMAUROCRAEA	57	F	L
CLADONIA ARBUSCULA	6	F	L
*CLADONIA BACILLARIS	1	F	L
*CLADONIA BACILLIFORMIS	3	F	L
*CLADONIA BELLIDIFLORA	2	F	L
*CLADONIA CARIOSA	2	F	L
CLADONIA CARNEOLA	4	F	L
CLADONIA CENOTEA	9	F	D
CLADONIA CHLOROPHAEA	39	F	L
CLADONIA COCCIFERA	15	F	L
*CLADONIA CONIOCRAEA	1	F	L
CLADONIA CORNUTA	25	F	L
CLADONIA CRISPATA	20	F	L
*CLADONIA CYANIPES	2	F	L
CLADONIA DEFORMIS	12	F	L
CLADONIA ECMOCYNA	4	F	D
CLADONIA FIMBRIATA	7	F	L
CLADONIA GRACILIS	87	F	D
CLADONIA MACROPHYLLA	4	F	L
*CLADONIA MAXIMA	1	F	D
*CLADONIA MEROCHLOROPHAEA	1	F	L
CLADONIA MITIS	144	F	L
CLADONIA MULTIFORMIS	8	F	D
*CLADONIA NORRLINII	3	F	L
CLADONIA PHYLLOPHORA	21	F	D

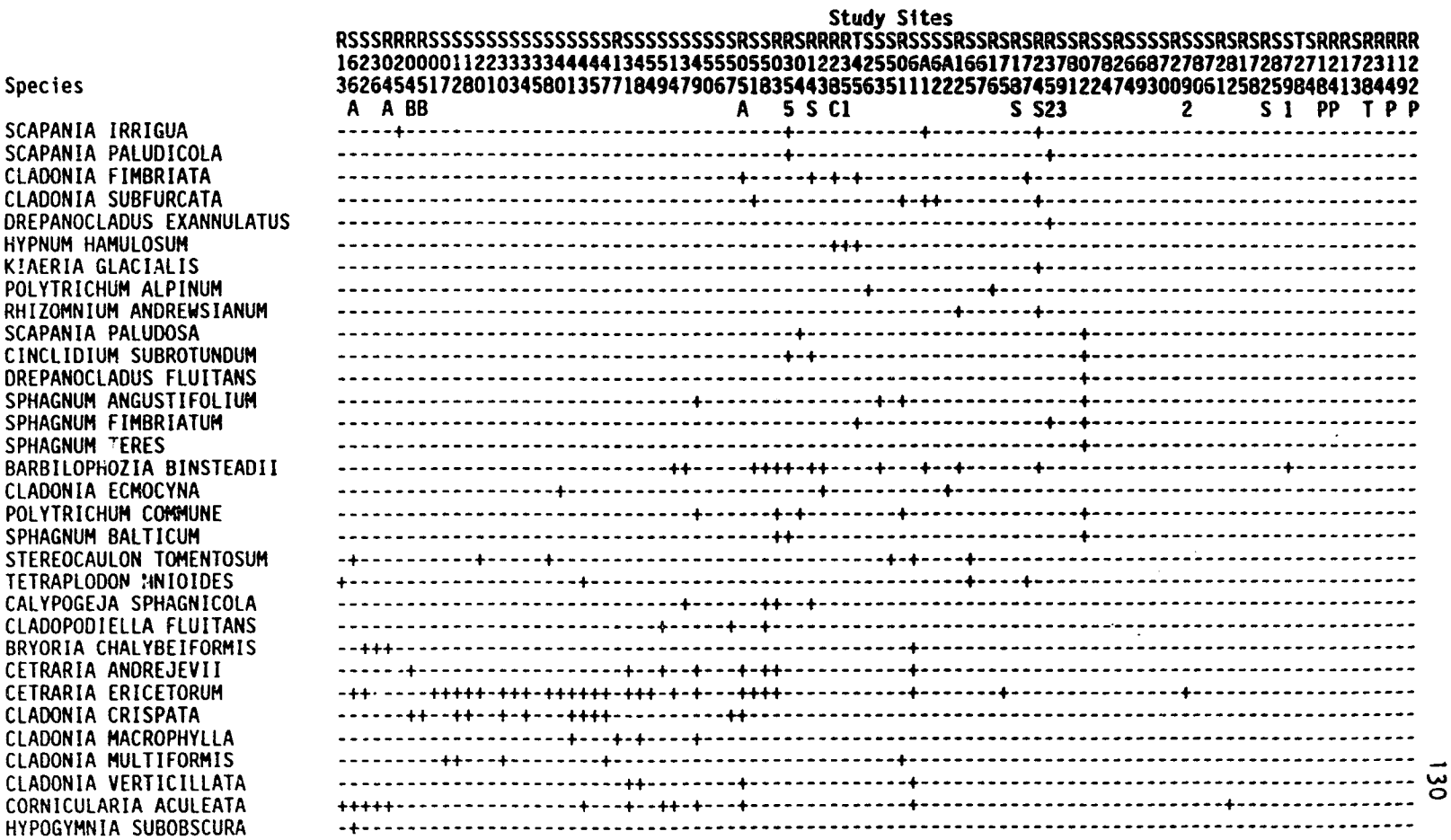
Appendix 12 continued.

