Fundy Model Forest

~Partners in Sustainability~

Report Title: Effects of Forestry Practices on Bryophyte Diversity 96-98 report

Author: K. Frego

Year of project: 1998

Principal contact information: University of New Brunswick Saint John
Biology Department
P.O. Box 5050 Saint John, N.B.
E2L 4L5
Phone: 506-648-5566

File Name:
Biodiversity_1998_Frego_Effects_of_Forestry_Practices_on_Bryophyte_Diversity_96_98_report

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

Effects of forestry practices on bryophyte diversity

Dr. K. Frego 1998

E11A

FUNDY MODEL FOREST
1996 -1998 Report

Principal investigator			Date:
Family Name: **FREGO**	Given name: **Katherine A.**	Position: **Associate Professor**	**March 1998**
Institution: **UNIVERSITY OF NEW BRUNSWICK (SAINT JOHN)**	Address: **Biology Dept., UNBSJ P.O. Box #5050 Saint John, NB**		Postal code: **E2L 4L5**
Phone: (B) **(506)-648-5566**	(H) **(506)-849-6257**	(FAX) **(506)-648-5811**	

Research Topic:

Short Title:
Effects of forestry practices on bryophyte diversity

10 Key Words:
bryophyte, moss, diversity, disturbance, regeneration, forest floor, recovery

Summary:

Bryophytes (mosses and liverworts) are an important part of mixed and coniferous forest ecosystems, with great impact on water and nutrient budgets. Their bio-diversity is poorly documented in mature forests, and their recovery after anthropogenic disturbances is even less known. If bryophyte species distribution is determined by micro-habitat, forest management practices which alter the micro-habitat would be expected to strongly influence bryophyte diversity. Alternatively, bryophyte distribution may be controlled primarily by dissemination of propagation units. Regeneration would then be encouraged by management practices that retain scattered patches of viable plants. This project is designed (a) to document the diversity of bryophytes in mature mixed forests, (b) to document the changes in diversity after a variety of forestry practices, (c) to determine which practices minimize reduction in diversity, and (d) to identify potential indicators of closed canopy forest bryophyte communities.

CONTENTS

ABSTRACT

Bryophytes (mosses and liverworts) are important components of the temperate forest community, influencing soil temperature, moisture and nutrient retention and providing a habitat for numerous vertebrates and invertebrates. However, the species composition of the bryophyte community is poorly documented for New Brunswick, and little is known of its response to perturbation of any sort, including anthropogenic disturbance (e.g. forest harvest). In order to ensure conservation of biodiversity, it is critical that we know (a) what species are typically present in a closed canopy forest, (b) what species are at risk after forest harvest, (c) what aspects of forest harvest constitute the risk, (d) how (or if) the species regenerate with the regrowth of the forest, and (e) what indicator effectively assesses the status of the bryophytes and related organisms that are most at risk.

In this sequence of studies, the species compositions of a number of stands in the Hayward Brook watershed were documented by surveying permanent plots, to provide baseline data on biodiversity. After the stands were harvested, disturbance variables and bryophyte abundances were surveyed and the relationships examined using trend-seeking ordination techniques. Of the 106 species encountered, a large proportion are clearly at risk immediately after harvest. The critical variables appeared to be (a) changes to the substrate (e.g. exposure of mineral soil, deposition of additional substrates) and (b) accumulation of slash, which reduces light intensity and air movement. The most extreme levels of both were associated with the combination of cutting followed by scarification.

The potential for community recovery from a soil propagule bank was investigated using germination studies. Twenty-five taxa germinated; only 4 were absent from the pre harvest community. This indicates that at least some of the species judged to be at risk (above) are capable of regenerating from naturally occurring spores.

The impact of slash and substrate changes were tested on two common species in an experimental manipulation in the field. The results will not be obtained until next year, to give the plants an opportunity to respond to the experimental conditions.

Based on observations in the pre and post harvest surveys (above), *Bazzania trilobata* was selected as a potential indicator of bryophyte community composition. Its tolerance to conditions experienced on cut-overs, including dessication and increased light intensity, were tested experimentally and compared with plants from a 2-year-old cut-over and from a closed forest (control). Metabolic rates (respiration and photosynthesis) indicated that the species is sensitive to these stresses, but can recover if the damage is not severe. After a recovery period, plants from the cut-over showed increased metabolic activity, growth, and pigment recovery while those from 2-month drying treatments did not recover. A clear colour differentiation was associated with degree of damage; this may be used as a criterion for scoring the indicator species in the field, using a simple, commercially prepared, colour calibration.

INTRODUCTION

Rationale for approach

Bryophytes are so poorly known that we have scant data on the most basic facts: what species occur in this area, their relative abundances, specific habitat requirements, and responses to disturbance. This is partly because bryophytes have no direct economic importance (so are rarely studied), but also because they require levels of sampling intensity and of taxonomic expertise that are generally not available (Bates 1982). However, bryophytes have great indirect value in terms of their own biodiversity, and in terms of their roles in forest growth, soil quality, and ecosystem processes. Under closed canopies of coniferous temperate and boreal forests, their extensive mats influence soil water relations (Busby and Whitfield 1978), as well as nutrient availability (e.g. Carleton and Read 1991) and soil temperature (Bonan 1992), all of which directly impact tree growth. In mixed and deciduous forests, bryophytes may be less prominent but may still greatly affect seedling emergence and establishment (cf. Keizer et al. 1985) and nutrient relationships (Rieley et al. 1979).

This series of studies, begun in 1995, was designed as a sequence of questions addressed on a "need to know" basis, i.e. the answer to each step requires an answer to the steps preceding it (Table 1). In 1995, baseline data on species and their distribution within a closed canopy bryophyte community were collected in a group of stands slated to be cut. In subsequent years, the same community was (and will continue to be) assessed, in order to document specific responses to disturbance. Although it will be a number of years before we can determine whether the community returns to its pre harvest state in terms of species and abundances (note that long-term monitoring will continue outside the FMF II), a number of specific questions can be addressed on the basis of the data collected in the early post harvest community. Our ultimate goal is to propose **specific, calibrated indicators of the health of the closed canopy bryophyte community**, for application in management plans to conserve biodiversity of this component of the forest ecosystem.

Table 1. Sequence of questions, the studies undertaken (with co-investigators indicated), and the year(s). (Note that continued surveys of the bryophytes in the permanent plots are required to answer the ultimate recovery of the forest floor community, however this is not expected to continue as part of FMF II. Frequency of assessments will also decline as the community stabilizes, i.e. from annual to 5 yr to 10 yr intervals.) Results for studies marked with asterisk have been submitted to FMF; those with ** are preliminary results.

Essential questions	**Study**	**Year(s), co-investigator**
1. What is "normal" biodiversity? (a) what species occur in the closed canopy forests of the area? (b) in what relative abundances?	Survey of bryophytes in permanent plots before harvest	1995 * (Sims)
2. How do specific silvicultural practices affect the bryophyte community overall? (a) How does the community change? (b) What is the precise nature of the disturbances?	Survey of the permanent plots immediately after harvest, (a) bryophytes (b) disturbance variables	1996 * (Peterson)
3. How do bryophytes respond over time? (a) Do they continue to decline, or recover? Ultimately, does the community return to its pre-disturbance state? (b) By what mechanisms do they recover?	(a) Continued surveys of the bryophytes (b1) Evaluation of the soil propagule bank (b2) Evaluation of species tolerance (factorial transplant experiment)	1997- ? 1997** (Peterson) 1997-1998 (Peterson)
4. What species are most at risk? These may be low in abundance, or unique to certain sites	Evaluation of survey data	1997-8**
5. What species are candidates for indicator species? These must be abundant, recognizable, and respond readily (but not terminally!) to changes in habitat conditions. (a) Precisely how does the candidate respond to specific disturbance variables? (b) Precisely what does it indicate, i.e. habitat conditions, associated species, etc.?)	Evaluation of survey data (a) Tolerance of *Bazzania trilobata* to drying and light (b) Re-evaluate survey data	1996 - ongoing 1997 * (Sollows) 1998

Objectives:

1. Baseline data collection (YEAR ONE): Document diversity of forest floor bryophytes in mature (closed canopy) mixed forests in the Hayward Brook Watershed (using permanent plots).

2. Document disturbance associated with each harvest treatment, and compare immediate effects of disturbance (harvest) on bryophyte community (YEAR TWO).

3. Determine changes in composition and diversity of bryophytes with successional time in response to human disturbance (YEARS 3-5).
   (a) Document early recovery of bryophytes in harvested areas, (i) in permanent plots and (ii) from soil propagule banks (YEAR THREE).
   (b) Sampling of the permanent quadrats will continue annually, as planned.

4. Evaluate candidate species #1 (*Bazzania trilobata*) as potential indicator species in future conservation-oriented management (YEAR THREE).

Deliverables and specific milestones of project:

This report of the results from 1996-7 and 1997-8 contains the following deliverables:

1. Continued **documentation of bryophyte species**, their abundance, and their habitat distribution before harvesting, relative to site characteristics. Our species list to date shows species that have not previously been reported for this geographical area; new species have been added with each year of sampling.

2. Continued **documentation of survival of bryophyte species** and their micro site distribution immediately after various harvesting procedures, relative to site characteristics and disturbance characteristics. This also provides information on availability of persistent vegetative propagation units which are critical to regeneration and hence conservation.

3. Documentation of **regeneration of bryophytes following harvest**, relative to site and disturbance. This longer-term aspect is particularly valuable because it has not been presented in the literature.

4. Identification of **bryophyte species that may be at risk** under specific harvesting and site-preparation treatments. This information is not available in the literature.

5. Evaluation of ***Bazzania trilobata* as a possible indicator species** for the mature-forest bryophyte community. With refinement, this species may be utilized in guidelines for forest management to ensure bryophyte species diversity is maintained, including species which are

rare and/or at risk. A simple colorimetric evaluation technique for viability of *Bazzania* in the field was assessed.

METHODS

Study site

The study area is a 56 ha watershed containing a mixed forest of spruce, balsam fir, birch, aspen, and maple located near Petitcodiac in Westmorland County, NB (lat. 45° 53'N, long. 65° 11'W). Two harvest blocks, north and south, are separated by the west branch of Hayward Brook. There were 8 dominant stand types, i.e. groupings of trees and associated vegetation, including 4 coniferous stand types in the low lying areas near the brook, 2 deciduous stands on a well drained ridge, and 2 mixed stands that were intermediate in elevation. (For detailed description, see Hovey, unpubl.)

Data collection

1. **Permanent plots** - used for bryophyte survey and assessment of disturbance characteristics

Pre harvest. In 1995, two blocks designated 6-North and 6-South by J.D. Irving, Ltd. foresters were delimited on either side of the Hayward Brook. In each, transects were laid out approximately perpendicular to the stream. Transects varied in length from 100-850 m depending on the geography of the area. Permanent quadrats (n=155) were placed at 50-m intervals along each quadrat. 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, unpubl.). Pre-harvest (baseline) data were collected June through August 1995. Two transects (n=34 quadrats) were added in the forested buffer area in June 1996.

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:
(a) **Canopy** closures of deciduous and coniferous trees were estimated using the average of two readings from a spherical densiometer, taken by two different workers 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.

(b) 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) 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=absent and 3=100%. Litter samples were analysed in the lab of Dr. Mark Roberts (UNB, Forestry) using standard methodologies, as reported in Sims (unpubl.).

(c) Micro **topography** was recorded as presence/absence of pits or mounds for each quadrat. Slope and aspect were estimated using a Suunto clinometer and a compass, respectively. Aspect, i.e. compass-bearing of the slope, was expressed as the sine and cosine, indicating "northness" and "eastness" respectively.

