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FUNDY MODEL FOREST
YEAR END REPORT

Effects of Forestry Practices on Species Composition, Diversity, Stand Structure, and Succession

by

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INTRODUCTION

Importance of Diversity in Forest Management

National and global forestry organizations have recognized the need to manage for biodiversity. The Canadian Council of Forest Ministers state that the following principle should be part of a national forest strategy: "*Forest land-use will maintain a diversity of plant and animal species and their habitats.*" The Tenth World Forestry Congress affirmed in The Paris Declaration "*...that the integral conservation of particular forests for the protection of biodiversity constitutes a management objective.*"

Many ecologists agree that biological diversity cannot be conserved effectively in natural reserves alone (Hansen et al. 1991). There is also a critical need to integrate biodiversity objectives into management of all landscapes (Harris 1984, Franklin 1988, Hunter 1990). The current challenge is to design and manage these multipurpose lands (Westman 1990). As Hansen et al. (1991) pointed out, however, rigorous comparisons of disturbance regimes in managed and natural stands cannot be made because of insufficient knowledge. Understanding the effect of current practices is an essential first step in designing future management approaches.

Forest managers need to know the potential effects of different types of silvicultural treatments on diversity patterns over time in order to design environmentally sound management practices. A range of management intensities currently exists, from clearcutting with intensive site preparation, artificial regeneration, and herbiciding to selection systems. Comparing succession following different treatments to natural forest succession will allow us to identify those human disturbance scenarios that most closely approximate natural disturbances in terms of diversity patterns.

Biodiversity is expressed at three levels of biological organization: population, community, and landscape. Population diversity may be assessed as the genetic diversity of breeding populations or species. Components of community diversity include taxonomic diversity (alpha or beta diversity, for example) and structural diversity. At the highest level, landscape diversity can be expressed in the following measures: gamma and delta diversity, patch size and distribution, porosity, connectedness and fragmentation. We focus on the population and community levels in this proposal because these provide the foundation for landscape-level diversity. In addition, because silviculture impacts diversity directly at the community level, identifying effects of forestry practices at the community level is the logical first step. We will pursue landscape diversity in a subsequent proposal.

Structural Diversity

One of the attributes of biodiversity is stand structural diversity (Franklin 1988, Schoonmaker and McKee 1988). In this study, stand structural diversity is the variability in physical plant structures, including heights, diameters and crown sizes of the woody stems. Stand structural diversity provides richness of habitats for fauna and flora (Hunter 1990, Elton 1966). For example, bird species diversity is highly correlated with foliage height diversity (MacArthur and MacArthur 1961). Standing dead trees and fallen logs also provide habitat for certain species (Franklin 1988, Hansen et al. 1991), including American marten (Martes americana) (NBDNRE 1991).

It has been shown that intensive forest management leads to a reduction of plant structural legacies (like down logs and snags). This results in more uniform stand structures (Hansen et al. 1991; Spies et al. 1988) and a loss of habitats.

To establish the knowledge necessary to plan proper forest management practices at the stand level, structures and species composition of stands with natural disturbance regimes should be compared with managed stands (Binkley 1993; Goldstein 1992; SAF 1993; Booth et al. 1993; Thompson and Welsh 1993). Measures of alpha diversity (Whittaker 1972) should be included in comparisons (Gove et al. 1991; Swindel et al. 1987) because they are important quantitative and objective emergent properties of plant communities and may be key considerations in planning for sustainable development (Burton et al. 1992).

Descriptions of the plant communities should be done for a successional chronosequence and at different scales if knowledge of stand dynamics is to be increased (Thórhallsdóttir 1990). The chronosequence provides insight into the direct effect of disturbance on stand structure as well as the subsequent structural and compositional development over time. The results depend on the spatial scale, corresponding to the scale of pattern in the plant community (Levin 1992; Reed et al. 1993).

Species Composition and Taxonomic Diversity

There is a general consensus that maintaining all forest successional stages is necessary to preserve diversity of plant and animal species (Hunter 1990, Hansen et al. 1991). However, studies of changes in diversity with succession in forest communities are relatively rare and have shown conflicting results (Monk 1967, Habeck 1968, Bormann and Likens 1979). Several studies have documented an increase followed by a decrease during succession (Auclair and Goff 1971, Shafi and Yarranton 1973, Schoonmaker and McKee 1988), which is consistent with the "intermediate disturbance hypothesis" (Huston 1979, Denslow 1980).

In disturbance-prone temperate forests, there is a strong tendency for one or a few shade-tolerant species to become dominant with increasing time since disturbance (Loucks 1970). Periodic disturbance may maintain diversity at the landscape level in temperate forests. The problem, then, is to determine the role that disturbances of various types play in controlling diversity and to identify the changes in diversity that occur with succession.

Diversity patterns in old-growth forests are commonly used as a standard of comparison for managed forests (e.g., Swindel and Grosenbaugh 1988). However, it would be more realistic to compare each stage in the managed stand succession to the equivalent stage from a natural successional sequence. This approach recognizes the natural role of disturbance in temperate forest ecosystems.

Objectives

1. Compare effects of human and natural disturbances on plant species composition, alpha diversity and structural diversity.
2. Determine changes in species composition and alpha diversity with successional time following human disturbances.
3. Determine changes in structural diversity at a variety of scales with successional time following human disturbances.
4. Develop hypotheses which explain the causes for observed diversity patterns by examining species abundance models and species life history characteristics.
5. Establish the knowledge base necessary to develop forest management systems that more closely approximate natural disturbance regimes in terms of impacts on biodiversity.

Hypotheses

1. Greater intensity of human disturbance will result in decreased diversity relative to natural stands.
2. Alpha diversity will peak at an intermediate stage of succession because the community will contain pioneer and climax species at this stage.
3. Structural diversity will increase with time following human-caused disturbance.
4. Species composition and alpha diversity following human disturbances will converge toward the naturally disturbed stands with successional time because of the gradual invasion of some late successional species and an increase in structural diversity.

STUDY AREA

The study area is within the Fundy Model Forest and encompasses Fundy National Park and surrounding freehold and Crown lands. This area is located within the Fundy Coast Section of the Acadian Forest Region (Rowe 1972). The climate is cool and wet to moist and is also strongly influenced by relief (Loucks 1960).

The soils in this area range from coarse sandy loams to clay loams, many of them shallow over the bedrock, and are composed of slates, shales, sandstones, and volcanic, hard metamorphic and igneous rocks (Loucks 1960). Humo-ferric podzol profiles are typical (Rowe 1972). In the Fundy Mountain District (Loucks 1960), from about 16 km inland, the soils are chiefly loams and sandy loams, moderately rich mineralogically. In many places the till is 1m or more in depth, but elsewhere it may barely cover the bedrock.

The vegetation of the Fundy Coast Region is comprised of balsam fir and red spruce as the predominant species, although white and black spruces are plentiful as well (Rowe 1972). On the highland slopes, white and yellow birch join the red spruce and beech, and sugar maple appears sparingly. The tolerant hardwoods achieve prominence on hilltops and north-facing slopes. Absence of the pines, eastern hemlock, and eastern white cedar is characteristic of this area. Trembling aspen, white and grey birch and red maple have re-populated old burns, and red spruce, balsam fir and white spruce have invaded abandoned old fields. The tolerant hardwoods may once have been prevalent, possibly mixed with balsam fir and red spruce.

METHODS

Work Accomplished

Study Design:

We have selected the following disturbance scenarios for study: 1) Intensively managed plantations (clearcutting with site preparation and planting with genetically improved stock), 2) naturally regenerated clearcuts, and 3) natural stands of spruce budworm origin. These are typical natural and human disturbances encountered in our forests.

We are sampling a chronosequence for each of the two human-caused disturbance scenarios. Because the natural stands have been affected by multiple budworm defoliation events, they are multi-cohort stands and cannot be assigned to a single age class. These stands represent the predominant natural disturbance scenario in the region and will be used as a control for comparison with the human disturbances. Only fully-stocked stands dominated by black/red spruce and balsam fir on imperfectly to moderately well drained sites have been selected.

Preliminary Study - Species-Area Curves:

The minimal area is the smallest spatial area providing the true characteristics of species and structure of a particular community type (Shimwell 1971). The method used to determine the minimum area to sample, based on the species composition, was the species-area curve.

Stands were selected which appeared to have relatively high species diversity to give us an indication of the upper limit of diversity and sample ares required. Species area-curves were compiled for each of the general vegetative growth forms, including herbs (<1m tall), shrubs (1-3 m) and trees (>3 m). Three stands were sampled for the herbaceous layer and 5 stands were sampled for the shrub and tree layers. The species area curves were compiled by plotting the area versus species number (Appendix III).

Conservative measures of plot sizes were maintained in order to get "robust" minimum sizes; the plot size at which 90% of the species were found was used as the minimum plot size (Oosting 1959). The minimum sample area to include was found to be $49m^2$ for the herb layer and 7200 m^2 for the shrub and tree layers.

Preliminary Study - Bivariate Interpolation:

The study of stand structural diversity includes the examination of the variability of stand structural variables (e.g. height and diameter) and diversity measures at a variety of scales. To examine the scale-effects on the variability of these variables of the natural, naturally regenerated stands and plantations, relative large areas need to be used. An square area or block of 1.44 ha was chosen (larger than determined with the species are-curve). Because of time constraints, the blocks needed to be subsampled.

Quadrats of 0.01 ha were chosen to be used for subsampling (Christensen 1977; Abbott 1984; Smith and Urban 1988). The question arose as to how many quadrats to use (i.e. what would be the sample intensity) to obtain satisfactory results with a minimum of sample time. This was determined in a preliminary study.

A commonly used method to assess values of variables in unsampled areas with scattered data points is that of bivariate interpolation. Tree map data from three differently treated stands in the central U.S. were available. The height and diameters of the trees in the 500x500 m stands were summarized into means and variances of diameter and height for 2500 0.01 ha quadrats. The statistics were attached to the x/y-coordinates of the mid-points of each of the subplots. Since real spatial data were available, different sample intensities (% sampled areas) could be tested for accuracy. Different numbers of quadrats were chosen from the data-base with which the statistics of the quadrats not sampled were inferred, using the bivariate interpolation technique available in the S-plus computer package. The "sampling" was done in a systematic fashion since it yields lowest sampling error (Spurr 1952) and is most practical for fieldwork. The accuracy of the bivariate interpolated values of the variables for each of the quadrats of the stands is graphically expressed as the magnitude of the residuals (true values of means and variance of the variables minus the bivariate interpolated values). This produces a response surface (Appendix IV).

The sample intensity to be used for each of the stand types was determined by visually comparing the graphs with each other. Flatter planes of the residual surfaces represent more accurate bivariate interpolated values. In about half the cases, the minimum sample intensity was determined as 4%, and the other half of the cases as 11.6 % for all three stand types (Appendix IV). These sample intensities correspond to 6 and 17 subplots of 0.01 ha respectively for a proposed block size of 1.44 ha. Since more intensive sampling requires more field time, a sample intensity between 4% and 11.6% was chosen, which corresponds to 12 subplots for a 120x120 m plot. However, 13 subplots give a more even distribution of quadrats across the blocks.

Stand Selection:

In order to make valid comparisons among the three disturbance types, pre-disturbance species composition and site conditions were held constant as much as possible. Three replicate stands in each of three age-classes (3-6, 10-12 and 14-19 years) were sought for the human disturbance types. The natural stands were all affected by the last spruce budworm disturbance of 1974-1976, as well as earlier defoliations in 1940-50 and 1910-20.

The managed stands were partly located with use of the GIS databases from the New Brunswick Department of Natural Resources and Energy (NBDNRE) and the Fundy Model Forest (FMF). The pre-disturbance species composition was chosen to be at least 70% spruce-fir overstory cover, but with no more than 70% spruce, and a maximum of 30% intolerant hardwoods. Plantations of black spruce were sought. A total of 25 natural stands, 71 naturally regenerated clearcuts and 66 plantations were visited during the summers of 1992 and 1993.

The New Brunswick Site Classification System (Zelazny et al. 1989) was used as a guide to locate stands with similar site conditions in the field. Sites with treatment unit (TU) 1, 2, 3 or 5 (generally moist, and poor in nutrients, characteristic for most coniferous sites in this region; Zelazny et al. 1989) were included. To limit the within stand variability in drainage, a maximum average slope of 5 percent was allowed.

Other stand selection criteria included stand size (3 ha minimum), accessibility, macroclimate, and location. Natural stands with a history of budworm disturbance are located in Fundy National Park. The managed stand types are located as close as possible to the Park boundary to insure that climatic conditions were are similar among stands.

Sampling Design and Field Methods:
A large sample block (120 X 120m) was used to insure reasonable estimates of species composition and stand structural variation. In two smaller study stands, a block size of 80 X 80m was used. Species-area curves (Shimwell 1971) were developed in a preliminary field study. The minimum area required to include 90% of the tree and shrub species in the stand was 7200 m^2 (89 X 89m).

Within the sample block, thirteen 10 X 10m quadrats were evenly distributed for sampling (Appendix I) in order to accommodate the assessment of stand structural diversity at a variety of scales. Systematic sampling was chosen because it is practical and yields the lowest sampling error (Spurr 1952).

Within each of the 13 quadrats per block, all live and dead woody plants >1 m tall were tallied by species in 2cm dbh classes and 1m height classes. In addition, height to live crown was recorded in 1m classes.

Percent cover and number of woody stems <1m tall and percent cover of ground vegetation was estimated by species in four 0.5 X 2m subquadrats within each of the thirteen 10 X 10m quadrats per block (see above). One subquadrat was located in each corner of the quadrat. The total sample area (52m^2 per block) was based on the species/area curve developed in a preliminary study. A complete species list was made within the entire 10 X 10m quadrat to insure that rare plants were represented. All vascular plants and the common mosses and liverworts were sampled.

At least one soil pit was dug in each sample block, depending on variability in site conditions. The soil profile was described, including thickness of diagnostic horizons, texture of each horizon, depth to mottling or gleying, and rooting depth. Rock fragments were examined to determine mineralogy. The spatial distribution of soil types, drainage, slope, and aspect within the blocks was determined and mapped.

Data Analysis to be Completed in 1993-94

Stand Structure:

Crown length will be derived from tree height measures and basal areas will be derived from the dbh measurements. Crown length will be calculated from tree height and height to live crown measures. The following stand descriptors will be used to characterize stand structure: plant height, diameter at breast height (dbh), crown length, total tree density (stems/ha), density by species, total basal area (m^2/ha), and basal area by species.

With bivariate interpolation, the values of all stand descriptors will be calculated for the 10 X 10m quadrats of the contiguous grid which were not sampled. These interpolated values will then be used in all subsequent analyses of stand structure.

Non-taxonomic richness and equitability diversity measures will be calculated for all stand structural descriptors (Toshihiko 1993, Kohyama 1993, Gove et al. 1991, McMinn 1992, Lu and Buongiorno 1993). The Berger-Parker index will be used as the measure of evenness, and the number of size-classes of each of the structural descriptors will be used as the measure of richness (Magurran 1988).

The jack-knife technique will be used to improve the estimate of a diversity statistic, to obtain the standard error of the estimate and to attach confidence limits. Jack-knifing produces a series of normally distributed pseudovalues, of which the mean is the best estimate of the diversity measure (Magurran 1988).

The standard deviation, derived from the variance measures (see below), will be used to compare absolute values of variability of each of the stand decriptors. To compare the relative change of variability of the stand descriptors with each other with scale and time, the coefficient of variation will be used as the variability measure (Johnson 1949, Freese 1961, Busing and White 1993). Both variability measures will be calculated from the sample means.

The degree of variability in each stand descriptor and its change over a range of scales from 10 X 10m to 120 X 120m will be determined. Estimates (quadrat-means) of each stand descriptor, standardized to 1.2 ha, will be compared to the corresponding mean value taken from all (replicate) stands within each age-class of a stand type at each of the scales or quadrat sizes. The results of this exercise depends on the starting point from which the sample quadrats (scales) expand within the block, thus all measures of the 5 possible starting positions will be used (Busing and White 1993).

The variability measures of the descriptors among samples at each scale will be calculated at 10 X 10m to 60 X 60m quadrat sizes in increments of 10 X 10m for the 1.2 ha blocks, or 10 X 10m to 40 X 40m in increments of 10 m for the 0.8 ha blocks. Variability measures of the central quadrats will be taken from 10 X 10m to 40 X 40m scales. Variability measures from larger quadrats up to 120 X 120m (or 80 X 80m) will be taken from one randomly chosen corner of each of the blocks (Busing and White 1993).

An ANOVA will be used separately for each stand descriptor to determine if differences exist in the variability of stand descriptors at different scales of similar-aged plantations. Further, an ANOVA will be used separately for each stand descriptor to determine if differences exist between the age-classes at each of the scales of the plantations.

Coarse woody debris will be sampled by size class, species, and vertical angle during the summer of 1994 using line transect methods adapted from fuel inventory work. These methods are currently being defined. Habitat relationships for American marten will be developed in cooperation with personnel from NBDNRE and Wildlife Habitat Canada.

Species Composition and Taxonomic Diversity:

Measures of species richness, evenness, and species lists will be used to characterize stand-level (alpha) diversity. The Shannon-Wiener index is one of the most commonly used measures (Peet 1974) and meets the criteria established by Elliot (1990). This index will be calculated for each sample plot from the number of species and relative cover of each species. Species richness will be expressed simply as the total number of species per plot. Evenness or equitability will be calculated as a ratio of the observed diversity (Shannon-Wiener index) to maximum diversity.

The pattern of species abundances within each community will be examined graphically as described by Magurran (1988). A community may follow one of several possible species abundance models which are thought to reflect the way in which species partition resources. Change in the abundance pattern, for example after disturbance or with succession, indicates that there has been a change in resource partitioning within the community.

Additions, deletions and changes in abundances of species will be examined for all species individually. This is necessary because large compositional changes can occur without changes in the diversity indices. This analysis will be facilitated by grouping species into categories based on function (reproductive characteristics, rooting habit, etc.) or life-form. Changes in the abundance of species or functional groups will be plotted over time (development stage) for each disturbance scenario and site type combination. These changes will be compared to the species requirements to develop hypotheses which explain the functional relationships between disturbance and diversity patterns.

RESULTS AND DISCUSSION

Approximately 75% of our field time in 1992 and 50% in 1993 was spent in locating sample stands. In addition, Dr. J. Loo-Dinkins assisted in stand location as part of a related study of genetic diversity. A large number of potential stands generated from the GIS data bases were visited in the field to assess suitability. In addition, DownEast Timberlands Ltd. and J.D. Irving Ltd. provided stand type maps which were used to determine stand composition before harvesting on private lands.

Careful attention was paid to insuring that all sample stands were comparable in terms of stand type and site conditions. Stands that did not meet the minimum criteria of pre-disturbance vegetation type, soil type, drainage, age and disturbance type were rejected. In addition, because of the land-use history in the region, a large number of stands occurred on old fields. These were rejected because they appeared to differ in stand structure and composition. Many other stands were rejected because they were too small in size or had evidence of recent cutting. Of the 25 natural budworm-origin stands that were visited, 4 were selected and sampled. Three of 71 naturally regenerated clearcuts were sampled. Nine (3 per age class) plantations were selected and sampled from a total of 66 plantations that were visited. Most of the plantations were black spruce, although two white spruce and one Norway spruce plantations were included as well. All sampled stands are listed in Appendix II.

Because of the shortage of naturally regenerated clearcuts, data analysis in 1993-94 will concentrate on describing diversity patterns over time in plantations and comparing plantations to budworm-origin stands. These two disturbance types, intensive human disturbance and natural disturbance, will give realistic estimates of the range of disturbance-diversity effects to be expected in this region. Work in 1994-95 will concentrate on locating and sampling additional naturally regenerated clearcuts. Our objective is to sample at least three stands per age class, as we did in the plantations. This will allow direct statistical comparisons of diversity patterns over time between plantations and naturally regenerated clearcuts.

Drainage was assessed by inspection of depth of mottling or gleying, thickness of forest floor, and rooting depth. All stands have a mix of well drained to poorly drained sections, mainly due to micro-relief. The average slope of the stands is about 4%. Most sites are predominantly imperfectly to moderately well drained (Zelazny et al. 1989). Soil types (ST) in the stands include ST 1, 2 and 3. The vegetation types (VT) include predominantly VT 1, 2 and 3 (Zelazny et al. 1989). Relatively uniform stands of red spruce, black spruce and balsam fir occur on these sites.

Results of the preliminary studies regarding species-area curves and sample intensity for stand structure analysis are presented in Appendices III and IV. These results were applied in the sampling carried out in 1993 and will be used in all future sampling. Because relatively little research has been done on variability in stand structure resulting from different disturbances, the methods developed in this study will have immediate application in biodiversity research.

Fundy Model Forest Component

This project is a large, integrated study of diversity which is funded by Forestry Canada Green Plan (Forestry Practices), the Cooperation Agreement on Forest Development (NBFRAC), and the Fundy Model Forest (FMF). Funding from FMF was used to support fieldwork in fall 1993, particularly related to the assessment of site conditions (site class). Funds have been used for undergraduate student salaries, travel purchase of supplies and equipment.

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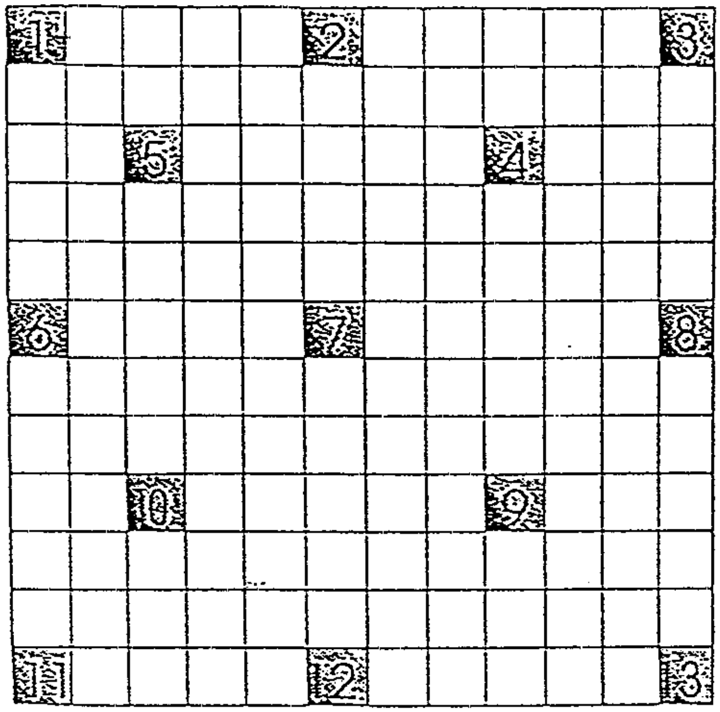
APPENDIX I

Layout of the 10 X 10m sample quadrats within a 120 X 120m block. The thirteen 10 X 10m quadrats within the 80 X 80m blocks are similarly arranged.



APPENDIX II

List of Sampled Stands

Abbreviations:

FNP = Fundy National Park.
NS = Norway spruce
bF = balsam fir
rS = red spruce
bS = black spruce
wS = white spruce
wB = white birch.

