Fundy Model Forest

~Partners in Sustainability~

Report Title: Disturbance of Forest Floor Bryophytes in a North Temperate Forest

Author: M. Sims

Year of project: 1995

Principal contact information: University of New Brunswick
Saint John

File Name:
Biodiversity_1995_Sims_Disturbance_of_Forest_Floor_Bryophytes_in_a_North_Temperate_Fo
rest

The Fundy Model Forest…
…Partners in Sustainability

"The Fundy Model Forest (FMF) is a partnership of 38 organizations that are promoting sustainable forest management practices in the Acadian Forest region."

Atlantic Society of Fish and Wildlife Biologists
Canadian Institute of Forestry
Canadian Forest Service
City of Moncton
Conservation Council of New Brunswick
Fisheries and Oceans Canada
Indian and Northern Affairs Canada
Eel Ground First Nation
Elgin Eco Association
Elmhurst Outdoors
Environment Canada
Fawcett Lumber Company
Fundy Environmental Action Group
Fundy National Park
Greater Fundy Ecosystem Research Group
INFOR, Inc.
J.D. Irving, Limited
KC Irving Chair for Sustainable Development
Maritime College of Forest Technology
NB Department of the Environment and Local Government
NB Department of Natural Resources
NB Federation of Naturalists
New Brunswick Federation of Woodlot Owners
NB Premier's Round Table on the Environment & Economy
New Brunswick School District 2
New Brunswick School District 6
Nova Forest Alliance
Petitcodiac Sportsman's Club
Red Bank First Nation
Remsoft Inc.
Southern New Brunswick Wood Cooperative Limited
Sussex and District Chamber of Commerce
Sussex Fish and Game Association
Town of Sussex
Université de Moncton
University of NB, Fredericton - Faculty of Forestry
University of NB - Saint John Campus
Village of Petitcodiac
Washademoak Environmentalists

Natural Resources Canada   Ressources naturelles Canada

Canada

DISTRIBUTION OF FOREST FLOOR BRYOPHYTES

IN A NORTH TEMPERATE FOREST

by

Mary R. A. Sims

A THESIS PREPARED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
Bachelor of Science with
Honours in Biology

THE UNIVERSITY OF NEW BRUNSWICK
SAINT JOHN
March 11, 1995

ABSTRACT

Bryophyte community structure may be influenced by underlying environmental factors at various spatial scales. What proportion of the observed bryophyte species distribution pattern is directly attributable to environmental variables? Within the Hayward Brook Watershed (Westmorland County, NB), bryophyte species abundance, as well as canopy, litter and topographical variables were recorded in 155 1.25-m^2 quadrats. Partial Canonical Correspondence Analysis (PCCA) was used to partition out the individual and combined influences of environment on species distribution. Environmental variables accounted for 26% of the total species pattern (3.564 of the 13.641 total inertia). Of the environmental variables, the unique contribution of litter accounted for the largest proportion of the species distribution pattern (14.3%), followed by topography (7.72%); canopy alone accounted for the least (1.71%). The remainder (1.99%) was attributable to combinations of these variables. Litter may influence bryophytes in several ways: (1) physically, e.g. acting as substrate or barrier, and/or (2) chemically, as a source of e.g. nutrients or toxins. The remaining 74% of species pattern may be influenced by factors such as other environmental variables, interspecific relationships, spore/gemmae dispersal and establishment, or chance.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

INTRODUCTION

Biodiversity

Biodiversity may be defined as the variety and variability of life-forms, both contemporary and extinct, at the gene, species, or ecosystem level (Savage 1995). Species diversity is composed of species richness and evenness. Richness is the number of species in a given area; evenness is the distribution of individuals among species, or species equitability (Barbour *et al.* 1987).

Only recently has the value of biodiversity been recognized as a global resource. Biodiversity underpins the healthy functioning of the earth's many environments and provides essential products (food, shelter, fibre, fuel, clothing and medicine) both from nature and from domesticated plants and animals. Ironically, recognition of the value of biodiversity arose from the observation that exploding human population and human activities are accelerating the loss of substantial numbers of organisms. An estimated 1.4 to 1.5 million living species of microorganisms, fungi, plants, and animals have been discovered, described and named, of which 950,000 and 250,000 are insects and plants, respectively (Anonymous 1995; Savage 1995). It has been estimated that the number of undiscovered species ranges from 10 to 100 million (Savage 1995). These known and undiscovered species represent a storehouse of information about the world. The dangers of losing this wealth are immense and far-reaching.

The disciplines of medicine, forestry, agriculture, fisheries, soil science, natural resource management, and conservation, as well as virtually all biological research, pure and applied, depend on studies of biodiversity. Biodiversity studies, i.e. documentation of the species components of an ecosystem or community via collections or presence/absence

studies, provide baseline data essential to further studies on the ecological, chemical, physiological, and genetic features of any or all components of the ecosystem.

Background

Conservation of biodiversity presupposes knowledge of what is present to ensure that it persists, hence, baseline data are essential to developing strategies for biodiversity preservation.   Baseline data consist of basic descriptions and documentation of an environment via specimen collection for preservation (in herbariums, museums, etc.), surveys, or presence/ absence studies. Data on vascular plants are reasonably extensive in North America and in New Brunswick (Bates 1982; Anderson *et al.* 1969) for New Brunswick, possibly due to their importance to agriculture, forestry practices, forest management, and medicine in the realms of genetic engineering, and pest and disease control. However, the documentation, identification, and study of bryophytes is still in its infancy (Økland 1994; Hedenäs 1994, 1989; Wyatt 1985), possibly because of their small size and difficulty in field identification. For example, in ecological studies of forest communities, bryophytes are often overlooked (Frego, pers. comm.) and data on reproductive isolation, gene flow, physiology and chemistry of bryophytes are still limited (Stark 1985; Wyatt 1985). As well, quantitative studies such as correlations between bryophyte communities and environmental factors are scarce (Økland 1994; Bates 1982). North American studies have focused on west coast rain forests and boreal, taiga and tundra vegetation zones which are characterized by an abundance of mosses (e.g. Kooijman and Bakker 1995; Frego 1994; Økland 1994; Økland and Eilertsen 1994; Gignac *et al.* 1991; Carleton 1990, 1984; Robinson *et al.* 1989; Alpert and Oechel 1982; Kenkel and Bradfield 1981; La Roi and Stringer 1976). However, there have been few

such studies for New Brunswick or the Maritime provinces. Moreover, herbarium

collections of bryophytes for New Brunswick are very sparse, representing only tiny

patches of ecosystems in a few New Brunswick Counties (Bruce Bagnell, New Brunswick

Museum, pers. comm.). Collections are important as reference material for the correct

identification of species, which in turn is essential to other studies. Collections also

represent an historical record of the distribution of species within an area (Anonymous

1995), hence, they are critical baseline compilations for conservation of biodiversity.

Documentation of existing biodiversity is also an essential component of forest

management (Roberts and Gilliam 1995). Yet bryophytes are frequently overlooked in

both biodiversity and forest description studies, presumably because they are small and

difficult to identify in the field. They are important components of the forests, as will be

discussed following. Further, as a result of differences in morphology and anatomy, major

differences might exist in the way bryophytes and vascular plants respond to various

environmental gradients. As a result, vegetation variation and diversity in one stratum

(e.g. the tree layer) may not be representative of patterns of the diversity in all other

vegetational strata (Watson 1980). "Foresters in northern Europe have recognized for

some time that bryophytes and lichens often make better indicators of species of site

conditions than many of the vascular plants" (Carleton 1990). Thus, understanding the

species structure and functioning of bryophyte communities is of increasing interest to

forest land management agencies.

Plant Community Ecology

The term "community" can refer to vegetation types of any scale or longevity (Barbour *et al.* 1987). For example, it can be applied to one stratum, such as the herbs, woody seedlings, and mosses comprising the forest floor, or to a widespread regional vegetation type. It can be applied equally to systems that are transitory or stable (Barbour *et al.* 1987). There are two schools of thought concerning what controls community structure (i.e. species composition and pattern): competition and stochastic theories. Competition models are generally based on the concept of the niche, i.e. community composition results as species with specific ranges of tolerance displace others for limiting resources. Species coexistence results from species partitioning the niches available to them. Stochastic models view community structure as the end-point of a series of random events (e.g. disturbance, chance dispersal of propagules) each narrowing the field of more or less equally suitable "applicants" (Frego 1994).

Situations which support both theories can be found in nature. For example, Whittaker (1977) stated that in local biotopes, community diversity is highest in intermediate environments and lowest in both harsh and favourable habitats. In harsh environments, diversity is thought to be low due to the limited number of species which have physiologically adapted to the conditions (opportunistic or fugitive colonization) - space is not saturated and, thus, there is no competition for resources; in favourable habitats, however, diversity may be lowered by saturated space and competitive exclusion of species for limited resources.

Gap-regeneration theories, which may include either competitive or stochastic models, suggest that regeneration and heterogeneity of microenvironments might play more important roles in species distribution (Grubb 1977). When a gap is created, the

replacement species that fills the gap may or may not be the same species as the original, depending on the environmental features of the gap relative to species tolerances, dispersal mechanisms of nearby species, and chance.

Bryophyte Biology and Community Ecology

Bryophytes *sensu lato* traditionally constitute three divisions of plants: (1) Hepatophyta, the liverworts, (2) Anthocerophyta, the hornworts, and (3) Bryophyta, the mosses. This discussion will focus on the latter, of which there are currently 14 000 to 21 000 named species (Smith 1982). Bryophytes are small, haploid plants with a dominant and photosynthetic gametophyte. The sporophyte, or diploid generation, remains attached to the gametophyte and is usually nutritionally dependent on it. Nutrients and water are primarily obtained through precipitation, and the "wicking action" of rhizoids, phyllidia ("leaves"), branches, and paraphyllia (linear or branched structures attached to the stem of some mosses). Mosses do not have specialized water and nutrient conducting cells (i.e. vascular tissue) but some, the endohydric mosses such as those in the Class Polytrichidae, have interior conducting cells called leptoids and hydroids; these lack the specialized wall thickenings of equivalent cells in vascular plants. Mosses are categorized into two major growth forms: acrocarpous and pleurocarpous. Acrocarpous mosses grow upright and produce sporophytes from their growing tip, i.e. apical cell. Pleurocarpous mosses creep along the substrate and produce sporophytes from their lateral apical cells, thus, they are able to continue growth during and after sexual reproduction.

The distribution of bryophytes worldwide, through a wide range of habitats, reflects their diverse means of sexual and/or asexual reproduction (Kimmerer 1994) as

well as ranges of environmental tolerances. Asexual reproduction involves the dispersal of

gemmae from splash cups or brood branches (e.g. *Dicranum flagellare*). Sexual

reproduction utilizes haploid spores produced by the diploid sporophyte. Bryophytes

depend on water as their dispersal mechanism for sexual reproduction. Sperm are located

in splash cups called antheridia at the tips of moss shoots. Falling raindrops splash the

sperm out, often dispersing them widely, where they either land on an archegonium, or

swim short distances through accumulated moisture in the moss turf to archegonia.

Insects may also carry drops of water rich in sperm to neighbouring or isolated female

gametophytes (Raven *et al.* 1992). Once fertilization takes place, the diploid sporophyte

develops from the archegonium. At maturity, the sporogenous tissue in the sporophyte

undergoes meiosis to form haploid spores which are released into the environment by

various dispersal mechanisms. Because of the small size of the spores, moss spores may

drift into the upper atmosphere and can travel great distances (Chopra and Kumra 1988).

If environmental conditions are suitable, the spores germinate into delicate filamentous

protonemata (singular: protonema). Moss shoots then develop from minute budlike

structures on the protonemata.

Despite their small size, bryophytes play significant roles in many ecosystems. In

mountain stream habitats bryophytes are important biological contributors since they

constitute a major part of the primary production (Slack and Glime 1985). In these areas

they are also important as a substrate for insects (Glime and Clemons 1972, Minkley 1963,

and Babcock 1949 *in* Slack and Glime 1985) and as a food source for insect larvae (Jones

1949 *in* Slack and Glime 1985). Indirectly, bryophtyes contribute significantly to the food

sources for fish. Thus, bryophytes and their community structure are important to the

dynamics of the stream ecosystem. Terrestrial bryophytes can be found growing below

translucent rock in the Mojave Desert (Werger and During 1989), to the Antarctic (Smith 1988). In bogs and polar regions they constitute the main primary producers, and in montane rain forests the large biomass of epiphytic bryophytes has a definite influence on water retention in whole watersheds (During and van Tooren 1987). In the boreal forest, extensive moss carpets also influence water relations (Busby and Whitfield 1978), as well as nutrient availability (Denison 1979, 1973, and Pike 1978 *in* McCune & Lesica 1992; Carleton and Read 1991; Kenkel & Bradfield 1981; Weetman 1968) and soil temperature (Bonan 1992; Viereck 1983; Larsen 1980). In temperate zones, bryophytes are less prominent but still may greatly effect seedling emergence and establishment (Keizer *et al.* 1985 *in* During and Verschuren 1988), nutrient relationships (Rieley *et al.* 1979 *in* During and Verschuren 1988), and possibly other processes.

Studies of bryophyte vegetation address topics of community structure, community variation, species strategies and community function (Bates 1982). However, these might be hampered by technical difficulties: the small size of mosses, the often fragmentary nature of their communities, the tendency of many species to grow on highly irregular surfaces, their often low biomass in communities dominated by other vegetation types, their lack of economic importance leading to restricted financial support for research (Bates 1982) and the practical difficulties of accurate field identification. Nevertheless, community ecology studies are accumulating, and understanding of bryophytes and their environment is improving.

Assumptions of competition vs. stochastic models are apparent in ecological studies of bryophytes (e.g. Økland 1994; Herben 1988). Competitive-based theories argue that plants occupy predictable areas because they are specifically adapted to tolerate conditions within certain parts of environmental gradients (Robinson *et al.* 1989).

However, competitive interaction between bryophyte species is considered by some to be of little importance in bryophyte communities (e.g. McAllister 1995; Grime 1977 *in* Robinson *et al.* 1989; Watson 1980) due to such factors as: (a) predominance of fine-grained, density-independent mortality in mosses (During and van Tooren 1987; Watson 1980); (b) slow growth rates relative to the life spans of suitable habitats; and (c) failure to fully saturate habitats with propagules due to limited dispersal (Watson 1980). Also, in temperate forests where bryophytes often are restricted to raised topographical features such as rotting logs, competition plays little role in bryophyte community structure due to slow growth rates and the temporary nature of the decomposing logs (McAllister 1995). Lee and La Roi (1979 *in* Watson 1980) and Slack (1977) suggested that bryophytes may provide environmental buffering for each other to tolerate adverse environmental conditions. For example, in drought conditions, mosses may extend the period of hydration, and hence metabolism, by growing in crowded mats, wefts, and cushions creating intershoot spaces between shoots of the same or different species. Thus, competing to rid neighbouring moss species may not be advantageous.