Post harvest. The stands were harvested in autumn 1995. Post-harvest data were collected in the permanent plots to:
(a) assess bryophyte status in 1996 and 1997 (using methodology described above) and
(b) document disturbance in 1996. For the latter, types and severity of disturbance were quantified for permanent quadrats in stands classified as either uncut, cut, or cut and scarified. Categories of disturbance included aerial additions (i.e. slash), substrates exposed or added (e.g. litter removed to expose mineral material, vs bark or wood chips), and compression due to vehicle tracks (Table 2).

2. Other studies

Based on the results of the bryophyte survey above, three related studies were undertaken:

Soil propagule bank (Co-investigator Jennifer Peterson). Vascular plants often regenerate from dormant seeds which persist in a soil bank (e.g. see MacInnis, unpubl). However bryophytes reproduce from tiny, relatively primitive spores, the longevity of which is essentially unknown. Further, few spore bank studies have been undertaken to determine their species composition (e.g. During et al. 1987, Lewis-Smith 1987, Leck 1980), and none were in ecosystems comparable to New Brunswick forests.

Soil samples were obtained from the permanent plots at Hayward Brook on 28 September 1996; n=76 plots x 4 samples each. Using standard seed bank methodology (e.g. Fenner 1985), the four 225-ml samples were combined, air-dried, and sieved through a 4 mm mesh sieve to remove stones, twigs, and other vegetative matter. A subsample of 100 ml was placed into a large petri dish (150 mm diameter, 20 mm deep), thoroughly moistened with distilled water, and placed in a warm greenhouse. The samples were monitored and watered as needed. Vascular plant seedlings were removed and discarded as they appeared, to avoid interference with spore germination.

Bryophytes were allowed to grow until they were large enough to identify, at which time a census was taken. Because gametophyte growth precludes quantification of individuals (i.e. a single spore may produce any number of vertical shoots, from its filamentous protonemal stage), the density of individual plants could not be determined. The spore bank composition was therefore recorded as presence/absence, and related to the pre harvest bryophyte community, and to stand type and harvest procedure.

Effect of slash on survival of *Pleurozium schreberi* and *Dicranum polysetum* (Co-investigator Jennifer Peterson). Comparison of silviculture techniques (cut vs cut and scarified) indicated two main differences: degree of substrate disturbance (organic vs mineral soil exposed) and amount and type of slash left on site. Bryophyte survey data suggested that these factors play an important role in the survival of established plants. A factorial experimental design was set up to test the combined effects of two substrate types (organic from the uncut forest and mineral soil exposed in the cut and scarified stand) and three slash loads (none, light and heavy coverage) on two common species. Experimental frames were built to enclose each replicate block of treatments, plastic rings approx 30 cm in diameter were sunk into the existing substrate, filled with the experimental substrate, and a pre-measured amount of the bryophyte was transplanted into the centre. The condition of the transplants was recorded photographically in autumn 1997. The final evaluation will be done in autumn 1998. (Preliminary results are not available because the co-investigator, M.Sc. candidate Jennifer Peterson, is on maternity leave until August 1998.)

Use of *Bazzania trilobata* as an indicator species (Co-investigator Mary Sollows). *Bazzania trilobata* is a large, easily recognizable leafy liverwort, in the Family Lepidoziaceae, Order Jungermanniales, Class Hepaticae (Smith 1990). It is common in temperate and warm temperate climates, in humid low-light intensity areas, on moist rocks, soil, bases of trees and on rotting wood (Ireland and Bellolio 1987, Schuster 1969). In New Brunswick, it is found in closed canopy coniferous and mixed temperate forests. Results of the bryophyte survey indicated that it persisted, but was clearly damaged, in cut-overs. The damage appeared as colour change, e.g. paler green to yellow or brown, and dry brittle texture relative to forest colonies. These characteristics are typical of bryophytes exposed to light intensity and dessication beyond their normal limits of tolerance, such that pigments are degraded, and externally-held moisture is depleted. However, pigments can often be repaired, and many bryophytes exhibit physiological drought resistence, so even damaged individuals may still be alive (Hicks 1992).

Because the species fits the initial profile of a candidate indicator species, an experiment was designed to test its tolerance for habitat conditions found in cut areas, i.e. increased light intensity and desiccation. Samples were collected from both the forested buffer strip and the open clear cut. Plants from the forest were subjected to one of two drying regimes (sun-dried vs shade-dried), after which they were compared to controls (fresh buffer strip plants) and field-dried shoots (from the clear cut). Comparisons were based on:

(a) metabolic activity (respiration, photosynthesis), using an Infra Red Gas Analyzer (IRGA),
(b) colour, using a Munsell Colour Chart for Plant Tissues (Wilde and Voigt 1977), and
(c) size (initial length in cm).
All shoots were then given a recovery period of 2 months, during which they received optimum conditions of light, temperature and humidity. They were reassessed as above, to determine their resilience (i.e. ability to recover to conditions similar to the controls). For details of methodology, see Sollows (unpubl.).

Statistical analyses

(1) **Disturbance** characteristics were analysed using Correspondence Analysis (CA), a multivariate analysis procedure performed by CANOCO 3.12 (ter Braak 1988). In addition, summary stats were compiled and compared by silvicultural treatment using Analysis of Variance (ANOVA, SAS Institute Inc. 1989).

(2) **Bryophytes.** (a) Species compositions of pre and post harvest communities were documented, and (b) compared in terms of species richness, evenness, total and mean covers. (c) The patterns in, and relationships between, bryophyte community data and disturbance were assessed with a series of multivariate analyses, as above. Basic CAs were performed on bryophyte data from 1995 and 1996 using parallel procedures for comparison. (Ultimately, data for 1995, 1996 and 1997 will be combined and re-assessed using a statistical programme that combines data over time to identify vectors of change, e.g. in succession.) (d) In addition, Canonical Correspondence Analyses (CCA) and Partial Canonical Correspondence Analysis (PCCA) were used to relate pre harvest bryophyte data to canopy, litter and topography, and to relate post harvest bryophyte data to disturbance variables.

(3) **Soil propagule bank.** A species list summarizes the taxa present in each silvicultural treatment. Although densities of spores could not be determined, species distributions were calculated in terms of species richness and evenness, standard measures of biodiversity.

(4) ***Bazzania trilobata* as an indicator.** The responses of this liverwort in terms of metabolism and growth were analysed using ANOVA, with Tukey's t-tests used to compare those treatment effects with significant contributions. Colour change was assessed using frequency charts to illustrate ranges and shifts in hue.

Table 2. Abbreviation, name, and definition of the environmental variables identified in the disturbance dataset for the Hayward Brook Watershed Project. #1-8 slash, 9-23 substrate, 24-25 skidder tracks.

Var #	Abbrev.	Name	Description
1	slhwfine	slash hardwood fine	% cover of slash <0.5cm in diam. suspended above ground. Includes attached leaves.
2	slswfine	slash softwood fine	as above, includes attached needles.
3	slbig	slash big	% cover of all other slash that is 0.5<slash<7cm.
4	slht	slash height	height under which 90% of the slash cover occurred
5	slclump	slash clumped	distribution of slash (c=clumped, n=not)
6	lslhw	living slash hardwood	% cover of living hardwood trees with stems greater than 1m tall at >45° off horizontal.
7	lslsw	living slash softwood	as above, % cover of the softwood trees.
8	lslht	living slash height	height under which 90% of the living slash occurred
9	subinv	substrate invisible	% of forest floor substrate not visible through dense slash
10	subrck	substrate rock	% cover of rocks >7cm (1%).
11	substmp	substrate stump	% cover of stumps and exposed roots attached to stumps.
12	sublitd	substrate disturbed litter	% cover of disturbed litter (parts removed, clumped, mixed, compressed, or dragged and deposited).
13	submin	substrate mineral	% cover of exposed mineral soil including rocks < 7 cm
14	subslfin	substrate slash fine	% cover of substrate slash 2-7 cm in diameter
15	subslbig	substrate slash big	% cover of substrate slash >7cm
16	subrotw	substrate rotten wood	% cover of rotten wood (easily crumbled, presumed to predate harvest)
17	subbrk	substrate bark	% cover of bark contacting the ground
18	chipcov	chip cover	% cover of fragmented wood or chips (fresh) on the ground
19	chipclp	chip clumped	distribution pattern of the chips (c=clumped, n=not)
20	sublitun	substrate litter undisturbed	% cover of undisturbed litter within the quadrat.
21	subscat	substrate scat	% cover of animal scat
22	subcone	substrate cones	% cover of spruce cones (approx 25 cones=1%)
23	subtrnk	substrate trunks	% cover of tree trunks
24	trkcov	track cover	% cover of skidder tracks in the quadrat
25	trktyp	track type	L=litter, S=soil, M=mixed litter and soil, W=crushed wood, LW=litter and wood, SW-soil and wood

RESULTS

1. Disturbance

Correspondence analysis (Figs. 1,2) identified two components of the disturbance pattern: substrate disturbance and slash deposition. The first axis was associated with substrates, separating characteristics of undisturbed forest (Substrates: tree trunks, undisturbed litter, rotten wood) from those of highly disturbed areas (Substrates: exposed mineral, disturbed litter, wood chips, and rocks; and skidder tracks). The second axis further isolated the slash effect, ranging from no slash to a high proportion of "invisible substrate". The spread of quadrats on these two axes (Fig. 2) supported the relationship to silvicultural treatment: uncut stands were located low on both Axes one and two, while scarified stands were high on Axis one; cut stands were midway on Axis one, but high on Axis two, in keeping with the high slash load.

Analysis of variance and Tukey's t-tests have shown significant differences among the three forest treatments in all disturbance variables except rotting wood (Table 3). The uncut stands served as a control, indicating the levels of these features that would occur naturally in the sampled stands, against which the harvested areas were compared.

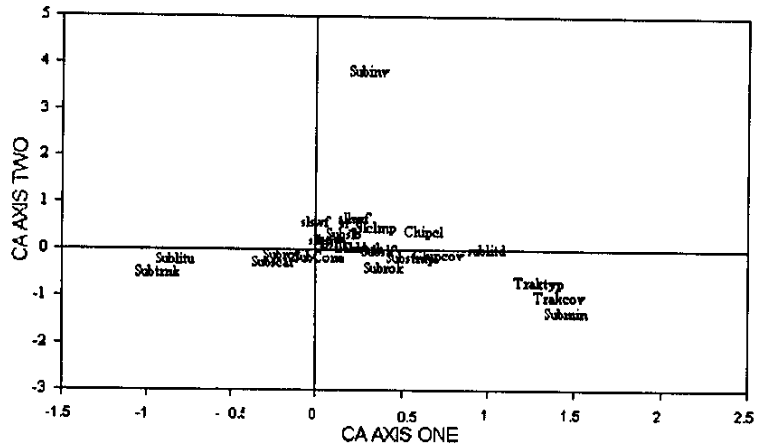

Figure 1. Correspondence analysis of disturbance variables (see Table 2), axes one and two. Axis 1 separates Substrates (undisturbed litter, trunk) from (tracks, mineral, disturbed litter). Axis 2 separates slash levels, from none to high.