NATURAL STANDS

Stand identification: FNP X.
Latest budworm disturbance: '76.
Site class: ST: 2

Stand identification: FNP XII.
Latest budworm disturbance: '76.

Stand identification: FNP XIII.
Latest budworm disturbance: '76.
Site class: ST: 2

Stand identification: FNP #10.
Latest budworm disturbance: '76.
Site class: VT: 4 or 1, ST: 2 or 6, TU: 8 or 2.

NATURALLY REGENERATED CLEARCUTS

Map: 5958
Stand: 9053 and 9051
Year of cut: approx. '89

Map: 5958
Stand: 2889 and 2493
Year of cut: approx. '75.

Map: 6255
Stand: 8560
Year of cut: '50 to '55.
Site class: ST: 4

ARTIFICIALLY REGENERATED CLEARCUTS

Plantations 3 to 6 years:

Map: 6156
Stand: 6211 and 6207
Year of planting: '87.
Site class: VT: 1, ST: 1, TU: 5.

Map: 6057
Stand: 5134
Year of planting: '87.

Stand identification: probably map: 6058, stand: 9091
Year of planting: approx. '87
Site class: VT: 1, ST: 1 and 2, TU: 5.

Plantations 10 to 12 years:

Map: 6058
Stand:3153
Year of planting: '83
Site class: VT: 2, ST: 4 or 7, TU: 2 or 1.
Note: wS

Map: 6058
Stand: 4744
Year of planting: '83.
Site class: VT: 1 or 2, ST: 4, TU: 2
Note: wS

Map: 6058
Stand: 6244
Year of planting: '81
Site class: VT: 6, ST: 3 or 4, TU: 9 or 7.
Note: Block size of 80x80 m.

Plantations of 14 to 19 years:

Map: 6058
Stand: 3818
Year of planting: '79
Site class: VT: 2, ST: 1, TU: 5.

Map: 5957
Stand: 7509
Year of planting: '79

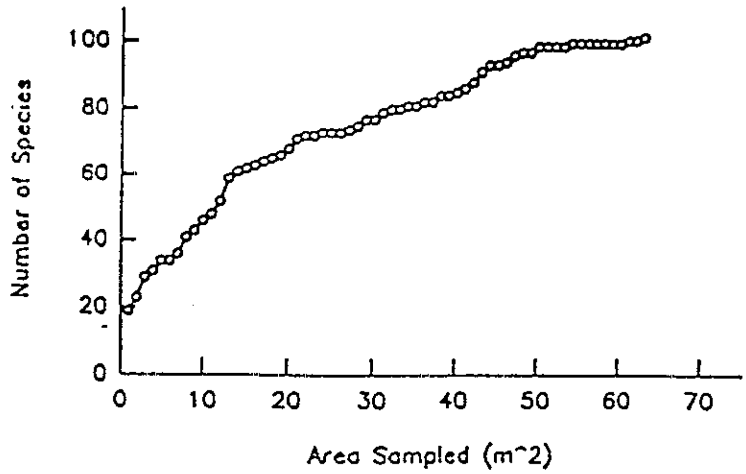
Map: 6056
Stand: 3676 and 3875
Year of planting: '76
Site class: VT: 1, ST: 1 or 6, TU: 5 or 2.

Plantation 73 years:

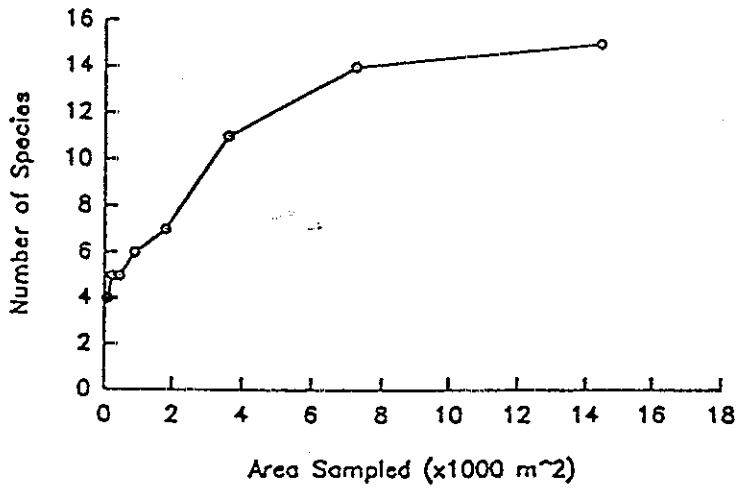
Stand identification: St. Martin.
Year of planting: '20.
Site class: ST: 4 or 6
Notes: NS plantation. Block size of 80x80 m.

Species Area Curves by Vegetation Layer

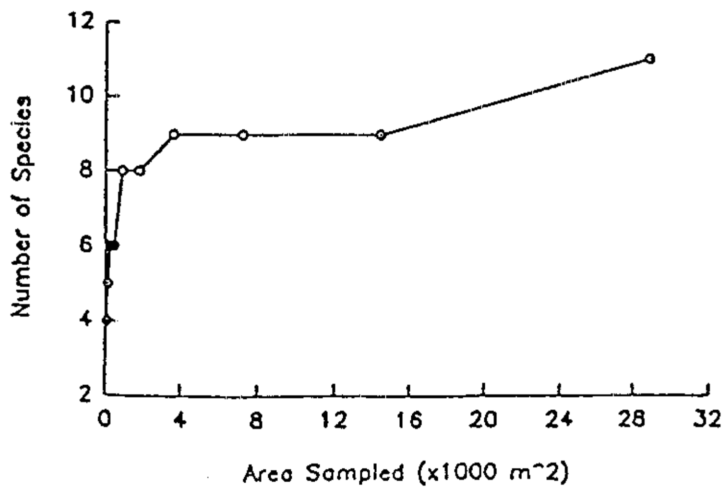
Herbaceous Stratum



Shrub Stratum



Tree Stratum

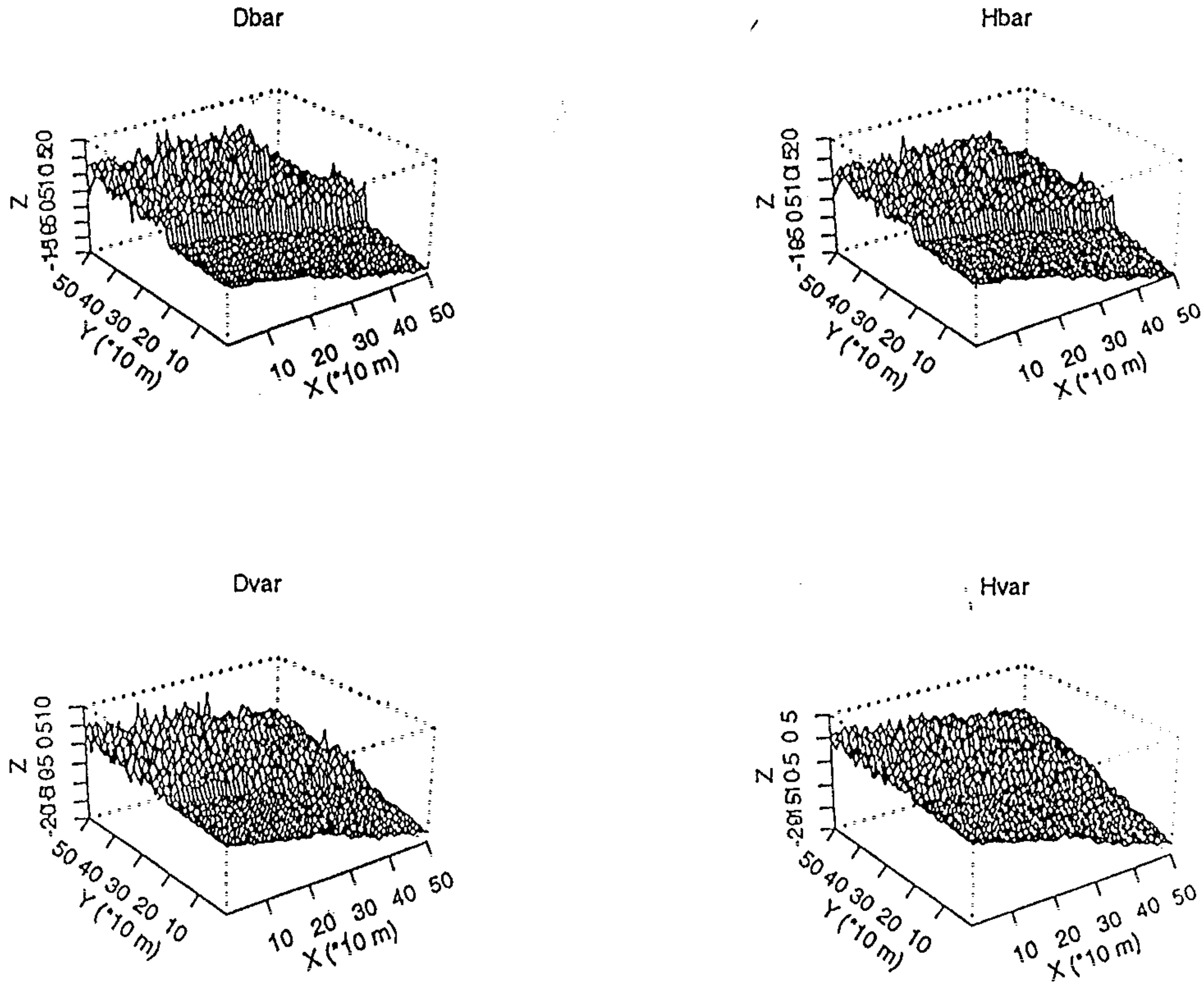


APPENDIX IV

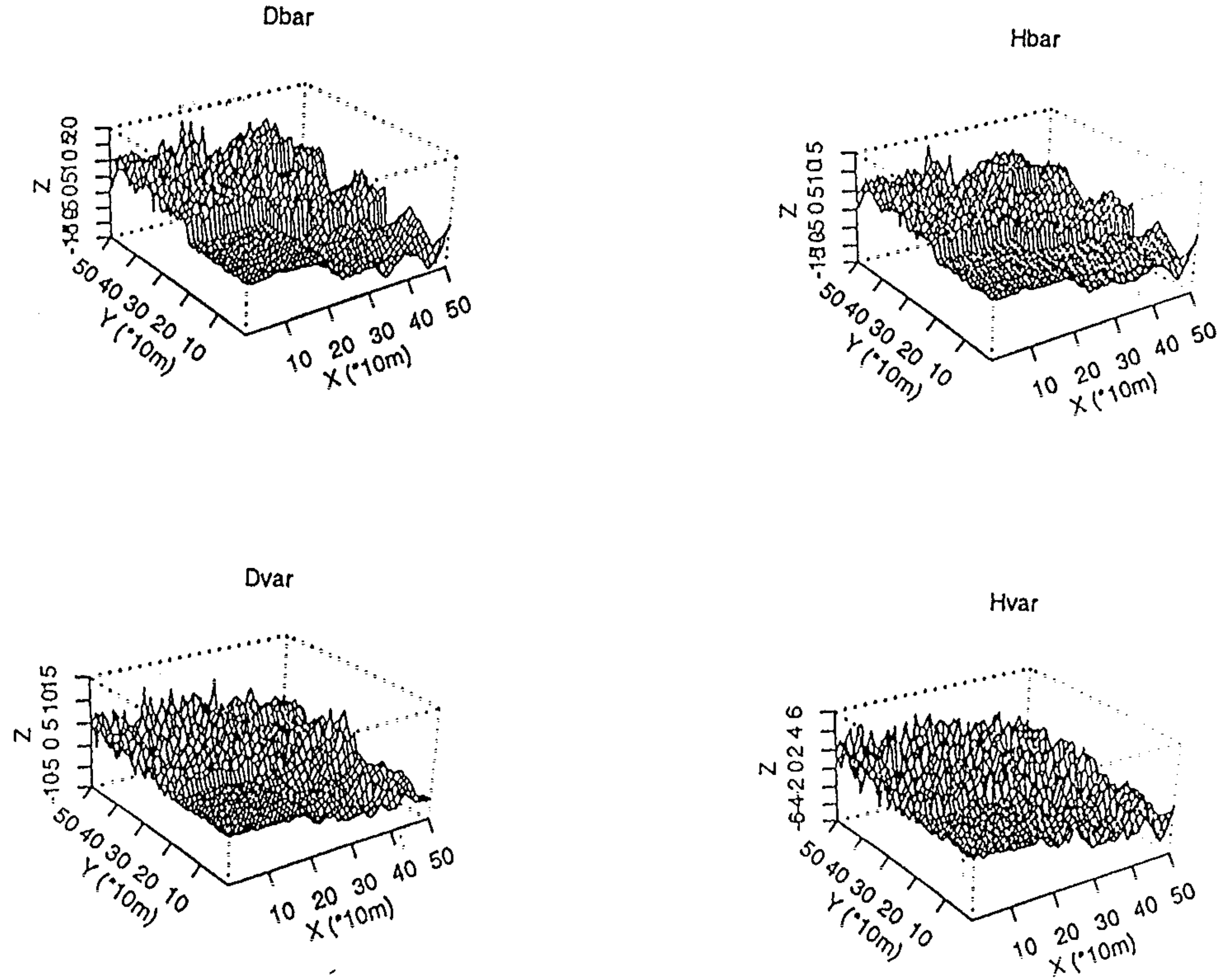
Results of Bivariate Interpolation With Different Sample Intensities

Sample intensity = percent of total stand area sampled, corresponding to number of 10 X 10m quadrats sampled
Dbar = mean tree diameter (per 10 X 10m quadrat)
Hbar = mean tree height
Dvar = variance of diameter
Hvar = variance of height

Residuals (Obs.-Exp.) of Forest 2
A 500*500 m Plot, uniformly sampled with 5 10*10 m Subplots
(Sample intensity: 1/5%, ncp=4)



Residuals (Obs.-Exp.) of Forest 2
A 500*500m Plot, uniformly sampled with 289 Subplots
(Sampling Intensity: 11.%, ncp=4)



FUNDY MODEL FOREST
YEAR END REPORT
1995

PROJECT: Effects of Forestry Practices on Species Composition, Diversity, Stand Structure and Succession

M.R. Roberts, Faculty of Forestry and Environmental Management, University of New Brunswick

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GOALS:

1. Enhance the capability to predict and minimize the impact of forestry practices on the ecosystem.

2. Establish the knowledge base necessary to develop forest management systems that more closely approximate natural disturbance regimes in terms of impacts on biodiversity.

3. Develop practical forest management guidelines for conserving biodiversity.

OBJECTIVES:

1. Assess response of herbaceous species to harvesting with and without site preparation.

2. Determine effects of different disturbance severities on herbaceous layer species composition and diversity.

PROJECT DESCRIPTION:

Phase 1:
The overall project was initiated in 1993 with the following objectives: 1) Compare effects of human and natural disturbances on plant species composition, alpha diversity and structural diversity, and 2) Determine changes in composition and diversity of vascular plant species and stand structure with successional time in response to human disturbance *vis a vis* spruce budworm disturbance.

A chronosequence for each of the human-caused disturbance scenarios on poor-moist sites was selected (Appendix 1). Three black spruce plantations in each of three age classes (5-7, 10-12, and 14-16 years) were sampled (total of 9 plantations). Three multi-aged stands of spruce budworm origin and 3 naturally regenerated clearcuts (7, 18 and 38 years) were sampled. The naturally disturbed (spruce budworm origin) stands are being used as a control for comparison with the human-caused disturbances.

Changes in structural diversity with spatial scale (10X10m to 60X60m) and stand age have been analyzed and compared among the three disturbances. The measures used are the coefficient of variation of stem density, tree diameter, height, crown length and basal area, and diversity indices for each structural variable based on the number of density or size classes present (Appendix 2).

The disturbance history of each stand has been documented (Appendix 3) and the effect of treatment and stand age on diversity (Shannon-Wiener index, Simpson index and species richness) of ground vegetation is currently being analyzed (Appendix 4). Analysis of changes in species composition of the dominant species and rare species in the ground layer is also in progress. Coarse woody debris has been sampled in each stand and analysis is in progress. A refereed journal article is in press (Ecological Applications) and other papers based on this work have been presented at meetings of the Model Forest Network, the Greater Fundy Ecosystem Research Group, and meetings of several other national and international ecological organizations. Final results on stand structural diversity were published in a M.Sc. theses this year. Two B.Sc. senior theses, which summarize results on taxonomic diversity and coarse woody debris, will be completed in May 1996.

The key findings from Phase 1 of this study with respect to structural diversity are as follows:

1. Based on the coefficient of variation of the structural variables used in this study, structural diversity in 5-16 year-old plantations may equal or exceed that in natural stands.

2. Residual stems (larger and older stems which survived the disturbance) are an important source of structural variability.

3. Structural diversity in natural stands was related to the wide range in stem sizes resulting from the spruce-budworm outbreak.

4. Structural diversity in young plantations was related to the presence of residual stems. Decreases in diversity with plantation age were apparently related to the mortality of many residual stems.

5. In addition to the coefficient of variation, absolute stem densities and sizes should also be considered for a clearer picture of stand structural diversity.

The key findings with respect to species composition and diversity are as follows:

1. There were no obvious effects of time and treatment on species diversity and composition in cutover stands.

2. There were noticeable differences in species composition and diversity in response to changes in site conditions from VT-2 to VT-7.

3. Cutovers were dominated by Sphagnum spp., bunchberry (Cornus canadensis), Schreber's moss (Pleurozium schreberi), and haircap moss (Polytrichum spp.). Budworm-origin stands were much the same, with the addition of Dryopteris spp.

Phase 2:

The second phase of this study was established in 1995, within the Hayward Brook Watershed (south of Petitcodiac in the Fundy Model Forest) to assess effects of treatments in the first year after disturbance (Appendix 1). This study is integrated with bryophyte studies at UNBSJ (Department of Biology). The objectives are to assess the response of herbaceous species to harvesting with and without site preparation and to assess effects of different disturbance severities on herbaceous layer species composition and diversity. This portion of the study complements the first phase by providing information on initial response of herbaceous layer species following harvesting.

A total of 169, $5m^2$ herb plots were located in two distinct blocks separated by a branch of the Hayward Brook (Appendix 5). The harvested blocks covered approximately 55ha. Plots were placed on transects which started in the riparian buffer strip and ran upslope. The spacing between plots was 50m and approximately 50m between the transects. The overstorey and understorey of each stand in the harvest blocks were sampled and each stand was assigned to a site class (Appendix 6).

All sample plots were established and sampled before harvest from May 16 to July 14, 1995. The area was harvested August 1-19 and portions were scarified on September 19-22. Post-disturbance measurements will be done next year due to the late date of site preparation this season. Some plots located in buffer zones and in the uncut stand surrounding of the harvested site will be used as controls for this study.

For sampling the pre-harvest herbaceous layer, each $5m^2$ herb plot was divided into four quadrats. Percent cover of all species of vascular plants was estimated by quadrat. A preliminary list of the species found before harvest is given in Appendix 7.

Environmental data collected on each plot included macrotopography, microtopography, crown closure, and nutrient availability. Macrotopography consisted of slope, slope position, aspect, stand type and substrate. The microtopography measured in each quadrat included forest floor depth, forest floor composition (coniferous, deciduous or moss), slope and slope position. Crown closure was estimated with a densiometer in quadrats one and three based on the average of two readings from two different observers. Adjacent to all the quadrats, litter, soil and plant tissue (Maianthemum canadense) samples were collected for laboratory analysis. Samples were gathered in brown paper bags, and air dried (soil and forest floor) or oven dried (plant tissue).

The following laboratory analyses were conducted on the mineral soil and forest floor samples: pH, carbon-nitrogen (C/N) ratio, organic matter content (OM), concentrations (meq/100g) of calcium (Ca), potassium (K), magnesium (Mg) and concentration (ppm) of phosphate (P). Soil texture (proportion of silt, clay and sand), was also assessed for 88 sample plots located on every second transect.

Maianthemum canadense was chosen for plant tissue analysis because it was a ubiquitous species within the study area. Tissue nutrient concentrations provide another measure of nutrient availability in addition to forest floor and mineral soil nutrients. Approximately 20 leaves were collected outside each plot within a 3m radius. Plant tissue analysis was conducted for Ca, K, Mg, P and N concentrations.

All laboratory analyses have been completed. Analysis of data collected during the 1995 field season is in progress. The main topic of a B.Sc. Honors Thesis in Biology is the pre-harvest species composition in the sample plots and how it is related to variation in the environmental (site) factors. These results will establish the baseline information needed to assess post-disturbance vegetation response.

The schedule below was followed during the 1995 field season:

- May 16 / June 1
  - Layout of 169 permanent sample plots
- June 1 / June 12
  - Overstorey sampling and site classification
- June 13 / July 14
  - Pre-harvest inventory
  - Collection of litter, soil, plant samples

° July 15 / August 31
  - Laboratory analysis of litter, soil and plant samples
  - Computer data entry

° August 31 / Present
  - Data analysis

DELIVERABLES:

The deliverables for Phase 1 of the project (see 1994 proposal) are stated below:

1. Graphs of changes in species richness and diversity indices over time on each of the human disturbances.

2. Graphs of changes in stand structure variability over time on each of the human disturbances.

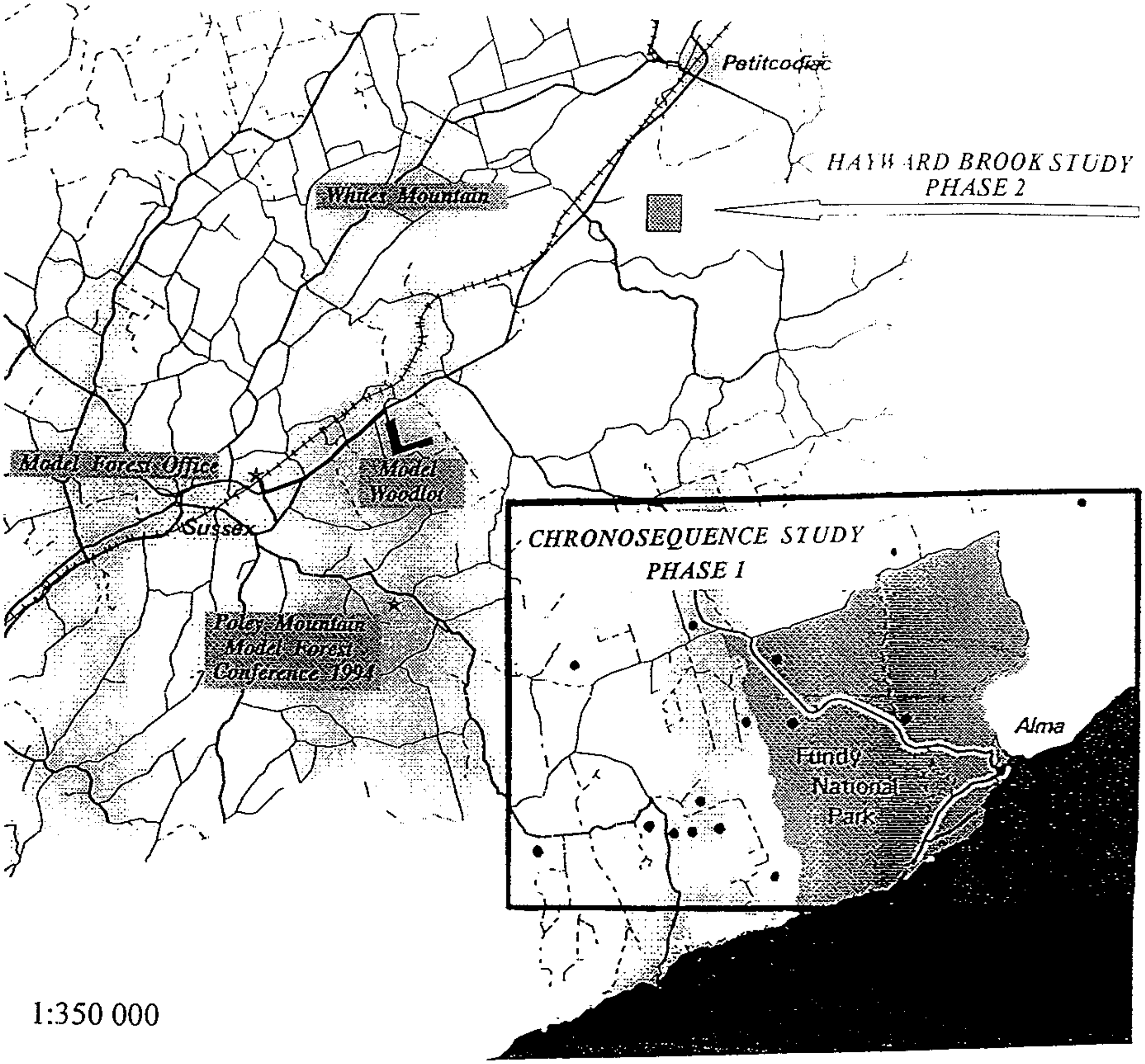
3. Comparisons of species diversity and structural diversity after human disturbances with spruce budworm disturbance.