SPECIES	#	FRUTICOSE/ NON-FRUTICOSE	LIGHT/ DARK
CLADONIA PLEUROTA	18	F	L
CLADONIA POCILLUM	24	F	L
CLADONIA PYXIDATA	45	F	L
CLADONIA RANGIFERINA	110	F	L
*CLADONIA SP.	8	F	L
*CLADONIA SQUAMOSA	2	F	L
CLADONIA STELLARIS	22	F	L
CLADONIA SUBFURCATA	5	F	L
*CLADONIA SUBULATA	1	F	L
*CLADONIA SULPHURINA	1	F	L
CLADONIA UNCIALIS	48	F	L
CLADONIA VERTICILLATA	5	F	L
CORNICULARIA ACULEATA	31	F	D
CORNICULARIA DIVERGENS	84	F	D
CORNICULARIA MURICATA	5	F	D
DACTYLINA ARCTICA	17	F	L
DACTYLINA RAMULOSA	6	F	L
*EVERNIA DIVARICATA	1	F	L
*EVERNIA PERFRAGILIS	1	F	L
*FULGENSIA BRACTEATA	3	N	L
*HYPOGYMNIA AUSTERODES	1	N	D
HYPOGYMNIA PHYSODES	8	N	L
HYPOGYMNIA SUBOBSCURA	6	N	D