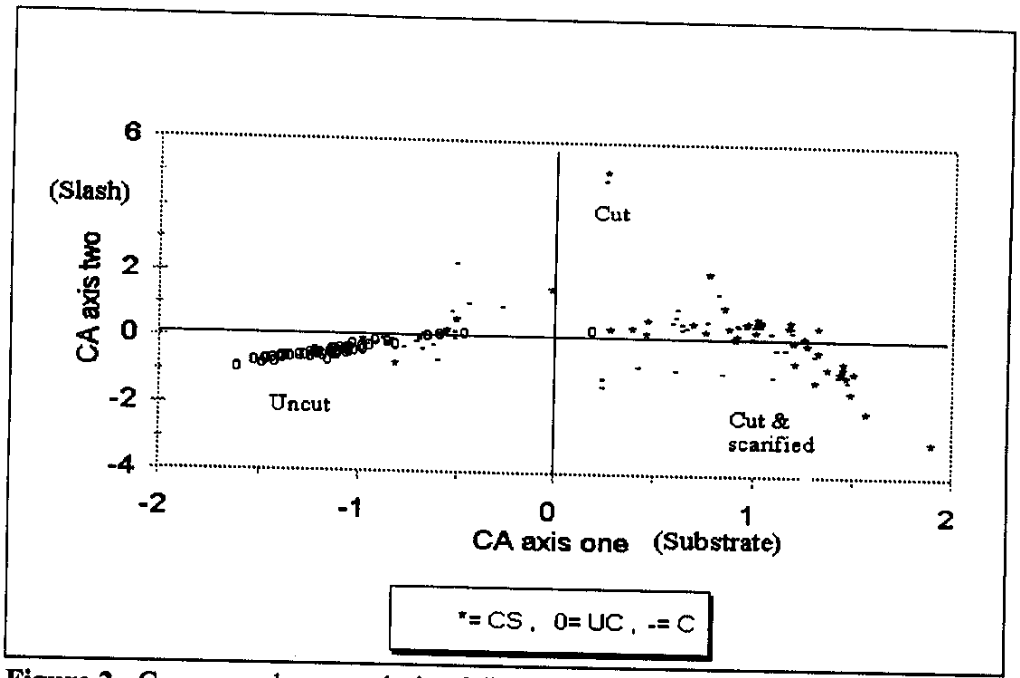

Figure 2. Correspondence analysis of disturbance variables, showing positions of quadrats by silvicultural treatment. Axis 1 separates closed canopy (uncut) from cut and scarified, while Axis 2 further separates cut stands with heavy slash loads.

It was evident that harvest (both cut and cut-and-scarified) resulted in increased slash load and soil disturbance. All characteristics of slash load, including both coverage and depth, increased significantly with cutting, and were highest in cut and scarified areas. Living slash (trees broken or bent to the ground, but still alive) also covered significantly greater areas in cut areas.

Harvested areas contained higher proportions of exposed rock, stumps, bark, chips and fallen trunks than the uncut stands. In particular, scarified sites contained significantly more disturbed litter, fine slash and vehicle tracks. More animal scat was found in cut but unscarified quadrats. It is noteworthy that the treatments did not differ in proportion of rotting wood substrate, which is typically associated with undisturbed forests.

Although some of these patterns (e.g. the link between scarification and exposed mineral soil) are not surprising, this study allows us to quantify the variables, and link them directly to bryophyte responses. More refined statistical analyses are required to quantify the relationship between disturbance characteristics and bryophyte response, however these preliminary data allow us to select and test pertinent variables, and use realistic levels in the experiments.

Table 3. Comparison of disturbance variables for three forest treatments at Hayward Brook watershed site (1996). Values are mean % cover (unless otherwise designated) ± standard error; those followed by the same letter within a row are not significantly different at $p<0.05$. HW= hardwood, SW=softwood.

	Uncut (n = 383)		Cut (n=260)		Cut & scarified (n=197)		Total (n=840)	
	mean	std err	mean	std err	mean	std err	mean	std err
Slash								
HW <.5cm	1.17	0.06 *a*	1.71	0.16 *b*	2.41	0.38 *c*	1.63	0.11
SW <.5cm	1.96	0.22 *a*	7.15	0.75 *b*	3.85	0.58 *c*	4.01	0.30
>.5cm	5.57	0.35 *a*	15.02	0.82 *b*	14.58	0.80 *b*	10.60	0.39
depth (cm)	18.98	1.07 *a*	33.38	1.45 *b*	24.46	1.13 *c*	24.72	0.74
clumping (rank)	low		medium		high			
Living slash								
HW	0.04	0.02 *a*	0.26	0.10 *b*	0.24	0.11 *b*	0.15	0.04
SW	0.73	0.35 *a*	4.02	0.60 *b*	0.72	0.14 *a*	1.75	0.25
height (cm)	1.34	0.44 *a*	24.26	2.25 *b*	8.29	1.35 *c*	10.07	0.86
Substrate								
invisible	0.01	0.01 *a*	5.02	1.06 *b*	5.35	1.35 *b*	2.81	0.46
rock	0.04	0.02 *a*	0.14	0.07 *a*	0.66	0.12 *b*	0.22	0.04
stump	0.17	0.04 *a*	0.75	0.16 *b*	1.05	0.26 *b*	0.55	0.08
disturbed litter	4.36	0.66 *a*	37.15	2.45 *b*	59.72	2.27 *c*	27.49	1.25
mineral	0.04	0.01 *a*	0.65	0.20 *a*	10.56	1.49 *b*	2.70	0.39
fine slash	1.52	0.09 *a*	2.28	0.18 *b*	3.24	0.21 *c*	2.16	0.09
coarse slash	0.37	0.09 *a*	2.10	0.31 *b*	1.70	0.24 *b*	1.22	0.12
rotting wood	2.41	0.20 *a*	1.94	0.24 *a*	1.88	0.27 *a*	2.14	0.13
bark	0.81	0.09 *a*	1.39	0.13 *b*	1.69	0.11 *b*	1.19	0.06
chips	0.08	0.02 *a*	1.06	0.15 *b*	1.10	0.13 *b*	0.63	0.06
undisturbed litter	89.10	0.76 *a*	47.26	2.58 *b*	12.68	1.84 *c*	58.23	1.44
scat	0.08	0.01 *a*	0.16	0.03 *b*	0.03	0.01 *a*	0.09	0.01
cones	0.08	0.01 *a*	0.23	0.03 *b*	0.03	0.01 *a*	0.11	0.01
trunks	1.25	0.23 *a*	0.11	0.03 *b*	0.44	0.23 *b*	0.71	0.12
Tracks								
% cover	0.00	0.00 *a*	8.41	1.36 *b*	18.86	2.45 *c*	7.03	0.76
depth (cm)	n/a		1.65	0.37 *a*	1.97	0.27 *a*	0.97	0.13

2. Bryophyte community and response

(a) The bryophyte species list (Table 4) has been updated from 1995, to a total of 106 species (3 lichens, 73 mosses and 29 liverworts). Seven new species were encountered in the harvested area; the buffer zone added 50 species.

- 23 species, including the rare species *Cirriphylum piliferum* (located in 2 quadrats in 1995), have not been found post harvest. These are species that should be considered "at risk".
- 19 species found in 1995 and 1996 were not found in 1997. These are species that persisted briefly after the harvest but succumbed.
- 39 species were found in all three years. Of these, 34 are clearly declining, so should be considered at risk. The remaining 5 apparently increased briefly in abundance in 1996, but have since declined.
- 3 species have appeared or increased in abundance post harvest.

(b) The initial response of the bryoflora to harvesting shows declines in species diversity (specifically, richness and evenness) and cover:

(i) **Species richness** is the number of species per sampling unit. Pre harvest (i.e. 1995), approx 75% of the the quadrats contained 7-18 species, with a mean of 8.69 ± 0.31 (standard error), and a mode of 10-12 species (Fig. 3). Post harvest (1996), over 80% of the quadrats contained 9 or less species, with a mean of 5.95 ± 0.22 and a mode of 4-6 species. By 1997, 90% of the quadrats contained 7 or fewer species, with a mean of 4.65 ± 0.15 and a mode of 4 species.

(ii) **Species evenness** is a measure of commonness/rarity of individual species. Pre and post harvest, the species were heterogeneously distributed, with most species occurring in < 5% of the quadrats. However, pre harvest 7 species were very common (present in 60-80% of quadrats, Fig. 4), while post harvest only one species was common, and the top 6 species ranged from 31-70% of the quadrats. There was little discernable change in 1997, aside from the decline in number of species overall.

(iii) **Species cover** is the amount of forest floor occupied by species, expressed as a percentage of the total quadrat area. In temperate forests, total bryophyte cover typically varies from 0% in dry balsam fir sapling thickets to 100% under open spruce canopy. Pre harvest, 35% of quadrats contained > 10% bryophyte cover (Fig. 5). Post harvest, the frequency distribution had shifted dramatically: only 1% of the quadrats contained > 30% cover, and over 70% contained < 5% cover. This trend continued in 1997.

In all years, most species covered less than 0.25% cover overall (Fig. 6), equivalent to approx 30 cm^2. This very low percent cover is expected given the heterogeneity of distribution of the species over a wide range of habitats represented by 189 quadrats. However, *Pleurozium schreberi*, which averaged 5% cover pre harvest, was reduced to 1.7% post harvest, and further to less than 1% in 1997.

The cover of species in habitats to which they were adapted (i.e. mean cover when present) shifted slightly from 1995 to 1997 (Fig. 7): pre harvest, 40 species each covered less than 0.5% of the quadrat area, whereas only 35 species fell into this category in 1996-7 . This apparent increase in individual species' abundances is an artefact of the reduction in species present.

(c) Correspondence analysis (CA) summarized the characteristics of the pre harvest (1995) and post harvest (1996) bryophyte community. The pattern of species distribution throughout the quadrats was found to be very complex. In 1995, the first two axes of the CA captured 11.7% of the species pattern. CA axis one was defined by *Sphagnum squarrosum* and *Brachythecium rutabulum*, whereas axis two was defined by *Brotherella recurvens, Hylocomium splendens* and *Polytrichum juniperinum* (Fig. 8). These species were related to habitat conditions, as seen in the simultaneous ordination of quadrats (Fig. 9): both axes separated hardwood from softwood stands.

In 1996, 11.3% of the community variability was captured on the first two CA axes. On CA axis one, three quadrats containing *Bryhnia novae-angliae, Climacium dendroides, Rhizomnium appalachianum*, and *Plagiomnium ciliare* were isolated from the rest of the samples (Figs. 10, 11). On CA axis two, one quadrat with a high cover of *Hylocomium splendens* was isolated. On closer inspection, the main distribution of species and samples on axis one was drawn out to the right by *Polytrichum juniperinum* (a pioneer on mineral soil), *Plagiothecium laetum* and *Brachythecium salebrosum* (both common on decayed bark and wood). Axis two further separated *Sphagnum squarrosum* and *P. juniperinum* at the lower end from *Hypnum pallescens, Bazzania trilobata, Rhytidiadelphus triquetrus*, and *Sphagnum capillifolium* at the top.

In order to assess the possible relationship between species pattern and harvest treatment, the quadrats were plotted with symbols to indicate the latter (i.e. uncut, cut, and cut-and-scarified). No clear relationship was detected, suggesting that the post harvest community was more strongly influenced by its pre harvest composition than by the harvest treatment. We expect that this will change in the short term, as the impact of disturbance on habitat conditions further selects for tolerant species.

(d) In 1995 the PCCA on pre harvest data indicated that the community composition was most strongly related to litter chemistry (13.6%, Table 5), with lesser contributions from topography (7.77%) and canopy (1.71%). Although the canopy variables showed a weak relationship with the bryophyte composition, their long-term impact on litter chemistry is implicit. Hence the composition of the bryophyte community under a closed canopy is most closely related to a long history of that particular set of canopy characteristics. It is therefore likely that canopy removal will have far-reaching effects, not only in immediate micro-climatic change, but in profound changes to the dynamic litter layer, i.e. changes in litter input, rates of decomposition, etc.