All deliverables have been completed in full and results are presented in Appendices 2 and 4. It was not possible to assess changes over time in the naturally regenerated clearcuts because an insufficient number of stands of different ages was available to construct a chronosequence.

Deliverables for the first year of Phase 2 of the project will be completed by the end of the annual funding period (March 31, 1996).

APPENDIX 1

STUDY AREA



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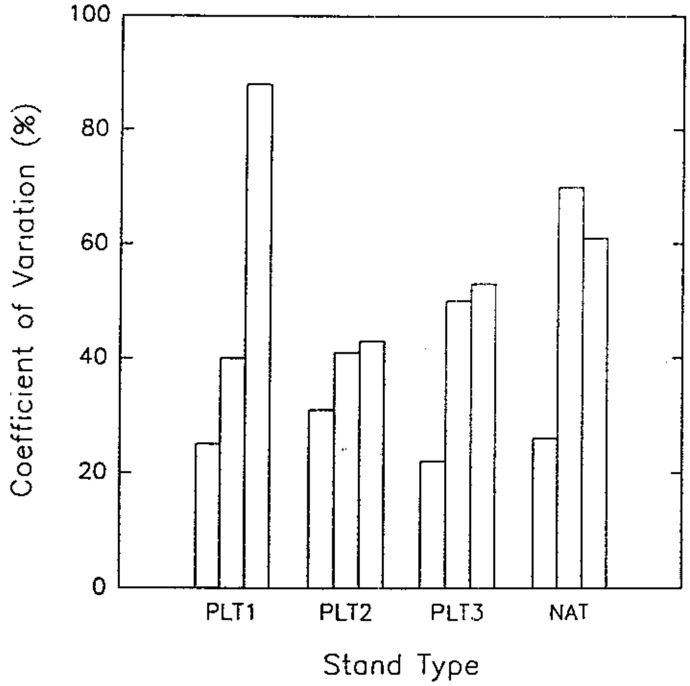
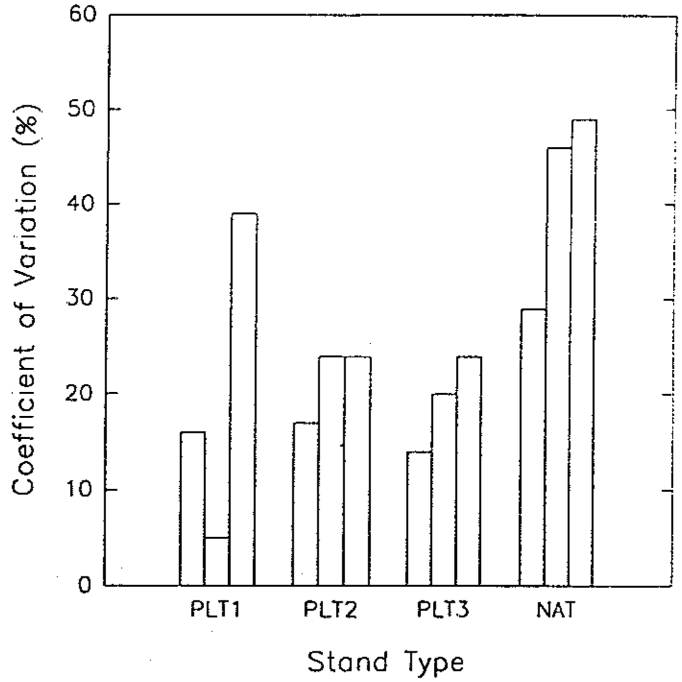


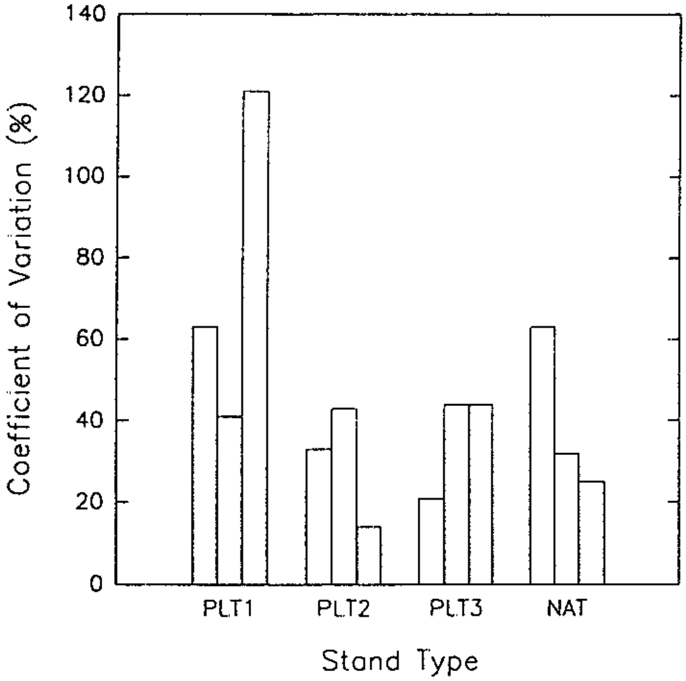
COEFFICIENT OF VARIATION FOR DENSITY IN INDIVIDUAL STANDS BY STAND TYPE.



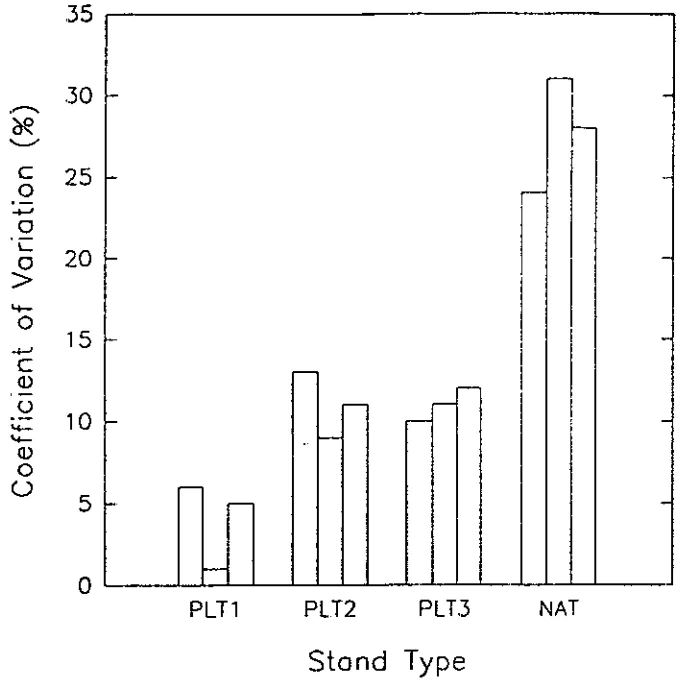
COEFFICIENT OF VARIATION FOR DBH IN INDIVIDUAL STANDS BY STAND TYPE.

LEGEND

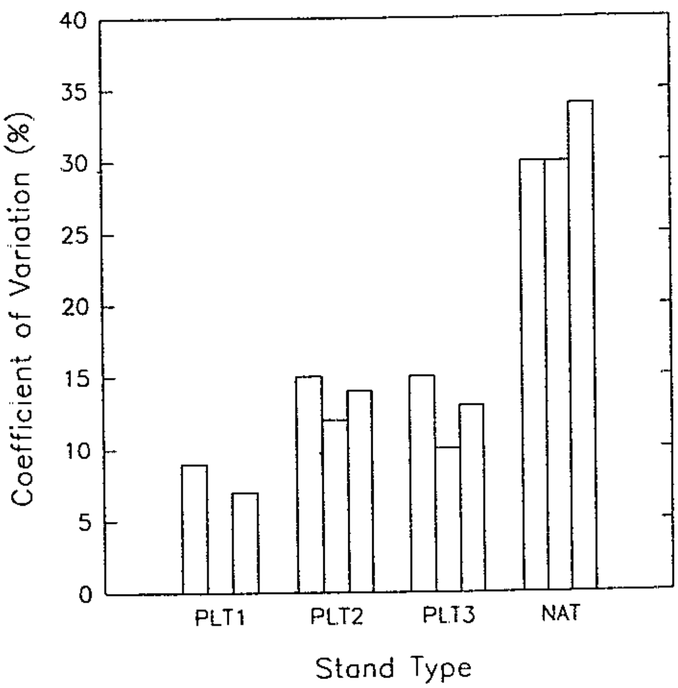
PLT1 - PLANTATIONS, 5-7 YEARS-OLD
PLT2 - PLANTATIONS, 10-12 YEARS-OLD
PLT3 - PLANTATIONS, 14-16 YEARS-OLD
NAT - NATURAL STANDS OF SPRUCE-BUDWORM ORIGIN



COEFFICIENT OF VARIATION FOR BASAL AREA IN INDIVIDUAL STANDS BY STAND TYPE.



COEFFICIENT OF VARIATION FOR HEIGHT IN INDIVIDUAL STANDS BY STAND TYPE.



COEFFICIENT OF VARIATION FOR CROWN LENGTH IN INDIVIDUAL STANDS BY STAND TYPE.

LEGEND

PLT1 - PLANTATIONS, 5-7 YEARS-OLD
PLT2 - PLANTATIONS, 10-12 YEARS-OLD
PLT3 - PLANTATIONS, 14-16 YEARS-OLD
NAT - NATURAL STANDS OF SPRUCE-BUDWORM ORIGIN

APPENDIX 3

Disturbance history and site information by study stand of (A) artificially regenerated clearcuts, (B) naturally regenerated clearcuts, and (C) stands of spruce-budworm origin

Stand no.	Treatment (date, type)	Scarification (date, type)	Date and species planted[a]	Herbicide (date, type)	Veg. type[b]	Soil type[b]	Slope (%)	Aspect (°Az)	Elev. (m)
A. Artificially regenerated clearcuts									
9091	1987 Clearcut	1987 Light chains	1988 NS	1990 Vision	2	1,2	3		270
6211	1984 Clearcut	1985 Chains	1986 bS	1988 Vision	6	1	4	250	270
5134	1983 Clearcut	1985 Chains	1987 bS	1988 Vision	2		1-5	90	290
3153	1981 Clearcut	1982 Crusher	1983 wS	1986 Vision	6	2,4,7	5		270
4744	1982 Clearcut	1982 Barrel and chain	1983 wS	1986 Vision	2	4	1-2		270
6244	1978-'80 Clearcut	1980 Barrel and chain	1981 bS	1983 245-T 1985 Vision	2	3,4	1-5		260
3818	1975-'76 Clearcut	1978 Barrel and chain	1979 bS	1983 245-T	7	1	2-3	80	270

APPENDIX 3 (continued)

Stand no.	Treatment (date, type)	Scarification (date, type)	Date and species planted	Herbicide (date, type)	Veg. type	Soil type	Slope (%)	Aspect (°Az)	Elev. (m)
A. Artificially regenerated clearcuts									
7509	1973 Clearcut	1978 Barrel and chains	1979 bs		2		4	136	290
3676	1976 Clearcut	1976[b] Barrel and chains[b]	1977 bS		2	1,6			300
B. Naturally regenerated clearcuts									
9054	1986 Clearcut				3	i	i		270
2889	1975 Partial clearcut			1985 Vision	2	i	i	44-240	270
8560	1955 Clearcut[d]				7	4,6	10	210	290

APPENDIX 3 (continued)

Stand no.	Treatment (date, type)	Scarification (date, type)	Date and species planted	Herbicide (date, type)	Veg. type	Soil type	Slope (%)	Aspect (°Az)	Elev. (m)
C. Stands of spruce budworm origin									
"FNP X"	Budworm origin				2	2	1- 3	60-340	300
"FNP XII"	Budworm origin				2		1-10	60-240	290
"FNP XIII"	Budworm origin				2	2	1		320

[a]Species codes: NS=Norway spruce (*Picea abies* (L.) Karst.); bS=black spruce; wS=white spruce.
[b]From NBDNRE site classification system (Zelazny *et al.* 1989).
[c]Approximate date and most probable treatment and apparatus.
[d]Naturally regenerated pasture.

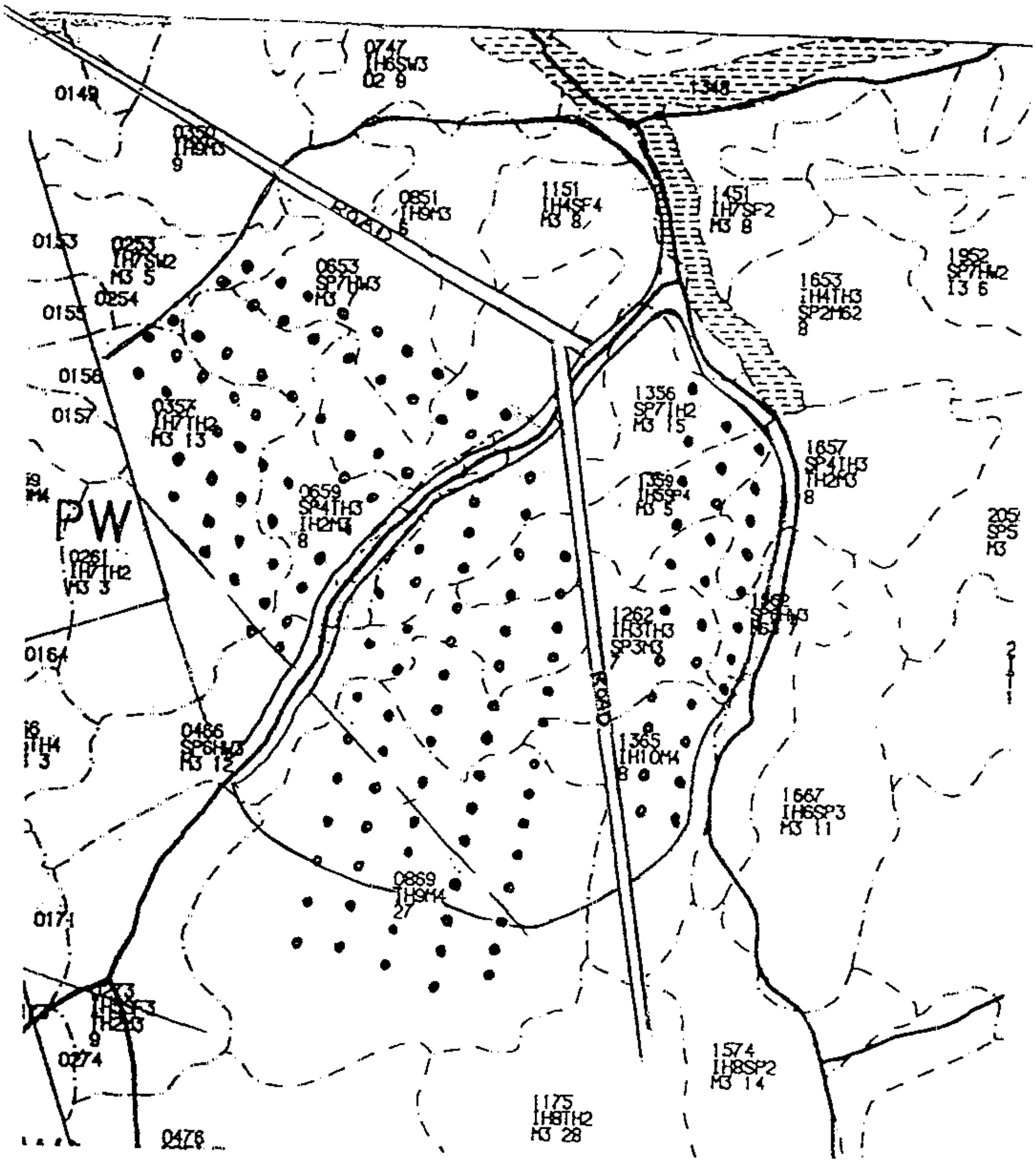
APPENDIX 4

Effect of treatment and time on stand composition (below one meter) as measured by three diversity indices

TREATMENT DATE	SHANNON INDEX	RECIPROCAL SIMPSON INDEX	SPECIES RICHNESS	MAP-STAND NUMBER
Herbicided plantations*				
1983	2.27	5.33	100	6058-3818
1985	1.77	3.37	65	6058-6244
1986	2.05	4.34	113	6058-3153
1986	1.82	3.25	74	6058-4744
1988	1.52	2.41	76	6057-5134
1988	3.00	10.91	112	6156-6211
Non-herbicided plantations*				
1973	1.95	3.45	75	5957-7509
1976	2.24	5.74	69	6056-3676
1987	2.24	6.28	64	6058-9091
Naturally regenerated clearcut				
1986	2.84	10.24	83	5958-9054
Naturally regenerated un-cultivated old field				
1955	2.86	8.62	110	6255-8560
Budworm origin				
Not Applicable	1.93	3.05	77	Fundy Park
Not Applicable	2.17	5.36	48	Fundy Park
Not Applicable	2.25	5.49	72	Fundy Park

*Stands listed by date of herbicide treatment or date of scarification

HAYWARD BROOK WATERSHED
STUDY AREA



HAYWARD BROOK
STAND OVERSTOREY AND UNDERSTOREY COMPOSITION

STAND NO.	OVERSTOREY [1] Dominant Species	Basal area m²/ha	Density #tree/ha	Mean dbh cm	UNDERSTOREY [2] Density # tree/ha	SITE CLASS [3] VT	ST	TU
1356	BS [4]	12.00	1207	15.11	800	7	3	10
	RM	6.67	345	15.56	0			
	RS	6.00	196	7.04	100			
466/1562/1657	BS	16.00	1226	13.41	1200	5	3	7
	WB	6.00	514	15.28	0			
	RS	3.50	146	9.42	1250			
1365/869	WB	11.50	848	10.75	0	8	6	12
	RM	7.50	1497	7.15	50			
	TA	4.50	212	14.75	0			
653	RM	8.00	318	20.07	0	7	5	12
	RS	8.00	265	22.60	267			
	TA	5.33	83	30.00	0			
1359	RM	6.00	405	15.67	0	7	3	10
	WB	6.00	393	11.11	0			
	TA	3.33	50	19.67	0			
1262	TA	10.00	198	26.53	0	5	6	6
	WB	8.67	627	15.67	0			
	RM	4.00	537	10.67	33			
659	WS	13.33	320	26.90	133	11	2	9
	RM	10.00	496	20.81	0			
	BF	5.33	459	17.33	2300			
357	WB	21.33	1158	17.20	0	9	5	12
	RM	14.00	2237	10.67	33			
	WP	2.00	14	32.33	33			

1. Based on the average of 3 to 4 prism sample plots (stems ≥ 5 cm dbh).
2. Based on the average of 3 to 4 , 5.64 m radius sample plots (stems < 5cm dbh).
3. Vegetation type (VT), soil type (ST) and treatment unit (TU) determined from the Field Guide to Forest Site Classification in New Brunswick, Harvey-Harcourt site region.
4. Species codes:

BF: Balsam fir
BS: Black spruce
RM: Red maple
RS: Red spruce
TA: Trembling aspen
WB: White birch
WP: White pine
WS: White spruce

HAYWARD BROOK WATERSHED - PRE-HARVEST SPECIES LIST

Abies balsamea
Acer pensylvanicum
Acer rubrum
Acer saccharum
Acer spicatum
Achillea millefolium
Actaea rubra
Alnus rugosa
Amelanchier spp.
Antennaria spp.
Apocynum androsaemifolium
Aralia nudicaulis
Aster acuminatus
Aster ciliolatus
Aster lateriflorus
Aster macrophyllus
Aster umbellatus
Athyrium filix-femina
Betula papyrifera
Botrychium matricariaefolium
Brachyelytrum erectum
Carex Arctata
Carex spp.
Carex umbellata
Chimaphila umbellata
Circaea alpina
Clintonia borealis
Coptis trifolia
Cornus canadensis
Corylus cornuta
Cypripedium acaule
Dalibarda repens
Dennstaedtia punctilobula
Dryopteris cristata
Dryopteris spinulosa
Equisetum sylvaticum
Fagus grandifolia
Fraxinus americana
Fragaria vesca
Galium circaezans
Galium triflorum
Gaultheria hispidula
Gaultheria procumbens
Goodyera tesselata
Poaceae
Gymnocarpium dryopteris
Hamamelis virginiana
Kalmia angustifolia
Lichens
Linnaea borealis
Lonicera canadensis
Luzula acuminata
Lycopodium annotinum
Lycopodium clavatum
Lycopodium complanatum
Lycopodium dendroides
Lycopodium lucidulum
Maianthemum canadense
Medeola virginiana
Melampyrum lineare
Mitella nuda
Mitchella repens
Moneses uniflora
Monotropa hypopithys
Orthilia secunda
Oryzopsis asperifolia
Osmunda cinnamomea
Osmunda claytoniana
Osmunda spp.
Oxalis montana
Picea glauca
Picea mariana
Picea rubens
Pinus strobus
Populus grandidentata
Populus tremuloides
Prenanthes spp.
Prunus virginiana
Prunella vulgaris
Pteridium aquilinum
Pyrola americana
Pyrola chlorantha
Pyrola elliptica
Ranunculus acris
Ribes americanum
Ribes lacustre
Rubus pubescens
Solidago flexicaulis
Solidago puberula
Sphagnum spp.
Streptopus amplexifolius
Streptopus roseus
Thelypteris noveboracensis
Thelypteris phegopteris
Trientalis borealis
Trillium undulatum
Vaccinium angustifolium
Vaccinium myrtilloides
Vaccinium vitis-idaea
Veronica officinalis
Viburnum cassinoides
Viola spp.