Other researchers (e.g. During and van Tooren 1987) believe that interspecific competition occurs. For example, Hërben (1988) found that interspecific competition determined the species sequence of *Sphagnum* spp. along topographical gradients in bogs. Robinson *et al.* (1989) suggest that whether mosses "behave" competitively or stochastically depends on the morphological nature of the species. Pleurocarpous species have the competitive advantage of being able to continue growing during and after initiation of sexual reproduction and to form extensive mats, enhancing their ability to compete with vascular plants for forest floor space (Robinson *et al.* 1989), whereas acrocarpous species are considered to be opportunistic, ruderal and stress-tolerant species

that are better adapted to colonizing exposed areas. Watson postulated that distribution patterns may also be influenced by competition among the juvenile stages of mosses: these delicate stages might have narrow ranges of tolerance for similar microhabitat conditions, thus, amount of available preferred sites would be limited (Watson 1980). However, this type of competition does not involve direct competition for limited resources, but rather interference competition, due to leakage of plant morphogenic substances into the substrate where they affect the growth of neighbours (Watson 1980).

Many apparent contradictions in understanding the factors determining bryophyte community structure may simply be a problem of scale. The scale of a study defines the limits of patterns that can be detected. For example, it may be expected that very small scale (i.e. microhabitat) features would play a more important role in bryophyte diversity and distribution than other "macro" features (e.g. canopy, altitude, slope) due to the organism's small size and the haploid genotype of the adult life stage; i.e. one would expect that the genetic repertoire of bryophytes would be relatively limited compared to the diploid vascular plants. Thus, they would presumably have evolved narrow ranges of tolerance to very specific microhabitats in which environmental variation is at a minimum. Such reasoning is supported by numerous studies. In her review of bryophyte distribution patterns in relation to environment, Watson (1980) concluded that the distribution of individual species correlates more strongly with micro characteristics of the environment, such as soil texture, pH, and substrate type, than with altitude (a macro characteristic).

La Roi and Stringer (1976) stated that mature bryophyte growth forms are substrate specific. For example, tufts and cushions of large mosses prefer humus while small bryophytes of short turfs, threaded mats, and smooth mats favour wood and bark surfaces, suggesting that the distribution and abundance of species on the forest floor are

strongly limited by the distribution and abundance of suitable substrates. Kenkel and Bradfield (1981) found that microclimate exerted a stronger influence in controlling distribution of epiphytic bryophytes than did substrate features. This contradicts La Roi and Stringer's (1976) findings (that substrate tends to control diversity and distribution), but supports micro characteristics as a stronger influence.

However, large scale variation in bryophytes is apparent. For example, studies comparing different forest stand types find that species and species abundances differ (e.g. Carleton 1990).

Also, bryophyte assemblages might not respond as a cohesive unit to a particular set of environmental variables, macro or micro, but rather may respond individualistically. In a study of bryophyte and microhabitat patterns by Kunkel (1975 *in* Watson 1980), individual species showed narrow distributional ranges on some environmental axes, and not on others; the critical habitat axes varied among species, i.e. for each species, different features of the environment were the primary determinant(s) of their niches. The species were extreme specialists in their habitat preferences.

Alternatively, bryophyte community structure may be due to factors other than the abiotic environment. For example, During and van Tooren (1987) suggest that interactions with microorganisms may play a more important role in bryophyte establishment and growth which together dictate species distribution patterns. Other factors may include range and frequency of propagule dispersal (Chopra and Kumra 1988), disturbance and gap regeneration (Frego 1994; Grubb 1977), and/or synchronous or asynchronous successional change (Coleman and Istock 1980). The null hypothesis is also possible, i.e. that observed differences in community composition may be due to chance occurrences of colonization and extinction, or chance effects of sampling (Coleman

and Istock 1980).

Ordination Techniques

By definition, community studies require simultaneous consideration of a number of species, i.e. a multivariate dataset. Ordination is a multivariate analysis technique which allows the detection of non-randomness (i.e. pattern) and the scale at which it occurs in species distributions (Bates 1982). "The method of looking for correlations of species occurrences, abundances or performances in the field with levels of environmental factors is one of several approaches for investigating the causal factors for species distribution patterns" (Bates 1982). Note however, that statistically significant correlation is no proof of a cause-effect relationship, and must be combined with studies using experiments under controlled conditions (Bates 1982). Most ordination techniques assume linear relationships between variables and ordination axes. Because most species show a bell-shaped range of tolerance to most variability, this assumption may be ecologically unrealistic in many instances, and may limit the successful exposure of vegetation gradients which are linked to underlying environmental gradients. However, Nichols (1977 *in* Kenkel and Bradfield 1981) stated that "for summarizing information and displaying overall relationships in a set of data, the methods are appropriate."

Ordination is a numerical approach commonly used in plant ecology to summarize complex relationships between vegetation patterns and components of the environment with minimal loss of information (e.g. Frego 1994; Carleton 1990, 1984; Robinson *et al.* 1989; Slack and Glime 1985; Kenkel and Bradfield 1981). Correspondence analysis (CA), also known as reciprocal averaging, is an indirect gradient analysis ordination technique. This technique reduces dimensionality in a hyper-dimensional dataset from discontinuous, nonlinear data to a continuous linear form that is more easily interpreted. It accomplishes this by ordinating the vegetation data in the vegetation by quadrat dataset through a

process of iterated reciprocal algorithms, finding the largest spread of variation (inertia) in the dataset, and summarizing it with linear axes (often 2) called eigen vectors. The derived axes are hierarchical and orthogonal; thus, the first axis goes through the greatest spread of variation, the second goes through the next largest spread at right angles to the first and is not correlated with the first. The "length" of the eigen vector (i.e. the spread of points it summarizes) is called the eigen value.

Canonical correspondence analysis (CCA) is a type of direct gradient analysis. It calculates the amount of variability captured when the CA is constrained by a linked set of variables. CCA orders two sets of linked data (i.e. vegetation and environment) simultaneously across their common range of samples (i.e. quadrats) by the same process (iterative reciprocal averaging) to capture the best fit of the environmental data and the vegetation by quadrat data. Thus, CCA captures only a portion of the total variability in the CA, the portion that is linearly related to the environmental variables. One criterion of this type of analysis is that the sample size should be higher than the number of species and environmental variables to prevent "unreasonably high canonical correlations" (Carleton 1984). In the present study, 79 species were quantified in 155 quadrats.

Partial canonical correspondence analysis (PCCA) is used to "partial out" one, or a group, of the environmental variables to determine the individual and combined effects of the various environment characters on the vegetation ordination. For example, it allows one to identify which environmental variables have the greatest and least links with the plant community. PCCA expands the scope of CCA and allows many new hypotheses to be tested regarding linear relationships between vegetation and environmental characteristics (Carleton 1984). It also quantifies potential overlaps in environmental gradients in the CA, which can lead to a confused ordination, to be teased apart and

examined independent of one another. For example, litter depth, composition and chemistry are affected by forest canopy, topography, and parent material. These variables must be partialled out to examine the unique individual influences of litter, topography, and canopy, excluding the shared, or overlapping, influences of the three variables; then each overlapping or shared variable influence is determined.

OBJECTIVES AND RATIONALE

Objectives

1) to document the terricolous bryophyte diversity of the forest floor in a mature mixed forest stand in the Hayward Brook Watershed (Westmorland County, New Brunswick), and

2) to relate bryophyte distribution pattern to selected environmental characteristics.

Rationale

Baseline and quantitative studies in New Brunswick are scarce, and the bryoflora of the Maritimes in general is poorly known. Only one manual exists on the bryophyte species of the Maritimes: Ireland's (1982) text, Moss Flora of the Maritimes. This manual is based on studies and herbarium collections from the area. Although this manual is thorough, collections on which it is based are limited, and much of New Brunswick's habitats have not been represented (Bruce Bagnell, pers.comm.). For Westmorland County, no collections, surveys, or literature exist (Bruce Bagnell, pers.comm.). Forested areas in Westmorland County, and specifically the Hayward Brook Watershed, are slated to be cut by Irving Forestry Ltd., with unknown consequences for biodiversity. This study provides baseline data for long-term studies of regeneration following forest management

procedures, which have been undertaken within the Fundy Model Forest.

THE STUDY SITE

North-temperate mixed forests are a combination of deciduous and coniferous stands with diverse and heterogeneous environmental and microenvironmental features. This forest type is a multilayered community with a dominant and subdominant canopy, a shrub stratum and a herbaceous stratum. The herbaceous understorey is composed of perennial angiosperms, ferns, mosses, and liverworts. The forest floor vegetation is subject to the microclimate heterogeneity influenced by canopy, topography, substrate, and moisture levels.

In the study site, eight ecologically diverse stand types were identified by Mark Roberts (unpublished) (Appendices I-III). These stand types were grouped as coniferous, mixed intermediate, or ridge hardwood. Coniferous stands (A, B, D, and E) were located at low altitudes nearest the stream and were dominated by Spruce (*Picea* spp.), Red Maple (*Acer rubrum*), and dead wood. The mixed intermediate stands (F and G) had rich soils high in organic matter and nutrients. Stand G had wet soils with many ground springs and was dominated by Spruce, Balsam fir (*Abies balsamea*), and Red Maple, while stand F was characterized by an abundance of Trembling Aspen (*Populus tremuloides*) and White Birch (*Betula papyrifera*). The mixed stands also contained tree species such as Ironwood (*Carpinus caroliniana*), White Ash (*Fraxinus* americana), Yellow Birch (*Betula lutea*), and Large Tooth Aspen (*Populus grandidentata*), which were absent from hardwood and coniferous stands. The ridge hardwood stands (C and H) were located at high altitudes on shallow rocky soil and were dominated by White Birch and Red Maple.

The areas chosen for study were two blocks (designated for clearcut harvesting by Irving Forestry Ltd. in 1995) in the Hayward Brook Watershed area of Westmorland County, New Brunswick, Canada. This area, located between the temperate and boreal zones of oceanic eastern Canada, is classified as Acadian Forest Region (Ireland 1982). It is an area of coniferous, deciduous, and mixed forests. Lower altitudes and valleys were wet, sometimes boggy, and dominated by Balsam Fir and Spruce, whereas higher elevations were dry, rocky, and dominated by Sugar Maple (*Acer saccharum*), Red Maple, Striped Maple (*Acer pennsylvanicum*), White Birch, Beech (*Fagus grandifolia*), and Trembling Aspen.

Climate

Average annual precipitation is approximately 130 cm. Late fall and early spring are the wettest, and late spring to early summer the driest, seasons. About 16% of the total annual precipitation falls as snow, often exceeding 300 cm (Gowan and Brodo 1988).

Geology

Two bedrock types, Pcu3 (PET 3 Geomorphological District) and Pbp3 (Boss Geomorphological District), underlie the Hayward Brook area (McLeod *et al.* 1994). PET3 form reddish or grey soils of fine to medium grained sandstone; grey, green and red mudstone and a minor proportion of grey and red , granule to cobble conglomerate and coal (McLeod *et al.* 1994). Boss lithologies are predominantly grey to greyish-green, plant-bearing quartzose sandstone and quartz pebble conglomerate; infrequently red sandstone and grey mudstone, and rarely red mudstone, impure coal, carbonaceous mudstone and fossiliferous, butuminous limestone (McLeod *et al.* 1994).

METHODS

Two blocks, designated 6-north and 6-south by the Irving Forestry crew were delimited on the north and south of the Hayward Brook stream, respectively. In each, transects were laid out approximately perpendicular to the Hayward Brook stream (Figure 1) in April - May 1995. Transects varied in length from 100 to 850 m depending on the geography of the area (roads, gravel pits, etc.). Permanent quadrats (n=155) were placed at 50 metre intervals along each transect. Each quadrat was 1.25-m^2, marked by a wooden stake at the southwest corner. Quadrats represented 1/4 of those used to sample the herbaceous layer as part of a separate study (see Hovey, unpublished). Data were collected June through August 1995.

In each plot, bryophyte species abundance was recorded as percent cover. Voucher specimens were placed in the University of New Brunswick Saint John and The New Brunswick Museum herbaria. Species composition was summarized at two scales: (1) meso (stand) scale - frequency and percent cover for all quadrats, and (2) micro (local) scale - frequency and percent cover for all quadrats in which the species was present. Environmental data on canopy, litter, and topography were gathered as follows:

(1) Canopy closures of deciduous and coniferous trees were estimated using the average of two readings from a spherical densiometer, taken by two different persons from the same point in the quadrat. As well, height to lowest branch, distance from centre of plot to nearest tree, and basal circumference of the nearest tree, were measured to further describe canopy characteristics.

(2) Vegetation litter was described by its gross and chemical composition. Percent covers of deciduous litter, coniferous litter, bark, twigs, and decorticated wood

were recorded for each quadrat. The depth of the LFH (Leaf Fibrous Humic layer, the upper organic layer which has not mixed with soil parent material) was measured on a 10 cm diameter circular section removed immediately outside the quadrat. Percent composition of moss, needles, and leaves in the LFH was estimated using a three point scale where 0 was "not present" and 3 was 100% composition. For example, an LFH sample could score 2 for leaf and 1 for needle composition meaning the LFH was 70% leaf and 30% needles.

Litter samples were collected for analysis in the lab of Dr. Mark Roberts (University of New Brunswick, Forestry). Litter chemistry was determined as follows: samples were oven-dried at 55 °C for 48 hours, then passed through a 2-mm sieve. Available phosphorus and exchangeable cations were determined for the extracted sub-samples. Exchangeable cations K, Ca, and Mg were determined by extraction with 1 N NH_4OAc, pH 7, and analysis of the extracts by atomic absorption spectrometry, using lanthanum chloride as the releasing agent for Ca and Mg (Baker and Shure 1982). Available phosphorus was determined by extraction with dilute sulphuric acid and colorimetric analysis of the extract, using the phosph-molybdo-blue method. Total nitrogen content was obtained using the Kjeldahl method (Bremmer and Mulvaney 1982) after grinding the sub-samples with a mortar and pestle.

(3) Microtopography were recorded as presence/absence of pits or mounds for each quadrat. Mounds and pits were defined as +/- 50 cm+ deep and coded: (0) flat, (1) slightly mounded, >5m apart, (2) moderately mounded, >1m apart , or (3) very mounded, mounds <1m apart. Slope and aspect were estimated using a Suunto clinometer and a compass, respectively. Aspect, i.e. compass bearing of slope, was expressed as the sine and cosine, indicating "northness" and "eastness", respectively.

Statistical Analysis

A series of multivariate analyses were performed using CANOCO 3.12 (ter Braak 1988) which is an extension of Cornell Ecology program DECORANA (Hill 1979). This program performs partial, detrended, and canonical correspondence analyses, as well as principal components and redundancy analyses. Basic correspondence analysis (CA), canonical correspondence analysis (CCA), and partial canonical correspondence analysis (PCCA) were used in this study. Analyses were performed as follows:

(1) CA (not detrended) was performed on the dataset of 79 bryophyte species in 155 sample quadrats, to obtain total inertia and scores of species and quadrats on the first two axes;

(2) CCA by simultaneous (canonical) ordination of the species by quadrat dataset and the environmental by quadrat dataset, to determine the proportion of species pattern (above) that was linearly related to the environmental variables; and

(3) PCCA. This statistical analysis tested each combination of environmental variables for relationship with the variance in species scores. The environmental dataset was partitioned into three components: topography, canopy, and litter. Individual and shared contributions of these components were obtained by systematically assigning categories of variables to be covariables, thereby including them in the linear axes, so that the canonical ordination was performed on the remaining (residual) environmental variable categories. The sum of the CCA eigen vectors was determined for each and expressed as percentages of total inertia determined in the CA (2, previous).