Canonical correspondence analysis (CCA) indicated that 22% of the post harvest species pattern was directly related to the disturbance variables (sum of unconstrained eigenvalues=14.768, sum of canonical eigenvalues=3.268; ratio=22.1%). The correlations between the species and disturbance variables were 0.8005 and 0.8476 for the first and second canonical axes, respectively.

These results suggest that the strong CA axes for disturbance variables, which identified substrate and slash factors, impose an impact on the post harvest bryophyte community. The next step will be to determine the relative contributions to regeneration: how much of the regenerated bryophyte community is directly related to the pre harvest community (through survival, propagules deposition, or stand micro habitat patterns) and how much is related to specific disturbance components? This can be explored using Partial Canonical Correspondence Analysis (PCCA).

Table 4. Bryophyte species frequency and mean cover values for 1995, 1996 and 1997 in permanent quadrats at Hayward Brook, NB. 1995 = pre harvest, 1996 = immediately post harvest.

Spp. #	Species	% Frequency			Mean % cover when present			Total Mean % cover		
		1995	1996	1997	1995	1996	1997	1995	1996	1997
Present in 1995 only										
1	*Ambylystegium serpens*	7.74	0	0	0	0	0	0	0	0
94	*Brachythecium reflexum*	0.65	0	0	0	0	0	0	0	0
88	*Brotherella recurvans*	3.23	0	0	1.68	0	0	0.1	0	0
56	*Calypogeja integristipula*	0.65	0	0	0.4	0	0	0	0	0
58	*Calypogeja muelleriana*	1.29	0	0	0	0	0	0	0	0
60	*Cephalozia bicuspidata*	3.23	0	0	0	0	0	0	0	0
89	*Cephaloziella spp.*	0.65	0	0	0	0	0	0	0	0
91	*Ceratodon purpureus*	0.65	0	0	0	0	0	0	0	0
95	*Cirriphylum piliferum*	1.29	0	0	3.55	0	0	0.1	0	0
77	*Crustose lichen*	0.65	0	0	0.7	0	0	0	0	0
80	*Dicranum viride*	1.94	0	0	0	0	0	0	0	0
87	*Disyscium foliosum*	0.65	0	0	0.2	0	0	0	0	0
61	*Frullania brittoniae*	0.65	0	0	0.1	0	0	0	0	0
84	*Frullania eboracensis*	1.29	0	0	0	0	0	0	0	0
62	*Frullania oakiana*	0.65	0	0	0	0	0	0	0	0
83	*Gymnocolea inflata*	0.65	0	0	0.5	0	0	0	0	0
29	*Hypnum pallescens var. protrubans*	3.23	0	0	0.1	0	0	0	0	0
31	*Leptodictyium riparium*	0.65	0	0	0	0	0	0	0	0
68	*Lophozia heterocolpos*	1.94	0	0	0	0	0	0	0	0
81	*Plagiothecium cavifolium*	1.94	0	0	4.83	0	0	0.1	0	0
30	*Platygyrium repens*	1.29	0	0	0.16	0	0	0	0	0
82	*Riccardia latifrons*	1.29	0	0	0.1	0	0	0	0	0
74	*Trocolea tomentalla*	1.29	0	0	0.1	0	0	0	0	0

Present in 1995 and 1996 only		1995	1996	1997	1995	1996	1997	1995	1996	1997
3	*Brachythecium campestre*	3.87	2.6	0	0.48	0.73	0	0	0	0
86	*Brachythecium populeum*	3.23	0.65	0	1.3	0.25	0	0	0	0
6	*Brachythecium rutabulum*	13.6	5.19	0	0.76	0.51	0	0.1	0	0
92	*Brachythecium velutinum*	3.23	1.95	0	0.63	0.42	0	0	0	0
8	*Bryhnia novae-anglais*	7.74	0.65	0	2.81	3.05	0	0.22	0	0
12	*Campylium stellatum*	3.23	1.95	0	0.16	0.6	0	0	0	0
59	*Cephalozia lunulifolia*	5.81	3.25	0	0	0.16	0	0	0	0
93	*Conocephalum conicum*	0.65	0.65	0	6	0.15	0	0	0	0
76	*Foliose lichen*	6.45	0.65	0	0.38	1.4	0	0	0	0
23	*Herzogiella striatella*	6.45	5.84	0	1.15	0.52	0	0.1	0	0
26	*Hypnum lindbergi*	0.65	0.65	0	0.6	0.25	0	0	0	0
65	*Lepidozia reptans*	8.39	10.4	0	0.43	0.32	0	0	0	0
75	*Lichen*	34.2	9.09	0	1.01	1.54	0	0.35	0.14	0
34	*Oncophorus wahlenbergii*	0.65	2.6	0	0.4	0.1	0	0	0	0
70	*Plagiochilla porelloides*	1.94	0.65	0	2.93	0	0	0.1	0	0
35	*Plagiomnium ciliare*	7.1	3.25	0	2.44	0.98	0	0.17	0	0
71	*Ptilidium ciliare*	7.1	5.19	0	0.75	0.75	0	0.1	0	0
47	*Rhizomnium appalachianum*	2.58	1.3	0	4.56	0.28	0	0.12	0	0
78	*Thuidium recognitum*	3.87	3.25	0	3.25	0.41	0	0.13	0	0
0	Unverified	1.29	1.3	0	2.5	0.78	0	0	0	0

Present in 1995, 1996 & 1997		1995	1996	1997	1995	1996	1997	1995	1996	1997
2	*Aulacomnium palustre*	7.74	9.74	6.85	1.57	0.89	1.97	0.12	0.1	0.13
54	*Bazzania trilobata*	12.3	5.19	4.11	2.59	1.35	0.8	0.32	0.1	0
55	*Blepharostoma trichophyllum*	5.81	2.6	0.68	0.1	0.1	0	0	0	0
4	*Brachythecium salebrosum*	12.9	7.14	4.79	0.91	0.46	0.37	0.12	0	0
5	*Brachythecium starkei*	59.4	30.5	37	0.8	0.41	0.45	0.47	0.13	0.16
9	*Callicladium haldanianum*	23.2	20.8	13	1.02	0.44	0.3	0.24	0.1	0
10	*Campylium hispidulum*	13.6	5.19	5.48	0.29	0.48	0.15	0	0	0
13	*Climacium dendroidium*	0.65	0.65	0.68	3.7	2.2	4	0	0	0
14	*Dicranum flagellare*	30.3	16.9	16.4	0.52	0.38	0.13	0.16	0.1	0
15	*Dicranum fuscescens*	26.5	33.1	9.59	0.93	0.58	0.19	0.25	0.19	0
17	*Dicranum montanum*	14.8	22.1	13.7	0.24	0.38	0.13	0	0.1	0
18	*Dicranum ontariense*	3.87	3.9	0.68	2.24	0.4	0.3	0.1	0	0
19	*Dicranum polysetum*	57.4	42.9	52.1	3.48	2.14	1.02	2	0.92	0.5
20	*Dicranum scoparium*	59.4	40.9	15.8	1.13	0.64	0.32	0.67	0.26	0.1
21	*Drepanocladus sononia*	24.5	7.14	17.8	0.44	0.27	0.19	0.11	0	0
85	*Eurychium pulchellum*	0.65	1.95	1.37	1.2	1.82	2.67	0	0	0
63	*Geocalyx graveolens*	17.4	3.9	14.4	0.1	0.22	0.28	0	0	0
24	*Herzogiella turfacea*	34.2	23.4	34.3	0.55	0.92	0.34	0.19	0.22	0.11
25	*Hylocomnium splendens*	7.74	4.55	4.79	4.59	5.8	1.96	0.36	0.26	0.1
27	*Hypnum imponens*	7.1	9.74	3.42	2.15	0.6	0.1	0.15	0.1	0
28	*Hypnum pallescens*	32.9	13	16.4	0.27	0.68	0.18	0.1	0.1	0
64	*Jamesoniella autumnalis*	41.9	23.4	14.4	0.34	0.21	0.24	0.14	0.1	0
66	*Lophocolea heterophylla*	47.7	13	1.37	0.17	0.11	0.1	0.1	0	0
69	*Nowellia curvifolia*	11.6	2.6	4.11	0.1	0.14	0	0	0	0
36	*Plagiomnium cuspidatum*	20.7	14.3	8.9	1.14	1.18	0.9	0.23	0.17	0.1
38	*Plagiomnium medium*	3.23	3.9	6.16	2.21	0.34	0.64	0.1	0	0

(Present in 1995-1997, cont'd)		1995	1996	1997	1995	1996	1997	1995	1996	1997
39	*Plagiomnium laetum*	11.6	13	4.79	0.1	0.42	0.24	0	0.1	0
41	*Pleurozium schreberi*	71.6	68.8	61.6	6.97	2.54	1.72	4.99	1.75	1
43	*Polytrichium commune*	10.3	16.9	22.6	1.64	0.51	0.89	0.17	0.1	0.19
44	*Polytrichium juniperinum*	6.45	5.84	8.22	1.33	1.22	0.31	0.1	0.1	0
72	*Ptilidium pulcherrimum*	69	43.5	35.6	0.69	0.46	0.35	0.48	0.2	0.12
45	*Ptilium crista-castrensis*	15.5	5.84	2.05	1.09	0.4	0.1	0.17	0	0
48	*Rhytidiadelphis triquestris*	3.87	3.25	2.05	11.4	0.31	0	0.44	0	0
73	*Scapania nemerosa*	1.29	0.65	0.68	0	0.15	0	0	0	0
90	*Sphagnum capillifolium*	0.65	0.65	1.37	14	3.3	7.75	0.1	0	0.1
49	*Sphagnum girgensohnii*	0.65	0.65	0.68	0.3	1	0	0	0	0
51	*Sphagnum squarrosum*	1.94	1.3	2.05	3.5	1.43	0	0.1	0	0
52	*Tetraphis pellucida*	14.8	1.95	2.74	0.47	0.14	0	0.1	0	0
53	*Thuidium delicatulum*	1.94	0.65	4.79	1.07	1.3	0.28	0	0	0
Present in 1996 only										
103	*Campylium chrysophyllum*	0	0.65	0	0	0.4	0	0	0	0
97	*Dicranum brevifolium*	0	0.65	0	0	0.25	0	0	0	0
98	*Marchantia polymorpha*	0	0.65	0	0	0.25	0	0	0	0
99	*Plagiomnium drummondii*	0	0.65	0	0	0.1	0	0	0	0
96	Protonema	0	1.3	0	0	0.3	0	0	0	0
100	*Pseudobryum cinclidiodes*	0	0.65	0	0	1.95	0	0	0	0
Present in 1996 and 1997 only										
102	*Frullania bolanderi*	0	0.65	0.68	0	0	0	0	0	0
Present in 1997 only										
106	*Dicranella heterophylla*	0	0	0.68	0	0	0	0	0	0
Present in 1995 and 1997 only										
42	*Pohlia nutans*	1.29	0	6.16	0	0	0.29	0	0	0

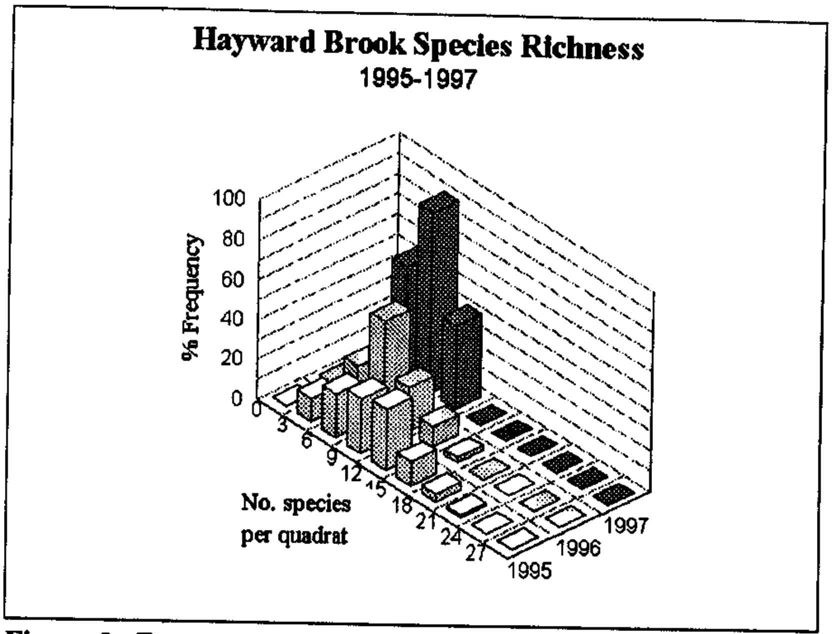

Figure 3. Frequency distribution of number of bryophyte species per quadrat, over three years. 1995=pre harvest, 1996-7=post harvest. The mode for pre harvest richness shifts from 10-12 spp. per quadrat, to 4-6 in 1996-7.