FUNDY MODEL FOREST

FINAL REPORT

NOVEMBER 13, 1997

(For 1996-97 Project Year)

Effects of Forestry Practices on Species Composition, Diversity, Stand Structure and Succession

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Fredericton, N.B. E3B 6C2

ABSTRACT

This report presents results of Phase II (Harvesting Effects Study) of the project, which was established in the Hayward Brook Watershed in spring 1995. The pre-harvest distribution of species in relation to environmental factors within the study area was determined in the first year (1995-96). Vegetation was resampled and disturbance conditions were described after harvesting in the second year (1996-97).

The study area occurs within the Continental Lowlands Ecoregion of New-Brunswick and the Anagance Ridge Ecodistrict 29 (NBDNRE 1996). Eight stand types were characterized based on overstory composition.

Percent cover of all vascular and non-vascular plants $\leq$ 1 m tall was recorded by species in 169 circular 5 m^2 sample plots before harvesting in 1995. Non-vascular plants were recorded in three broad groups (*Sphagnum spp.*, other mosses and lichens). A total of 106 species and species groups were found. Diversity indices such as the Simpson Index, Shannon-Wiener Index, maximum H' and evenness showed slight differences between stand types before harvesting. Species evenness was relatively low, i.e. 80% of the species occurred in $\leq$ 20% of the plots. Species richness averaged 15 species/5 m^2 plot. Two stands contained the greatest richness with 70-72 species. These stands occurred in portions of the watershed that contained seepage springs.

Canonical correspondence analysis (CCA) showed that 24% of the species pattern was correlated with the environmental variables chosen in this study (canopy, topography and litter). Partial canonical correspondence analysis (PCCA) was employed to partition out the individual and combined effects of the environmental variables; litter nutrient content (particularly pH, Ca, and Mg) was most highly correlated with the species pattern. Changes in community composition after catastrophic disturbance were predicted using both equilibrium and non-equilibrium models.

Disturbance intensities differed in the two harvesting treatments in the first year after harvesting. In one area that was clearcut without site preparation and planting (C), more softwood slash was created, less litter was disturbed and less mineral soil was exposed than in the other area that was clearcut, scarified (barrels and chains) and planted (CS)

Harvesting treatments had different effects on species composition and species richness In the CS treatment, 23 species were lost, 20 species invaded, and species richness decreased from 82 (pre-harvest) to 79 (the first year after harvesting). The Shannon-Wiener diversity index

decreased from 0.7842 to 0.7377. In the C treatment, 19 species were lost and 10 invaded; species richness changed from 60 (pre-harvest) to 51 (the first year after harvesting); and the Shannon-Weiner index increased from 0.5966 to 0.6578 after harvesting. The species that were lost or significantly reduced in abundance provide easily identifiable indicators of sustainable forest management which can be readily monitored. These species include *Actaea rubra, Aster ciliolatus, Aster macrophyllus, Brachyelytrum erectum, Cypripedium acaule*, *Dalibarda repens*, *Dennstaedtia punctilobula, Dryopteris sp.*, *Gaultheria hispidula*, *Goodyera tellelata, Linnaea borealis, Luzula acuminata, Lycopodium annotinum, Lycopodium complanatum, Medeola virginiana, Mitella nuda*, *Moneses uniflora, Monotropa hypopithys, Orthilia secunda, Oryzopsis asperifolia, Osmumda spp.*, *Oxalis montana*, *Prunella vulgaris, Ribes lacustre, Solidago flexicaulis, Sphagnum spp.*, *Streptopus amplexifolius*, *Streptopus roseus*, *Thelypteris noveboracensis*, *Vaccinium vitis-idaea* and *Veronica officinalis*.

Areas within the watershed containing unique vegetation communities and high diversity were delineated. These areas should be monitored closely to determine effects of harvesting on species and communities. In addition, all community types should be monitored to insure that representative examples of each type are maintained.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

INTRODUCTION

Environmentally sustainable forest resource use and development requires knowledge of how forestry practices impact the composition, diversity, structure and dynamics of the forest ecosystem. Measures of diversity along with assessments of species composition provide indices of the health of the ecosystem. Baseline data on species composition and diversity before and after harvesting have been provided by this study. Quantitative assessments of successional changes in composition and structure are essential for predicting and modeling long-term ecosystem dynamics.

The Chronosequence Study (Phase I of the overall study) provided an analysis of general patterns of change in stand structure, composition and diversity over relatively long time periods, starting at a minimum stand age of 5 years. Phase I was supported by Canada's Green Plan (Forestry Practices), Canada/New Brunswick Cooperation Agreement on Forest Development, and the Fundy Model Forest and was completed in 1995. Results were presented in a final report to the Canadian Forest Service (Roberts and Methven 1996). Phase II, the Harvesting Effects Study, complements the Chronosequence Study by providing information on the initial effects of harvesting disturbance on plant composition and diversity. This report presents results from the first two years (1995-97) of Phase II.

The first year (1995-96) of the Harvesting Effects Study focussed on the pre-harvest distribution of species in relation to site factors within the study area. The second year (1996-97) addressed disturbance conditions and vegetation response in the first growing season after harvest.

Objectives

1. Identify patterns of herbaceous layer composition and diversity in relation to soil and site conditions before harvest.
2. Assess response of herbaceous layer species to harvesting with and without site preparation.
3. Determine effects of different disturbance severities on herbaceous layer species composition and diversity.

STUDY AREA

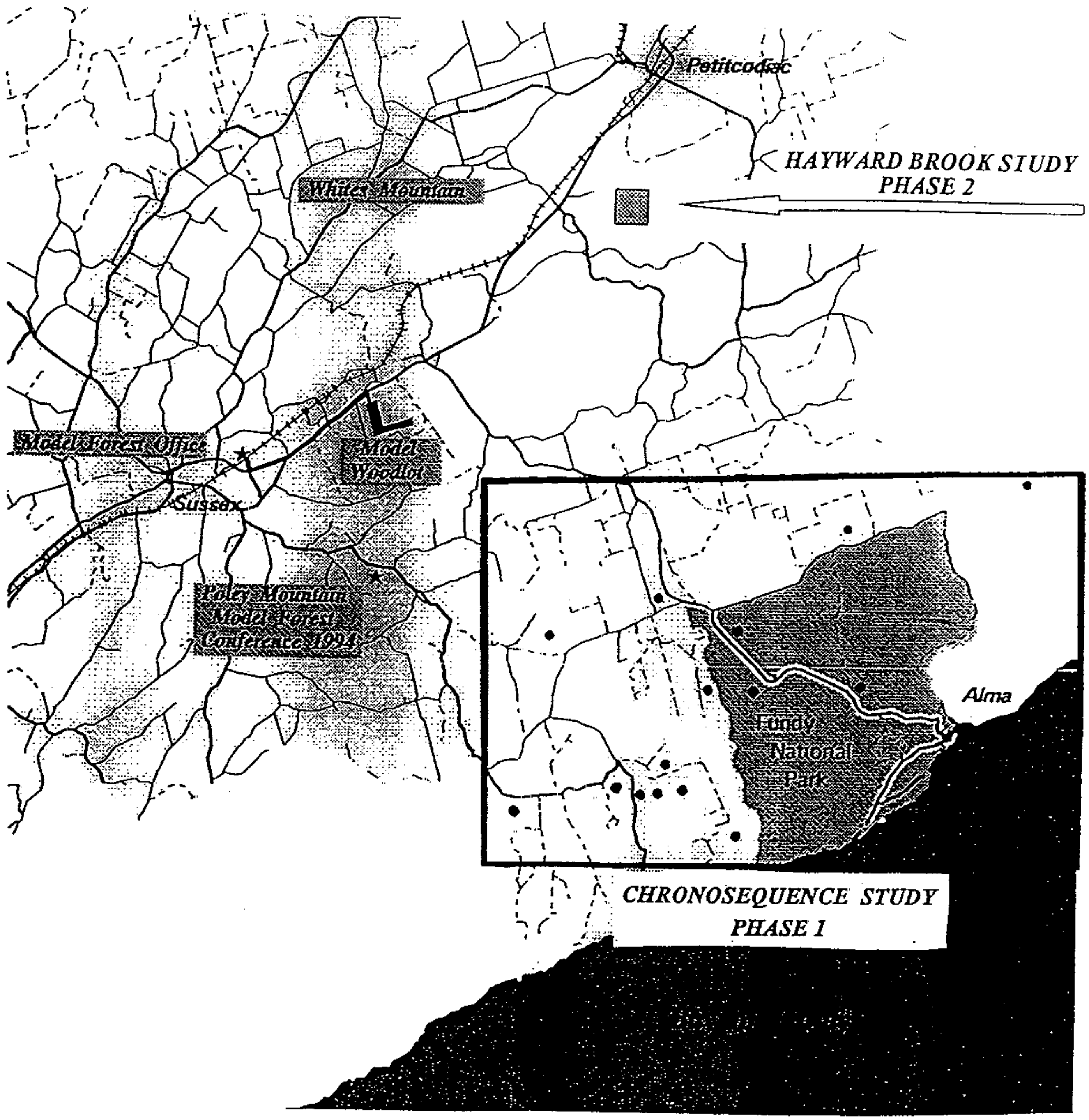
This study was established in 1995, within the Hayward Brook Watershed, south of Petitcodiac, N.B., in the Fundy Model Forest (latitude 45°53'N, longitude 65°11'W) (Figure 1). This study is integrated with bryophyte studies at UNBSJ (Department of Biology). The study area is a portion of the Hayward Brook Watershed which covers approximately 110 ha, and has predominantly NW aspect and SE aspects separated by a branch of Hayward Brook. The elevation above sea level ranges from 200 to 400 feet. The study area occurred within the Continental Lowlands Ecoregion of New-Brunswick (NBDNRE 1996). This area is part of the Acadian Forest Region (Ireland 1982).

The study area has hardwood ridge tops of white birch (*Betula papyrifera* Marshall), red maple (*Acer rubrum* L.), trembling aspen (*Populus tremuloides* Michx.) and large-tooth aspen (*Populus grandidentata* Michx). Within this stand type, the soil is well drained with a thin layer of organic matter. On mid-slopes, red spruce (*Picea rubens* Sarg.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Miller) BSP), red maple and balsam fir (*Abies balsamea* (L.) Miller) constitute the mixedwood stands. The bottom slopes are predominantely wet areas with black spruce, red spruce, red maple and balsam fir, and a thick layer of organic matter. White pine (*Pinus strobus* L.) is scattered throughout the entire area as well as a few red pine (*Pinus resinosa* Aiton) and jack pine (*Pinus banksiana* Lambert). Stand types are best described by NBDNRE's Anagance Ridge Ecodistrict 29.

Two bedrock types underlay this site. One is formed of grey-red sandstone, grey-green and red mudstone, with minor, grey and red, granule to cobble conglomerate and coal. The second bedrock, most likely infertile, is formed of greyish-green, plant bearing quartzose sandstone and quartz pebble conglomerate, with minor, red sandstone and grey mudstone, fossiliferous, bituminous limestone (McLeod *et al.* 1994).

The Sunbury and Parry soil series are found in this study area. Soil types included 2, 3, 5, and 6 which range from poorly to well drained soils. The vegetation types included 5, 7, 8, 9 and 11. These soil and vegetation types were associated with treatment units 6, 7, 9, 10 and 12 which represent dry-moderately poor mixedwood stands, moist-moderately poor mixedwood stands, moist-rich softwood stands, moist-rich mixedwood stands and dry-rich mixedwood stands (Zelazny *et al.* 1989).

Figure 1. **Location of the study area.**



METHODS

Study Design

A total of 169 permanent 5 m^2 circular plots were systematically located in two distinct blocks separated by a branch of the Hayward Brook (see Figure 3, p. 19). The plots were placed on transects which started in the riparian buffer strip and ran upslope. The spacing was 50 m between plots and approximately 50 m between the transects. All sample plots were established and sampled before harvest from May 16 to July 14, 1995. To facilitate relocating plots after harvest, the center of each plot was marked with a wooden stake flush with the ground. The three nearest trees >10 cm dbh were painted at the stump and their distances and bearings from the plot center were recorded.

The area was harvested by a Feller-buncher, the trees were delimbed on site and carried out on a Porter (6-wheel drive) from August 1 to 19, 1995. Portions of the study area were scarified by a Tree Farmer Skidder with barrels and heavy-chains, from September 19 to 22. Plot centers were relocated in spring 1996. Disturbance and vegetation measurements were done in summer 1996.

Pre-Harvest Sampling

Herbaceous layer variables

For sampling the pre-harvest herbaceous layer, each 5 m^2 herb plot was divided into four quadrats. Percent cover of all species of vascular plants was estimated by quadrat. Non-vascular plants were recorded in three broad groups: *Sphagnum spp.*, other mosses and lichens. The herbaceous layer was defined as extending from the forest floor to 1 m height, hence tree species $\leq$ 1 m tall were included. Table 1 lists all the species found in the sample plots before harvest.

Environmental variables

(a) Litter. A litter sample was taken from just outside each quadrat using a 10 cm diameter circular-cutter and the depth for each sample was determined. Percent composition of moss, needles, and leaves in the LFH layer of this sample was estimated using a 3 point

Table 1. Species list and abundances for Hayward Brook Watershed, NB., in order of frequency. Nomenclature follows Hinds (1986). Species codes are those used in plots of Correspondence and Canonical Correspondence Analyses.

Species	Species code	Frequency (%) (n=169)	Mean % cover when present	mean % cover (all quad.)
Moss spp.	66	97.63	12.38	12.09
Maianthemum canadense Desf.	58	97.04	0.82	0.80
Abies balsamea (L.) Mill	1	82.25	15.22	12.52
Cornus canadensis L.	29	79.88	2.90	2.32
Gaultheria procumbens L.	43	54.44	0.98	0.53
Vaccinium angustifolium Ait.	101	52.66	1.36	0.72
Vaccinium myrtilloides Michx.	102	51.48	1.21	0.62
Pteridium aquilinum (L.) Kuhn	82	50.89	6.76	3.44
Acer rubrum L.	3	50.30	1.94	0.98
Trientalis borealis Raf.	98	47.34	0.72	0.34
Picea glauca (Moench) Voss	73	45.56	3.52	1.61
Amelanchier sp.	9	41.42	0.38	0.16
Acer pensylvanicum L.	2	39.64	2.40	0.95
Corylus cornuta Marsh.	30	37.28	5.47	2.04
Viola spp.	106	33.14	0.62	0.21
Aralia nudicaulis L.	12	30.77	0.86	0.26
Grass spp.	45	29.59	0.47	0.14
Chimaphila umbellata (L.) Spreng.	25	25.44	0.59	0.15
Viburnum cassinoides L.	105	24.26	0.23	0.06
Coptis trifolia (L.) Salisb.	28	21.89	1.92	0.42
Lycopodium clavatum L.	54	18.34	2.96	0.54
Picea rubens Sarg.	75	18.34	5.26	0.97
Picea mariana (Mill.) BSP.	74	17.16	7.79	1.34
Lycopodium dendroidium Michx.	56	15.38	2.30	0.35
Pinus strobus L.	76	14.79	0.92	0.14
Rubus pubescens Raf.	89	14.20	3.49	0.50
Streptopus roseus Michx.	95	13.61	0.40	0.05
Kalmia angustifolia L.	48	13.61	1.27	0.17
Populus tremuloides Michx.	78	13.02	0.35	0.05
Carex spp.	23	12.43	0.65	0.08

Table 1 (cont'd)

Mitchella repens L.	63	11.83	0.38	0.04
Trillium undulatum Willd.	99	11.83	0.26	0.03
Aster macrophyllus L.	16	11.24	0.27	0.03
Lichen spp.	49	11.24	2.07	0.23
Linnaea borealis L.	50	11.24	0.93	0.10
Hamamelis virginiana L.	47	11.24	0.89	0.10
Athyrium filix-femina (L.) Roth	18	10.65	3.67	0.39
Clintonia borealis (Ait.) Raf.	27	10.06	0.25	0.03
Prenanthes spp.	79	10.06	0.88	0.09
Oxalis acetosella L. (Syn. O. montana Raf.)	72	9.47	2.44	0.23
Pyrola elliptica Nutt.	85	8.88	0.44	0.04
Dryopteris spp.	35	7.10	1.88	0.13
Medeola virginiana L.	59	7.10	0.34	0.02
Brachyelytrum erectum (Schreb.) Beauv.	21	7.10	1.74	0.12
Aster acuminatus Michx.	13	6.51	0.34	0.02
Lonicera canadensis Bartr.	51	5.92	0.40	0.02
Mitella nuda L.	62	5.92	1.06	0.06
Solidago puberula Nutt.	92	5.92	0.20	0.01
Osmunda sp.	71	5.33	5.78	0.31
Fagus grandifolia Ehrh.	37	5.33	2.47	0.13
Pyrola chlorantha Sw.	84	4.73	0.28	0.01
Galium triflorum Michx.	41	4.73	0.55	0.03
Betula papyrifera Marsh.	19	4.14	0.79	0.03
Moneses uniflora (L.) Gray	64	4.14	0.18	0.01
Sphagnum spp.	93	3.55	5.02	0.18
Pyrola americana Sweet	83	3.55	0.33	0.01
Fraxinus americana L.	38	3.55	0.60	0.02
Gymnocarpium dryopteris (L.) Newm.	46	3.55	5.88	0.21
Lycopodium annotinum L.	53	3.55	7.46	0.26
Fragaria vesca L.	39	3.55	0.85	0.03
Actaea rubra (Ait.) Willd.	7	3.55	0.31	0.01
Acer spicatum Lam.	5	2.96	0.33	0.01
Aster lateriflorus (L.) Britt.	15	2.96	0.30	0.01
Circaea alpina L.	26	2.96	1.20	0.04
Gaultheria hispidula (L.) Muhl.	42	2.96	0.25	0.01

Table 1 (cont'd)

Lycopodium complanatum L.	55	2.96	0.95	0.03
Melampyrum lineare Desr.	60	2.96	0.18	0.01
Equisetum sylvaticum L.	36	2.37	1.50	0.04
Cypripedium acaule Ait.	31	2.37	0.16	0.00
Orthilia secunda (L.) House	67	2.37	0.50	0.01
Ribes lacustre (Pers.) Poir.	88	1.78	0.54	0.01
Achillea millefolium L.	6	1.78	0.17	0.00
Thelypteris phegopteris (L.) Slosson	97	1.78	2.67	0.05
Osmunda cinnamomea L.	69	1.18	10.63	0.13
Luzula acuminata Raf.	52	1.18	0.09	0.00
Apocynum androsaemifolium L.	11	1.18	0.50	0.01
Aster ciliolatus Lindl.	14	1.18	0.44	0.01
Goodyera tesselata Lodd.	44	1.18	0.13	0.00
Monotropa hypopithys L.	65	1.18	0.25	0.00
Streptopus amplexifolius (L.) DC.	94	1.18	0.25	0.00
Dennstaedtia punctilodula (Michx.) Moore	33	1.18	3.00	0.04
Dryopteris cristata (L.) Gray	34	1.18	0.63	0.01
Thelypteris noveboracensis (L.) Niewl.	96	0.59	15.75	0.09
Vaccinium vitis-idaea L.	103	0.59	0.38	0.00
Lycopodium lucidum Michx.	57	0.59	0.13	0.00
Veronica officinalis L.	104	0.59	0.25	0.00
Acer saccharum Marsh.	4	0.59	0.13	0.00
Antennaria sp.	10	0.59	0.25	0.00
Alnus incana (L.) Moench. (syn. A. rugosa (DuRoi) Preng.)	8	0.59	0.25	0.00
Unknown	100	0.59	0.13	0.00
Dalibarda repens L.	32	0.59	0.25	0.00
Prunus virginiana L.	80	0.59	0.25	0.00
Prunella vulgaris L.	81	0.59	0.13	0.00
Populus grandidentata Michx.	77	0.59	0.25	0.00
Oryzopsis asperifolia Michx.	68	0.59	0.25	0.00
Osmunda claytoniana L.	70	0.59	1.25	0.01
Galium circaezans Michx.	40	0.59	0.13	0.00
Carex umbellata Schkuhr	24	0.59	0.75	0.00
Aster umbellatus Mill.	17	0.59	0.13	0.00

Table 1 (cont'd)

Solidago flexicaulis L.	90	0.59	0.50	0.00
Solidago sp.	91	0.59	0.38	0.00
Ribes americanum P. Mill.	87	0.59	0.13	0.00
Carex arctata Boott	22	0.59	0.25	0.00
Botrychium matricariifolium A. Br.	20	0.59	1.13	0.01
Ranunculus acris L.	86	0.59	0.13	0.00
Grand mean ± s.e.		22.77±3.39	1.74±0.28	0.46±0.17

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 30% leaf and 70% needles. The samples were dried at 55 ° Celsius for 48 hours and passed through a 2 cm wire mesh, removing leafs, branches and other forms of large debris. The pH was determined with a pH meter after adding deionized water to form a thin paste and allowing the mixture to equilibrate for one hour (McKeague 1978). Total nitrogen was determined for the sub-samples by the Kjeldahl method (Bremmer and Mulvaney 1982) using a Buchi autoanalyser distillation unit. Exchangeable cations (K, Ca and Mg) were determined by extraction of samples with 1 N NH_4OAc, pH7, and analysis of samples by atomic absorption spectrometry, using lanthanum chloride as the releasing agent for Ca and Mg (Baker and Shure 1982). Available phosphorus was obtained by extraction with dilute sulphuric acid and colorimetric analysis of the extract, using phospho-molybdo-blue method (Baker and Shure 1982). Percent carbon and organic matter were determined by dry combustion using a Leco Carbon Determinater and the formula O.M.= %C*1.72 (Anonymous 1977, Walkley 1946).

(b) Mineral soil. Mineral soil samples were taken from just outside each quadrat using a soil-corer. Samples were collected for 88 sample plots located on every second transect. Samples were dried at 55 ° C for 48 hours and passed through a 2 mm sieve, removing any prevalent root clumps. The pH, total nitrogen, exchangeable cations (K, Ca and Mg), available phosphorus, percent carbon and organic matter were measured following the same methodology as the forest floor analysis. In addition, soil texture was measured (proportion of silt, clay and sand) by the sedimentation method (Bouyoucos 1953).

(c) Plant tissue. Adjacent to each plot, 20 leaves of False lily-of-the-valley (*Maianthemum canadense* Desf.) were collected. The plant tissue of this ubiquitous species was analyzed in the laboratory for concentrations of phosphorus (P), nitrogen (N), potassium (K), calcium (Ca) and magnesium (Mg). Tissue nutrient concentrations provide an additional measure of nutrient availability.

The plant tissues samples were oven dried at 70 ° Celsius for 72 hours, ground in a Thomas-Wiley Mill / (Model ED-5) then reduced to ash in a furnace at 450 ° Celsius for three hours. The ash residue was moistened with distilled water and then 5 ml of 8NHCl was added. The samples were then placed in a 95 ° Celsius water bath for 20 minutes to allow cooling. The ashes were then filtered through a Whatman #541 filter paper using a long stemmed funnel into a 50 ml volumetric flask. The ashes were diluted to 50 ml with deionized water. This final solution was mixed with HCl-vanadate-molybdate to induce color development. Percent transmittance of all the plant tissue samples were determined using the spectrophotometer, and converted into ppm of phosphorus.