For both the CA and CCA, quadrats were also plotted as stand type (ie. coniferous, mixed, or hardwood) on CA and CCA scatter plots to illustrate the relationship between stands and environmental variables. The outliers found in the CA were not included in the plot in order to magnify the tight cluster of sample scores (now represented by stand type letters) to enable better detection of patterns.

RESULTS

Community Composition and Pattern

(1) Species richness

The cryptogam flora consisted of 76 species (53 mosses, 23 liverworts), and three lichen types designated only as crustose, foliose, or fruticose (Table 1). Approximately 75% of the 1.25-m^2 quadrats contained 7 to 18 species, 10% contained ≤ 3 species, with a mean of 10.37 ± 0.398 and a mode of 7 to 9 (Figure 2).

(2) Species frequency

Figure 3 illustrates the frequency distribution of species in 155 quadrats. Thirty-nine of the 79 species (49%) occurred in $\leq 5\%$ of the quadrats: seven species occurred in 60 - 80% of the quadrats, i.e. *Ptilidium pulcherimum* (see Table 1 for nomenclature), *Pleurozium schreberi*, *Dicranum scoparium*, *D. polysetum*, *Brachythecium starkei*, *Lophocolea heterophylla* and *Jamesoniella autumnalis* (Table 1).

(3) Species cover

At the stand scale (i.e., in 155 quadrats), 69 species (87%) had total mean percent cover values $\leq 0.25\%$, whereas 9% averaged 0.26 - 0.75% cover (Figure 4). Only

Pleurozium schreberi and *Dicranum polysetum* differed from this pattern, with total mean percent covers of 5.89% and 2.20% respectively (Table 1). At the local scale, average bryophyte cover per species was 1.23% $\pm$ 0.23 (Table 1), representing local abundance or dominance of a species. Sixty-six species (84%) had mean cover values $\leq$ 2% (Figure 5). *Pleurozium schreberi, Dicranum polysetum,* and *Hylocomium splendens* had maximum cover values of 78.0%, 40.0%, and 30.0% respectively. *P. schreberi* was the most abundant moss both in frequency (76.13%) and cover (mean cover when present of 7.74%), whereas *Ptilidium pulcherimum* had higher frequency (79.35%), but much lower cover, when present (0.69%) (Table 1). *Hylocomium splendens, Plagiothecium cavifolium , Sphagnum squarrosum* and *S. nemoreum* were locally abundant, but not frequent (Table 1). *S. nemoreum* had a high mean cover value when present (14%) but a total mean cover value of only 0.09%, as it was encountered only once.

Variation in species richness was high among stands. A few dry, coniferous fir thickets contained no discernable bryophytes, whereas other quadrats contained almost 100% cover in bryophytes.

Two quadrats contained the rare species *Cirriphylum piliferum*, previously only reported in Victoria and Queen's counties in New Brunswick (Ireland 1982). These quadrats were also characterized by other infrequent species ($\leq$ 7.75% of quadrats) such as *Bryhnia novae-angliae, Climacium dendroides, Plagiomnium ciliare, Aulocomnium palustre, Thuidium delicatulum , T. recognitum, Blepharostoma trichophyllum, Riccardia latifrons,* and *Brachythecium reflexum.*

(4) CA

The total inertia (variability) of the species and quadrat matrix captured in the CA was 13.641, of which the first two axes captured 6.1% and 5.6%, respectively. Species defining CA axis 1 were *Sphagnum squarrosum* and *Brachythecium rutabulum;* axis 2 was defined by *Brotherella recurvans* and *Polytrichum juniperinum* (Figure 6). The same axes were defined by quadrat H-2 block 6 south and I-5 6 north for axis 1; N-4 block 6 north and I-7 block 6 south for axis 2 (Figure 7). The mixed stand types overlapped the softwood and hardwood stands; the softwood and hardwood stands showed divergence along axis 1 and axis 2 (Figure 11).

Relationships Between Species Distribution and Environment

(1) CCA

The CCA gave a constrained inertia of 3.523, i.e., the 26 environmental variables correlated with approximately 26% (3.523/13.641) of the species pattern obtained in the CA (Table 2; Figure 10). CCA axis 1 explained 17.1% of the CCA inertia, while axis 2 accounted for an additional 12.9%. The CCA algorithm was successful in aligning the species and environmental axes, ($r^2 = 0.9269$, 0.8730 for axes 1 and 2, respectively). Litter, pH, calcium and magnesium, and cosine (northward slope) defined the first axis, whereas litter depth, moss litter component, and potassium defined axis 2. Axis 3 did not show any strong environmental correlations with species axis 3, thus, only axes 1 and 2 will be included here.

Scatter plots of species scores and quadrat scores with superimposed environmental biplot scores illustrated the patterns of species-environment relationships (Figures 8 and 9). The species which most commonly occurred (i.e. *Pleurozium schreberi,*

Dicranum spp., *Ptilium crista-castrensis, Ptilidium pulcherimum, Drepanocladus uncinnatus, Herzogiella* spp.) are located in the centre of the scatterplot; hence, their distribution is not strongly linked to the environmental variables included in this analysis. Species that occurred less regularly are found at the outer ends of the axes (Figure 8), thus, they define the axes. Axis 1 was defined by *Dicranum ontariense* at the negative end, and *Plagiothecium cavifolium* at the positive end. Axis 1 was simultaneously correlated with the environmental variables cosine of aspect (northward) and litter characteristics (carbon:nitrogen ratio, magnesium, calcium, and pH). Axis 2 was defined by *Sphagnum nemoreum, S. squarrosum* and *Bazzania trilobata.*

(2) PCCA

Of the environmental variables, litter pattern alone (i.e. main effect) accounted for the largest proportion of the species distribution pattern (14.3%), followed by topography (7.72%); canopy accounted for the least (1.71%) (Table 2; Figure 10). Shared variables (i.e. interaction effects) had little influence.

(3) CCA of stand groups

The three stand groups overlapped on CCA axes (Figure 12) but the mixed stand group was associated with basic soils with high concentrations of calcium, magnesium and nitrogen.

DISCUSSION

Community description

Overall, bryophyte species richness in this study (79 cryptogamic species) was comparable to that of other mixed forests. At the quadrat scale (i.e. $1.25\text{-}m^2$), richness in this study varied from 0 - 27 species per quadrat with a mean value of 10.36. Although direct comparison of species richness is only meaningful among spatially equal units, general comparisons are useful. In the Interior Highlands of North America, Redfearn (1986) identified 109 bryophyte species (mosses and hepatics), and reported similar values in the Appalachian Mountains. The bryoflora of other forest types may vary, e.g. in the taiga, Frego (1994) reported 14 bryophyte species in seven mature black spruce stands, whereas, in the tropical rain forest of Africa, Pocs (1978 *in* Pocs 1982) reported 170 liverworts and 30 moss species in epiphyllous communities. A survey of bryoflora associated with trails near Mountain Lake in Virginia revealed a total of 35 species (Studlar 1980). In a more specialized mountain stream habitat, Slack and Glime (1985) identified 36 species; the lower richness reflects the higher degree of specialization required in this environment.

Mean bryophyte cover for the study site was low ($0.20\% \pm 0.08$, Table 1) compared to Frego's (1994) study where cryptogam cover averaged 86.7%, but low cover values are typical of temperate eastern forests (During and van Tooren 1987) where the bryophyte stratum tends to be discontinuous and patchy. Almost half of the 79 species (49%) occurred in $\leq 5\%$ of the quadrats (Figure 3). This suggests that the majority of species were not ubiquitous; only a very small proportion of species occurred in 60-80% of the quadrats (Figure 3). Also, 84% of the species had very low mean cover values when present (2% or less); many of these species are liverworts (23 species) which tend to

grow among moss shoots in low abundance (this would account for a large proportion of the species having low cover values). The relatively large total mean percent cover (5.89%) for *Pleurozium schreberi* found in this study, which was significantly higher than those for the remaining species (Table 1), is consistent with its distribution at a larger scale. *P. schreberi* is ubiquitous in the Northern Hemisphere and dominates much of the bryoflora of boreal zones which cover 11% of the earth's land masses (Bonan and Shugart 1989; Wein *et al.* 1983 *in* Frego 1994); this suggests effective dispersal mechanisms and broad ranges of environmental tolerance.

The dense clustering of species and samples in the CA indicates that there was great overlap in species composition among quadrats. The outliers scattered to the periphery, *Brotherella recurvans, Sphagnum squarrosum, Hylocomium splendens* and *Calypogeia muelleriana* (Figure 6), were locally abundant but very infrequent. For example, *S. nemoreum* had a cover value of 14.0% but occurred in only one quadrat (Table 1). When the cluster of quadrats was magnified (Figure 11), the apparent separation of stand types (softwood - mixed - hardwood) indicates variation in canopy type at the local scale, which may influence the distribution of bryophyte species locally.

Interpretation of Patterns

Variables that might influence the bryophyte community are seemingly infinite. Some include competition factors (e.g. features of the abiotic and biotic habitat), stochastic factors (e.g. the history of the area), and regeneration abilities of the species. Bates (1982) stated that vegetation patterns generally reflect trends in controlling environmental conditions. However, the relationships between community structure and environment may be too complex to be attributable to one or a few factors; as is common

in nature, a network of interconnected influences may be involved (During and Verschuren 1988).

The complexity of several of these environmental gradients was evident from the CCA, as seen in the species-environmental biplots where elements of canopy, topography, and litter were all represented. Under mixed canopies, one group of species (*Climacium dendroides, Cirriphyllum piliferum, Rhytidiadelphus triquetrus, Bryhnia novae-angliae, Plagiothecium cavifolium, Plagiomnium cuspidatum, Brotherella recurvans, Thuidium recognitum, Hypnum imponens, Dicranum viride, Brachythecium reflexum, B. salebrosum* and hepatics *Plagiochila porelloides* and *Riccardia latifrons*) was associated with microsites characterized by high deciduous canopy cover with resulting deep deciduous litter, and high concentrations of nitrogen, calcium, magnesium and high pH, on generally south-facing slopes. Roberts (unpublished) found that the mesic, nutrient-rich mixed stands F and G contained tree species unique to the study area, such as Ironwood, Yellow Birch, Large Tooth Aspen, and White Ash. These species and associated environmental variables indicated a community that is very different from those of the coniferous and deciduous stands. Moreover, the bryophyte species mentioned previously were abundant locally but very infrequent, which further supports the distinction of this habitat. The association of these bryophytes species with stands F and G might be attributable to the unusual canopy species. Alternatively, both canopy and bryophyte composition may reflect a common controller. For example, the composition of stands F and G might represent the remnants of ancient microenvironment features.

At the opposite end of the gradient represented by CCA axis 1, a second group of species (*Dicranum ontariense, D. polysetum, Diphyscium foliosum, Pleurozium schreberi, Oncophorus wahlenbergii,* and hepatics *Lophozia heterocolpos, Calypogeia*

integristipula, and *Frullania eborascensis*) was associated with a predominantly coniferous canopy, shallow coniferous litter, and deeper moss litter with low pH and high potassium, on generally north-east facing slopes. These environmental features and species are typical of coniferous stands (Carleton 1990).

The deciduous stands overlapped the coniferous stands on the CCA considerably (Figure 12), hence, the bryophyte species present in both these stand types were similar. These quadrats contained the ubiquitous species *Ptilidium pulcherinum, Pleurozium schreberi, Dicranum scoparium, D. polysetum, Lophocolea heterophylla, Brachythecium starkei,* and *Jamesoniella autumnalis.* These may be very tolerant species capable of exploiting a variety of microhabitat conditions. The observed association between moss occurrence and mounds is common in deciduous stands which have high litterfall that may act as a physical barrier to bryophytes. Mosses tend to colonize raised topographical features such as mounds, decaying logs and stumps which shed litter (Sveinbjörnsson and Oechel 1992).

In a parallel study of the relationship of terricolous bryophytes and lichens with environment and stand types, Carleton (1990) found similar trends in complex gradients. The main axes of separation were that of dry, nutrient poor coniferous stands verses moist, fertile deciduous stands; the mixed forest was intermediate. Bryophyte richness and cover were higher in moist, nutrient-rich deciduous stands and dry, nutrient-poor, coniferous stands, rather than in the mesic-mixed area. The mixed, nutrient-rich, mesic area showed a higher density of vascular plants, which was also observed in our mesic stands F and G (Appendices VII and VIII). As in this study, *P. schreberi, Dicranum polysetum* and *Cladina rangiferina* were predominant in the coniferous stand and *Brachythecium* spp. were dominant in the deciduous stands. *Drepanocladus uncinnatus*

and *Dicranum fuscescens* were predominant in the mesic, mixed stand characterized by abundant herbaceous plants.

The Hayward Brook data also revealed an association between bryophyte growth form (*sensu* During 1992) and stand type. Acrocarpous species dominated the coniferous stand, whereas pleurocarpous species dominated the deciduous stand. Acrocarpous species are characteristic of sites with acidic, coarse-textured, dry soils, and low vascular plant species (Robinson *et al.* 1989). Pleurocarpous species are adapted to mesic habitats relatively stable habitats; their growth form enhances their ability to compete with forest floor vascular plants (Vitt 1984 *in* Robinson *et al.* 1989).

The results of this study indicate that bryophyte community composition at the local scale is closely related to certain aspects of the microhabitat, specifically to combinations of canopy, litter and topography. Species distribution patterns seem to be most related to litter, while macro habitat features such as topography, aspect, and canopy seem less important (Table 2, Figure 10). Although this study is not experimental, it is useful in that it generates hypotheses that can be further tested. Future studies can examine isolated effects of these environmental components.

Litter

The effects of litter on bryophyte establishment and growth may be either positive or negative, chemical or physical, and immediate or long-term. One negative physical effect of litter is shading or burial. This is especially true in deciduous stands where broad leaf litter is shed in annual pulses and tends to remain on top of moss colonies; coniferous needles, however, tend to fall between the moss shoots due to their geometry and continuous shedding (Sveinbjörnsson and Oechel 1992). This explains the more

continuous moss carpets (i.e. higher total cover) under coniferous canopies than under deciduous canopies. Under deciduous stands mosses form cushions or small moss carpets on hummocks or other topographically raised features such as tree stumps and fallen logs which shed litter. The herbaceous stratum also contributes litter (Sveinbjörnsson and Oechel 1992). The yearly die-off of annuals or above-ground shoots of perennials such as bracken fern can contribute substantially to litter burial and shading of bryophytes.

Broad-leaf litter may dramatically reduce the amount of light reaching the bryophyte community. As a result, photosynthesis may decrease, thus, decreasing or arresting growth, or causing etiolation. In extreme cases where bryophyte shoots receive insufficient light, death may occur. Broad-leaf litter burial may also physically alter the microclimate above bryophytes by raising the local temperature or local relative humidity. Decaying leaf litter is often dark in colour and is easily warmed by the sun to temperatures greater than air temperature. Litter may reduce evaporation or even trap moisture between the moss carpet and the litter. Both these effects might have a positive effect on bryophyte photosynthesis and respiration: (1) the higher temperatures might allow bryophytes to photosynthesize in air temperatures that would normally prevent this, and (2) most bryophytes desiccate rapidly as they depend on atmospheric moisture (rain, dew, fog, mist, and humidity) and have no means of water storage and internal water conduction (except endohydric mosses, e.g. Polytricaceae). This study provides no evidence that litter presence or depth acted as a barrier above the bryophytes.