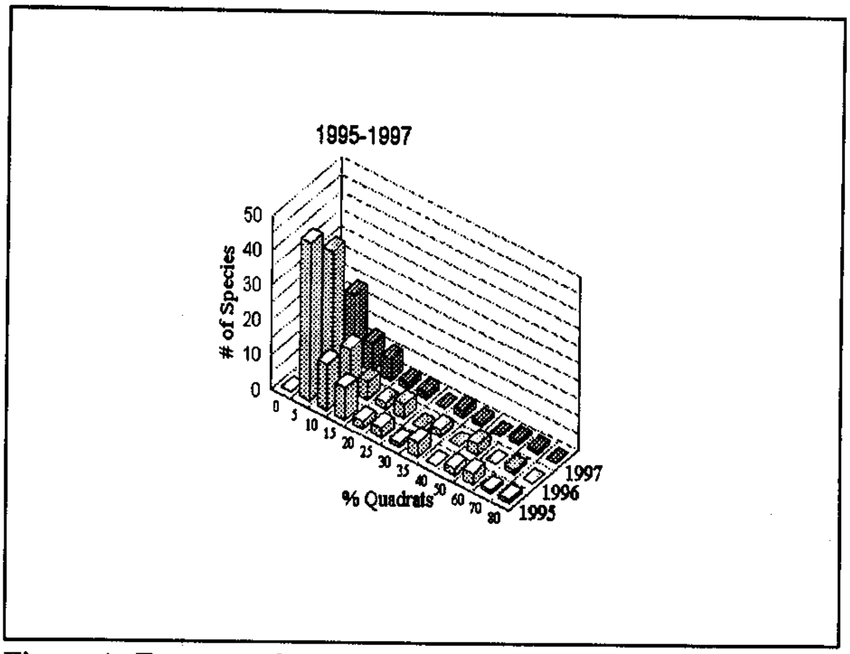

Figure 4. Evenness of species in quadrats over three years. Pre harvest, species were heterogeneously distributed, with most occurring in < 5% of quadrats, however 7 spp. were very common (in 60-80% of quadrats). Post harvest, only one species was common (51-60%) and all others occurred in less than 50% of quadrats.

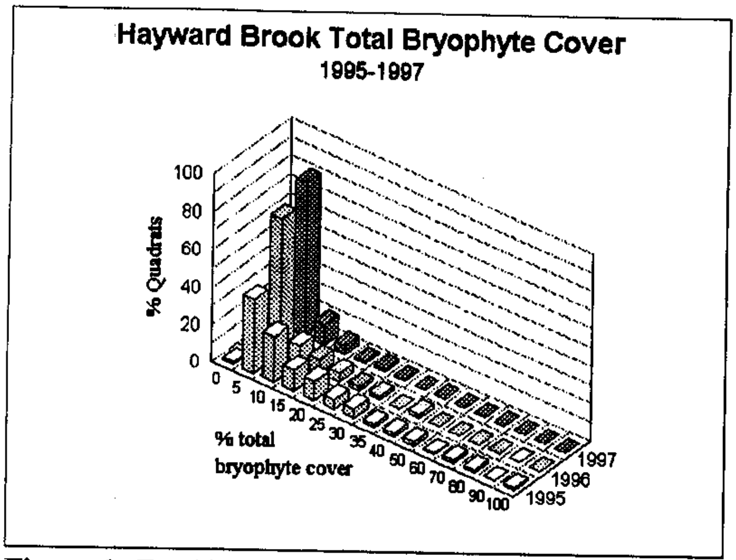

Figure 6. Total bryophyte cover in permanent quadrats over three years. Pre harvest, 35% of quadrats contained more than 10% bryophyte cover, with some containing 50-100% cover. Post harvest, all quadrats contained less than 50% cover, and over 70% contained less than 5% cover.

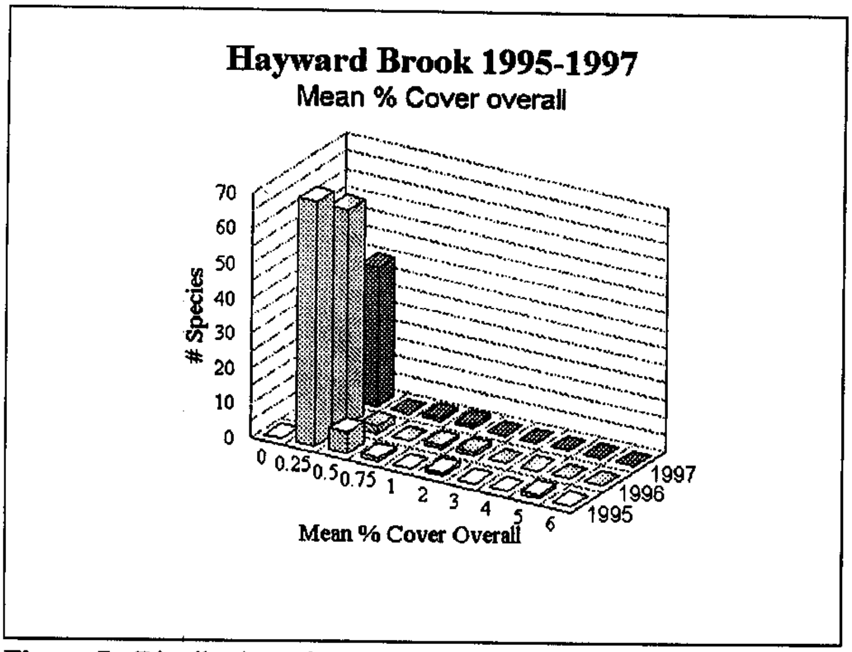

Figure 7. Distribution of species by mean % cover. Over three years, most species covered 0.25% of the quadrat, equivalent to approx 30 cm^2. However pre harvest, the one species that averaged over 5% cover dropped to 1.7% in 1996 and further to less than 1% in 1997.

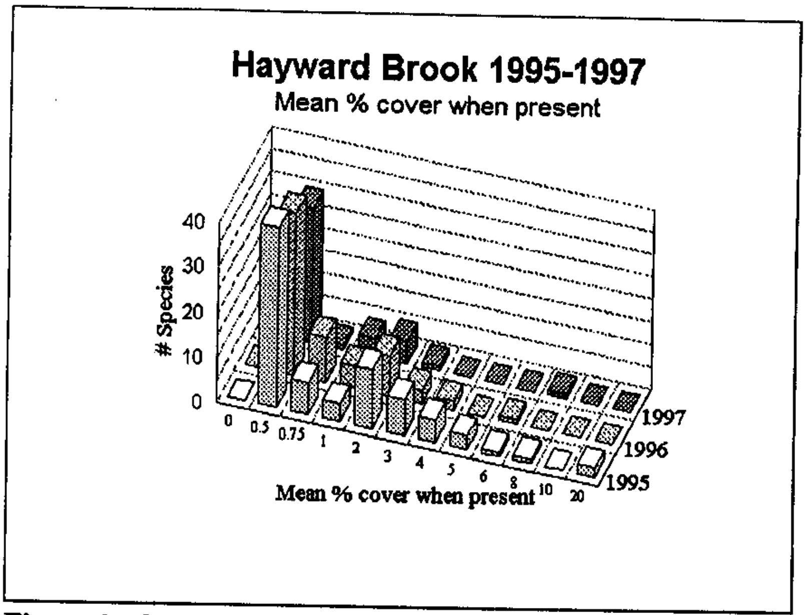

Figure 8. Cover of species in habitats to which they were adapted, over three years. Pre harvest, a number of species covered more than 5% of the quadrats; however post harvest most averaged less than 4%.

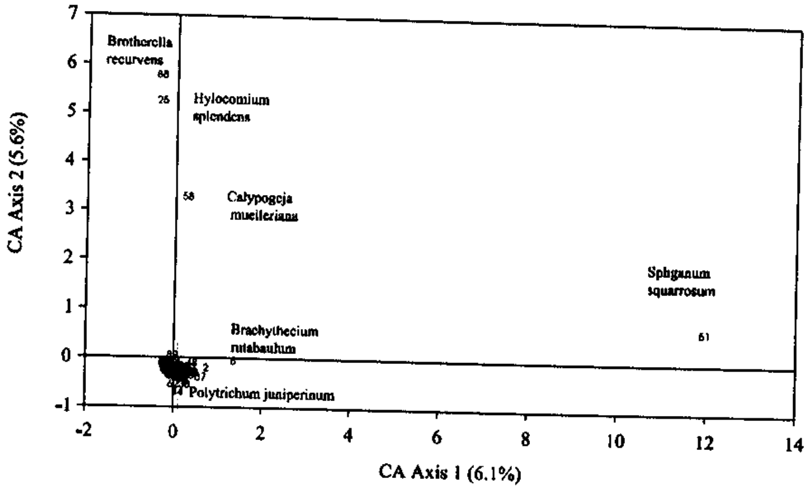

Figure 9. Species scores on first two axes of CA, pre harvest (1995) bryophyte community. Species defining the axes are shown.