A similar process was used to determined the amount of exchangeable cations (K, Ca, Mg) but the final solution was mixed with deionized water and lanthanum-chloride. The transmittance was recorded with the spectrophotometer and converted into ppm of K, Ca, Mg (Skoog 1969).

(d) Canopy. Canopy closure was estimated in each plot with a densiometer using the average of four readings. The observations were taken in the first and third quadrats above the herbaceous layer. Two readings were taken at the same point in each quadrat, by two people reading from different directions to account for observer effects (Vales and Brunnell 1988). Total canopy closure as well as proportion of deciduous and coniferous canopy were tallied. The general stand type was described, looking at the dominant tree species in the canopy around each sample plot.

(e) Macrotopography and aspect. Macrotopography was recorded as presence/absence of pits or mounds (visually +/- 50+cm deep) and coded as flat (0), to slightly mounded and >5 m apart (1), to moderately mounded and >1 m apart (2), to very mounded and <1 m apart (3). Aspect and slope were estimated using a compass and a Suunto clinometer respectively. Aspect, i.e. compass bearing of slope, was expressed as the sine and cosine of azimuth, indicating the degree of "northness" and "eastness" respectively. Slope position was also recorded and expressed as follow (1)ridge top, (2) upper slope, (3) mid slope, (4)lower slope and, (5) flat at bottom of slope.

Stand type characterization

Stand types were delineated within the study area from stand cover type maps provided by the New Brunswick Department of Natural Resources and Energy (NBDNRE) (see Figure 3, p. 19). To describe the stand types within the study area three overstorey and understorey sample plots were measured for each stand. Also one soil pit was described within each stand type using the Field Guide to Forest Site Classification in New Brunswick (Zelazny *et al.*, 1989) to identify soil types.

A prism count was done on trees $\geq$ 5 cm dbh (overstorey), and a fixed sample plot (5.64 m radius) was used for the stems < 5 cm dbh (understorey). Number of trees and dbh were tallied for each tree species. The data from the three plots were averaged together by stand type for the overstorey and understorey samples separately. The vegetation type was also determined, using Field Guide to Forest Site Classification in New Brunswick, Harvey-Harcourt region (Zelazny *et al.*, 1989). The results are condensed in Table 2, showing the density, basal area, and the mean dbh by species for the overstorey. Density of the understorey tree species, vegetation types and soil types are also shown. Overstorey composition (% basal area) in each stand is presented in Figure 2.

Post-Harvest Sampling

The summer of 1996 was the first growing season after the harvesting disturbance. On the 169 plots established in 1995, disturbance data, herbaceous vegetation data and canopy closure data were collected. As done in the pre-harvest sampling, each plot was divided into 4 quadrats. The disturbance and herbaceous vegetation data were collected on each quadrat. Canopy closure was measured in quadrat one and quadrat three of each plot and then averaged to represent the canopy closure of the plot.

The schedule below was followed during the 1996 field season:

--May 16/ May 26 - relocate plots

--May 27/June 14 - measure disturbance

--June 24/June 26 - establish 36 permanent sample plots in buffer strips

--July 2/July 31 - measure vegetation and canopy cover

-- September 1/ Present - enter and analyze data

Table 2. Overstory, understory and site caharacteristics by stand type.

STAND A: 1356

SPECIES	OVERSTOREY BA m2/ha	density #tree/ha	dbh-mean cm	UNDERSTOREY density #small trees/ha
BSP	9.00	905.51	11.33	825.00
RM	8.00	419.62	15.92	0.00
RSP	6.00	232.34	9.28	100.00
DEAD	4.50	285.90	20.83	0.00
TA	3.00	40.84	22.75	0.00
WB	2.00	83.81	13.00	0.00
WSP	1.50	83.51	8.25	50.00
BF	0.50	44.21	3.00	5975.00
HE	0.00	0.00	0.00	25.00
WP	0.00	0.00	0.00	25.00
ALD	0.00	0.00	0.00	25.00

SITE CLASS VT	ST	TU	Plot used PLOT
7	3	10	SJ01
			SHO1
			SX01
			SZ01

STAND B: 466/1562

SPECIES	OVERSTOREY BA m2/ha	density #tree/ha	dbh-mean cm	UNDERSTOREY density #small trees/ha
BSP	23.00	1226.46	19.49	150.00
WB	10.00	924.59	14.56	0.00
DEAD	6.00	401.35	25.25	100.00
RSP	3.00	164.46	8.33	600.00
BF	1.00	31.83	10.00	1050.00
WP	1.00	12.43	16.00	0.00
RM	1.00	64.96	7.00	0.00

SITE CLASS VT	ST	TU	PLOT
			SI03
			SY05

STAND C: 1365/869

SPECIES	OVERSTOREY BA m2/ha	density #tree/ha	dbh-mean cm	UNDERSTOREY density #small trees/ha
WB	11.5	848.486907	10.75	0
RM	7.5	1497.25862	7.152381	50
TA	4.5	211.764897	14.75	0
DEAD	3.5	197.726238	30.5	175
STM	1.5	253.529131	8	900
WSP	1	110.524251	8	475
BE	0.5	32.4806002	3.5	50
BF	0.5	44.2097058	3	800
WP				250
RSP				25
BSP				100
SM				75

SITE CLASS VT	ST	TU	PLOT
			SJ07
8	6	12	SH11
			SF12
			SY10

STAND D: 653

SPECIES	OVERSTOREY BA m2/ha	density #tree/ha	dbh-mean cm	UNDERSTOREY density #small trees/ha
RM	8.00	317.67	20.07	0.00
RSP	8.00	265.06	22.60	266.67
TA	5.33	83.21	30.00	0.00
WB	3.33	187.01	10.89	0.00
WSP	3.33	103.09	6.93	0.00
BF	2.67	147.46	10.67	3566.67
WP	1.33	18.17	10.33	66.67
STM				66.67
DEAD	7.33	485.99	32.89	8333.33

SITE CLASS VT	ST	TU	PLOT
			NF07
			NF05
7	5	12	NG03

Table 2 (cont'd)

STAND E: 1359

SPECIES	OVERSTOREY BA m2/ha	density #tree/ha	dbh-mean cm	UNDERSTOREY density #small trees/ha
BSP	6.5	736.348276	12.166667	1225
WB	5.5	346.984448	16.333333	0
RM	3.5	383.188525	10.625	0
RSP	2	63.3542066	5.25	1600
DEAD	1.5	63.1817847	14	0
TA	1.5	19.2493294	8	0
BF	0.5	44.2097058	3	6775
RP	0.5	1.89244876	14.5	0
WSP	0	0	0	200
WP	0	0	0	25

SITE CLASS VT	ST	TU	PLOT
5	3	7	SG03, SG04, SX04, SZ03

STAND F: 1262

SPECIES	OVERSTOREY BA m2/ha	density #tree/ha	dbh-mean cm	UNDERSTOREY density #small trees/ha
TA	10.00	198.36	26.53	0.00
WB	8.67	626.56	15.67	0.00
RM	4.00	537.28	10.67	33.33
BSP	3.33	537.00	14.44	1866.67
BF	2.67	312.68	10.89	3100.00
DEAD	2.00	102.66	11.00	0.00
LTA	0.67	5.88	12.67	0.00
WP	0.67	58.95	4.00	133.33
RSP	0.67	43.31	4.67	1233.33
WSP	0.00	0.00	0.00	600.00

SITE CLASS VT	ST	TU	PLOT
5	6	6	SI05, SH07, SX08

STAND G: 659

SPECIES	OVERSTOREY BA m2/ha	density #tree/ha	dbh-mean cm	UNDERSTOREY density #small trees/ha
WSP	13.33	320.49	26.90	133.33
RM	10.00	496.17	20.81	0.00
BF	5.33	458.55	17.33	2300.00
WB	4.67	92.19	30.50	100.00
WAS	3.33	295.03	10.17	33.33
DEAD	2.00	32.81	28.00	0.00
YB	1.33	32.27	7.67	0.00
TA	1.33	238.92	19.33	0.00
I	0.67	132.63	2.67	33.33

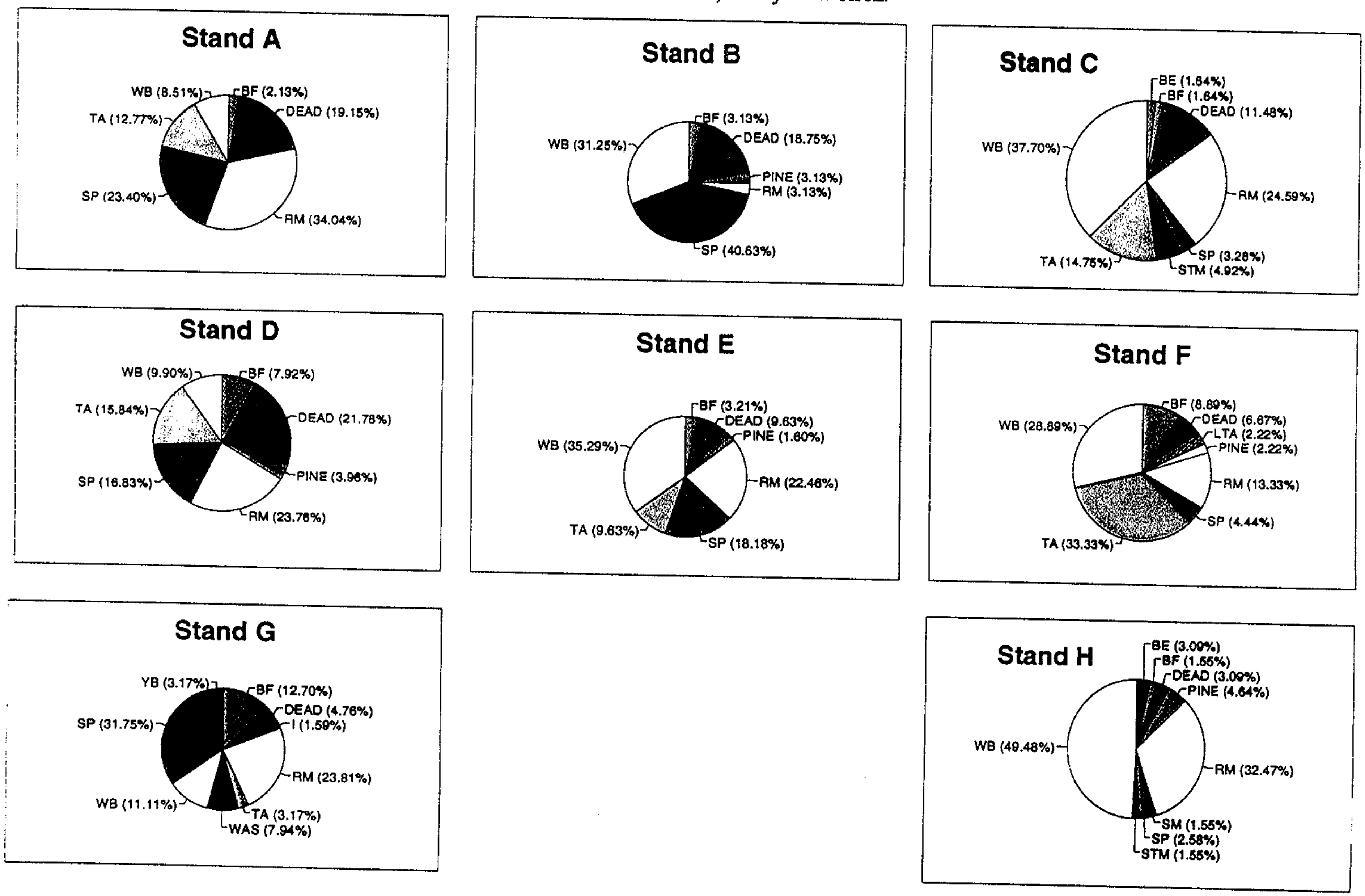
SITE CLASS VT	ST	TU	PLOT
11	2	9	NM01, NL02, NK03

STAND H: 357

SPECIES	OVERSTOREY BA m2/ha	density #tree/ha	dbh-mean cm	UNDERSTOREY density #small trees/ha
WB	21.33	1157.90	17.20	0.00
RM	14.00	2237.25	10.67	33.33
WP	2.00	14.39	32.33	33.33
WSP	2.00	64.96	6.67	166.67
DEAD	1.33	19.12	20.00	0.00
BE	1.33	268.94	7.33	33.33
BF	0.67	132.63	2.67	4033.33
BSP	0.67	21.22	6.67	33.33
STM	0.67	235.79	2.00	300.00
SM	0.67	235.79	2.00	33.33
RSP	0.67	17.54	7.33	100.00

SITE CLASS VT	ST	TU	PLOT
9	5	12	NM05, NL07, NK06

Figure 2. Basal area of overstory tree species by stand type. BE=beech, BF=balsam fir, DEAD=dead standing trees, I=ironwood, LTA=large-tooth aspen, PINE=pine species, RM=red maple, SP=spruce, SM=sugar maple, STM=striped maple, TA=trembling aspen, WAS=white ash, WB=white birch, YB=yellow birch.



The harvesting, especially scarification, destroyed some plot stakes and stumps of reference trees. From May 16 - May 26, all of the plots were relocated using available stakes or reference trees and marked with new plot stakes. In the cases where plot stakes were missing, the plot was relocated from the bearings to the reference trees which had been marked with red paint at their stumps last year before harvesting. Three reference trees were marked near each plot before harvest and at least one was found on each plot after harvest in 1996.

From May 27 to June 14, disturbance conditions were measured. To quantify disturbance, three groups of variables were measured, i.e., slash coverage, substrate and tracks. The following variables were measured:

1. *Treatment*. There were three kinds of treatments, including two harvesting methods and one uncut control in the study area, i.e., UC (uncut), CS (cut and scarified) and C (cut). In total, 65 plots were in the C treatment, 49 plots in the CS treatment and 96 plots in the UC treatment.

2. *Total Slash*. Any fresh (not rotten) wood or foliage material alive or dead. If touching the ground, they were also considered as substrate. Total slash included slash and living slash.

2.1. *Slash*: Dead twigs, branches, logs and foliage attached onto them. Four variables defined the Slash:

1). *< 0.5 cm HW*. The percentage cover of the dead hard wood twigs of diameter less than 0.5 cm and the foliage attaching to them.

2). *< 0.5 cm SW*. The percentage cover of the dead soft wood twigs of diameter less than 0.5 cm and the foliage attaching to them.

3). *Height*. The height under which 90% of the slash cover occurs.

4). *Clumped*. Whether the slash is clumped or not. The answer can only be' Y' (clumped) or 'N' (not clumped).

2.2. *Living Slash*. Living plants with stems higer than 1 m and with the angle from the stem to horizonal < 45°. Three variables were used to define living slash:

1). *HW*. The percentage cover of living hard wood.

2). *SW*. The percentage cover of living soft wood.

3). *Height*. The height under which 90% of the living slash occurs.

3. *Substrate*. The ground surface of the quadrat, divided into invisible substrate and visible substrate.

3.1 *Invisible Substrate*. The substrate that is under slash and can not be seen.

3.2 *Invisible Substrate*. The substrate that is not covered by slash. It is composed of the following items:

1). *Rocks*. The percentage cover of rocks with diameter > 7.5 cm.

2). *Stumps*. The percentage cover of fresh stumps.

3). *D. Litter*. The percentage cover of disturbed litter.

4). *Exp. Min. Soil*. The percentage cover of exposed mineral soil.

5). *Slash (2-7cm)*. The percentage cover of slash with diameter between 2 - 7 cm.

6). *Slash (7cm)*. The percentage cover of slash with diameter > 7 cm.

7). *Rotten Wood*. The percentage cover of rotten wood.

8). *Bark*. The percentage cover of bark.

9). *Chips*. Fragmented wood. Two variables were used to define chips:

a. *Cover*. Percentage cover of chips.

b. *Type*. The pattern of the distribution of chips. 'Y' = clumped; 'N' = not clumped.

10). *Undist. Litter*. Undisturbed Litter. The percentage cover of undisturbed litter.

11). *Scat*. Percentage cover of animal scat.

12). *Cones*. Percentage cover of cones.

13). *Trunks*. Percentage cover of trunks (stems of living trees).

4. *Tracks*. The tracks made by skidders. Three variables were used to define tracks:

1). *Cover*. Percentage cover of tracks.

2). *Type*. The type of track: L (litter), M (mixed litter and soil), S (soil), W (crushed wood), LW (litter and crushed wood) and WS (soil and crushed wood).

3). *Depth*. The depth of the track.

All of the above variables were measured visually except for the depth of track which was measured with a ruler. Percent canopy cover was measured with a densiometer at the ground surface in quadrats 1 and 3. The cover of bracken fern (*Pteridium aquilinum*) was ignored or avoided.

Thirty-six new plots were established in the buffer strips bordering the brook in 1996 to supplement the plots established in this area before harvesting. Along with the plots in the uncut area, they will be used as controls in data analysis. After disturbance conditions were measured and the plots in the buffer strips were established, the herbaceous vegetation on all the plots including the ones in the buffer strips was measured using the same methods used to sample preharvest vegetation.

Data Analysis

Correspondence analysis (CA) was performed on the pre-harvest vegetation x plot matrix to detect relationships in the species and samples using CANOCO (ter Braak 1988). No transformation, weighting, or detrending were used.

Canonical correspondence analysis (CCA) was used to simultaneously ordinate the pre-harvest vegetation x plot matrix and the environment x plot matrix. This constrained CA detects linear correlations between the patterns of the vegetation x plot matrix and the individual environmental variables. In CCA, environmental variables related to forest floor, forest canopy and macrotopography were used as canonical variables to determine the total species pattern (expressed as a sum of canonical eigenvectors) that can be directly related to the environmental data. The final groups of environmental variables that provided the best prediction of species composition were identified.

In Partial Canonical Correspondence Analysis (PCCA), effects of specific environmental variable categories (ie. litter, canopy, topography) were successively partitioned out as covariables, and CCA was run on the residual variation (Appendix I). The resulting sum of eigenvalues for each run represents the proportion of the total pattern captured in the residual CCA uniquely attributable to a particular environmental variable category. For example, to determine the unique contribution of topography, the litter and canopy variables were designated as covariables. Shared contributions were determined by subtraction of unique runs from combined runs.

Correspondence analysis (CA) was also performed on the post-harvest vegetation data. Plot locations in the ordination diagram were plotted by treatment to examine the relationships between harvest treatments and vegetation composition in the first year after harvesting.

Disturbance data were collected by quadrat and averaged by plot. Plot-level data were used to derive treatment means, which were compared graphically.

RESULTS

Pre-Harvest Patterns

Forest Types

The tree species in the Hayward Brook study area are predominantely white, red and black spruce, balsam fir, white birch, red maple and trembling aspen. Large red and white pines are scattered through the entire area. Hardwood stands represented by stand C and stand H, are located on ridge tops (Figure 3). White birch, red maple, sugar maple, trembling aspen, beech and striped maple are found in these deciduous stands in which softwood represents less than 13 % of the stand.

Stands A, B, D and E (Figure 3) are predominantly softwood forests of black, red and white spruce which also contain intolerant hardwood species such as red maple, white birch and trembling aspen. Hardwoods represent 20 to 45 % of these stands. Stands A, B, D and E are located near the streams. The two stands that make a transition between softwood and hardwood forest types are stand F and G which are mixedwood stands (Figure 3). Stand G is unique because it is on a wet site and contains yellow birch, white ash and ironwood which are not present elsewhere. Stand G is mainly a mixedwood stand of white spruce, red maple and balsam fir. The overstorey of stand F is mainly trembling aspen, white birch, red maple, black spruce and balsam fir.

Balsam fir was abundant in the understorey in all stand types (Table 2). Spruces were also abundant in the understorey of softwood and mixedwood stands. Striped maple was a dominant species in harwood stand understories along with balsam fir (Table 2).

Community Composition

Before harvest in 1995, the 169 plots contained 106 taxa including 15 tree species and 17 species of ferns and fern allies, and three groups of non-vascular plants (Table 1). On average, plots contained 15 species (Figure 4) with 59% total herbaceous cover (Figure 5). Taxa which occurred in the greatest number of plots were moss spp., *Maianthemum*

Figure 3. Map of stand types and sample transects in the Hayward Brook Watershed. Stand types: A (#26), B (#40), C (#41&42), D (#22), E (#34), F (#38), G (#29) and H (#30). Dots show quadrat locations. Dashed lines delimit north and south blocks (true north at top of page). Scale 1:30,000.

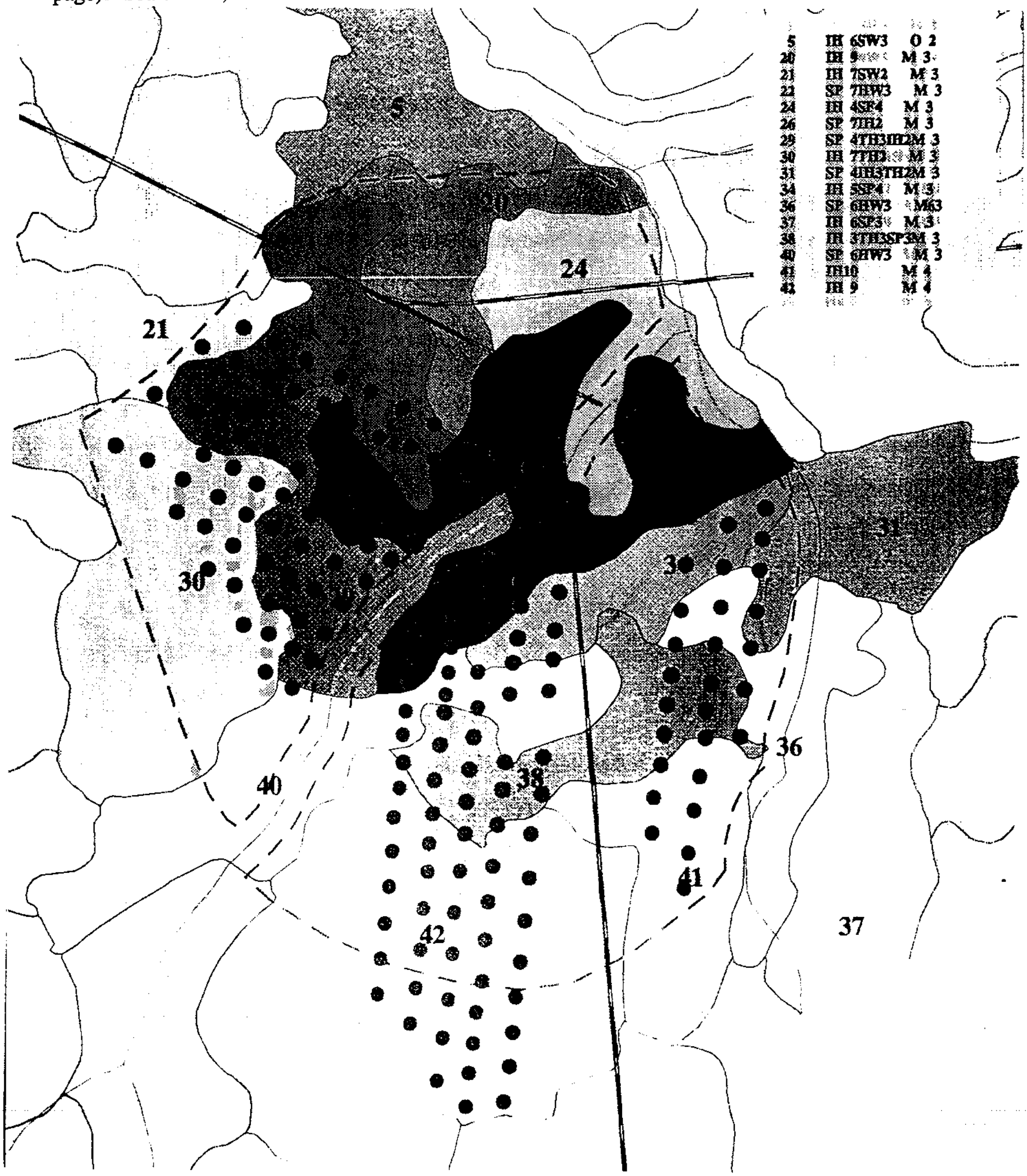


Figure 4. Frequency distribution of herbaceous species richness in 5m^2 quadrats (n=169 quadrats, 106 species).