The physical nature of litter may provide a positive influence by serving as a substrate for certain species. While few species are strictly substrate specific, many species of bryophytes have much stronger affinities for one or a few substrate types (La Roi and Stringer 1976). For example, *Hypnum pallescens* var. *protruberans* prefers tree

bases and rotten logs and is rarely found on rock (Ireland 1982); *Drepanocladus*

uncinnatus occurs exclusively on recent woody debris, small woody stems or even stems

of herbaceous plants (Carleton 1990).

This study indicated that litter chemistry was an important influence on bryophyte

community structure. This may be a positive or negative influence, depending on whether

the litter supplies nutrients or toxins from the decaying plant material. Upon

decomposition, minerals may leach out of tree and herbaceous litter through dripwater

which is readily absorbed by bryophytes. The literature supports the idea that the chemical

influence of litter more often enhances, rather than hinders, bryophyte growth (e.g. Frego

and Carleton 1995; Frego 1994; van Tooren *et al*. 1990). For example, in a study of five

bryophyte species in British grasslands, it was found that only one of the five species was

at all inhibited by litter, while the other four were either enhanced or not affected (Rincón

1988 *in* Sveinbjörnsson and Oechel 1992). The enhancement of bryophyte growth was

considered to be due to nutrient acquisition from the decomposing litter (Sveinbjörnsson

and Oechel 1992). However, bryophyte growth may also be negatively affected by toxins

in the plant debris (Frego, pers.comm.) and/or chemicals released from decomposer

microorganisms (Sveinbjörnsson and Oechel 1992).

Topography

Some aspects of topography were related to bryophyte community structure at the

local scale. At the macro scale, topography may affect features such as climate (e.g.

temperature, water drainage, height from water table, incoming radiation, and wind).

Aspect and slope affect the amount of incident light and radiation reaching the forest floor

as well as local temperatures, i.e. a south-facing slope will receive more light and more

warmth of the sun than north-facing slopes. High light levels can negatively affect growth and intraspecific inhibition in some species of bryophytes (e.g. Scandrett and Gimingham 1987). The steepness of the slope affects water drainage and, thus, water relations. Elevation may also affect bryophyte distribution patterns (Slack and Glime 1985); higher elevations tend to be lower in humidity (Kenkel and Bradfield 1981) and are farther from the water table. However, because bryophytes are very small, they are likely to respond to variation at the micro scale. Microtopographical features such as pits and mounds would be expected to greatly influence the distribution of bryophyte species. Pits formed by uprooted trees in the boreal forest tend to trap moisture and thus are often colonized by hydrophilic mosses such as *Sphagnum* spp., whereas those in mixed or deciduous stands tend to accumulate broad-leaf litter which may bury mosses (Sveinbjörnsson and Oechel 1992). In this study, mounds were associated with high deciduous canopy and litter (Figures 7 and 8). This is consistent with the observation that moss colonies tend to form on mounds and any raised topographical features that escape litter burial in mixed and deciduous stands.

Canopy

Canopy did not appear to affect moss communities directly, i.e. in terms of composition or percent cover. This may be because the tree stratum is generally several metres above the bryophyte layer. Canopy directly modifies such macroenvironmental features as temperature, precipitation (throughfall), humidity, light, and wind. Throughfall precipitation from the canopy can be enriched with nutrients derived from foliar leaching and wash off of dry deposition (Rieley *et al.* 1979 *in* During and Verschuren 1988). Canopy could be expected to affect bryophytes indirectly but at a more local scale by: (1)

providing litter in annual pulses e.g deciduous, or consistently e.g. coniferous; (2)

providing substrates in the form of litter, rotting logs, upturned trees (mineral soil), and

the vertical trees themselves (epiphyte communities); and (3) influencing the distribution

of herbaceous plants, which in turn influence the bryophyte stratum through local shading,

litter, toxins, and nutrients. Future analysis will examine the relationship between

bryophyte pattern and herbaceous vascular plants in the same quadrat (see Hovey

unpublished). In this study, percent canopy cover was much less significant than litter

composition, indicating that the impact of canopy operated at the finer scale of local litter

production, rather than the aerial effects.

Predicted effects of forest harvesting

This study documents the baseline bryoflora in the Hayward Brook Watershed. Its

contributions are threefold: (1) it documents the general biodiversity and distribution

patterns of bryophytes in such stand types in the Acadian Forest Region; (2) it allows for

detection of changes in species community composition following human intervention; and

(3) it allows for hypothesis generation of: (a) other possible variables that may explain the

vegetation distribution pattern (e.g. moisture, interspecific relations, regeneration, soil

texture and chemistry, etc.), and (b) cause and effect predictions from forestry practices.

For example, in this study, bryophyte communities were associated to some extent with

features of the canopy. If bryophytes are sensitive to variations in environment within a

given stand, many species will not likely tolerate the gross changes in environmental

conditions caused by canopy removal by clear-cutting, i.e. very high light intensities, low

humidity, exposure to wind, blowing snow and ice crystals, increased erosion, evaporation

or clogging of ground springs (due to disturbance and erosion) resulting in loss of wet

habitats, as well as the intense disturbance of scarification methods resulting in destruction of communities on rotting logs and stumps, and litter layers removed to expose mineral soil. Some species such as the thallose liverwort *Conocephalum conicum* cannot tolerate low humidities and die when mildly droughted (Sveinbjörnsson and Oechel 1992). Only species capable of existing in these new conditions will regrow; others may persist as moss fragments or diaspores in the soil, to regenerate when conditions are favourable once again (van Tooren *et al.* 1990). If the area is allowed to regrow naturally, the same stand types may or may not be re-assembled. Thus the 49% species of this area that were site-specific may not encounter the conditions required for regeneration in the regrown forest; the bryoflora and vascular flora (described in Hovey, unpublished) documented for this area may be an historically unique assemblage.

Alternatively, the previous forest stands may be replaced anthropogenically. A common practice of forestry is to replant harvested areas with monocultures of commercially viable species such as Black Spruce, Jack Pine, or other softwood species. The difference detected in this study between the bryophyte communities associated with coniferous stands versus the rich, mesic mixed stands, suggests that only bryophytes characteristic of coniferous stands will regenerate under the coniferous monocultures. Species such as *Cirriphyllum piliferum, Plagiomnium* spp., *Mnium* spp., *Thuidium* spp., *Plagiothecium cavifolium*, and others found at the rich, mesic mixed stands end of the axis (Figure 12), would, therefore, be lost from the bryoflora of the area; bryophyte biodiversity (species richness and evenness) would decline. Alternatively, biodiversity and particularly richness may increase with the invasion of weedy or more cosmopolitan species, but the species composition would still have been changed (van Tooren *et al.* 1990). Rare species especially may be more at risk. For example, in European chalk

grasslands, rare species only occur in sites that are 70 years old (van Tooren *et al.* 1990). In a regenerated site which was arable since 1960, rare bryophytes were still absent (van Tooren *et al.* 1990). This implies that once an ecosystem is changed, it may never be able to support the original species assemblage again. We predict that the bryoflora assemblage that regenerates in Hayward Brook after clearcutting will not be the same assemblage.

CONCLUSION

This study represents a record of the bryoflora assemblage in the Hayward Brook Watershed area of the Maritime Forest Region immediately prior to forest harvest. It illustrates the variation in bryophyte distribution patterns at both the stand scale and at the microscale. Environment was associated with 26% of the total variation in bryophyte distribution patterns, implying that environment has a significant influence on bryophyte community. Many important microhabitat features are directly or indirectly associated with the stand type. For example, while the ordination analysis showed that canopy cover was not strongly associated with species patterns, canopy will affect such microsite features as litter, nutrient levels, and pH which were strongly associated with the bryophyte community composition. Further research to explain more of the variation in bryophyte distribution patterns would include determining the influences of herbaceous plant distributions, moisture levels and other environmental variables not included in this study, along with interspecific relationships between bryophyte species, and their reproductive mechanisms.

Figure 1. Map of Hayward Brook Watershed study site. Red dots indicate location of

quadrats. Stand letters corresponding with numbers on map are: A=26, B=40, C=41 &

42, D=22, E=34, F=38, G=29, and H=30. Stands A, B, D, and E were classified as

coniferous, F and G as mixed intermediate, and C and H as ridge hardwood.

Figure 2. Frequency distribution of richness, i.e. number of species per quadrat (155 1-m^2

quadrats). Twenty-five percent of the quadrats had 7-9 species per quadrat,

approximately 22% had 13-15 species and 17% had 10-12 species.
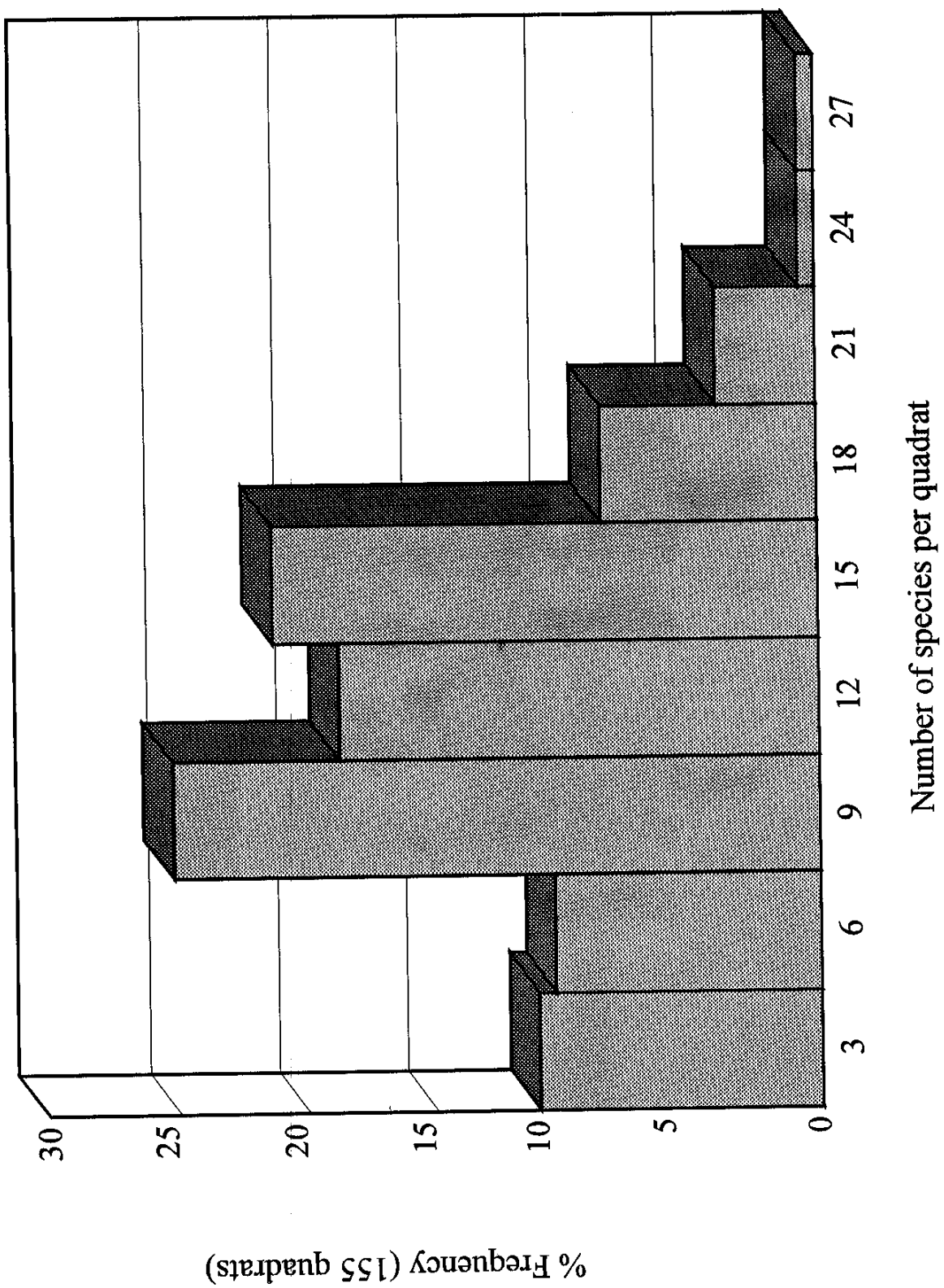
% Frequency (155 quadrats)

Number of species per quadrat

Figure 3. Distribution of frequency of occurrence of species in quadrats, e.g. 39 species were present in ≤ 5% of 155 quadrats.
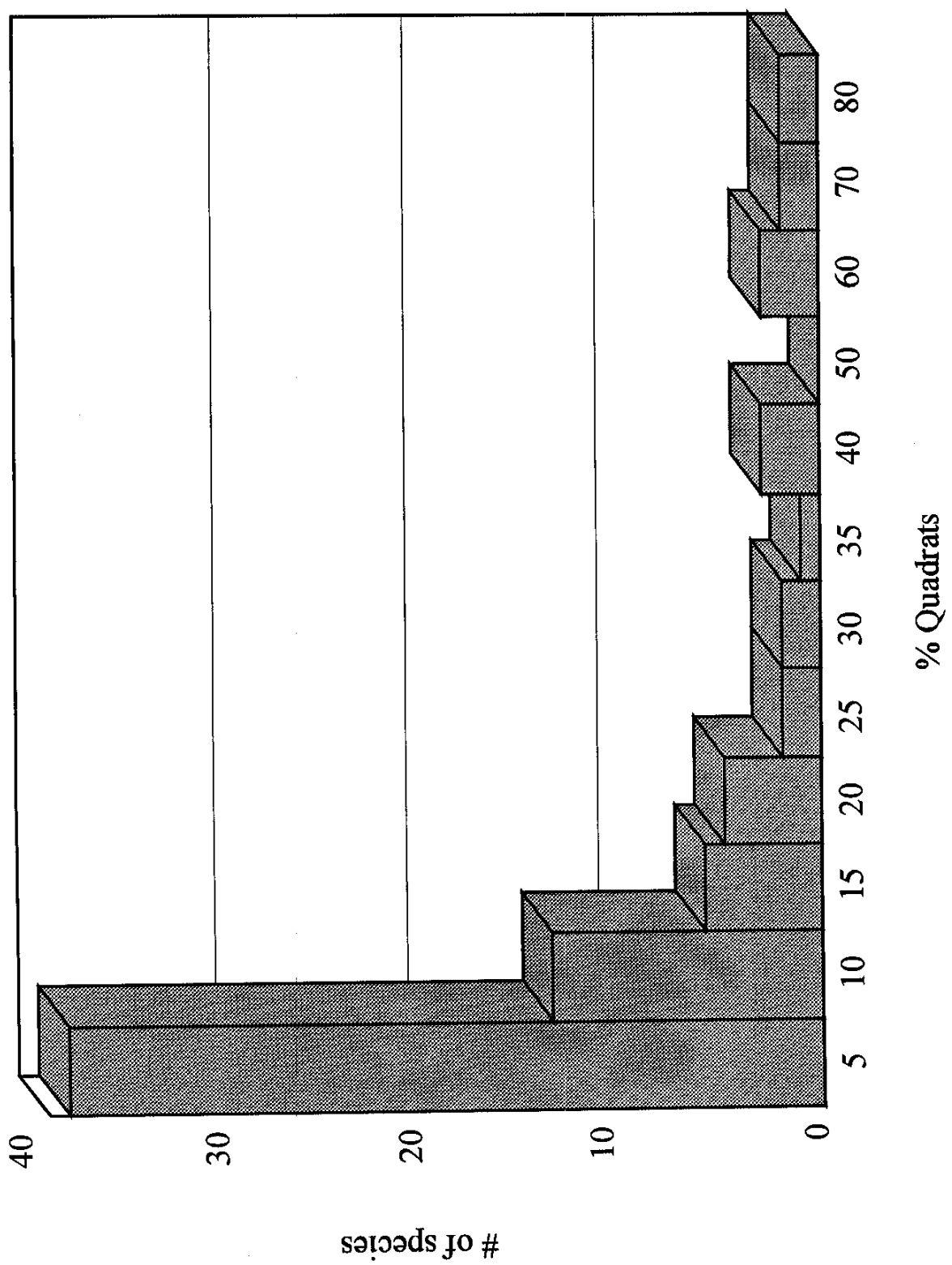
Figure 4. Distribution of mean % cover of species in 155 1.25-m^2 quadrats; 69 species had total mean cover $\leq$ 0.25%.