*ICMADOPHILA ERICETORUM	1	N	L
LECANORA EPIBRYON	9	N	L
*LECIDEA RUBIFORMIS	1	N	L
*LEPTOGIUM LICHENOIDES	1	N	D
*LEPTOGIUM SATURNINUM	1	N	D
MASONHALEA RICHARDSONII	16	F	D
NEPHROMA ARCTICUM	8	N	L
*NEPHROMA EXPALLIDUM	3	N	L
*NEPHROMA HELVETICUM	2	N	D
*OCHROLECHIA ANDROGYNA	1	N	L
OCHROLECHIA FRIGIDA	4	N	L
*OCHROLECHIA SP.	1	N	L
OCHROLECHIA UPSALIENSIS	6	N	L
*PACHYSPORA VERRUCOSA	1	N	D
*PARMELIA OMPHALODES	3	N	D
*PARMELIA SAXATILIS	2	N	D
*PARMELIA STYGIA	3	N	D
PELTIGERA APHTHOSA	41	N	D
PELTIGERA CANINA	34	N	L
*PELTIGERA HORIZONTALIS	1	N	D
PELTIGERA MALACEA	29	N	D
PELTIGERA POLYDACTYLA	6	N	D
*PELTIGERA SP.	2	N	D

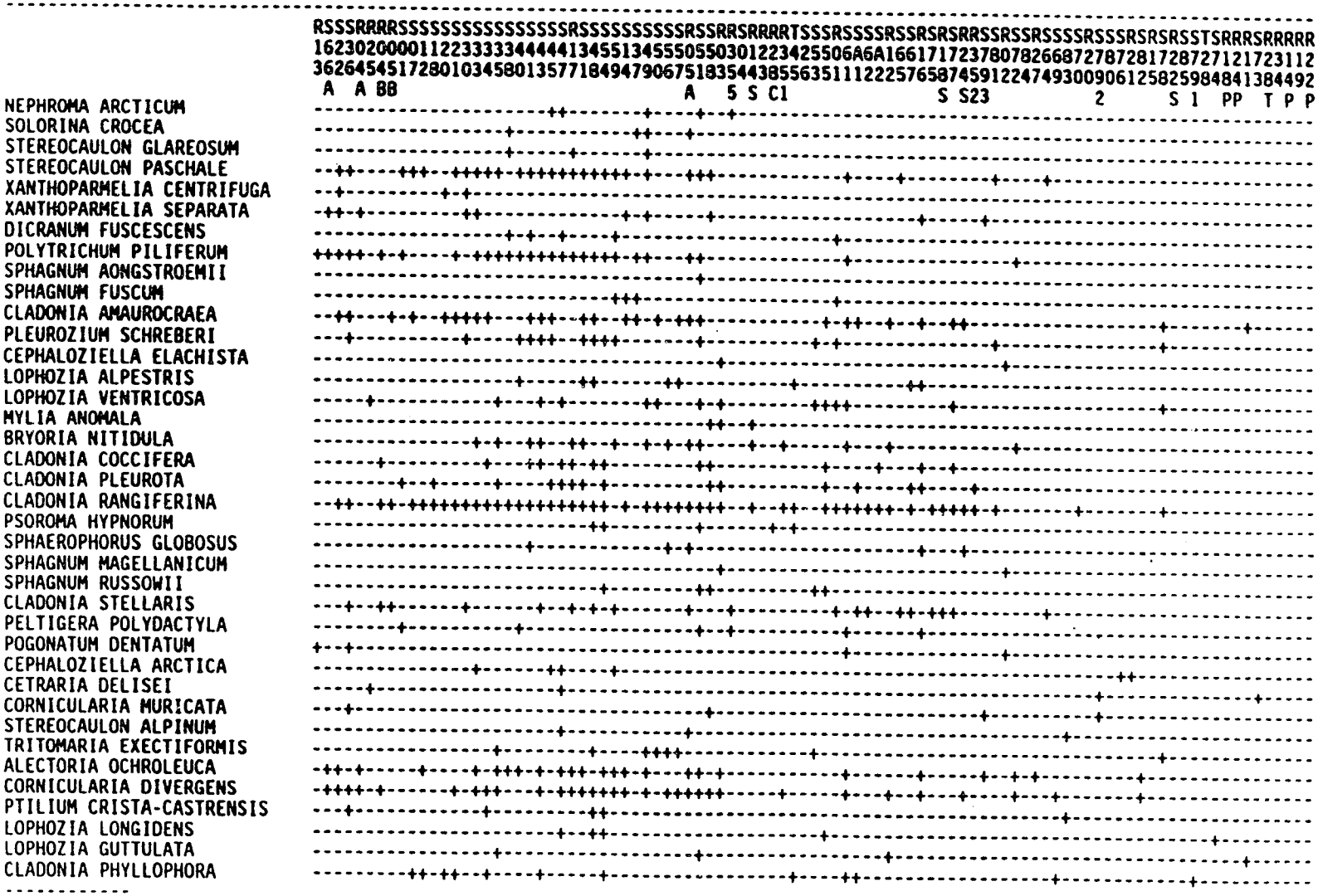
Appendix 12 concluded.