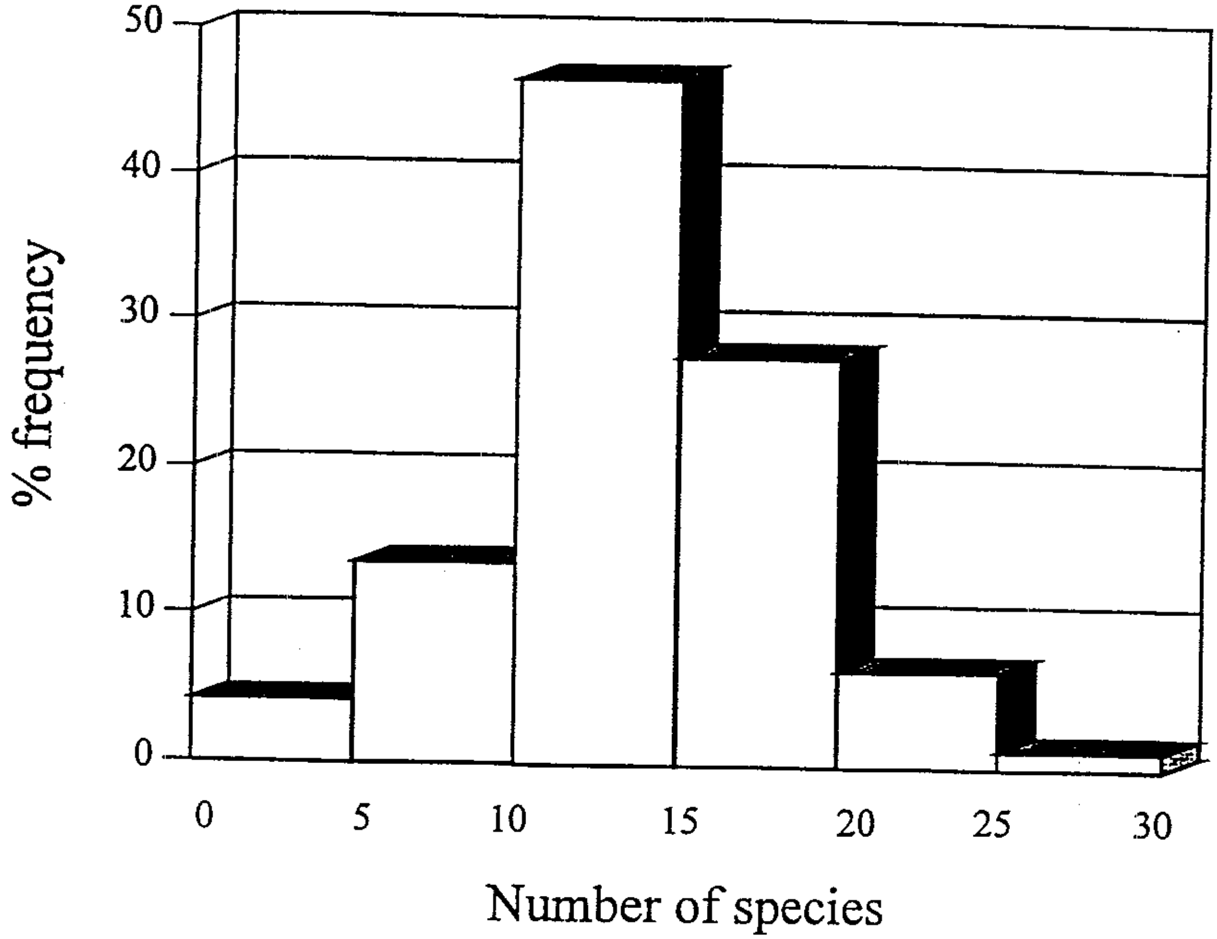
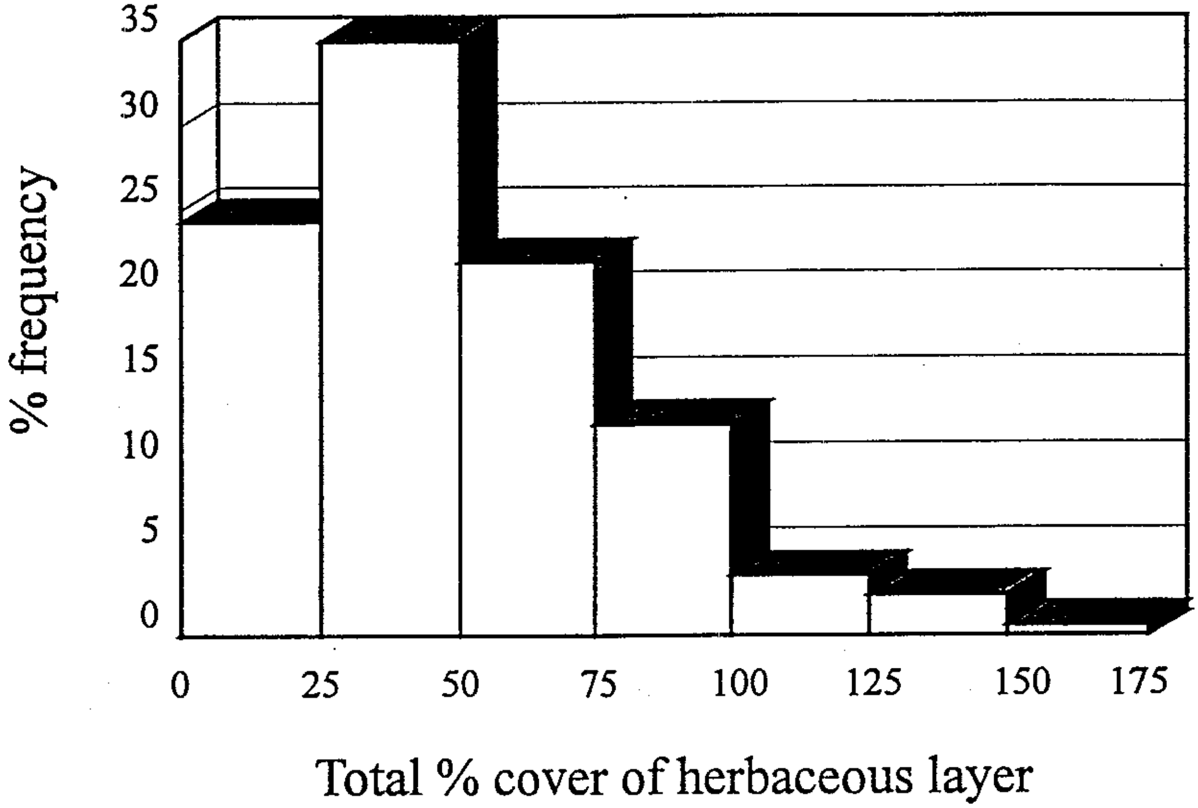


Figure 5. Frequency distribution of total percent cover of the herbaceous species in $5m^2$ quadrats (n=169 quadrats).



canadensis and *Abies balsamea*. Of the 106 species, 80 occurred in $\leq$ 20% of the plots (Figure 6). *Abies balsamea*, *Pteridium aquilinum* and moss spp. had the highest total cover in the study area; however, 98 species had cover values of $\leq$1% (Figure 7). At the local scale, i.e. cover when present in a plot, 69 species covered $\leq$ 1%, however three species regularly covered 13-18% (*Abies balsamea*, *Picea mariana* and *Lycopodium annotinum*) (Figure 8).

Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA)

Correspondence analysis (CA) showed that total variability (total inertia) in the species data was 6.581 before harvest (Table 3). The first CA axis captured 8.4% of this variability, while the second captured 6.7%. Species scoring high on CA axis one included *Thelypteris noveboracensis* (#96), *Sphagnum spp.* (#93), *Aster umbellatus* (#17), and *Prunella vulgaris* (#81) (Figure 9). At the low end of axis one was *Lycopodium annotinum* (#53), *Lycopodium dendroides* (#56), and *Alnus rugosa* (#8). The samples formed two groups along axis one: a string at the high end and a larger, denser cluster at the low end which separated somewhat on axis two. The softwood stands (A,B,D,E) formed two dense clusters at both ends of axis one (Figure 10). The hardwood stands C and H formed a string that ran parallel to CA axis two. The mixed stands (F,G) formed two clusters: G along the first axis, and F along the second.

The sum of all canonical eigenvalues was 1.582, or 24% of the total inertia (Table 3b). The remainder (76%) represents the loss of capture of the vegetation variability due to the compromise between species and environmental variable axes, to make them maximally parallel to one another. CCA axes one and two each captured slightly less of the species data variability than the CA axes (Table 3a&b). The species-environment axes were highly correlated: r^2 = 0.893 and 0.791 for axes one and two respectively (Table 3b).

Aster umbellata (#17), *Prunella vulgaris* (#81), *Solidago flexicaulis* (#90) scored high on CCA axis one (Figure 11). At the low end of axis one were *Populus grandidentata* (#77), *Fagus grandifolia* (#37), and *Vaccinium vitis-idaea* (#103). CCA was similar to CA in two ways: (1) plots separated along the first two CCA axes (Figure 12), with similar spread, and (2) plot 6NJ06 (#138) scored high on axis one, joined by 6NM02 (#160), and 6NK01 (#143). Unlike CA, plots at the low end of CCA axis one included 6SH11 (#74), 6SI14 (#92) and 6SX17 (#47).

Figure 6. Frequency distribution of frequency of species occurrence in $5m^2$ quadrats (n=169 quadrats).

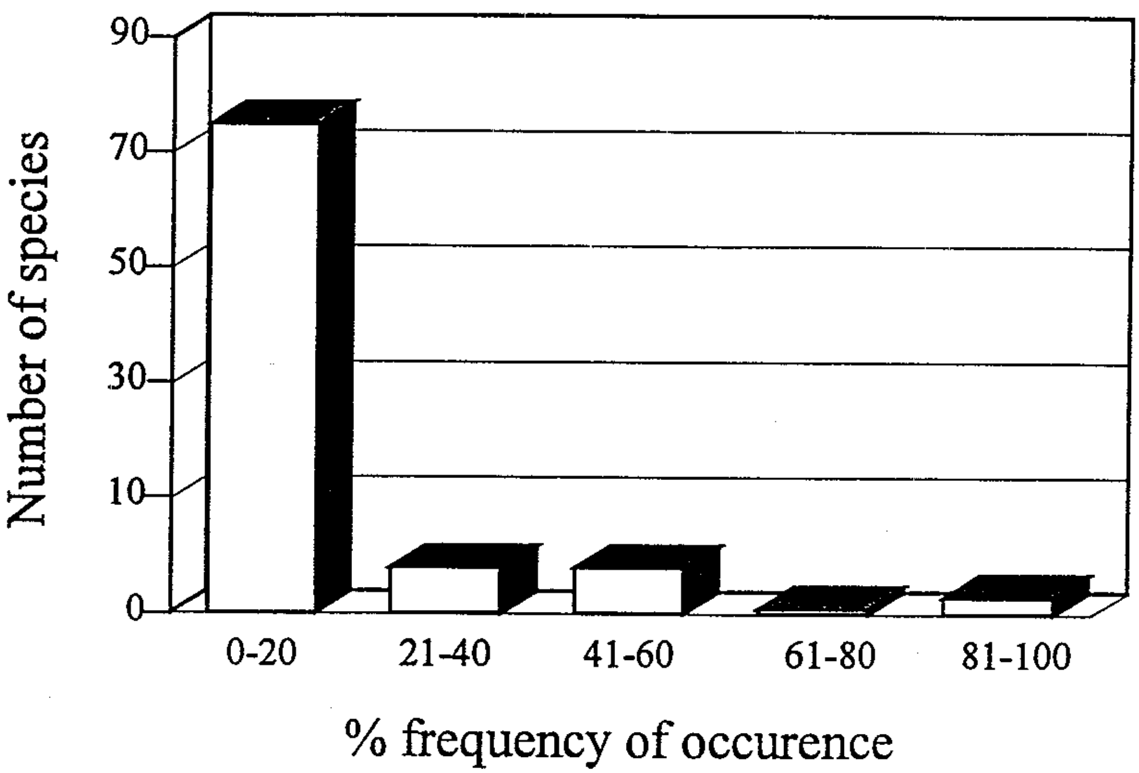


Figure 7. Frequency distribution of mean percent cover in $5m^2$ quadrats (n=169 quadrats, 106 species).

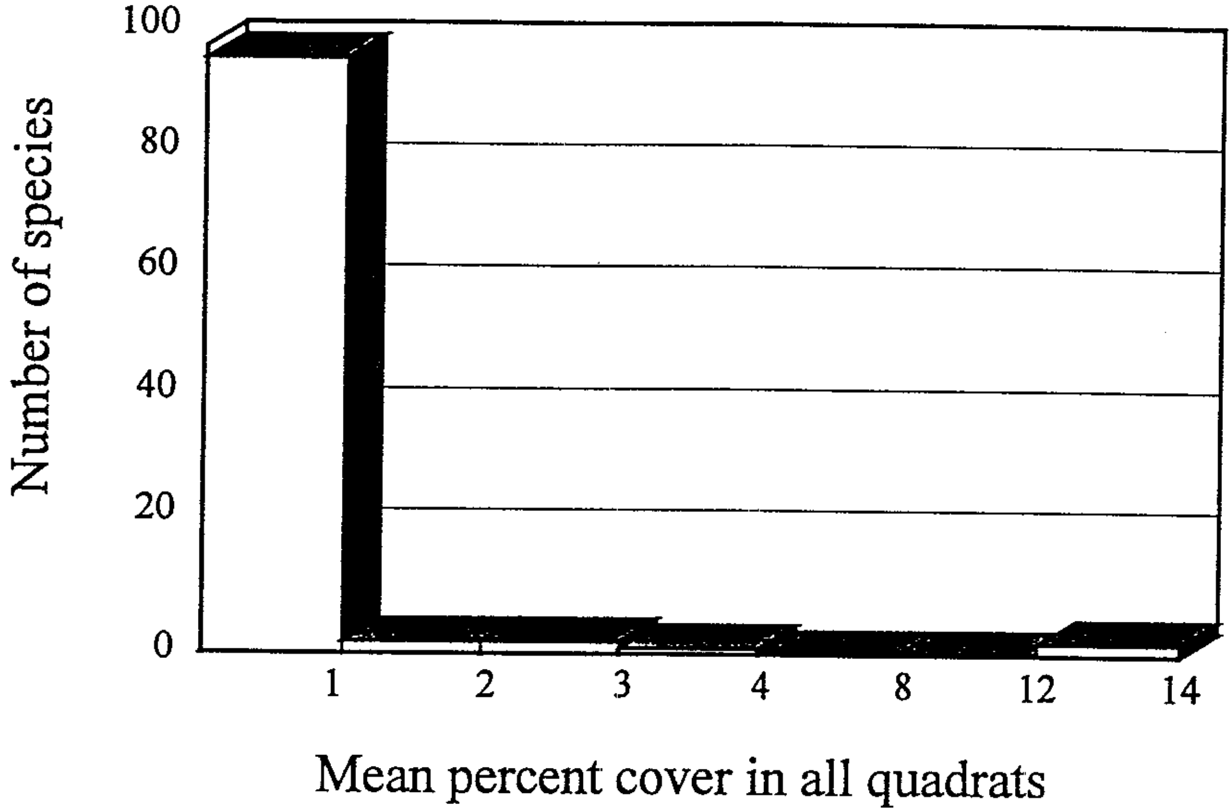


Figure 8. Frequency distribution of local mean percent cover, i e. cover when present, of 106 species in $5m^2$ quadrats

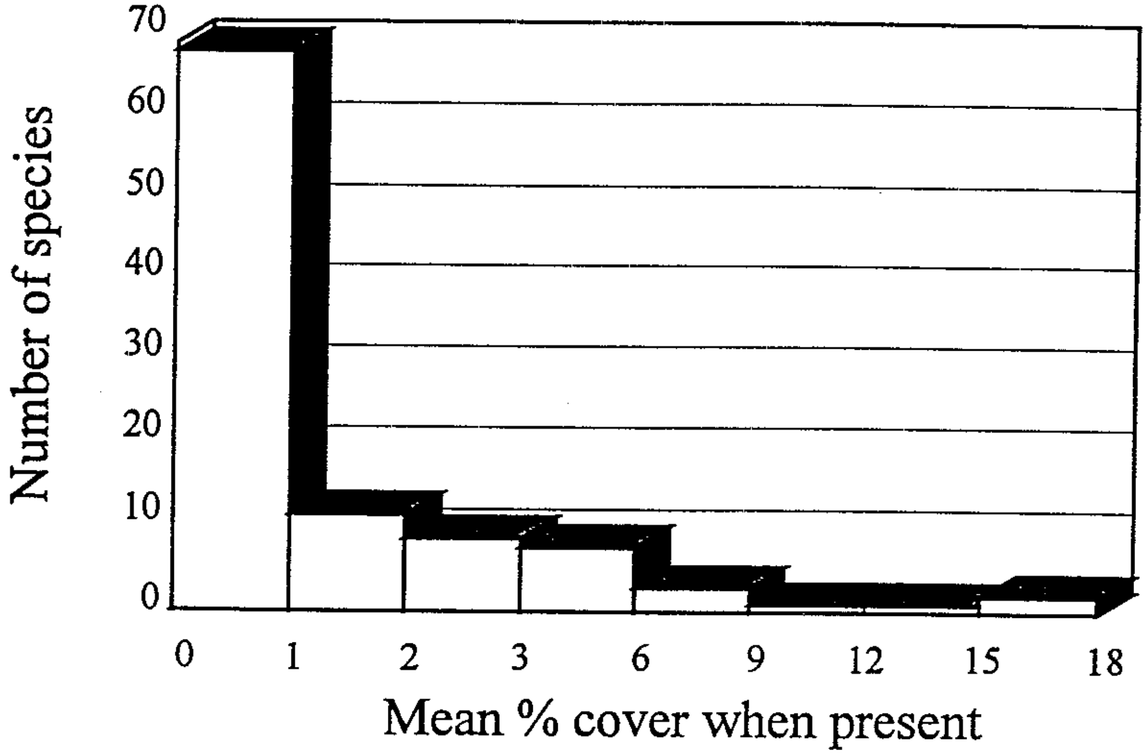


Table 3. Summary of the first axes of (a) CA and (b) CCA on herbaceous vegetation and environmental data before harvesting from Hayward Brook.

	(a) CA		(b) CCA		
	EV	%	EV	%	Sp/env r^2
1ST AXIS	0.551	8.4	0.408	6.2	0.893
2ND AXIS	0.442	6.7	0.257	3.9	0.791
INERTIA	6.581 (total)	100	1.582 (canonical)	24 of total	

Figure 9. Species scores on the first two axes of Correspondence Analysis (CA) on 106 species in 169 $5m^2$ quadrats. Numbers represent species codes (see Table 1).

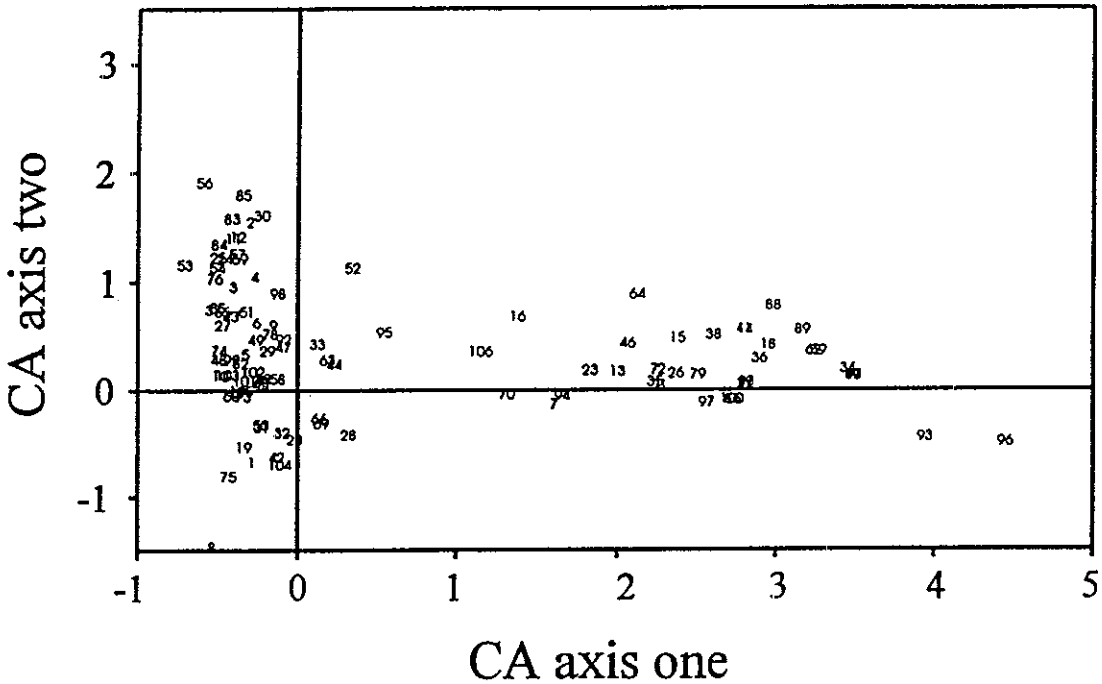


Figure 10. Distribution of 169 5m² quadrats (grouped by stand type) on the first two axes of Correspondence Analysis (CA). Softwood stand types A, B, D, E; mixed stand types F, G; hardwood stand types C, H.