Mean % cover overall
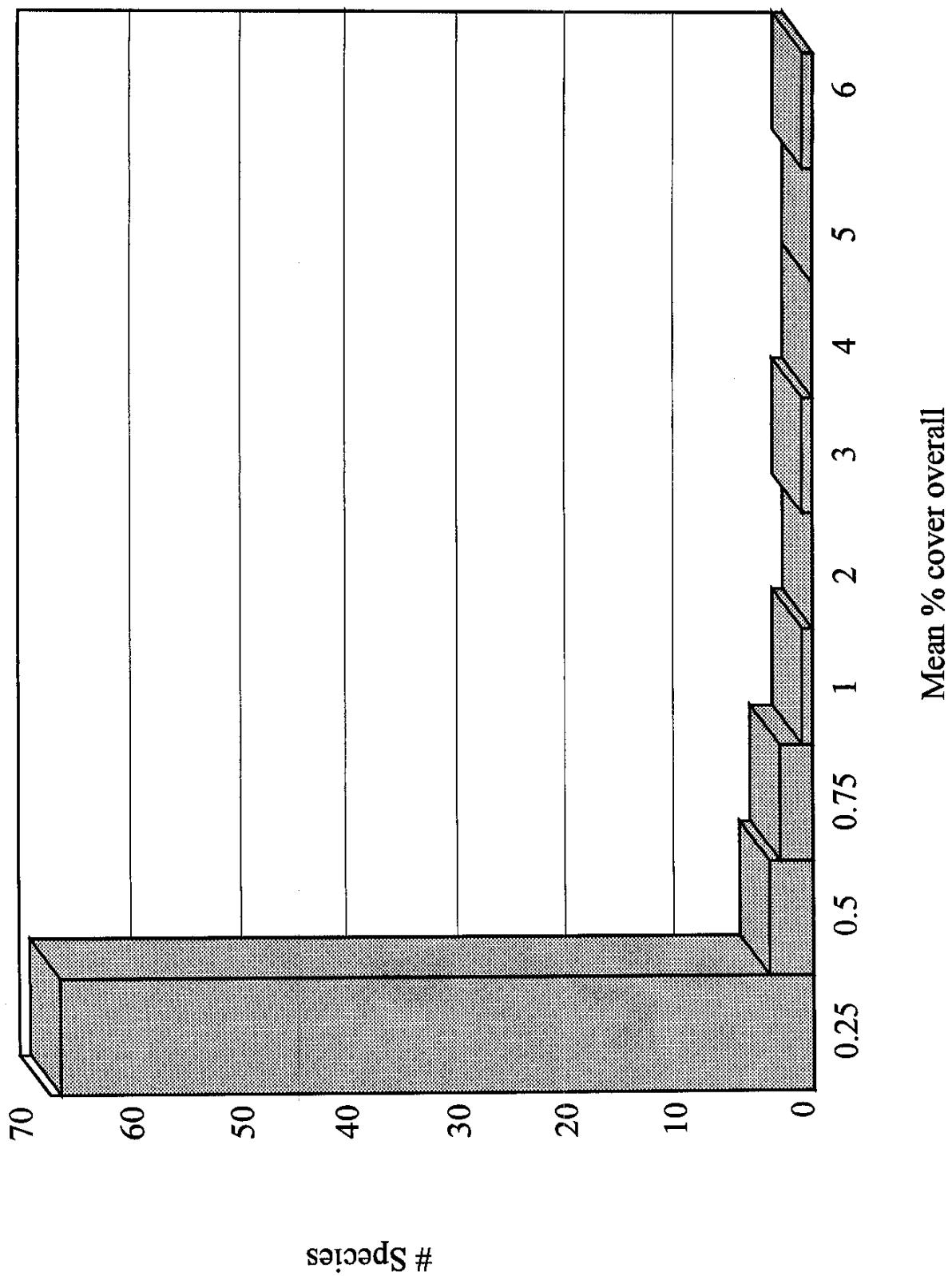
Species

Figure 5. Distribution of mean species abundance when present (n=155). In quadrats in which they were present, 66 species had ≤ 2% mean cover while *Sphagnum nemoreum* had a mean cover value of 14% (but occurred only once).
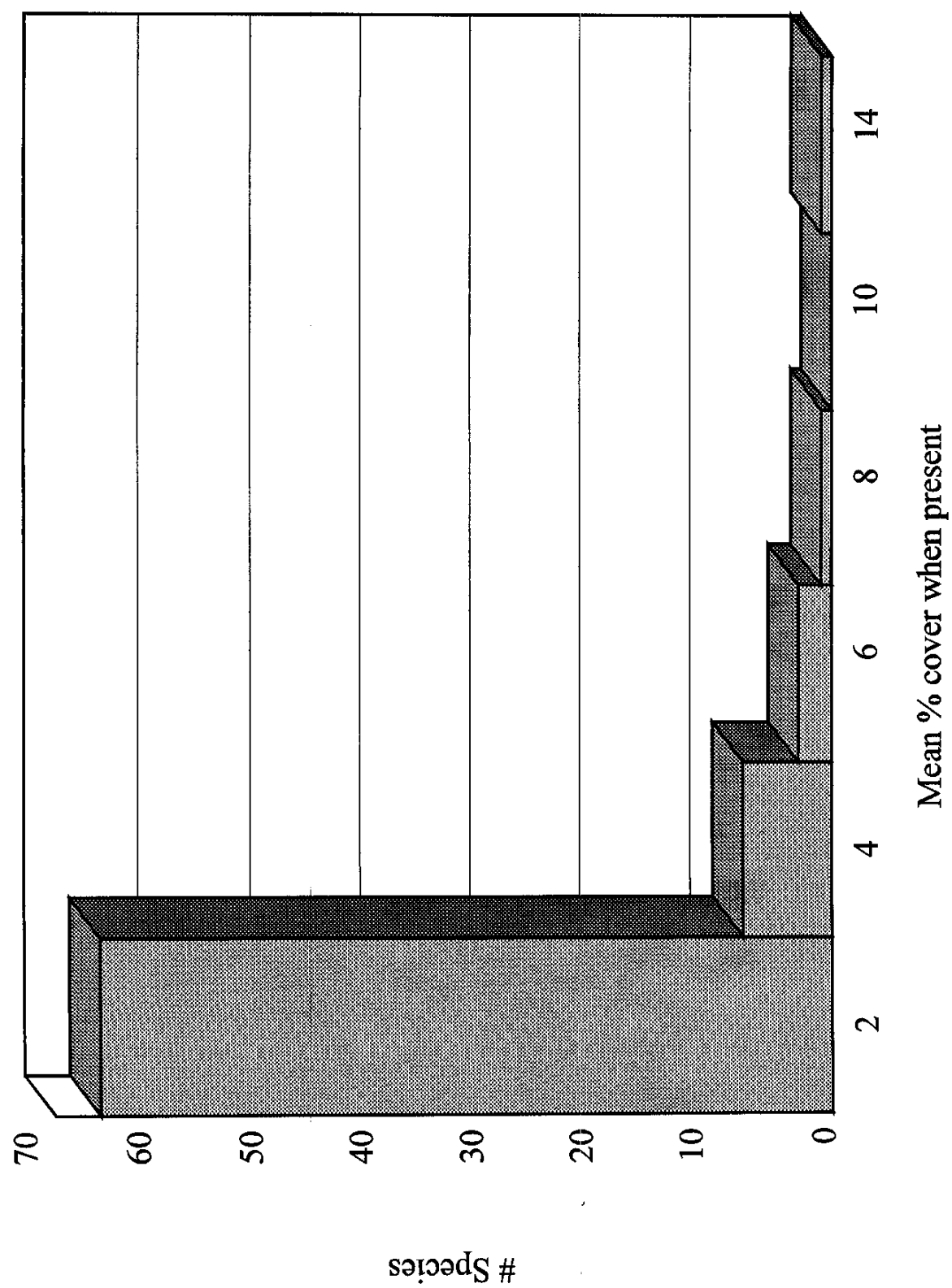
Figure 6. Species scores on first two axes of correspondence analysis (CA) in 155 1.25-m^2 quadrats at Hayward Brook Watershed. Total interia = 13.641. Contribution of each axis to total inertia is in parentheses.

Axis 1 (6.1%)

Axis 2 (5.6%)
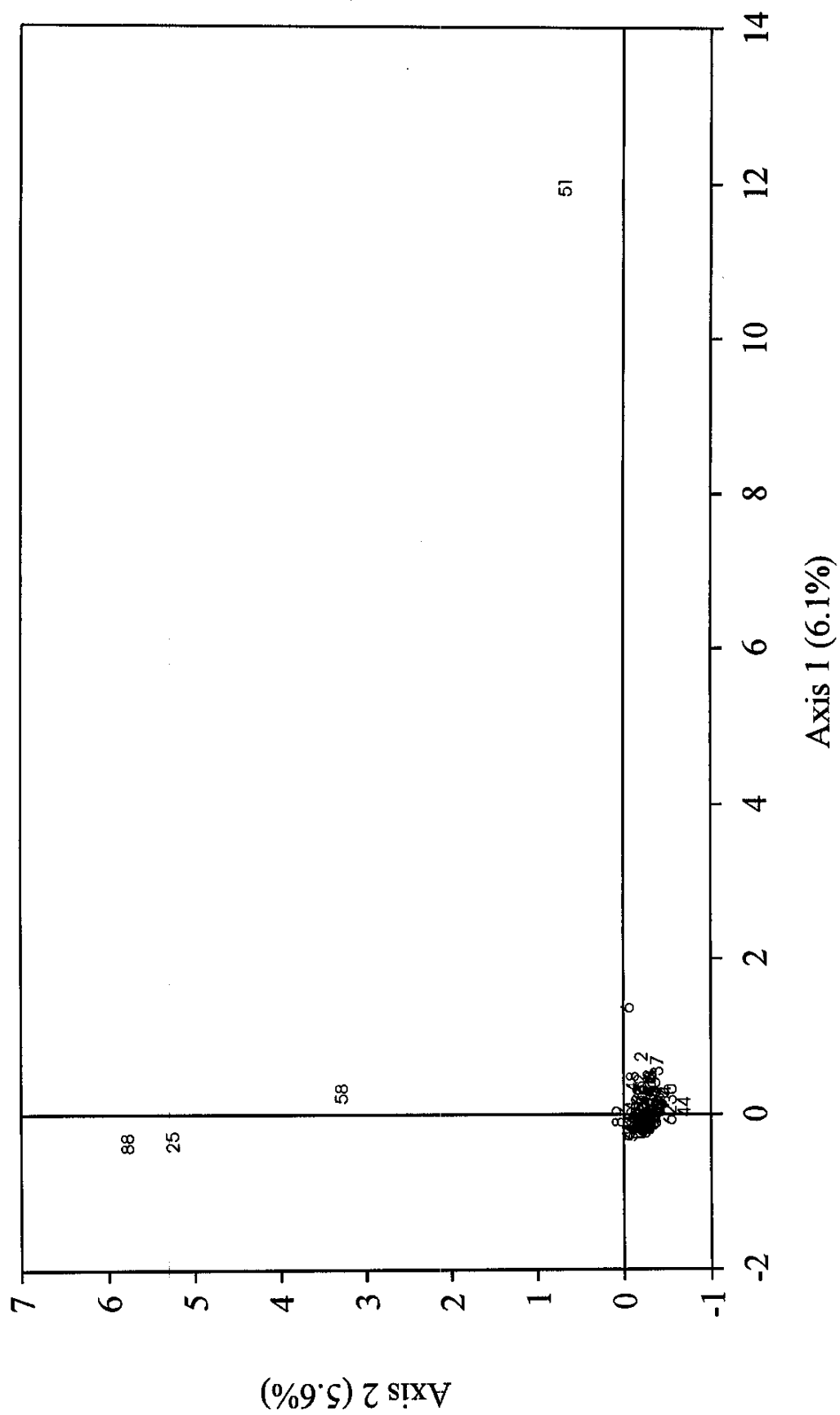
Figure 7. Quadrat scores on first two axes of CA in 155 1.25-m^2 quadrats. Total inertia = 13.641. Contributions of each axis to total inertia is in parentheses.

Axis 1 (6.1%)

Axis 2 (5.6%)
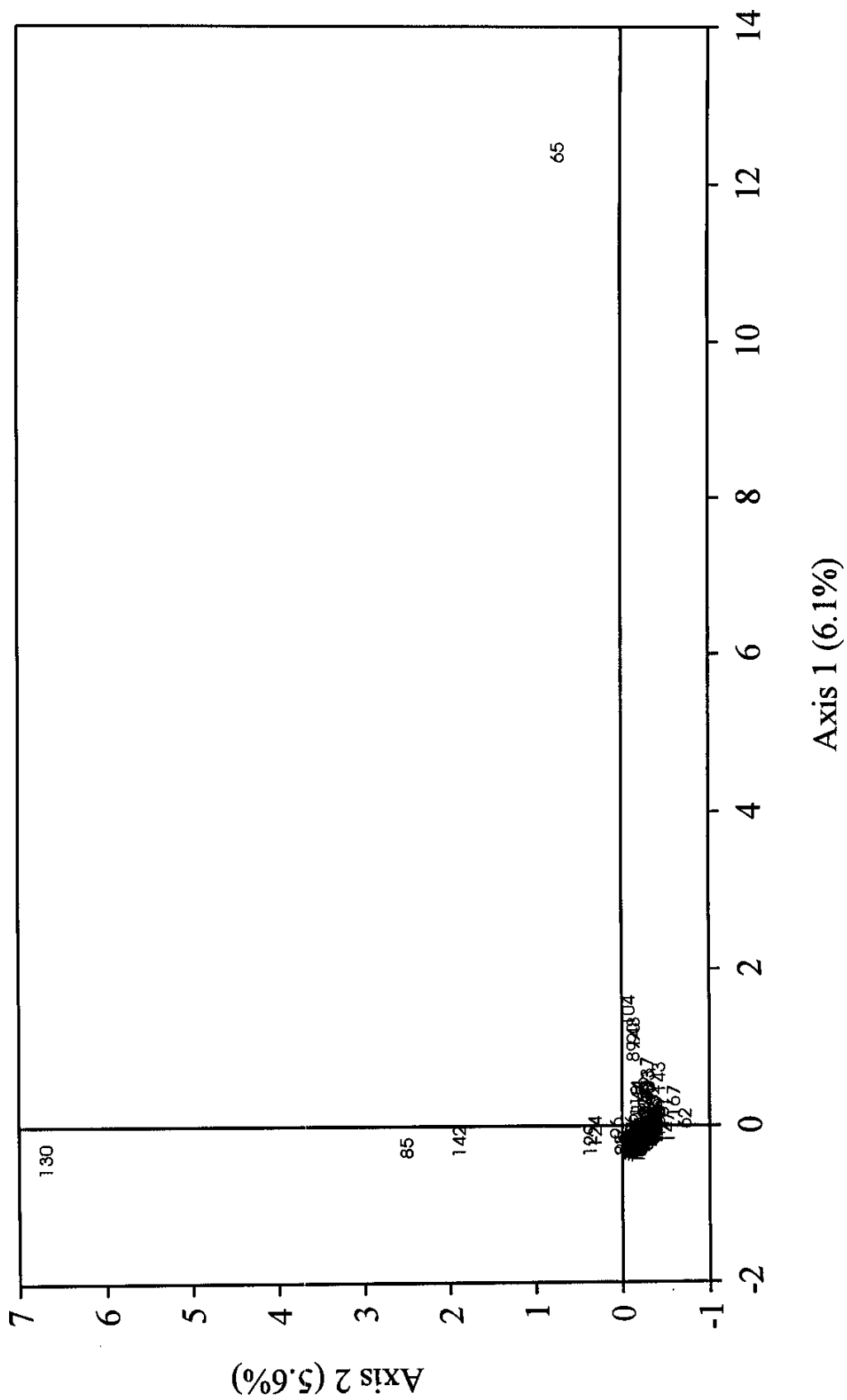
Figure 8. Species scores (numbers) on first two canonical correspondence analysis (CCA) axes with environmental biplot scores (vectors). Length and proximity of arrows to a particular axis show the correlation of that variable with the axis. Contribution of each axis to total inertia is in parentheses.