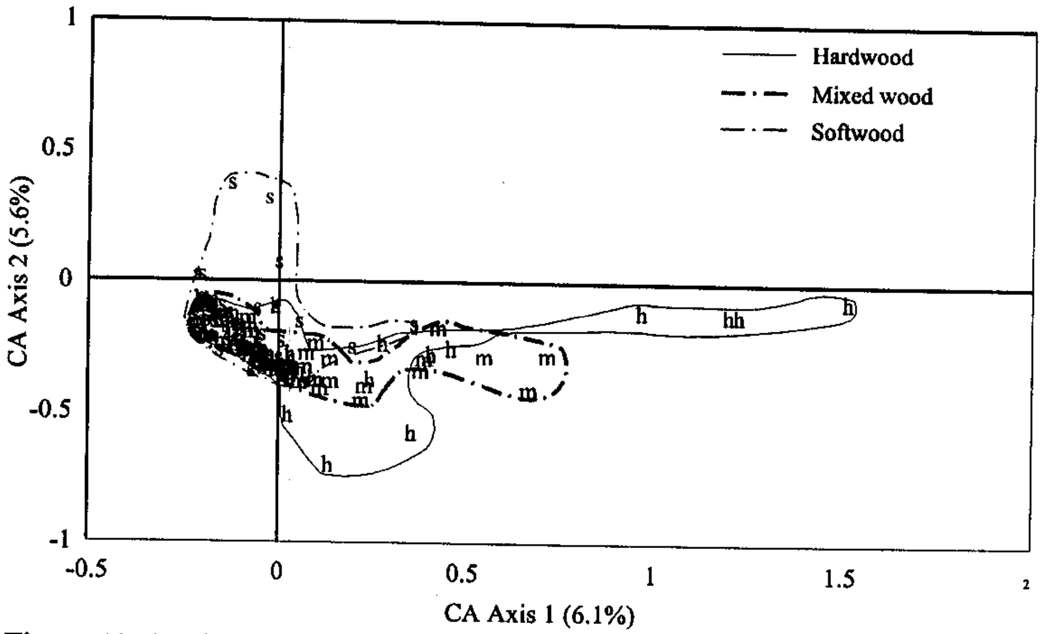

Figure 10. Pre harvest (1995) quadrat scores for first two CA axes, plotted by stand types. Hardwoods extend along the first axis, softwoods are separated on the second, and mixed wood stands are intermediate.

CA Species Scores 1996

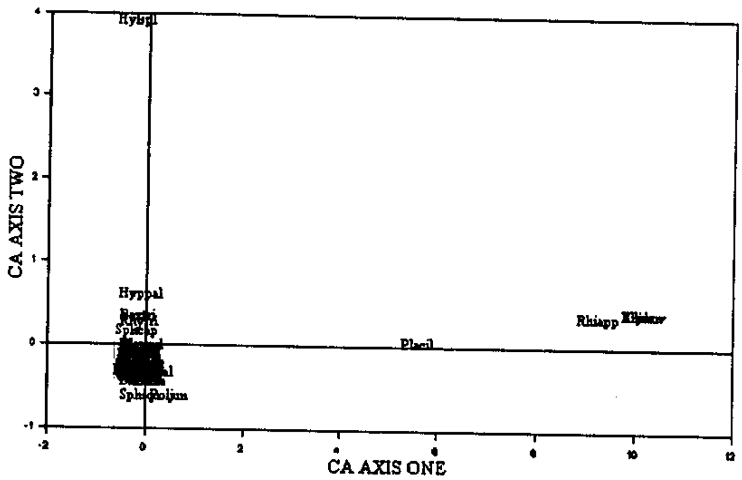

Figure 11. Species scores on first two CA axes, 1996 (post harvest). Species defining axes are shown.

CA quadrat scores by treatment 1996

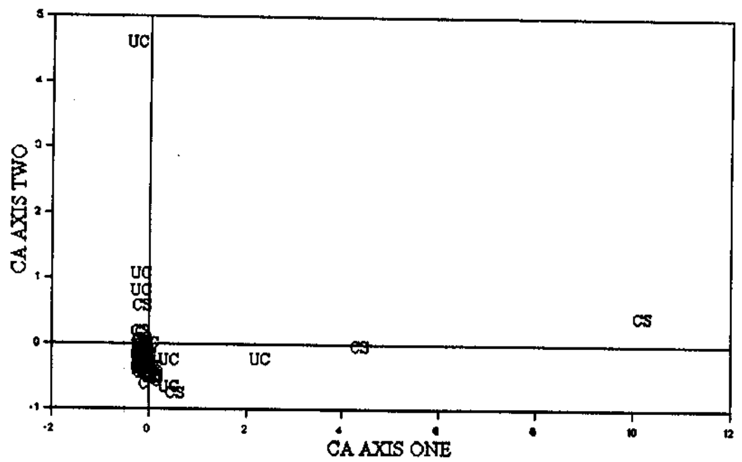

Figure 12. Post harvest (1996) quadrat scores on first two CA axes, plotted by harvest treatment. UC=uncut, C=clear cut, CS=cut and scarified.

Table 5. Partial Canonical Correspondence Analysis (PCCA) series showing unique and combined influences of litter, topography, and canopy variables on the pre harvest bryophyte species pattern. Litter alone showed the largest correlation with the species pattern. (from Sims, unpubl.)

Source	Sum of canonical eigenvalues	% of total CCA inertia	% of total CA inertia (species pattern)
Litter	1.957	54.91	13.64
Topography	1.060	29.74	7.77
Canopy	0.233	6.538	1.71
Topography x litter	0.176	4.938	1.29
Topography x canopy	0.051	1.431	0.37
Litter x canopy	0.046	1.291	0.34
Litter x topography x canopy	0.041	1.150	0.30
TOTAL	3.564	99.998	25.12

3. Soil spore bank.

A total of 25 species germinated from the soil spore bank. Surprisingly, the total richness (number of species) was similar for all stands, ranging from 19-21 (Table 6). Also, the most abundant species were similar and tended to be those associated with open areas. This is presumably because "pioneer" species generally have high spore production, hence their airborne spores are more likely to be ubiquitous. However, there were groups of species most common, and even unique, to specific forest treatments. Uncut stands contained more *Sphagnum* spp and *Atrichum crispum*, as well as the only colonies of *Ceratodon* sp. and the liverwort *Cephalozia bicuspidata* (Table 7); all but *Atrichum* are characteristic of shady, cool, moist areas under a closed canopy.

The cut stands were the only ones to produce *Bazzania trilobata*, but contained the same common species as the uncut stands. Two species, *Callicladium* sp. and *Dicranum scoparium*, were germinated only from the cut and scarified stands. This is intriguing, because these species are normally found in closed canopy forests.

At the quadrat scale, individual quadrats contained from 3-13 species, with mean of 8 species (Fig. 12). Individual quadrats in the uncut treatments had a higher mean and narrower range of richness, whereas both cut treatments had similar means but greater variation in richness (Fig. 13).

Seed bank studies (i.e. those considering propagation units of the "higher" plants) frequently report that the distribution and abundance of seeds appears completely unrelated to that of the vegetation on the site. Apparently, this is also true of spore banks: 4 taxa were absent from the pre harvest community, and the 14 species which were represented both pre and post harvest were not most abundant in the aboveground community. The same species were most common in the spore bank, regardless of recent disturbance, and were primarily robust pioneer species which typically invade disturbed areas.

There are three lines of investigation that must be followed before this information can be fully implemented: (a) to quantify the relationship between the spore bank contents and the pre-harvest vegetation, i.e. to determine if the rare species are likely to be able to regenerate from a spore source, (b) to determine the longevity of spores in the soil, i.e. to determine whether spores from a previously closed canopy community <u>can</u> persist until canopy closure, in order to contribute to the regenerating community, and (c) to quantify the relationship between the spore bank contents and the post-harvest regeneration in the permanent quadrats, i.e. to determine whether the recovering community <u>depends on</u> the presence of spores for its species composition.

Table 6. Bryophyte species distributions in soil propagule banks from three silviculture treatments at Hayward Brook (n=76 samples).

Summary	**Forest Treatment**			**Totals**
	Uncut	Cut	Cut/Scarified	
Total # taxa	21	19	20	25
Mean # taxa per sample	7.67	8.88	7.18	7.89
Standard error	0.30	0.28	0.50	0.22
Mean % frequency of taxa	30.67	35.67	28.73	30.47
Most frequent species	*Pohlia nutans* *Dicranella* *Atrichum sp.*	*Sphagnum sp.* *Pohlia nutans* *Polytrichum* *Sphagnum* *Dicranum spp.*	*Pohlia nutans* *Dicranella* *Polytrichum* *Dicranella*	*Pohlia nutans* *Dicranella* *Dicranum* *Sphagnum sp.*
Unique taxa	*Ceratodon sp.* *Cephalozia cuspidata*	*Bazzania trilobata* *red Sphagnum*	*Callicladium sp.* *Dicranum scoparium*	

Table 7. Percent frequency of germinated bryophyte species associated with specific habitat conditions in soils collected from three forest treatments at Hayward Brook. "Years" refers to the years in which each taxon was found in the permanent plot data (Table 4). Shaded species were absent from the aboveground pre and post harvest communities.

Species	Years			Forest Treatment			
	95	96	97	Uncut	Cut	Cut/Scarified	Totals
Open							
Pohlia nutans			▸	100.00	95.83	95.45	97.37
Polytrichum	▸	▸	▸	80.00	66.67	45.45	65.79
Bryum				10.00	20.83	27.27	18.42
Bryum argenteum				6.67	8.33	4.55	6.58
Ceratodon	▸			3.33	0.00	0.00	1.32
Open/Moist							
Dicranella			▸	100.00	95.83	81.82	93.42
Polytrichum	▸	▸	▸	96.67	95.83	77.27	90.79
Atrichum crispum				90.00	75.00	59.09	76.32
Philonotis fontana				3.33	8.33	9.09	6.58
Marchantia		▸		3.33	0.00	9.09	3.95
Closed							
Dicranum spp.	▸	▸	▸	46.67	91.67	81.82	71.05
Herzogiella spp.	▸	▸	▸	60.00	75.00	63.64	65.79
Tetraphis pellucida	▸	▸	▸	26.67	41.67	27.27	31.58
Pleurozium	▸	▸	▸	6.67	50.00	9.09	21.05
Plagiomnium	▸	▸	▸	6.67	0.00	31.82	11.84
Brachythecium	▸	▸	▸	6.67	12.50	13.64	10.53
Plagiothecium	▸			3.33	20.83	9.09	10.53
Bazzania trilobata	▸	▸	▸	0.00	8.33	0.00	2.63
Dicranum	▸	▸	▸	0.00	0.00	4.55	1.32
Callicladium	▸	▸	▸	0.00	0.00	4.55	1.32
Closed/Moist							
Sphagnum spp.	▸	▸	▸	96.67	100.00	59.09	86.84
Aulacomnium	▸	▸	▸	13.33	16.67	4.55	11.84
Calypogeja	▸			3.33	4.17	0.00	2.63
Cephalozia	▸			3.33	0.00	0.00	1.32
Red Sphagnum	▸	▸	▸	0.00	4.17	0.00	1.32

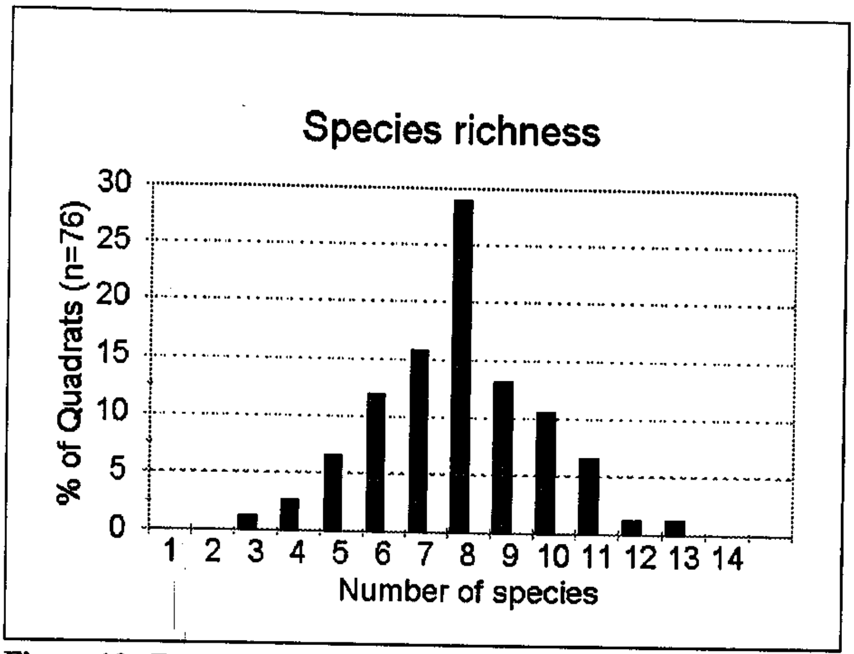

Figure 13. Frequency distribution of bryophyte species germinated from soil spore bank. For list of species, see Table 7.