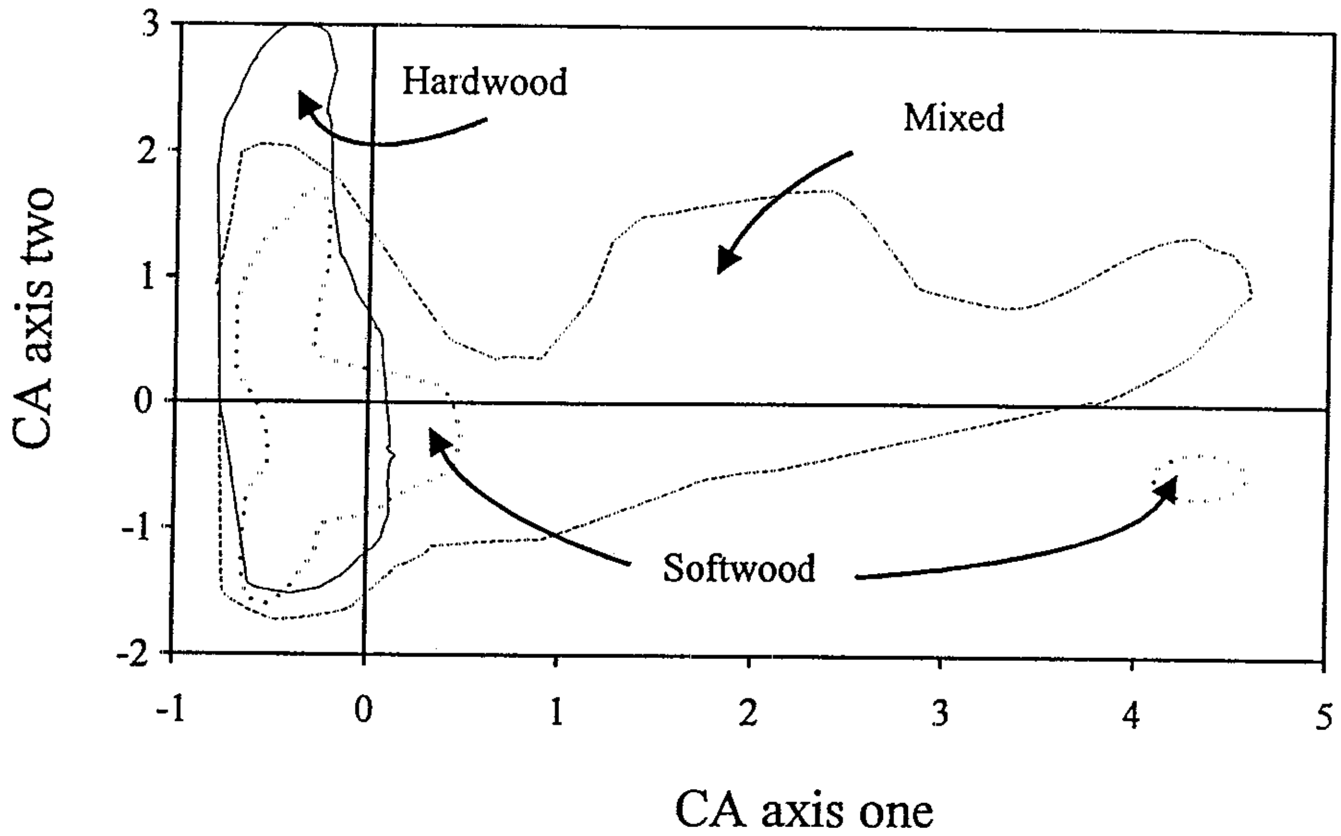


Figure 11. Species scores on the first two axes of Canonical Correspondence Analysis (CCA) with environmental biplots. Numbers represent species codes (see Table 1). TC=total canopy cover, DC=deciduous canopy, CC=coniferous canopy, DL=litter depth, LM=litter moss component, LD=litter deciduous component, LC=litter coniferous component, S1=slope of the microtopography, SLO=slope of the plot, PIT=pitted, MOU=mounded, FLA=flat, MAC= macrotopography, S2=slope of the area, POS=slope position, COS=cosine of azimuth, SIN=sine of azimuth, pH=litter pH, K=litter potassium, Ca=litter calcium, Mg=litter magnesium, P= available phosphorus (litter), C=percent carbon (litter), N=total nitrogen (litter), C/N=carbon to nitrogen ratio (litter), OM=percent organic matter (litter).

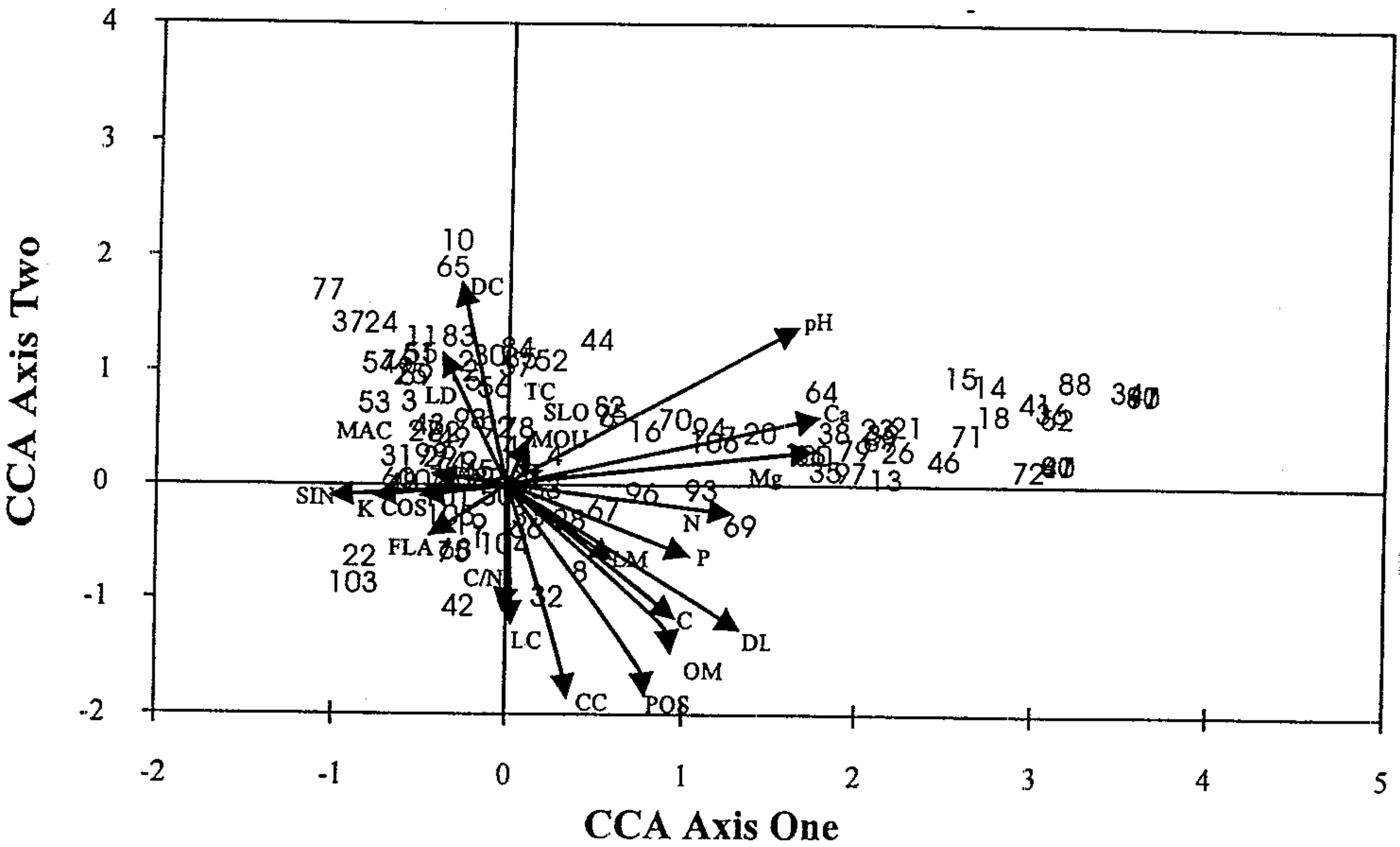
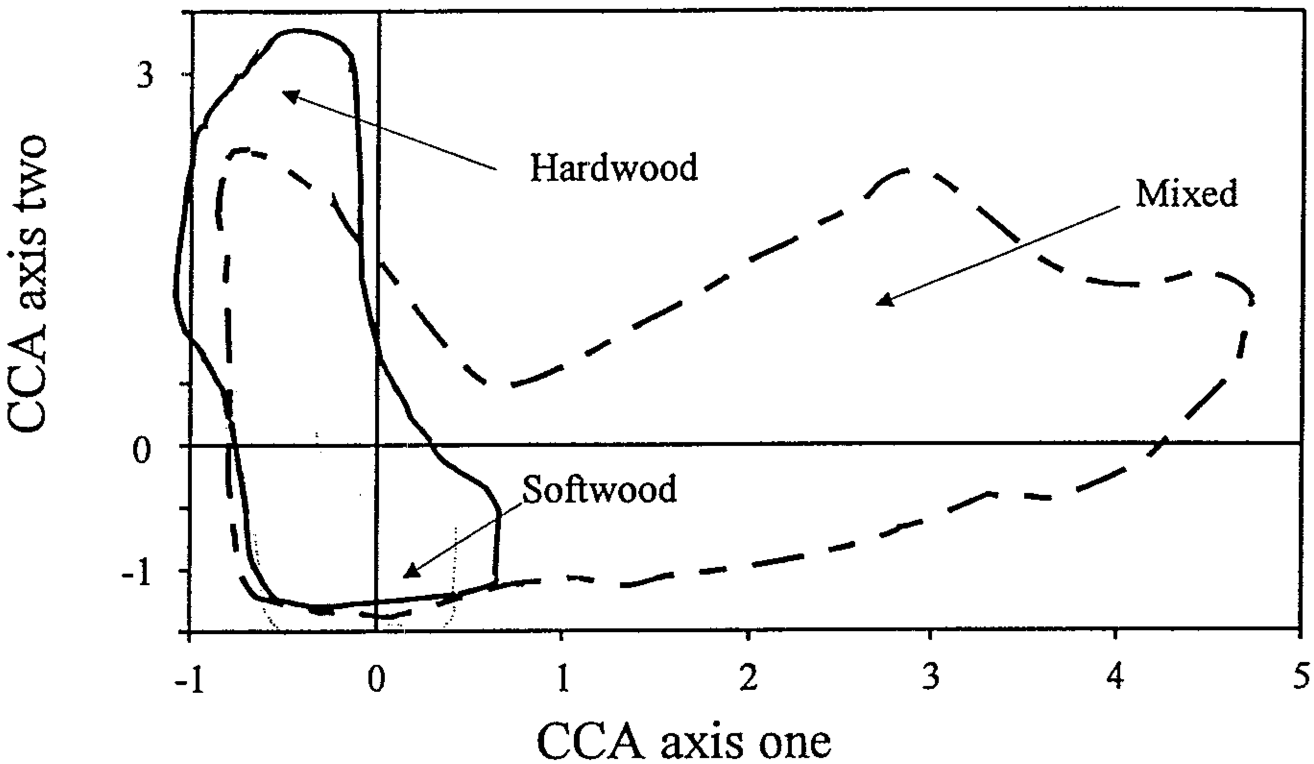


Figure 12. Distribution of 169 5m^2 quadrats (grouped by stand type) on the first two axes of Canonical Correspondence Analysis (CCA).



The distribution of the softwood mixed and hardwood stand types (Figure 12) were similar to the CA ordination (Figure 11), except the softwood stands occurred in a tighter cluster at the low end of both axes.

Biplot scores of the environmental variables (Figure 11) indicate that litter calcium (#20), magnesium (#15), and pH (#11) were most positively correlated with CCA axis one, whereas sine and cosine of the slope (#17, #16) and litter potassium (#19) were negatively correlated with it. CCA axis two was positively correlated with percent deciduous canopy cover (#2) and litter depth (#4), and negatively correlated with coniferous litter (#7) and canopy(#3). Interset correlations are shown in Appendix II.

PCCA showed that canopy and topography accounted for $<10\%$ of the total inertia, or $<30\%$ of the variability in the species that was related to environmental factors (Table 4). Litter, uniquely and in combination, contributed approximately 15% of the total, or $>60\%$ of the CCA total.

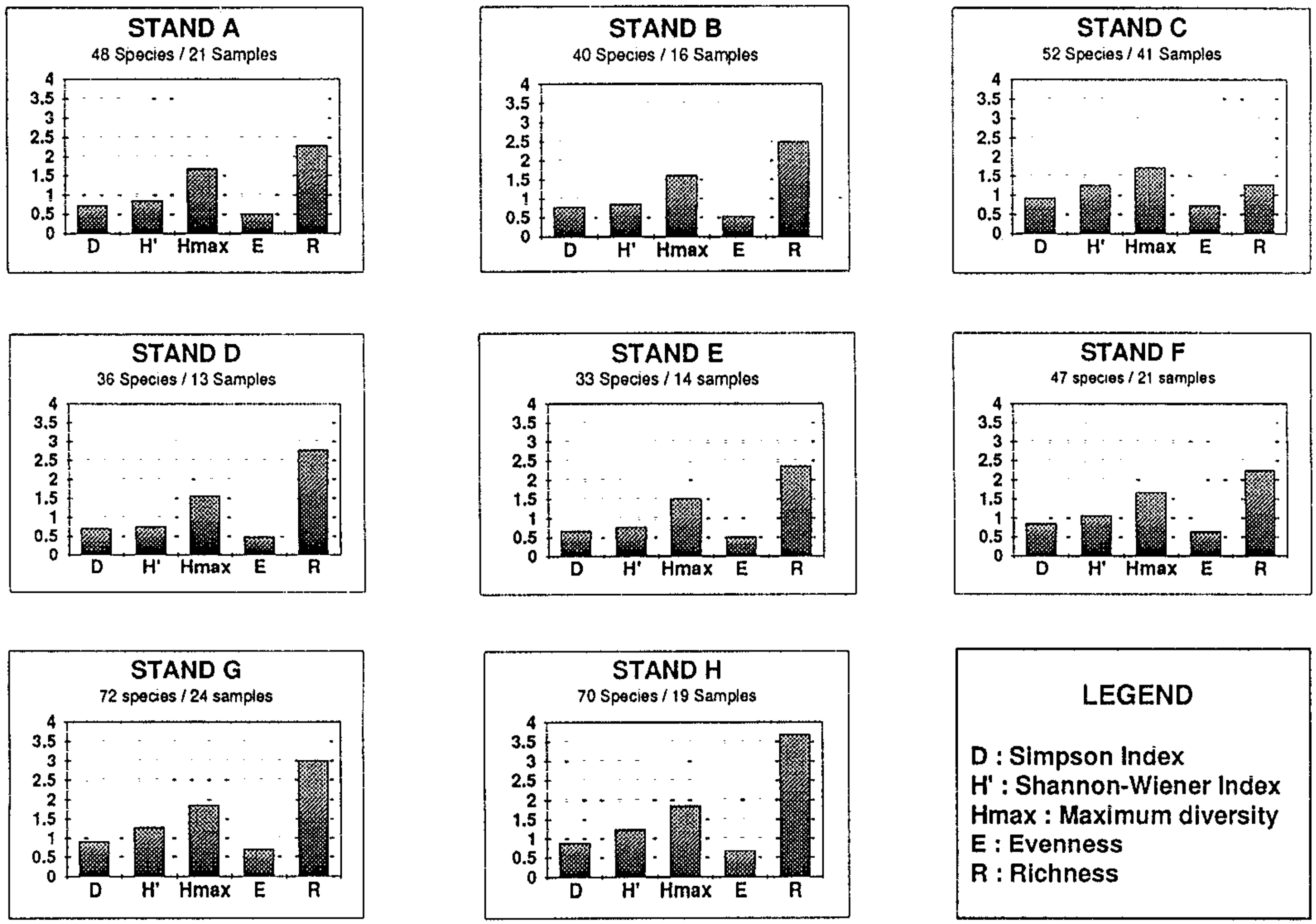
Table 4. **PCCA of the vegetation pattern in Hayward Brook, showing unique and shared contributions of environmental variables as a % of sum of canonical eigenvalues (= 1.582) and as % of the total inertia (= 6.582).**

	Environmental Variable Categories	Sum of eigenvalues	Percent of sum of canonical eigenvalues	Percent of total inertia (= 6.582)
Unique Effects	Litter	0.815	51.52	12.39
	Topography	0.347	21.93	5.27
	Canopy	0.108	6.83	1.64
Shared Contributions	Topography+ Litter	0.172	10.87	2.61
	Canopy+Litter	0.020	1.26	0.30
	Canopy+Topography	0.023	1.45	0.35
	Canopy+Litter+ Topography	0.097	6.13	1.47
	TOTAL	1.582	99.99	24.04

Diversity Indices

Diversity indices including the Simpson Index (D), the Shannon-Wiener Index (H'), maximum H', evenness and average richness were calculated for each stand type (Figure 13). Average richness was calculated as the total number of species in the stand divided by the number of samples (plots) in the stand. The differences between stands were small, except for average richness which may change from one stand to another because of the number of sample plots taken. Overall, stands A, B, D and E could be grouped together because of low Shannon-Wiener Index value ($H' < 1.0$), a low Simpson Index value ($D < 0.75$) and low evenness (approximately 0.5). Stands C, F, G and H had higher values than the above stands, with Shannon-Wiener Index values between 1.0 and 1.5, Simpson Index values from 0.75 to 1.0 and evenness above 0.5. Stands G and H had the greatest richness by far with 70-72 species (3.0-3.7 average richness). These results indicate that stands G and H contained the highest diversity of vascular plants before harvesting.

Figure 13. Diversity indices by stand type.



Post-Harvest Patterns

Disturbance Variables

The harvesting (both C and CS treatments) resulted in more softwood slash <0.5 cm than hardwood slash <0.5 cm. The C treatment caused more softwood slash <0.5 cm than the CS treatment, whereas the CS treatment caused more hardwood slash <0.5 cm than the C treatment (Figure 14 A-B). The cover of slash >0.5 cm had very little difference in the C and CS treatments (Figure 14 C).

Both the C and CS treatments created dense clumps of slash and areas with invisible substrate (Figure 14 D-E).

The CS treatment disturbed the forest floor more severely than the C treatment. The cover of disturbed litter, rock and exposed mineral soil was greater in the CS area than the C area (Figure 14 F-H). In addition, the cover of machine tracks was 20% in the CS area as compared to 8% in the C treatment. Conversely, cover of undisturbed litter was lowest in the CS treatment (10%) and highest in the UC treatment (90%).

Response of Herbaceous Layer Species to Harvesting

The initial effects of harvesting and site preparation were determined during the summer of 1996; these results represent vegetation response (survival and some initial germination) in the first growing season after harvesting. We will continue to monitor the plots in future years with a focus on the relationships between post-harvest species composition and disturbance factors (residual canopy cover, forest floor disturbance and slash levels).

Correspondence Analysis (CA) was applied to the herbaceous vegetation data collected in 1996. The plots were classified by treatment, i.e, clearcutting (C), clearcutting and scarification (CS) and uncut (UC). The results of CA showed that the total variation (inertia) of the herbaceous vegetation was 7.321 and the first four axes captured 26.1% of the variation.

The plots in the CS area tended to gather in the upper left quarter of the CA ordination of plots (Figure 15). The species diagram showed that many weedy species, hardwood seedlings and hardwood stump sprouts, such as *Acer spicatum, Prunus pensylvanica, Achillea millefolium, Aster lateriflorus* and *Epilobium angustifolium* occurred in these plots (Figure 16).

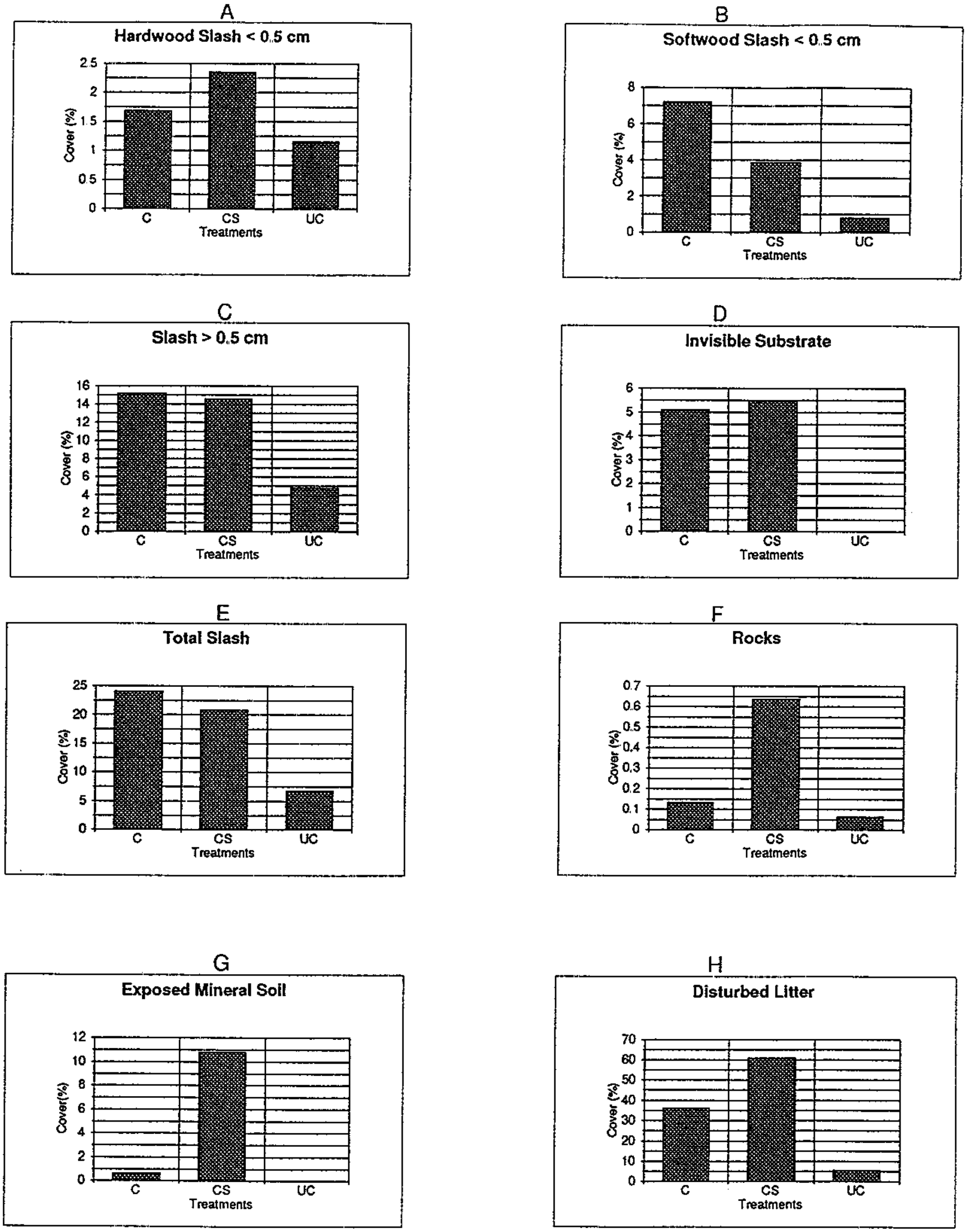


Figure 14 Disturbance conditions in the C, CS and UC areas

Figure 15. Plot scores on the first two axes of Correspondence Analysis (CA) on 169 - 5m^2 plots (grouped by treatment type) in the first year after harvest (1996). Codes indicate plot numbers.