CCA axis 1 (17.1%)

CCA axis 2 (12.9%)

calcium
pH
Mg
nitrogen
deciduous canopy
deciduous litter
litter
organic matter
phosphorus
carbon
position
macro
moss litter
flat
coniferous canopy
C/N
cosine
coniferous litter
potassium
sine
slope
canopy
slope
mound
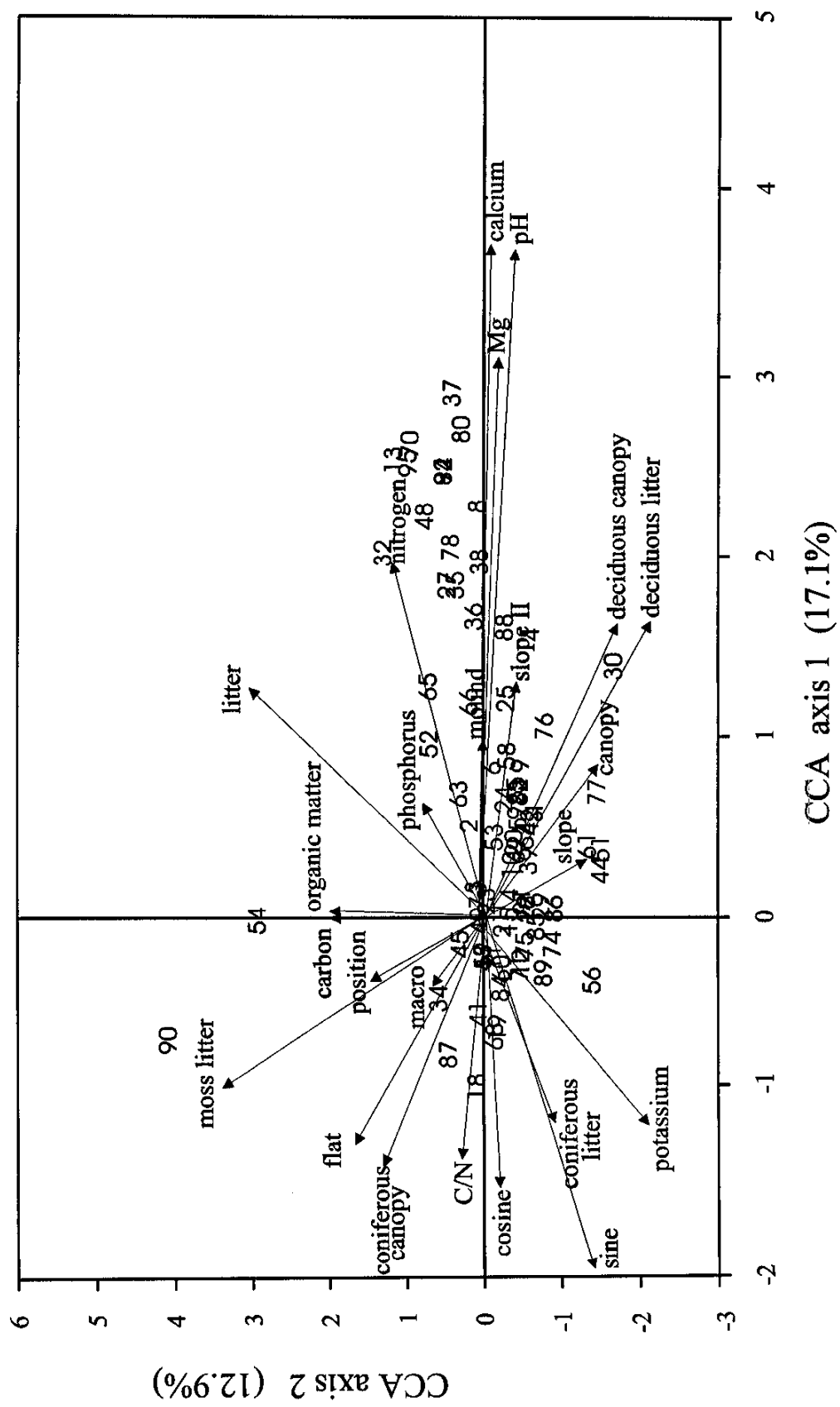
Figure 9. Quadrat scores (numbers) on first two CCA axes with environmental biplot scores (vectors). Length and proximity of arrows to a particular axis show the correlation of that variable with the axis. Contribution of each axis to total inertia is in parentheses.
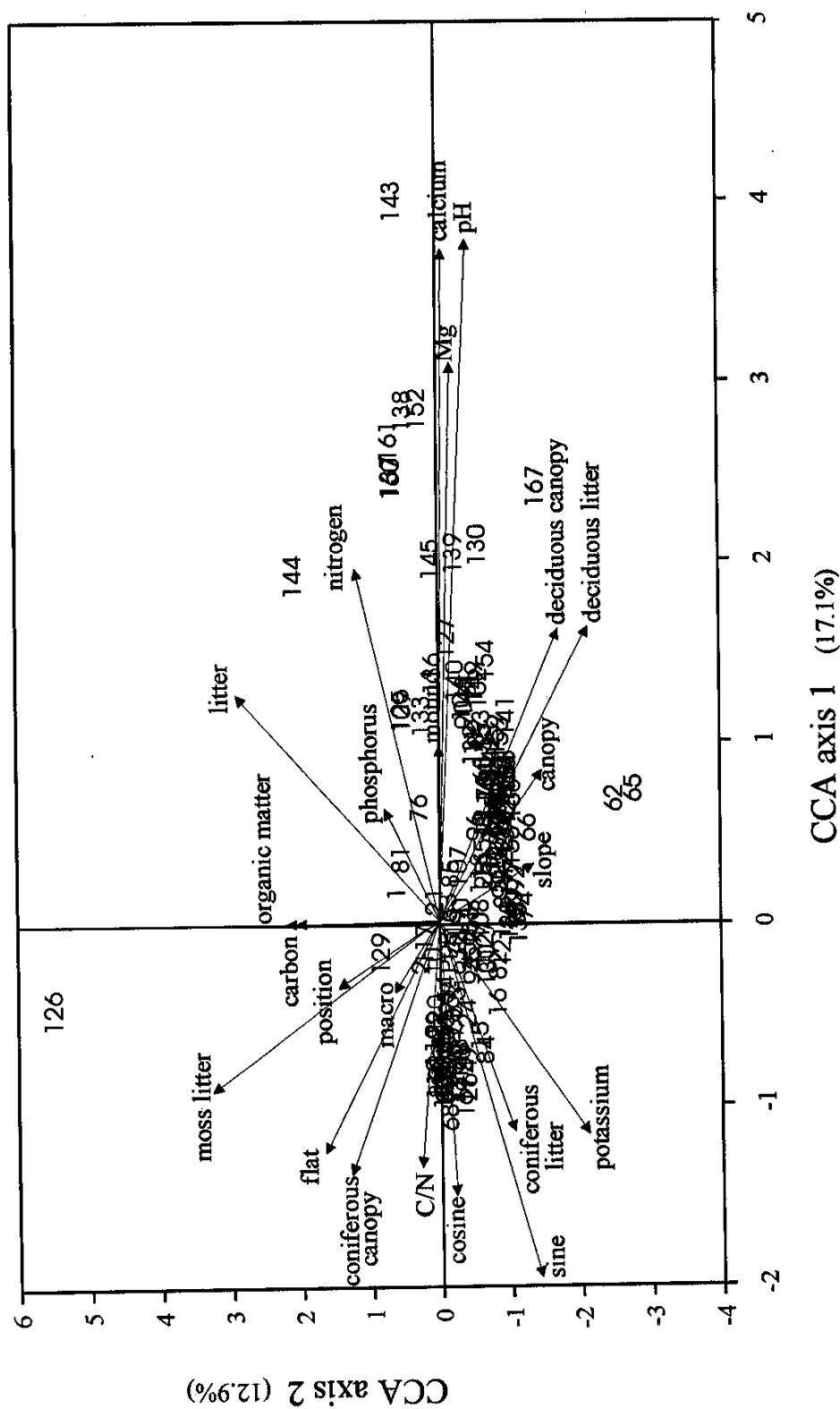
Figure 9. CCA scatter plot of sample scores (numbers) with environmental biplot scores (vectors).

Figure 10. Summary of multivariate analyses. Total inertia of the correspondence analysis

(CA) = 13.641. Environmental variables in the canonical correspondence analysis (CCA)

accounted for approximately 26% of the total inertia. Partial canonical correspondence

analysis (PCCA) revealed the unique and overlapping influences of topography, canopy

and litter. Litter alone showed the greatest influence.

PCCA

Topography

Canopy

Litter

Total variability

?

CCA

100

75

50

25

0
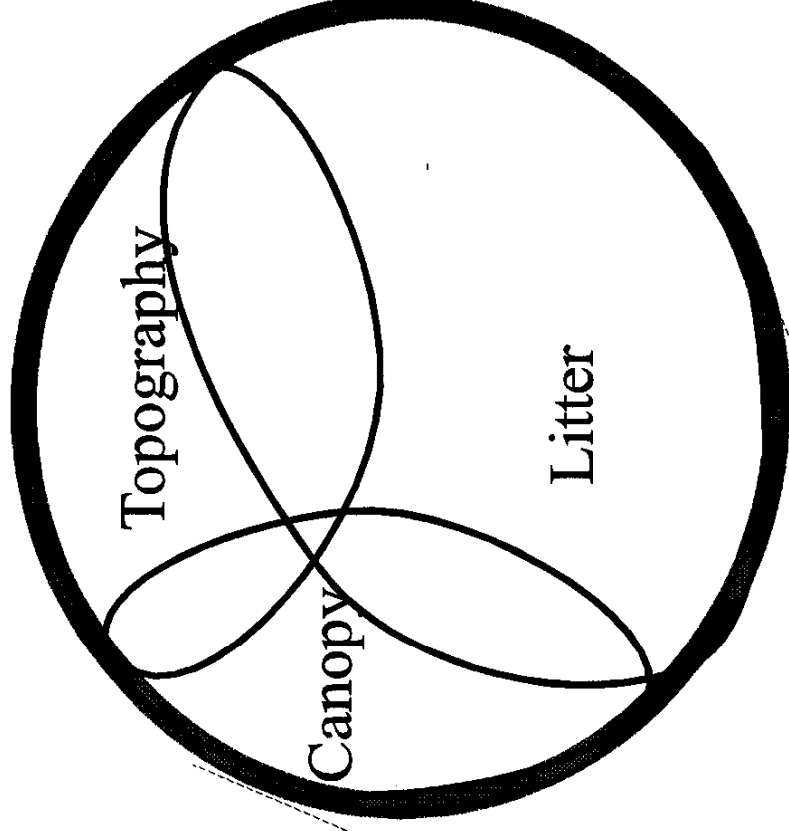
Figure 11. Quadrat scores on first two axes of CA, by stand type. Red = softwood, blue = mixed intermediate, and green = hardwood. The mixed stand overlaps the hardwood and softwood in the CA pattern.

Axis 1 (6.1%)

Axis 2 (5.6%)
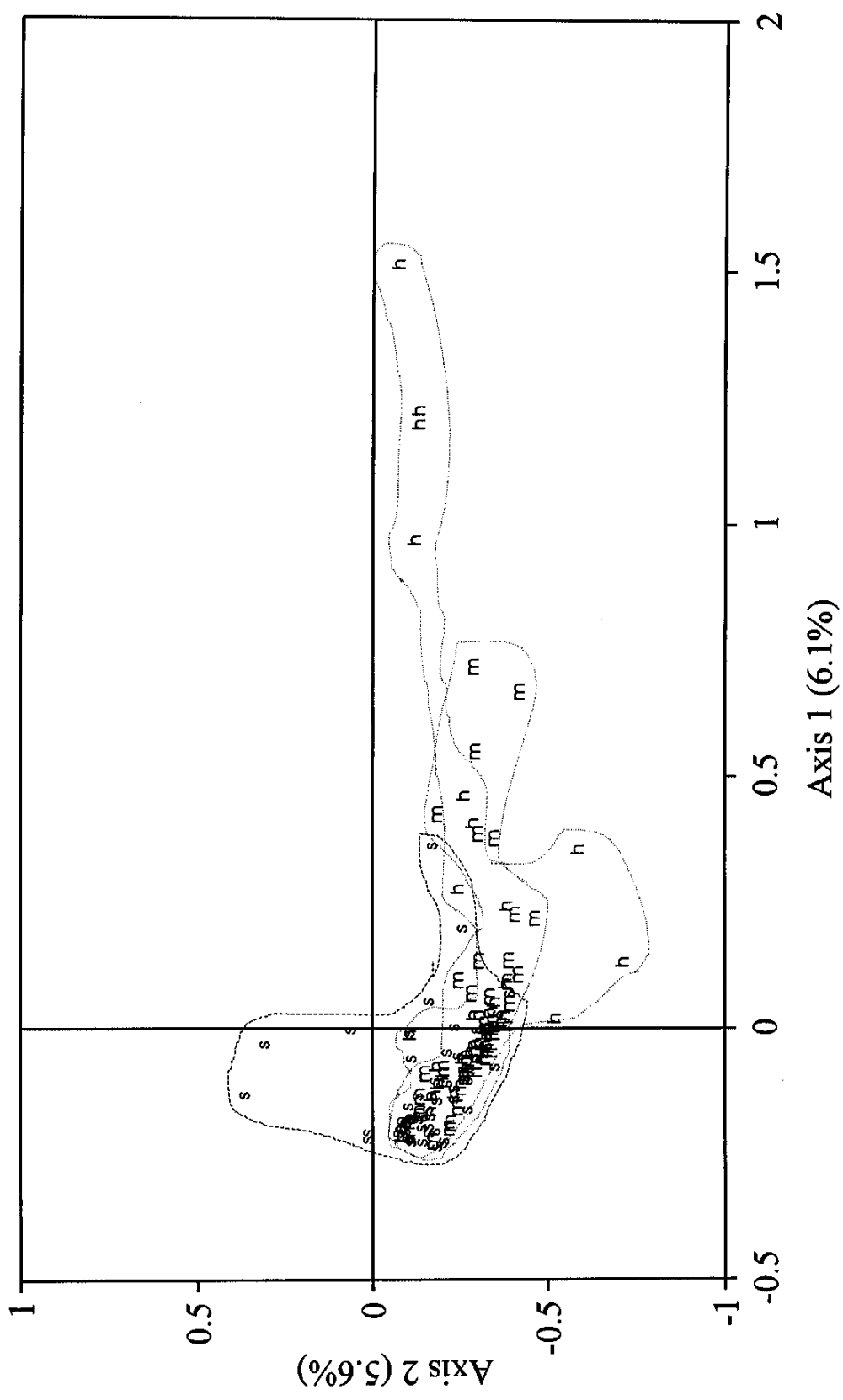
Figure 12. Quadrat scores on first two axes of CCA, by stand type. Red = softwood, blue = mixed intermediate, and green = hardwood. The mixed stand group shows a strong association with basic litter layers high in concentrations of calcium, magnesium, and nitrogen.