SPECIES	#	FRUTICOSE/ NON-FRUTICOSE	LIGHT/ DARK
*PERTUSARIA DACTYLINA	2	N	L
*PERTUSARIA SP.	1	N	L
PHYSCONIA MUSCIGENA	12	N	D
*PSEUDEPHEBE PUBESCENS	3	F	D
*PSORA DECIPIENS	2	N	L
PSOROMA HYPNORUM	6	N	D
*RINODINA SP.	1	N	D
*SOLORINA BISPORA	2	N	D
SOLORINA CROCEA	5	N	D
*SPHAEROPHORUS FRAGILIS	2	F	D
SPHAEROPHORUS GLOBOSUS	6	F	D
STEREOCAULON ALPINUM	3	F	L
STEREOCAULON GLAREOSUM	3	F	L
STEREOCAULON PASCHALE	80	F	L
*STEREOCAULON SP.	2	F	L
STEREOCAULON TOMENTOSUM	8	F	L
THAMNOLIA SUBULIFORMIS	33	F	L
*THAMNOLIA VERMICULARIS	1	F	L
*WHITE CRUSTOSE (unidentified)	2	N	L
XANTHOPARMELIA CENTRIFUGA	4	N	L
XANTHOPARMELIA SEPARATA	15	N	L

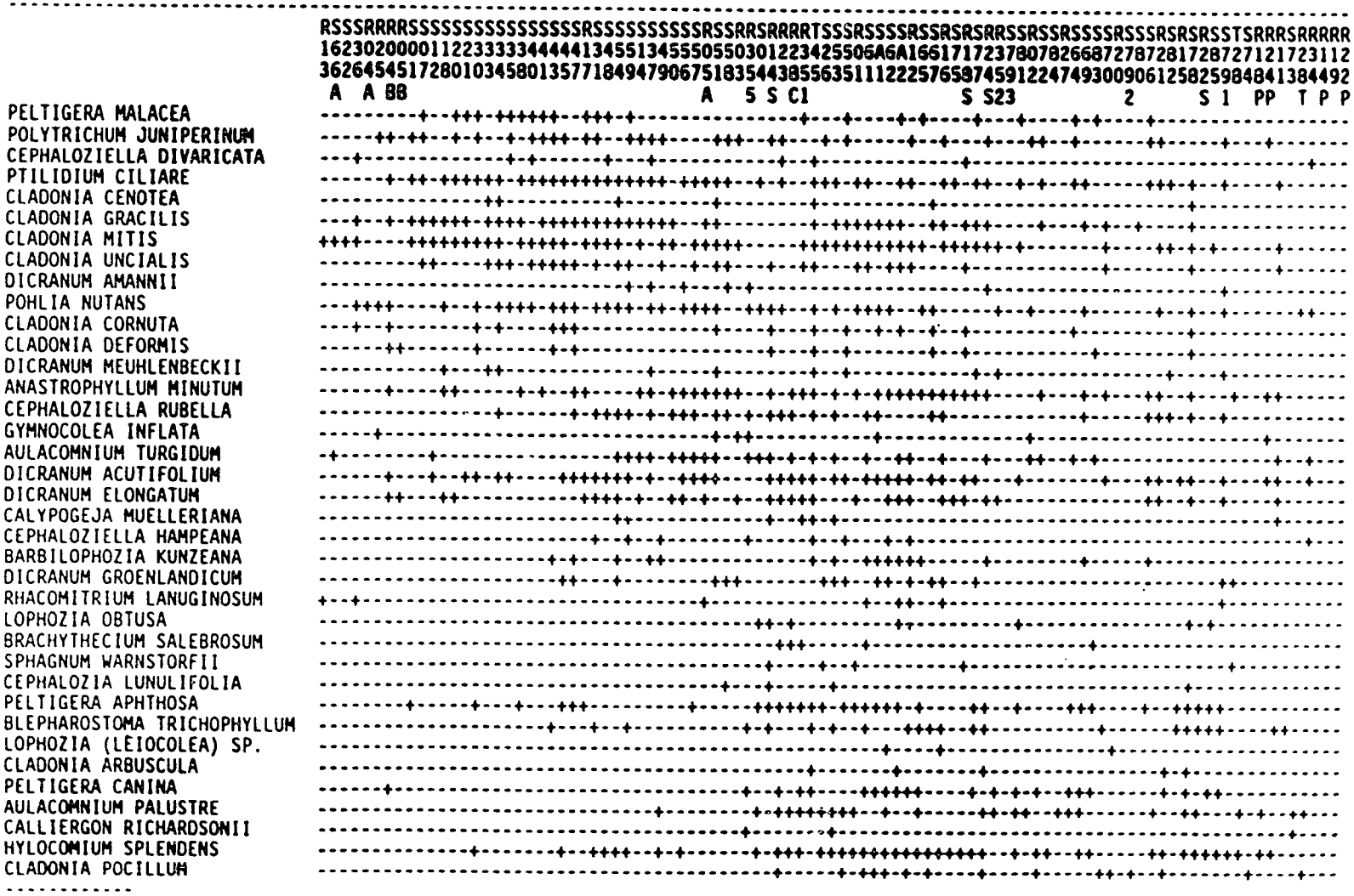
Appendix 13. Occurrence of bryophytes and lichens in the 95 study sites. Study sites are arranged by preferential and indicator species, and species are arranged by affinities in stand occurrence using TWINSPAN (Hill, M.O. 1979. TWINSPAN - A FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of Individuals and Attributes. Ecology and Systematics, Cornell University, Ithaca.). Site designations, e.g., R13, S66A, are those of Timoney (1988).