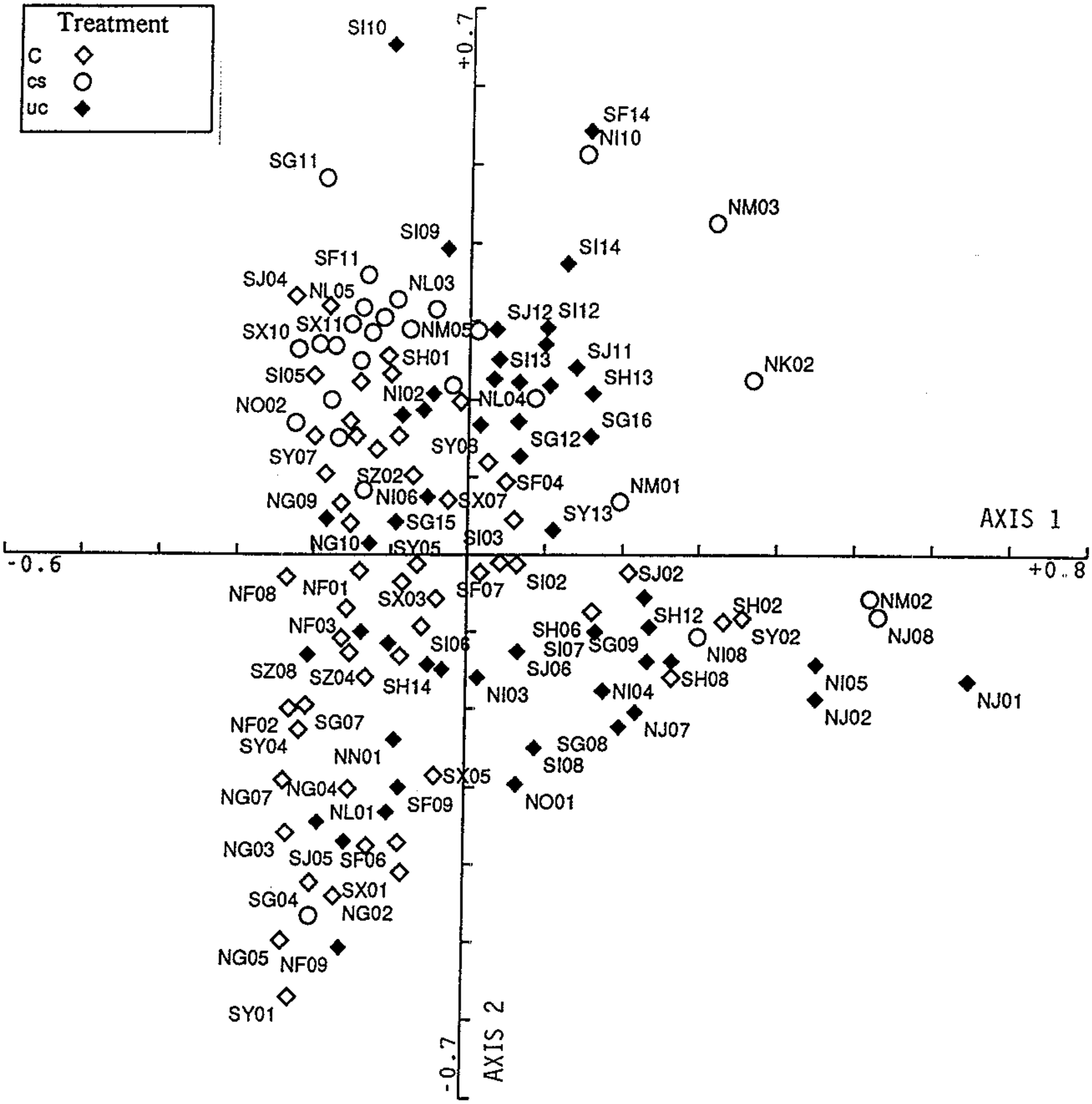
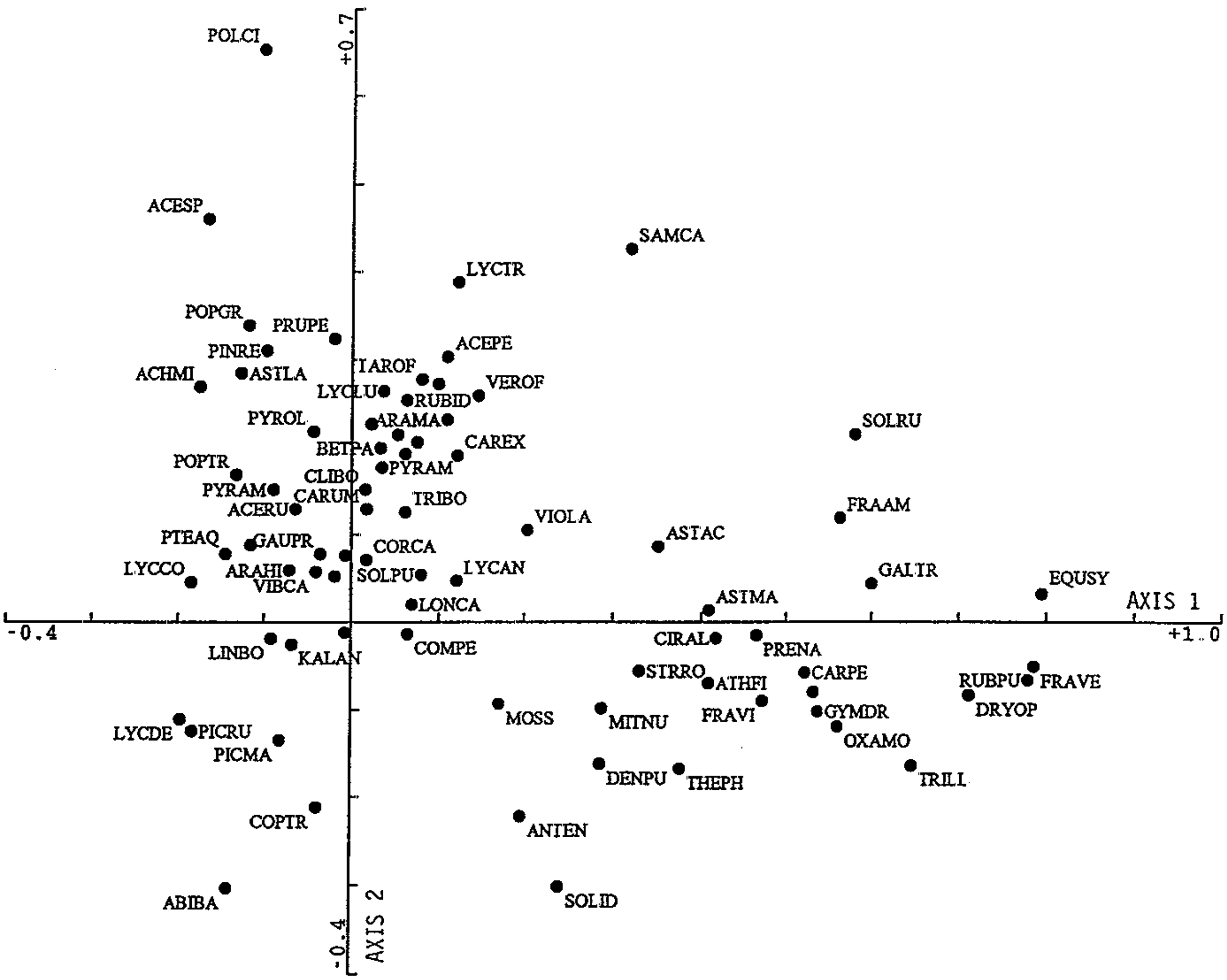


Figure 16. Species scores on the first two axes of Correspondence Analysis (CA) on 169 - $5m^2$ plots (grouped by treatment type) in the first year after harvest (1996).



Most of the plots in the C treatment were grouped in the left half of the plot diagram (Figure 15). In addition to the species listed above, many other species which are found in open and dry conditions occurred in these plots, such as *Populus tremuloides, Acer rubrum, Pinus strobus, Viburnum cassinoides, Aralia hispida, Pteridium aquilinum, Pinus resinosa, Lycopodium obscurum, Lycopodium dendroides, Vaccinium myrtilloides, Picea rubens* and *Maianthemum canadense* (Figure 16).

In the right-most portion of the plot diagram (Figure 15), most of the plots were those located in the bottom of the watershed, where conditions were relatively wet and rich. The species occurring in these plots were *Equisetum sylvaticum, Rubus pubesens, Fragaria vesca, Dryopteris sp., Trillium sp., Oxalis montana, Galium triflorum* and *Fraxinus americana* (Figure 16).

The species number in the whole study area decreased from 106 to 91 after harvesting. In the CS area, 23 species were lost and 20 species invaded after harvesting; species richness changed from 82 to 79. The species lost were *Acer saccharum, Actaea rubra, Aster ciliolatus, Brachyelytrum erectum, Dennstaedtia punctilobula, Goodyera tellelata, Linnaea borealis, Luzula acuminata, Lycopodium annotinum, Lycopodium complanatum, Medeola virginiana, Moneses uniflora, Monotropa hypopithys, Orthilia secunda, Osmunda spp., Prunella vulgaris, Ribes lacustre, Solidago flexicaulis, Sphagnum spp., Streptopus amplexifolius* and one unknown species. The species which invaded were *Anaphalis margaritacea, Aralia hispida, Betula papyrifera, Epilobium angustifolium, Fragaria virginiana, Hieracium sp., Lycopodium lucidulum, Lycopodium tristachyum, Mentha arvensis, Osmunda cinnamomea, Pinus resinosa, Plantago major, Polygnum cilinode, Prunus pensylvanica, Rubus idaeus, Sambucus canadensis, Solidago rugosa, Taraxacum officinale* and *Veronica officinalis*.

In the C area, 19 species were lost and 10 species invaded after harvesting, with a decrease in species richness from 60 to 51. The species lost were *Achillea millefolium, Alnus rugosa, Aster macrophyllus, Cypripedium acaule, Dalibarda repens, Dryopteris sp., Gaultheria hispidula, Medeola virginiana, Mitella nuda, Orthilia secunda, Oryzopsis asperifolia, Osmunda spp., Oxalis montana, Sphagnum sp., Streptopus roseus, Thelypteris noveboracensis, Vaccinium vitis-idaea* and *Veronica officinalis*. The species which invaded were *Aralia hispida, Comptonia peregrina, Epilobium angustifolium, Hieracium sp.,* *Lycopodium annotinum, Populus grandidentata, Prunus pensylvanica, Osmunda claytoniana, Rubus idaeus* and *Solidago sp.*.

Diversity indices were also changed by the harvesting. In the CS area, both average species richness per plot and the average Shannon-Wiener index per plot decreased after the harvesting. The average species richness per plot was 16.2 before harvesting and 15.5 after harvesting. The Shannon-Wiener index was 0.791 before harvesting and 0.759 after harvesting. In the C area, species richness per plot decreased but the Shannon-Wiener index increased. Species richness per plot was 11.83 before harvesting and 11.14 after harvesting. The Shannon-Wiener index was 0.5966 before harvesting and 0.6578 after harvesting.

DISCUSSION

Pre-Harvest Patterns

The Hayward Brook stand types are found in the Anagance Ridge Ecodistrict which contains coniferous vegetation of spruce and fir mixed with intolerant hardwoods and scattered pines. Higher hills with more fertile soils in this Ecodistrict contain tolerant harwood species such as beech, sugar maple, and yellow birch, with a minor component of white ash and ironwood according to NBDNRE (1996), although our stand type inventory showed a dominant forest canopy of intolerant hardwood such has white birch and red maple. Ironwood and white ash were present as minor species in one midslope stand (stand G). A long history of fire and forest cutting has favored the maintenance of trembling aspen and largetooth aspen which are found on this site (Rowe 1977). The large red and white pines and the jack pines might also have been favored by the past fires.

Measures of species richness determined that on average there were 15 species/5 m^2 within the study area. Comparisons with the literature are difficult due to the differences in scales; this study used 5 m^2 plots , whereas others generally use 1 m^2 plots for herbaceous vegetation (Smith 1980). Richness is expected to increase with plot size (Ashby 1971).

The total cover of herbaceous species ranged from 0-175% within the plots, with a low mean evenness (80% of species occurred in $\leq$ 20% of plots) (Fig. 5). This component of diversity showed that there were many infrequently represented species. Some were particularly uncommon both in the study site and in this geographical area, e.g., the orchids *Cypripedium acaule* and *Goodyera tesselata* and some of the Pyrolaceae, including *Chimaphila umbellata* and *Pyrola americana* (Table 1) (Hinds 1986).

Species evenness was determined to be relatively low primarily because there were many species that occurred infrequently or with low cover within the plots, whereas a few other species had consistently high frequency and cover, e.g. moss spp., *Maianthemun canadensis*, *Pteridium aquilinum*, and *Abies balsamea*.. The richness of the area was high, however, with a relatively large number of species present within the study area.

The first CA axis appears to represent a broad scale moisture gradient. *Sphagnum spp.*, *Moneses uniflora*, and many fern species (*Thelypteris noveboracensis*, *Thelypteris phegopteris*, *Osmunda spp.*, *Athyrium filix-femina*, and *Gymnocarpium dryopteris*) at the high end of CA axis one are characteristically associated with moist to wet habitats, whereas those at the other end (*Lycopodium spp.*, *Cornus canadensis*, and *Vaccinium vitis-idaea*) are generally associated with drier habitats. The stand types also demonstrated this moisture gradient, with both softwood (A) and mixed (G) stands at the high end of axis one. This study did not measure moisture directly, but moisture can be deduced from stand types as well as factors influencing drainage. For example, steepness of slope and position on the slope (e.g.. top vs. bottom) influence moisture retention and drainage directly.

Furthermore, steepness and aspect of the slope, along with canopy height, will determine the path and duration of insolation and will affect moisture availability (Collins *et al.* 1985). However, the PCCA indicated topography (including macro slope position, slope of the plot, and moundedness/pittedness of the area etc.) accounted for approximately 6% of the total inertia. The common influence of canopy and topography, which includes precipitation interception by the canopy, accounted for only 10% of the total inertia.

The second CA axis was related to canopy oriented factors. At the low end were predominately coniferous stands (A,B,D,E) and species which are common under a coniferous canopy, e.g.. *Gaultheria hispidula*, *Coptis trifolia*, and seedlings of *Abies* and *Picea* species. At the high end were typically deciduous stands (C, H) and species common under deciduous canopies: *Pyrola spp.*, *Aralia nudicaulis* , *Medeola virginiana*, and *Chimaphila umbellata*. Canopy type influences both the light available to the understorey, and rainfall interception (Anderson *et al.* 1969). However, canopy cover and its composition accounted for only 4% of the total inertia that could be captured by the environmental variables measured.

The pattern of herbaceous species is therefore only weakly correlated with the canopy and topography variables measured in this study. Species presence / absence at the plot scale is therefore not primarily related to the amount or composition of canopy cover, implied moisture levels, or even the drainage pattern of the area.

Other features related to canopy, such as the litter fall and decomposition, may have more intimate effects on the herbaceous understorey vegetation. The grouping of herbaceous species according to canopy may result from the type and amount of litter such canopy produces, as shown in the PCCA. Further, the litter variables most closely related to vegetation in this study were primarily litter chemistry: litter pH, and calcium and magnesium contents, which are influenced by the historical accumulation of past canopies.

Litter pH had the strongest correlation with vegetation composition. Its importance may be due to its influence on chemical availability of the nutrients from the decomposing litter in soil solution. The chemical forms, and thus solubility, of certain elements, change with pH (Mauseth 1995). Nutrients in the litter layer may also be in unavailable inorganic forms until after some microbial decomposition has occurred. The rate of the nutrient cycling varies with both the nature of the litter and the environmental conditions (Brady 1974). For example, coniferous litter with its high concentration of lignin is both mechanically difficult to break down and sufficiently acidic to inhibit many microbial decomposers. In contrast, litter from angiosperms and deciduous trees have a higher surface area to volume ratio, making it easier to mechanically break down and have a lower concentration of tannins, making it less acidic to the microbial decomposers. Similarly, the two types of litter decomposition are inhibited by waterlogged conditions.

There are several ways to account for the remainder (76.96%) of community structure that was not related to environmental variables used in this study.

1) Equilibrium models would predict that the herbaceous community is structured by some critical environmental variables that were not measured in this study, such as soil chemistry or moisture. The species present would be there because they have out-competed all competitors to utilize the resources available within the environment. Based on these models, the resulting post-disturbance community will return to pre-disturbance structure given enough time for the best competitors to re-establish themselves.

2) Non-equilibrium models would predict that the herbaceous community is structured by stochastic processes. For example, localized disturbances may displace superior competitors, allowing weaker competitors to persist in the community; this is the premise of gap dynamics models. Disturbances increase the heterogeneity of the landscape, and break up monospecific patches by allowing different species to become established (Thompson 1980). Other stochastic processes contribute to unique history of the stand (Smith and Cottam 1967). The past fire regime in the area may affect the herbaceous community, but this would more than likely be at the stand scale. The occurrence of isolated lightening strikes, however, may affect the herbaceous community at a localized scale. Based on these models, the post-disturbance community is unpredictable and may not resemble the pre-disturbance community.

3) The underlying pattern by which the vegetation was originally structured may have become blurred over time, and the resulting correlations with the habitat characteristics may no longer be detectable. For example rhizomatous species become established according to habitat preference, but clonal spread would increase their range by allowing surplus resources to be channeled into ramets in less suitable environments.

4) Sampling and analytical procedures affect the ability to detect patterns. Correspondence analysis detects only linear relationships within and between data (ter Braak 1988). It is possible that the relationship between species and environmental variables is non-linear, much like a bimodal or bell-shaped range of tolerance for a species. However, this technique is considered to be sufficiently robust to deal with some curvature, and a trial analysis using detrending (means of removing curvature) did not significantly increase information capture.

Similarly, pattern detection is influenced by the scale of sampling. The spatial scale of 5 m^2 used to sample vegetation and environmental features in this study may be unsuitable in that, factors affecting a small localized area may not be the same factors that affect populations at a larger scale. However, personal observation suggests that the scale was appropriate because: (a) the quadrat size was sufficient to capture most species in the area and (b) the environmental variables measured in this study appear to vary at the plot.

Post-Harvest Patterns

Harvesting treatments, both C and CS, removed the canopy and exposed the forest floor to sunlight and desiccating winds. The environmental conditions in the herbaceous layer were changed from favouring forest species, which need shade and moisture, to favouring weedy species, which need more sunlight. Though many forest species survived through the changes, some of them were lost while some weedy species invaded. In the CS area, the forest species that were lost included: *Actaea rubra, Brachyelytrum erectum, Goodyera tesselata, Linnaea borealis, Luzula acuminata, Medeola virginiana, Moneses uniflora, Monotropa hypopithys, Orthilia secunda, Solidago flexicaulis* and *Streptopus amplexifolius*. The weedy species which invaded were *Anaphalis margaritacea, Aralia hispida, Betula papyrifera, Epilobium angustifolium, Fragaria virginiana, Mentha arvensis, Plantago major, Polygnum cilinode, Rubus idaeus, Sambucus canadensis, Taraxacum officinale* and *Veronica officinalis*. In the C area, the lost forest species were *Cypripedium acaule, Dalibarda repens, Gaultheria hispidula, Medeola* *virginiana, Mitella nuda, Orthilia secunda, Oryzopsis asperifolia, Oxalis montana, Sphagnum spp., Streptopus roseus, Thelypteris noveboracensis* and *Trillium undulatum*. The weedy species which invaded were *Aralia hispida, Comptonia peregrina, Epilobium angustifolium, Populus grandidentata* and *Rubus idaeus*.

The physical damage that resulted from harvesting also might have caused the loss of some species, especially the rare ones, which occurred in very few plots before harvesting. In the CS area, *Acer saccharum, Dennstaedtia punctilobula, Lycopodium annotinum, Prunella vulgaris* and *Ribes lacustre* were such rare species. In the C area, *Achillea millefolium, Alnus rugosa, Aster macrophyllus, Dryopteris sp., Vaccinium vitis-idaea* and *Veronica officinalis* were such rare species.

Some rare forest species, such as *Goodyera tesselata* in CS area, were susceptible to both changes in environmental conditions and physical damage caused by harvesting.

It was found that more forest species were lost and more weedy species invaded in the CS area than in the C area. This is due to the difference in the disturbance intensities caused by the two harvesting treatments. In the CS area, the canopy was removed and the advance regeneration was mostly destroyed in the harvesting, while in the C area, much of the advance regeneration was retained and provided some shade to the forest floor after harvesting. In addition, the CS treatment caused more physical damage to the herbaceous layer than the C treatment.

After the C and CS treatments, many forest species were lost but not as many weedy species invaded to take their place in the first year just after the harvesting, resulting in an overall decline in species richness. The Shannon-Wiener index increased in the C treatment and decreased in the CS treatment. The Shannon-Wiener index is made up of two components: species richness and evenness. The C treatment increased diversity by reducing the dominance of a few species and increasing evenness since the species richness after harvesting in C area was lower than before harvesting. How the Shannon-Wiener index was reduced in the CS treatment is not clear; species richness declined but evenness may or may not have decreased.

This study has identified a number of species that are eliminated or significantly reduced in abundance by harvesting. These species could be used as criteria and indicators of sustainable forest management and should be the focus of monitoring efforts. Additional species may be lost and some of the species that were initially lost may reinvade with time. Additional monitoring will be required before a complete list of indicator species can be finalized.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Correspondence analysis of the pre-harvest herbaceous community in the Hayward Brook Watershed, southeastern New Brunswick, indicated that the community composition was most highly correlated with litter variables (> 60%) and less so with those of canopy, topography and aspect. Composition was strongly related to litter chemistry, specifically pH, and calcium and magnesium components. The herbaceous community had low species evenness. However, the community was rich with species that are particularly uncommon for the area; this increased the relative diversity of the area.

There is concern that many of the rare species, i.e. those that were infrequent or had low cover values, will be at risk following forest harvest. Catastrophic disturbance such as clearcutting would be expected to have profound effects on herbaceous community diversity: it may eliminate these species locally, it may increase the chance of new species colonizing the area, it may change the relative abundances of the species that were present in the pre-disturbance community, or a combination of these may result. It is essential to track the post-disturbance response of species in relation to stand development stages and site quality to determine the effects of forest management practices and the effect of clearcutting on the biodiversity of the herbaceous vegetation in a mixed forest setting. This study provides baseline data against which changes can be detected.

It is also important to determine where unique herbaceous communities and uncommon species occur within the study area to propose strategies for protecting or managing these areas. This study has delineated the stand types and herbaceous communities associated with those stand types within the study area. In addition, the relationships between these communities and environmental factors have been identified. With this information, predictions of the location of certain communities can be made based on simple environmental factors, including topography and canopy composition. This will simplify the sampling of herbaceous communities and will facilitate management planning.

This study has also provided critical information for identifying indicator species of sustainable forst management. Those species that were lost or significantly reduced by harvesting provide a focus for monitoring and assessment.

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Appendix I. Summary of PCCA procedure. In each analysis (numbered), the environmental data set was successively partitioned to isolate individual environmental variable groups by assigning the remainder as covariates. The sum of eigenvectors (CEV) represents the unique contribution of the canonical variables.

	Canonical	Covariate	CEV
1.	All	None	1.582
	Topography+Litter	Canopy	1.334
	Topography	Canopy+Litter	0.347
2.	Topography+Canopy	Litter	0.478
	Canopy	Topography+Litter	0.108
3.	Litter+Canopy	Topography	0.943
	Litter	Topography+Canopy	0.815