CCA axis 1 (17.1%)

CCA axis 2 (12.9%)

6
5
4
3
2
1
0
-1
-2
-3
-4

-2
-1
0
1
2
3
4
5

143

calcium
pH

Mg

138
152

181 6

nitrogen

144

145
139
130

167

deciduous canopy
deciduous litter

litter

organic matter

phosphorus

109

carbon

position

macro 129

moss litter

flat

coniferous
canopy

C/N

cosine

sine

coniferous
litter

potassium

canopy

slope

62
65

76

81

126

66
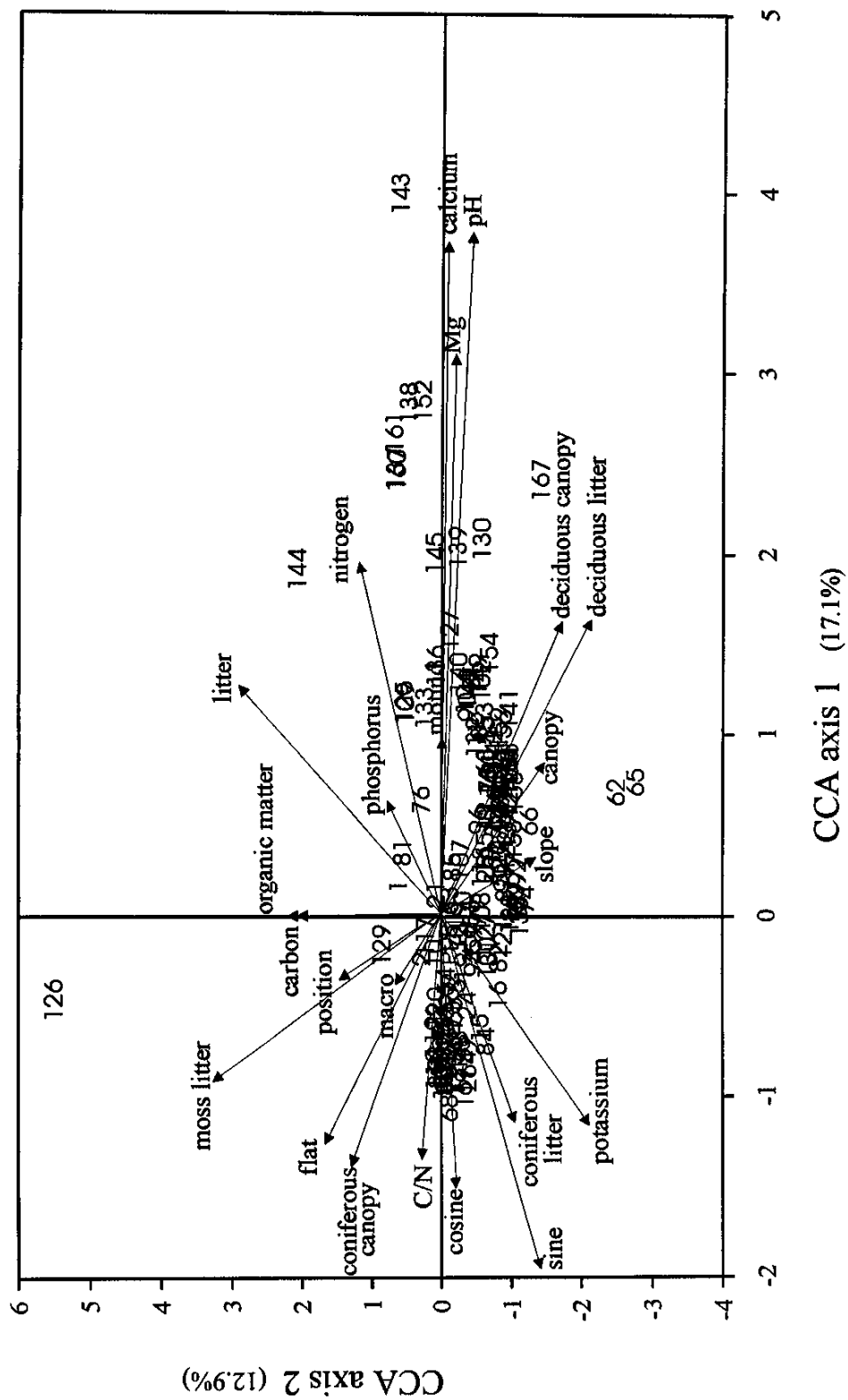
Table 1: Species frequency and mean cover values, ordered by descending frequency of occurrence in 155 quadrats. Nomenclature follows Ireland (1982), and Ireland and Bellolio-Trucco (1987).

Species	species #	% Frequency	Mean % cover when present	Total mean % cover
Ptilidium pulcherinum (G. Web.) Hampe	72	79.35	0.69	0.55
Pleurozium schreberi (Brid.) Mitt.	41	76.13	7.74	5.89
Dicranum scoparium Hedw.	20	68.39	1.31	0.89
Dicranum polysetum Sw.	19	67.74	3.25	2.20
Lophocolea heterophylla (Schrad.) Dum.	66	56.77	0.18	0.10
Brachythecium starkei (Brid.) B.S.G.	5	55.48	0.72	0.40
Jamesoniella autumnalis (DC.) Steph.	64	51.61	0.38	0.20
Fruticose lichen	75	38.06	0.99	0.38
Herzogiella turfacea (Lindb.) Iwats.	24	37.42	0.56	0.21
Hypnum pallescens (Hedw.) P.Beauv.	28	35.48	0.26	0.09
Dicranum flagellare Hedw.	14	31.61	0.53	0.17

Species	species #	% Frequency	Mean % cover when present	Total mean % cover
Drepanocladus uncinnatus (Hedw.) Warnst.	21	29.68	0.40	0.12
Dicranum fuscescens Turn.	15	28.39	1.00	0.28
Plagiomnium cuspidatum (Hedw.) Kop.	36	23.23	0.87	0.20
Callicladium haldanianum (Grev.) Crum	9	22.58	0.96	0.22
Ptilium crista-castrensis (Hedw.) De Not.	45	18.06	1.01	0.18
Geocalyx graveolens (Schrad.) Nees	63	18.06	0.13	0.02
Tetraphis pellucida Hedw.	52	17.42	0.50	0.09
Plagiothecium laetum B.S.G.	39	16.77	0.13	0.02
Dicranum montanum Hedw.	17	16.77	0.28	0.05
Bazzania trilobata (L.) S. Gray	54	14.84	3.57	0.53
Nowellia curvifolia (Dicks.) Mitt.	69	12.90	0.10	0.01
Brachythecium rutabulum (Hedw.) B.S.G.	6	12.90	0.66	0.09
Campylium hispidulum (Brid.) Mitt.	10	12.26	0.33	0.04

Species	species #	% Frequency	Mean % cover when present	Total mean % cover
Polytrichum commune Hedw.	43	12.26	1.41	0.17
Brachythecium salebrosum (Web. & Mohr) B.S.G.	4	10.97	0.76	0.08
Hylocomium splendens (Hedw.) B.S.G.	25	9.68	5.65	0.55
Hypnum imponens Hedw.	27	9.03	2.21	0.20
Lepidozia reptans (L.) Dum.	65	9.03	0.44	0.04
Herzogiella striatella (Brids.) Iwats.	23	8.39	1.25	0.10
Ptilidium ciliare (L.) Hampe	71	7.74	0.72	0.06
Plagiomnium ciliare (C. Müll.) Kop.	35	7.74	3.32	0.26
Aulocomnium palustre (Hedw.) Schwaegr.	2	7.74	1.57	0.12
Amblystegium serpens (Hedw.) B.S.G.	1	7.74	0.07	0.01
Foliose lichen	76	7.74	0.36	0.03
Blepharostoma tricophyllum (L.) Dum.	55	7.10	0.10	0.01
Cephalozia lunnifolia (Dum.) Dum.	59	7.10	0.60	0

Species	species #	% Frequency	Mean % cover when present	Total mean % cover
Polytrichum juniperinum Hedw.	44	6.45	1.36	0.09
Bryhnia novae-angliae (Sull & Lesq. *ex.* Sull.) Grout	8	5.81	0.92	0.05
Dicranum ontariense Peters.	18	5.16	3.21	0.17
Campylium stellatum (Hedw.) C. Jens.	12	3.87	0.16	0.01
Brachythecium velutinum (Hedw.) B.S.G.	92	3.87	0.57	0.02
Brachythecium campstre (C. Müll.) B.S.G.	3	3.87	0.48	0.02
Thuidium recognitum (Hedw.) Lindb.	78	3.87	0.89	0.03
Brachythecium populeum (Hedw.) B.S.G.	86	3.23	1.49	0.05
Brotherella recurvans (Michx.) Fleisch.	88	3.23	1.43	0.05
Hypnum pallescens var. *protruberans* (Brid.) Aust.	29	3.23	0.09	0
Cephalozia bicuspidata (L.) Dum.	60	3.23	0.50	0
Rhytidiadelphus triquetrus (Hedw.) Warnst.	48	2.58	2.15	0.06

Species	species #	% Frequency	Mean % cover when present	Total mean % cover
Plagiomnium medium (B.S.G.) Kop.	38	2.58	1.78	0.05
Plagiothecium cavifolium (Brids.) Iwats.	37	1.94	4.83	0.09
Scapania nemerosa (L.) Dum.	73	1.94	0.05	0.
Lophozia heterocolpos (Thed.) M.A. Howe	68	1.94	0.07	0
Dicranum viride (Sull & Lesq. *ex.* Sull) Lindb.	80	1.94	0.07	0
Plagiochila porelloides (Torrey *ex.* Nees) Lindenb.	70	1.29	1.65	0.02
Thuidium delicatulum (Hedw.) B.S.G.	53	1.29	0.85	0.01
Platygyrium repens (Brid.) B.S.G.	30	1.29	0.18	0
Cirriphyllum piliferum (Hedw.) Grout	95	1.29	3.55	0.05
Pohlia nutans (Hedw.) Lindb.	42	1.29	0.05	0
Calypogeia muelleriana (Schiffn.) K. Müll.	58	1.29	0.05	0
Riccardia latifrons	82	1.29	0.05	0

Species	species #	% Frequency	Mean % cover when present	Total mean % cover
Frullania eborascensis Gott.	84	1.29	0.05	0
Sphagnum girgensohnii Russ.	49	1.29	0.30	0
Sphagnum squarrosum Crome	51	1.29	5.20	0.07
Trichocolea tomentalla (Ehrh.) Dum.	74	0.65	0.05	0
Mnium sp.	32	0.65	0.05	0
Cephalozia sp.	89	0.65	0.05	0
Frullania oaksiana Aust.	62	0.65	0.05	0
Ceratodon purpureus (Hedw.) Brid.	91	0.65	0.05	0
Brachythecium reflexum (Starke & Web. *ex.* Mohr.) B.S.G.	94	0.65	0.05	0
Frullania brittoniae Evans	61	0.65	0.10	0
Eurynchium pulchellum (Hedw.) Jenn.	85	0.65	1.20	0.1
Crustose lichen	77	0.65	0.70	0
Sphagnum nemoreum Scop.	90	0.65	14.00	0.09
Climacium dendroides (Hedw.) Web. & Mohr	13	0.65	3.70	0.02

Species	species #	% Frequency	Mean % cover when present	Total mean % cover
Calypogeia integristipula Steph.	56	0.65	0.40	0
Diphyscium foliosum (Hedw.) Mohr	87	0.65	0.20	0
Gymnocolea inflata (Huds.) Buch	83	0.65	0.50	0
Oncophorus wahlenbergii Brid.	34	0.65	0.40	0
Mean	-	13.11	1.23	0.20
standard deviation	-	18.85	2.05	0.70
n	-	79	79	79
standard error	-	2.12	0.23	0.08

Table 2. PCCA series results showing unique and combined influences of litter, topography, and canopy on the bryophyte species pattern. Litter alone showed the largest correlation with the species pattern, followed by topography; the three-way overlap showed the smallest correlation with the species pattern.

	Contribution of categories of environmental variables to CCA	Sum of all canonical eigenvalues	% of total CCA inertia	% of total CA inertia
Unique contribution	litter	1.957	54.91	13.64
	topography	1.060	29.74	7.77
	canopy	0.233	6.538	1.71
Combined contributions	topography + litter overlap	0.176	4.938	1.29
	topography + canopy overlap	0.051	1.431	0.37
	litter + canopy overlap	0.046	1.291	0.34
	litter + canopy + topography overlap	0.041	1.150	0.30
Total		3.564	99.998	25.12

LITERATURE CITED

Anonymous. 1995. Systematics: An impending crisis. Federal Biosystematics Group. Canadian Museum of Nature. Ottawa. pp. 5,11.

Alpert, P. and Oechel, W. C. 1982. Bryophyte vegetation and ecology along a topographic gradient in montane tundra in Alaska. Holarctic Ecol. 5:99-108.

Anderson, R. C., Loucks, O. L. and Swain, A. M. 1969. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. Ecology 50:255-263.

Babcock, R. M. 1949. Studies in stream life in tributaries of the Welsh Dee. J. Animal Ecol. 18:193-208. *Cited in* Slack, N. G., and Glime, J. M. 1985. Niche relationships of mountain stream bryophytes. Bryologist 88:7-18.

Baker, D. E. and Shure, N. H. 1982. Atomic absorption and flame emission spectrometry. *In* Methods of soil analysis, Part 2: Chemical and microbiological properties, Second Ed. *Edited by* A. L. Page. Agron. Monogr. No.9, Part 2. Am. Soc. Agron., Inc., and Soil Sci. Am., Inc. Madison, WI.

Bates, J. W. 1982. Quantitative approaches in bryophyte ecology. *In* Bryophyte Ecology. *Edited by* Smith, A. J. E. Chapman and Hall, Ltd. New York, NY. pp.1-45

Barbour, M. G., Burk, J. H., and Pitts, W. D. 1987. Terrestrial Plant Ecology. The Benjamin/Cummings Publishing Company, Inc. pp.223-228.