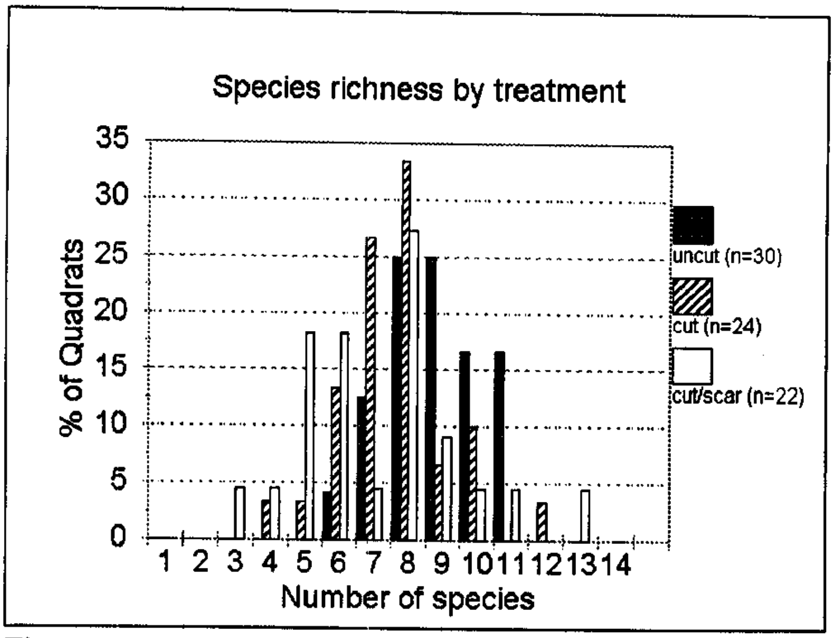

Figure 14. Frequency distribution of bryophyte species germinated from soil spore bank, grouped by silvicultural treatment category of quadrats. For list of species, see Table 7.

4. Use of *Bazzania trilobata* as an indicator

Metabolic responses. All samples showed evidence of respiration before and after the recovery period, indicating that they were viable. For details of the results, see Sollows (unpubl.).

Overall, the field-dried shoots showed the highest respiration rate (Fig. 14), while the shade-and sun-dried shoots were equal and lowest. Respiration of the three drying treatments did not change after recovery, however that of the control shoots increased significantly. A high respiration rate indicates one of two states: (a) the organism may be actively metabolizing and utilizing its stored energy sources for growth and/or reproduction, or (b) it may be using its fuel reserves to repair damaged membranes, photosynthetic pigments, etc. It is therefore necessary to examine other responses (e.g. photosynthesis) to interpret the respiration results.

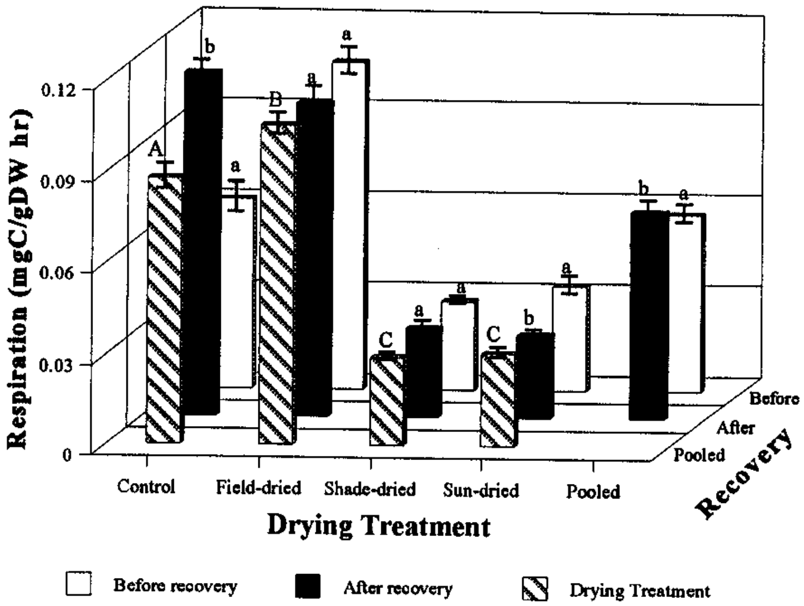

Figure 15. Respiration rates for *Bazzania trilobata* samples. Pooled effect values represent the impacts of the drying treatment or recovery period alone. Bars are means ± 1 s.e. Those with different letters are significantly different ($p < 0.05$). Upper case letters refer to the drying treatment effect; lower case letters refer to differences between treatments before and after recovery period.

Net photosynthesis is the overall gain in energy and carbon after the needs of respiration have been met; it represents the surplus that is available for growth and reproduction. Net photosynthesis was negligible for all dried samples before recovery, while that of the controls was much higher (Fig. 15) After recovery, the rate dropped for the controls, but rose significantly in field-dried shoots. The increase in net photosynthesis for field-dried shoots clearly indicates that the pre recovery respiration rates were related to damage repair, as there was no net gain.

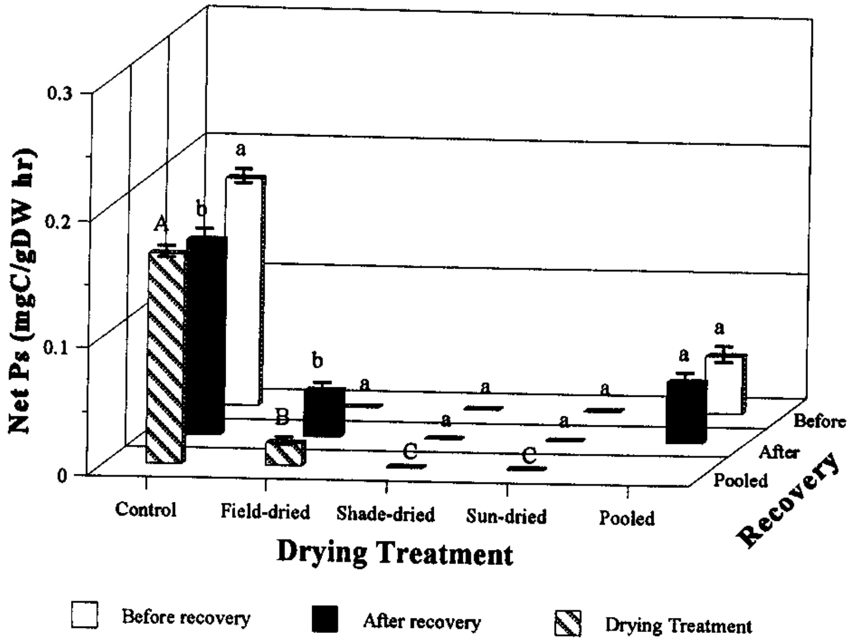

Figure 16. Net photosynthetic rates (Net Ps) for *Bazzania trilobata* samples. Pooled effect values represent the impacts of the drying treatment or recovery period alone. Bars are means ± 1 s.e. Those with different letters are significantly different ($p<0.05$). Upper case letters refer to the drying treatment effect; lower case letters refer to differences between treatments before and after recovery period.

However it appears that the repairs were effective during the recovery period, after which a surplus was available. The sun- and shade-dried shoots showed no sign of recovery.

Growth. These patterns were supported by growth measurements (Fig. 16). Control shoots elongated by a mean of nearly 0.7 cm in two months, and field-dried shoots by only 0.1 cm. This is consistent with the hypothesis that field-dried shoots that utilized a large proportion of their reserves to repair membranes and pigments during recovery, but were then able to allocate the small surplus to growth. The growth of sun-and shade-dried shoots, mean <0.06 cm, was sufficiently low to be attributable to experimental error. They did not recover, nor did they grow. It is therefore possible that the very low respiration, initially interpreted as indicating viability, was due to microbial respiration, i.e. the metabolism of bacteria clinging to the shoots.

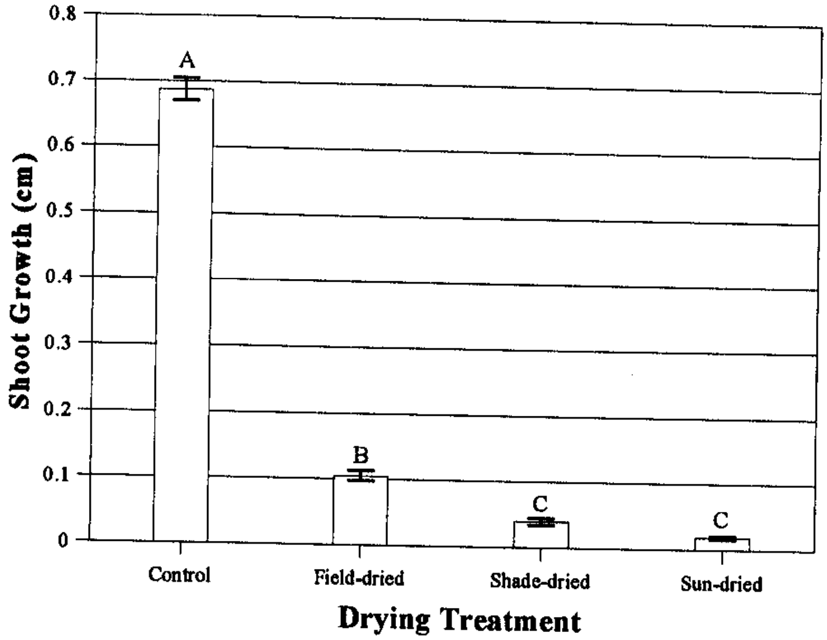

Figure 17. Shoot growth (elongation) during a two month recovery period for different treatments of *Bazzania trilobata* shoots. Bars represent means ± 1 s.e. Those with different letters are significantly different ($p<0.05$).

Colour. The plants' colour changes were easily discernible using the Munsell Colour Charts. The control samples all fell within a narrow range (5 Green-Yellow), before and after recovery (Fig.17); this colour range was therefore assumed to represent the healthy state. The field-dried samples fell within a range from pale Green-Yellow through Yellow to Yellow-Red, indicating severe pigment degradation (Fig. 18). However, after the recovery period, the distribution shifted strongly toward Yellow and Green-Yellow, indicating recovery that is consistent with the increased net photosynthesis and growth noted above. After drying, shade- and sun-dried shoots appeared less damaged than the field-dried ones, ranging from 5GY to Yellow (Figs. 19, 20). Their colour deteriorated after the recovery period, with all shoots falling within the Yellow hue. Again, this is consistent with the absence of recovery noted in metabolism.

Conclusions. *Bazzania trilobata* was clearly damaged by dessication, however it remains viable and able to recover after two years in a clear cut. This suggests that clumps of established plants left on a cut-over are capable of recovering, assuming that they are remain viable until optimum environmental conditions return. It appears that the experimental drying treatments, which lasted less than 2 months, caused more severe, and irreversible, damage than did two years in a clear cut. It may be that the drying treatments, which were abrupt and constant, were somewhat unrealistic. Canopy removal was an abrupt habitat change, however remaining slash and undergrowth may slow the dessication process. In addition, occasional precipitation and regular dew formation presumably made the drying process more gradual.