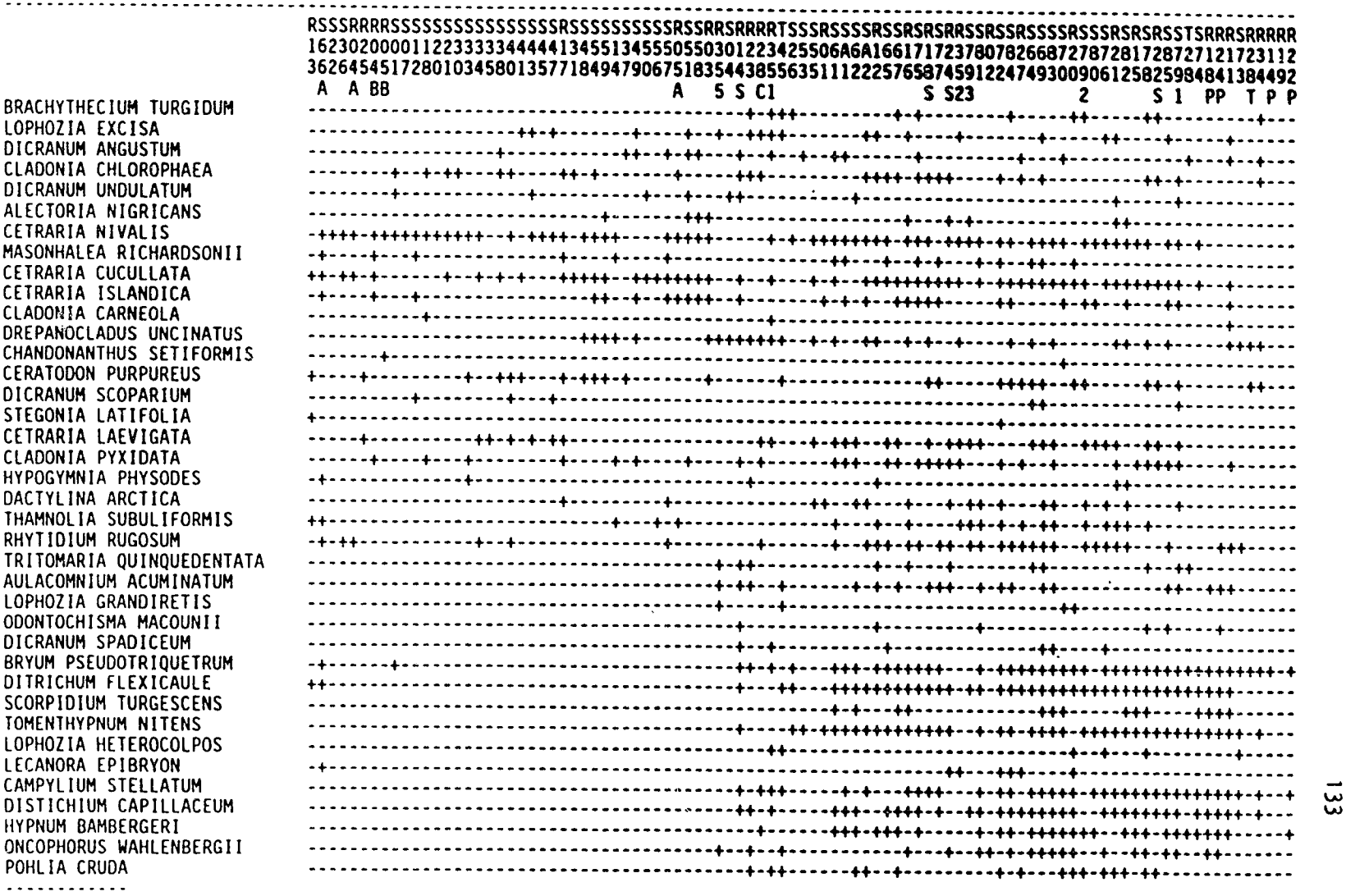
Appendix 13 continued.