Bonan, G. B. 1992. Soil temperature as an ecological factor in boreal forests. *In* A systems analysis of the global boreal forest. *Edited by* Shugart, H. H., Leemans, R. K. and Bonan, G. B. Cambridge University Press. pp.126-143.

Bonan, G. B. and Shugart, H. H. 1989. Environmental factors and ecological processes in boreal forests. Ann. Rev. Ecol. and Systematics 20:1-28.

Bremmer, J. M. and Mulvaney, C. S. 1982. Nitrogen-total. *In* Methods of Soil Analysis, Part II: Chemical and Microbiological Properties; 2nd Ed. *Edited by* A. L. Page. Agron. Monogr. No.9, part 2. Am. Soc. Agron., Inc., and Soil Sci. Soc. Am., Inc. Madison, WI.

Busby, J. R. and Whitfield, D. W. A. 1978. Water potential, water content, and net assimilation of some boreal forest mosses. Can. J. Bot. 56:1551-1558.

Carleton, T. J. 1990. Variation in terricolous bryophyte and macrolichen vegetation along primary gradients in Canadian boreal forests. J. Veg. Sci. 1:585-594.

Carleton, T. J. 1984. Residual ordination analysis: a method for exploring vegetation-environment relationships. Ecology 65:469-477.

Carleton, T. J. and Read, D. J. 1991. Ectomycorrhizas and nutrient transfer in conifer-feather moss ecosystems. Can. J. Bot. 69:778-785.

Chopra, R. N. and Kumra, P. K. 1988. Biology of Bryophytes. Wiley Eastern Limited. New Delhi, India. 350 p.

Coleman , B. B., and Istock, C. A. 1980. Ecological pattern in the moss species ensembles of a Hemlock-hardwood forest mosaic. Evolutionary Theory 5:1-27.

Denison, W. C. 1979. Lobaria oregana, a nitrogen-fixing lichen in old-growth Douglas-fir forests, pp. 266-275. In symbiotic Nitrogen Fixation in the Management of Termperate Forests. Edited by Gordon, J. C., Wheeler, C. T., and Perry, D. A. Forestry Research Laboratory, Oregon State University, Corvallis. Cited in McCune, B. and Lesica, P. 1992. The trade-off between species capture and quantitative accuracy in ecological inventory of lichens and bryophytes in forests in Montana. The Bryologist 95:296-304.

Denison, W. C. 1973. Life in tall trees. Scientific American 228:74-80. Cited in McCune, B. and Lesica, P. 1992. The trade-off between species capture and quantitative accuracy in ecological inventory of lichens and bryophytes in forests in Montana. The Bryologist 95:296-304.

During, H. J. 1992. Ecological classification of bryophytes and lichens in a changing environment. In Bryophytes and lichens in a changing environment. Edited by Bates, J. W. and Farmer, A. M. Clarendon Press, Oxford. pp.1-31.

During H. J., and van Tooren, B. F. 1987. Recent developments in bryophyte population ecology. TREE 2:89-93.

During, H. J. and Verschuren, G. A. C. M. 1988. Influence of the tree canopy on terrestrial bryophytes communities: microclimate and chemistry of throughfall. In Dependent Plant Communities. Edited by Barkham, J.J. and Sykora, K. V. Academic Publishing, The Hague, The Netherlands.

Frego, K. A. and Carleton, T. J. 1995. Microsite tolerance of four bryophytes in a mature black spruce stand: reciprocal transplants. The Bryologist 98:452-458.

Frego, K. A. 1994. Factors influencing the local distribution of four bryophyte species in mature upland black spruce forest. Ph.D. thesis, Department of Botany, University of Toronto. Toronto.

Gignac, L. D., Vitt, D. H., and Bayley, S. E. 1991. Bryophyte responses along ecological and climatic gradients. Vegetatio 93:29-45.

Glime, J. M. and Clemons, R. M. 1972. Species diversity of stream insects on Fontinalis spp. Compared to diversity on artificial substrata. Ecology 53:458-464. *Cited in* Slack, N. G. and Glime, J. M. 1985. Niche relationships of mountain stream bryophytes. The Bryologist 88:7-18.

Gowan, S. P., and Brodo, I. M. 1988. The lichens of Fundy National Park, New Brunswick, Canada. Quart. J. Amer. Bryological and Lichenological Soc. 91:255-325.

Grime, J. P. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Amer. Nat. 111:1169-1194. *Cited in* Robinson, A. L., Vitt, D. and Timoney, K. P. 1989. Patterns of community structure and morphology of bryophytes and lichens relative to edaphic gradients in the subarctic forest-tundra of northwestern Canada. The Bryologist 92:495-512.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. 52:107-145.

Hedenäs, L. 1994. The basal pleurocarpous diplolepidous mosses - a cladistic approach. The Bryologist 97:115-243.

Hedenäs, L. 1989. Some neglected character distribution patterns among the pleurocarpous mosses. Quart. J. Amer. Bryological and Lichenological Soc. 92:157-163.

Herben, T. 1988. The ecology of the invasion of *Orthodontium lineare* Schwaegr. in central Europe. Symp. Bio. Hung. 35:323-334.

Hill, M. O. 1979. DECORANA - A FORTRAN Program for Detrended Correspondence Anlysis and Reciprocal Averaging. Section of Ecology and Systematics, Cornell University, Ithaca, New York.

Ireland, R. R. 1982. Moss Flora of the Maritime Provinces. National Museums of Canada, Ottawa. p.24.

Ireland, R. R. and Bellolio-Trucco, G. 1987. Illustrated guide to some hornworts, liverworts and mosses of eastern Canada. National Museums of Canada, Ottawa.

Jones, J. R. E. 1949. A further ecological study of calcareous streams in the 'Black Mountain' district of south Wales. J. Animal Ecol. 18:142-159. *Cited in* Slack, N. G., and Glime, J. M. 1985. Niche relationships of mountain stream bryophytes. The Bryologist 88:7-18.

Keizer, P. J., Tooren, B. F. van and During, H. J. 1985. Effects of bryophytes on seedling emergence and establishment of short-lived forbs in chalk grassland. J. Ecol. 73:493-504. *Cited in* During, H. J. and Vershuren, G. A. C. M. 1988. Influence of the tree canopy on terrestrial bryophytes communities: microclimate and chemistry of throughfall. *In* Dependent Plant Communities. *Edited by* Barkham, J.J. and Sykora, K. V. Academic Publishing, The Hague, The Netherlands.

Kenkel, N. C., and Bradfield, G. E. 1981. Ordination of epiphytic bryophyte communities in a wet-temperate coniferous forest, South-Coastal British Columbia. Vegetatio 45:147-154.

Kimmerer, R. W. 1994. Ecological consequences of sexual verses asexual reproduction in *Dicranum flagellare* and *Tetraphis pellucida*. The Bryologist 97:20-25.

Kooijman, A. M., and Bakker, C. 1995. Species replacement in the bryophyte layer in mires: the role of water type, nutrient supply and interspecific interactions. J. Ecol. 83:1-8.

Kunkel, G. P. 1975. Microhabitat abd phytosociological studies of cryptogamic chasmo- and lithophytes. M. A. Thesis. Univ. of Colorado. *Cited in* Watson, M. A. 1980. Patterns of habitat occupation in mosses - relevance to consideration of the niche. Bull. Torr. Bot. Club 107:346-372.

La Roi, G. H., and Stringer, M. H. L. 1976. Ecological studies in the boreal spruce-fir forests of the North American Taiga. II. Analysis of the bryophyte flora. Can. J. Bot. 54:619-643.

Larsen, J. A. 1980. The boreal ecosystem. Academic Press Inc. New York. 500p.

Lee, T. D. and La Roi, G. H. 1979. Bryophyte and understorey vascular plant beta diversity in relation to moisture and elevation gradients. Vegetatio 38:29-38. *Cited in* Watson, M. A. 1980. Patterns of habitat occupation in mosses - relevance to consideration of the niche. Bull. Torr. Bot. Club 107:346-372.

McAllister, S. 1995. Species interactions and substrate specificity among log-inhabiting bryophyte species. Ecology 76:2184-2195.

McCune, B. and Lesica, P. 1992. The trade-off between species capture and quantitative accuracy in ecological inventory of lichens and bryophytes in forests of Montana. The Bryologist 95:296-304.

McLeod, J. J., Johnson, S. C. and Ruttenburg, A. A. 1994. Geological map of southeastern New Brunswick. NBDNRE, Mineral Resources Division. NR-6.

Minkley, W. L. 1963. The ecology of a spring stream, Doe Run, Meade County, Kentucky. Wildlife Monographs 11. 124 pp. *Cited in* Slack, N. G., and Glime, J. M. 1985. Niche relationships of mountain stream bryophytes. The Bryologist 88:7-18.

Nichols, S. 1977. On the interpretation of principal components analysis in ecological contexts. Vegetatio 34:191-197. *Cited in* Kenkel, N.C. and Bradfield, G. E. 1981. Ordination of epiphytic bryophyte communities in a wet-temperate coniferous forest, South-Coastal British Columbia. Vegetatio 45:147-154.

Økland, R. H. 1994. Bryophyte and lichen persistence patterns in a Norwegian boreal coniferous forest. Lindbergia 19:50-62.

Økland, R. H. and Eilertsen, O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. J. Veg. Sci. 5:117-126.

Pike, L. H. 1978. The importance of epiphytic lichens in mineral cycling. The Bryologist 81:247-257. *Cited in* McCune, B. and Lesica, P. 1992. The trade-off between species capture and quantitative accuracy in ecological inventory of lichens and bryophytes in forests in Montana. The Bryologist 95: 296-304.

Pocs, T. 1982. Tropical forest bryophytes. pp 59-104. *In* Bryophyte Ecology. *Edited by* Smith, A. J. E. Chapman and Hall, Ltd. New York, NY. 511p.

Pocs, T. 1978. Bryophytorum bibliotheca. 13:681-713. *Cited in* Pocs, T. 1982. Tropical forest bryophytes. pp 59-104. *In* Bryophyte Ecology. *Edited by* Smith, A. J. E. Chapman and Hall, Ltd. New York, NY. 511p.

Raven, P. H., Evert, R. F. and Eichhorn, S. E. 1992. Biology of Plants. 5th Ed. Worth Publishers, Inc., New York. pp. 298-315.

Redfearn, P. L. Jr. 1986. Bryogeography of the Interior Highlands of North America: taxa of critical importance. The Bryologist 89:32-34.

Rieley, J. O., Richards, P. W. and Bebbington, A. D. C. 1979. The ecological role of bryophytes in a North Wales woodland. J. Ecol. 67:497-527. *Cited in* During, H. J. and Verschuren, G. A. C. M. 1988. Influence of the tree canopy on terrestrial bryophytes communities: microclimate and chemistry of throughfall. *In* Dependent Plant Communities. *Edited by* Barkham, J.J. and Sykora, K. V. Academic Publishing, The Hague, The Netherlands.

Rincón, E. 1988. The effects of herbaceous litteron bryophyte growth. J. Bryol. 15:209-217. *Cited in* Sveinbjörnsson, B. and Oechel, W. C. 1992. Controls on growth and productivity of bryophytes: environmental limitations under current and anticipated conditions. *In* Bryophytes and Lichens in a Changing Environment. *Edited by* J. W. Bates and A. M. Farmer. Oxford University Press, Oxford. pp. 77-97.

Robinson, A. L., Vitt, D. H., and Timoney, K. P. 1989. Patterns of community structure and morphology of bryophytes and lichens relative to edaphic gradients in the subarctic forest-tundra of Northwestern Canada. The Bryologist 92:495-512.

Roberts, M. R. and Gilliam, F. S. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecological Applications 5:969-977.

Savage, J. M. 1995. Systematics and the Biodiversity Crisis. BioScience 45:673-679.

Sandrett, E. and Gimingham, C. H. 1989. Experimental investigation of bryophyte interactions on a dry heathland. J. Ecol. 77:838-852.

Slack, N. G. 1977. Species Diversity and Community Structure in Bryophytes: New York State Studies. Bulletin 428, New York State Museum, Albany, NY.

Slack, N. G., and Glime, J. M. 1985. Niche relationships of mountain stream bryophytes. The Bryologist 88:7-18.

Smith, R. I. L. 1988. Bryophyte oasis in Ablation Valleys on Alexander Island, Anarctica. The Bryologist 91:45-50.

Smith, A. J. E. 1982. Bryophyte Ecology. Chapman and Hall Ltd., New York, NY. 511p.

Stark, L. R. 1985. Phenology and species concepts: a case study. The Bryologist 88:190-198.

Studlar, S. M. 1980. Trampling effects on bryophytes: Trail surveys and experiments. The Bryologist 83:301-313.

Sveinbjörnsson, B. and Oechel, W. C. 1992. Controls on growth and productivity of bryophytes: environmental limitations under current and anticipated conditions. *In* Bryophytes and Lichens in a Changing Environment. *Edited by* J. W. Bates and A. M. Farmer. Oxford University Press, Oxford. pp. 77-97.

ter Braak, C. J. F. 1988. CANOCO - a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis (version 2.1). TNO Inst. Appl. Comp. Sci. Stat. Dept. Wageningen, Wageningen.

van Tooren, B. F., Ode, B., During, H. J., and Bobbink, R. 1990. Regeneration of species richness in the bryophyte layer of Dutch chalk grasslands. Lindbergia 16:153-160.

Viereck, L. A. 1983. The effects of fire in black spruce ecosystems of Alaska and Northern Canada. *In* The role of fire in northern circumpolar ecosystems. *Edited by* Wein, R. W. and MacLean, D. A. John Wiley and Sons. New York. pp. 201-220.

Vitt, D. H. 1984. Classification of the Bryopsida. *In* New Manual of Bryology 2. *Edited by* Schuster, R. M. Nichinan. pp.696-759. *Cited in* Robinson, A. L., Vitt, D. H., and Timoney, K. P. 1989. Patterns of community structure and morphology of bryophytes and lichens relative to edaphic gradients in the subarctic forest-tundra of Northwestern Canada. The Bryologist 92:495-512.

Watson, M. A. 1980. Patterns of habitat occupation in mosses - relevance to consideration of the niche. Bull. Torr. Bot. Club 107:346-372.

Weetman, G. 1968. The relationship between feather moss growth and the nutrition of black spruce. *In* Proc. Third International Peat Congregation. *Edited by* Lafleur, G. and Butler, J. Quebec. pp.366-370.

Wein, R. W., Riewe, R. R. and Methven, I. R. (eds.). 1983. Resources and dynamics of the boreal zone. Association of Canadian Universities for Northern Studies.

Ottawa. *Cited in* Frego, K. A. 1994. Factors influencing the local distribution of four bryophyte species in mature upland black spruce forest. Ph.D. thesis, Department of Botany, University of Toronto. Toronto.

Werger, M. J. A. and During H. J. 1989. A subterranean moss greenhouse in the Californian desert. The Bryologist 92:411-412.

Whittaker, R. H. 1977. Evolution of species diversity in land communities. Evol. Biol. 10:1-68. *In* Watson, M. A. 1980. Patterns of habitat occupation in mosses - relevance to consideration of the niche. Bull. Torr. Bot. Club 107:346-372.

Wyatt, R. 1985. Species concepts in bryophytes: Input from population biology. The Bryologist 88:182-189.