Identification of species that are good indicators of forest conditions is important in evaluating and predicting the effects of forest management activities (Woodley and Forbes 1997), however in order to use this species as an indicator, it must be carefully calibrated. Aside from determining its range of tolerance (conditions and duration), we also must quantify its relationship to species assemblages. The survey data will provide information on the bryophytes associated with *Bazzania*. In addition, observations in the field suggest that it may also be a useful indicator for some animal species. Toads, snakes and spiders were observed on and in the colonies of *Bazzania* in the closed forest, but were absent from those in the clear cut. Conversely, ants were observed only in the field-dried samples.

Colour appears to be a useful criterion for assessing *Bazzania* in the field, however further refinement is needed to determine the colours that indicate critical damage. Although the experimentally dried shoots appeared more similar in hue to the controls than did the field-dried samples, they ultimately deteriorated. It was noted that specific textures were associated with the metabolic status; an assessment criterion that includes both colour and texture may be both accurate and feasible.

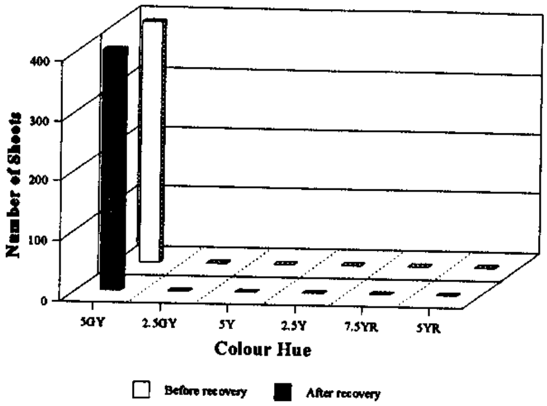

Figure 18. Control samples: Number of shoots (n=400) of *Bazzania trilobata* that fell into 7 colour hues as described by Wilde and Voigt (1977). Visual assessments were made before and after the 2 month recovery period.

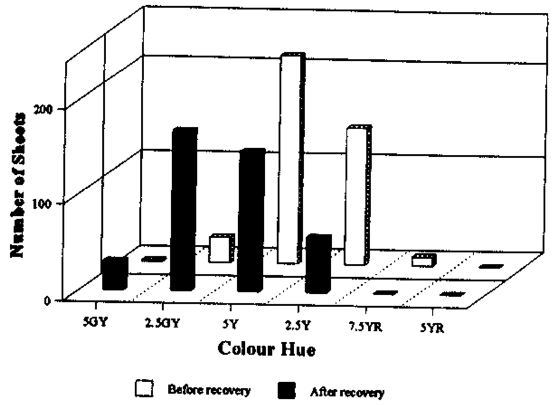

Figure 19. Field-dried samples: Number of shoots (n=400) of *Bazzania trilobata* that fell into 7 colour hues as described by Wilde and Voigt (1977). Visual assessments were made before and after the 2 month recovery period.

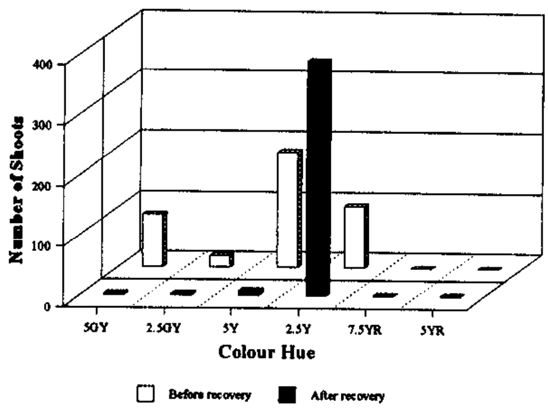

Figure 20. Sun-dried samples: Number of shoots (n=400) of *Bazzania trilobata* that fell into 7 colour hues as described by Wilde and Voigt (1977). Visual assessments were made before and after the 2 month recovery period.

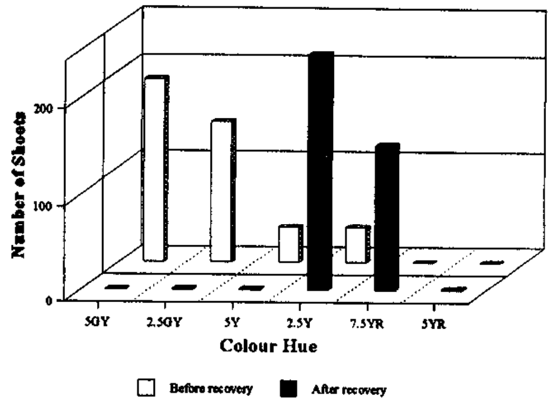

Figure 21. Shade-dried samples: Number of shoots (n=400) of *Bazzania trilobata* that fell into 7 colour hues as described by Wilde and Voigt (1977). Visual assessments were made before and after the 2 month recovery period.

EXECUTIVE SUMMARY OF RESULTS

DISTURBANCE. Aside from the obvious removal of canopy, harvest disturbances of two general types occur: addition of slash, and changes to the substrate. As expected, scarification was associated with greatest soil disturbance, e.g. exposure of parent material and rocks, and greatest extent of vehicle tracks. Slash accumulation was most common on unscarified sites, presumably because they were most frequently coniferous. However, scarification also altered the spatial pattern of slash to make it even more heterogeneous at the micro scale.

While physical damage to the forest floor and its soil are likely to have profound negative effects on established plants, slash may provide shade and increased humidity to offset canopy removal. The effects of slash and substrate disturbance on survival of several forest floor species are being tested by experimental manipulation (by Jennifer Peterson, MSc candidate); these results will be available in 1999.

BRYOPHYTE COMMUNITY RESPONSE. Baseline data (1995, pre harvest) indicated that the bryophyte community was most strongly related to the litter chemistry, which is a cumulative feature characteristic of a particular forest canopy. As predicted, removal of that canopy was followed by declines in species diversity and cover. Of 106 species identified in the pre harvest community, 23 species were lost after harvest, 19 persisted for one year, and 34 are clearly declining. A large proportion of these species are likely to be at risk, however (a) some may persist and regenerate from damaged but viable material (e.g. *Bazzania trilobata*, below), (b) some may regenerate from the soil spore bank (see Spore Bank study, below) and/or (c) some may re-establish through long distance spore dispersal. At least 3 "colonist" species, which were not part of the closed canopy community, have appeared in the disturbed quadrats.

Approximately 22% of the post harvest species pattern was related to disturbance vectors, with similar degrees of relatedness to slash and substrate variables. The greatest impact was clearly related to scarification. Further analyses will be needed to determine the overall, community-level, changes over time, and to determine whether the bryophyte community will ultimately return to its pre harvest state.

SOIL SPORE BANK. An initial assessment of the complement of spore in the soil showed 25 taxa, of which only four were not found in the pre harvest community. (These species are likely to be pioneers with high spore output, which typically invade disturbed micro sites.) While it is clear that only a small proportion of the bryophyte community is represented in the spore bank, it is important to note that (a) *Bazzania trilobata* was among them, and (b) at least 6 of the species judged to be most "at risk" were regenerated from the spore bank.

***BAZZANIA TRILOBATA* AS AN INDICATOR.** This leafy liverwort shows potential as an indicator of the closed canopy bryophyte community. A colour assessment may be calibrated to use as an indicator of the plant's viability, and the species itself may be calibrated to indicate species assemblages and habitat conditions. However, rapidly dried specimens appeared to retain their colour until rewetted, at which point pigment degeneration followed. It would therefore be useful to refine the colour scale (a) to determine colours associated with critical damage, and (b) to include a texture (brittleness) component.

LITERATURE CITED

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

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

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

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

During, H.J. 1979. Life strategies of bryophytes: A preliminary review. Lindbergia 5: 2-18.

During, H.J., M. Brugues, R.M. Cros, and F. Lloret. 1987. The diaspore bank of bryophytes and ferns in the soil in some contrasting habitats around Barcelona, Spain. Lindbergia 13: 137-149.

Fenner, M. 1985. Seed ecology. Chapman and Hall. New York.

Hicks, M.L. 1992. Guide to the liverworts of North Carolina. Duke University Press, Durham and London.

Hovey, A. 1996. Structure of the herbaceous community in a mixed forest in the Hayward Brook Watershed, New Brunswick. Unpublished B.Sc.(Hons.) thesis. Department of Biology, University of New Brunswick (Saint John).[1]

Ireland, R.R. and T.G. Bellolio. 1967. Syllogeus 62. Illustrated guide to some Hornworts, Liverworts and Mosses of Eastern Canada. National Museum of Natural Sciences, National Museum of Canada, Ottawa.

Jonsson, B.G. 1993. The bryophyte diaspore bank and its role after small-scale disturbance in a boreal forest. J. Veg. Sci. 4: 819-826.

Keizer, P.J., B.F. van Tooren, and H.J. During. 1985. Effects of bryophytes on seedling emergence and establishment of short-lived forbs in chalk grassland. J. Ecol. 73: 493-504.

Leck, M.A. 1980. Germination in Barrow, Alaska, tundra soil cores. Arc. Alp. Res. 12: 343-349.

---

[1] Shaded citations were studies undertaken in the Hayward Brook Watershed, Westmorland County, New Brunswick.

Lewis-Smith, R.I. 1987. The bryophyte propagule bank of Antarctic fellfield soils. Sym. Biol. Hung. 35: 233-245.

MacInnis, B. 1997. Small scale variability in a mixed temperate forest seed bank. Unpublished B.Sc.(Hons.) thesis. Department of Biology, University of New Brunswick (Saint John).

Rieley, J.O., P.W. Richards, and A.D.C. Bebbington. 1979. The ecological role of bryophytes in a North Wales woodland. J. Ecol. 67: 497-527.

Rydgren, K. and G. Hestmark. 1997. The soil propagule bank in a boreal old-growth spruce forest: Changes with depth and relationship to aboveground vegetation. Can. J. Bot. 75: 121-128.

SAS Institute Inc. 1989. Cary, North Carolina.

Sims, M.R. 1996. Distribution of forest floor bryophytes in a North Temperate forest. Unpublished B.Sc.(Hons.) thesis. Department of Biology, University of New Brunswick (Saint John).

Schuster, R.M. 1969. The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian. Vol. II. Columbia University Press, New York.

Smith, A.J.E. 1990. Liverworts of Britain and Ireland. Cambridge University Press, Cambridge.

Sollows, M. 1998. Recovery of *Bazzania trilobata* (L.) S. Gray following dessication. Unpublished B.Sc. (Hons.) thesis. Department of Biology, University of New Brunswick (Saint John).

ter Braak, C.J.F. 1988. CANOCO: A FORTRAN program for canonical community ordination. Vers. 2.1. Microcomputer Power. Ithaca, New York.

Wilde, S.A. and G.K. Voigt. 1977. Munsell colour chart for plant tissues. Kollmorgen Instruments Corporation. New Winsor, New York.

Woodley, S. and G. Forbes. 1997. Forest management guidelines to protect native biodiversity in the Fundy Model Forest. New Brunswick Co-operative Fish and Wildlife Research Unit, University of New Brunswick (Fredericton).

EXPENDITURES
for 1996/7 and 1997/8

Category	Amount	Details
Salaries (students)	$37,500	augmented by NSERC, JET Stream and Summer Career Placement 1996-8
Vehicle	900	truck rental 1997-8
Gas	350	1997-8
Accommodation	1,700	rental 1996-8
Other	1,400	includes photographic supplies, compressed gases for IRGA, photocopying, data logger and sensors etc.
Total	**$41,850**	