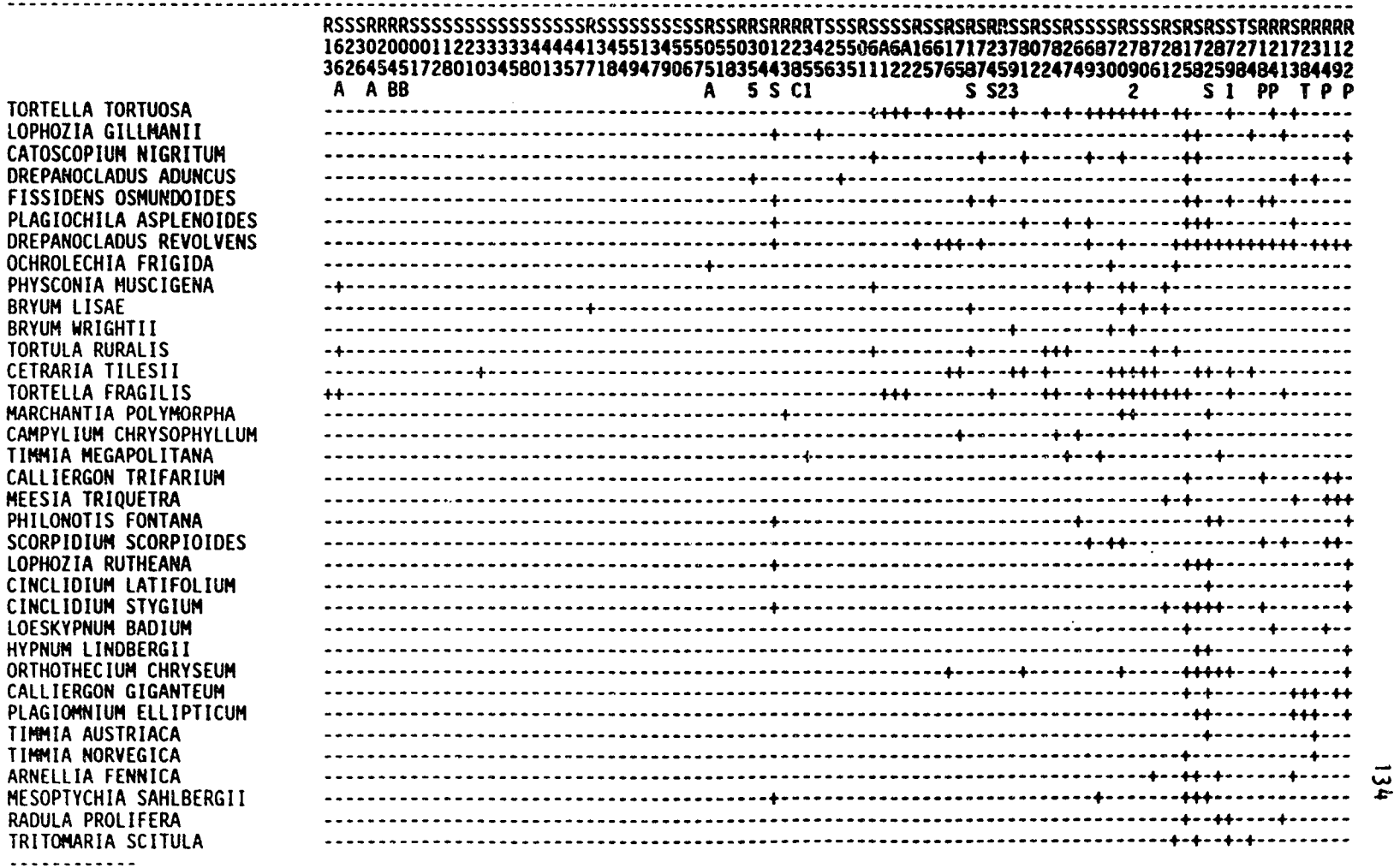
Appendix 13 continued.



Appendix 13 continued.



Appendix 13 continued.



Appendix 13 concluded.