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THE UNIVERSITY OF ALBERTA

UNDERSTORY DEVELOPMENT IN ASPEN-WHITE SPRUCE FORESTS IN
NORTHERN ALBERTA

by

ROBERT A. ELLIS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE
IN
PLANT ECOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

SPRING 1986

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled UNDERSTORY DEVELOPMENT IN ASPEN-WHITE SPRUCE FORESTS IN NORTHERN ALBERTA submitted by ROBERT A. ELLIS in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in PLANT ECOLOGY.

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Date... *January 17, 1986*

Abstract

Forty-five stands located on well-drained upland sites in the Boreal Mixedwood Ecoregion of Alberta were investigated. *Picea glauca* and *Populus tremuloides* were the dominant tree species present though *Abies balsamea* and *Populus balsamifera* were important in a few stands. Orthic Grey Luvisols were the predominant soils.

Three groupings of stands, based on canopy evergreenness, were recognized using Detrended Correspondence Analysis. These stand groupings were related to community and species attributes.

Canopy cover and the development of a moss carpet were the two factors found to be most important in influencing understory structure and composition. Species richness (R), species diversity (H') and total vascular plant cover decreased with increasing evergreen canopy cover while species dominance (C) and heterogeneity, patchiness, increased.

Understory evergreen species become more important than summergreen species as evergreen canopy cover increases. Understory evergreenness appears to be related to canopy evergreenness and not to stand age.

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1. Introduction

The Boreal Mixedwood Ecoregion, the largest ecoregion in Alberta, covers approximately 290,000 km² extending from the Aspen Parkland Ecoregion in the south to the Boreal Northlands Ecoregion in the north (Strong and Leggat 1981). Analogous to the Boreal Mixedwood Section (B18a) of the Boreal Forest (Rowe 1972), the Boreal Mixedwood Ecoregion is dominated by trembling aspen (*Populus tremuloides*) a species well adapted to the frequent fires which occur in the region.

The forests of central and northwestern Alberta have been described in terms of floristic composition and ecological relationships by Moss (1932, 1953). More intensive quantitative studies have been done on the development of white spruce-balsam fir (*Picea glauca-Abies balsamea*) (Achuff and LaRoi 1977) and jack pine (*Pinus banksiana*) (Carroll and Bliss 1982, Purchase and La Roi 1983) forests in Alberta but aspen forests have been largely ignored. Research on the development of aspen-white spruce mixedwood communities has been done in Saskatchewan (Rowe 1956, Dix and Swan 1971) as a component of more comprehensive studies on the dynamics of boreal forest communities.

Overstory-understory relationships in the boreal forest have been studied in Saskatchewan (Swan and Dix 1966) and Ontario (Carleton and Maycock 1980, Carleton and Maycock 1981).

Vascular plant nomenclature follows Moss and Packer (1983).
Bryophyte nomenclature follows Crum (1976).

The primary objectives of this thesis are (1) to describe long-term autogenic succession in the understory structure and composition of aspen-white spruce mixedwood forests in northern Alberta, and (2) to investigate the effect of shifting tree canopy dominance from broadleaf deciduous to needleleaf evergreen on the understory structure and composition of aspen-white spruce mixedwood forests in northern Alberta.

The following hypotheses, proposed by Odum (1969) in his ecosystem model, were tested:

H₁: Species richness is low in the developmental stages of succession and high in the mature stages.

H₂: Species diversity (equitability component) is low in the early stage of succession and high in the mature stages.

H₃: Spatial heterogeneity (pattern diversity) is poorly organized in the early stages of succession and well organized in the mature stages.

1.1 Definition of Terms

Summergreen species are species which retain their leaves for most of one growing season.

Wintergreen species are species which retain their leaves for a one year period and then replace them with the next annual cohort.

Evergreen species are species which retain their leaves for two or more years.

2. Study Region

2.1 Climate

The climate of the study region (Fig. 1) is continental, humid to subhumid, microthermal (Dcf Koeppen System), characterized by short, cool summers and long, cold winters (Longley 1970). Mean annual precipitation, mean annual temperature and growing degree-days above 5°C decrease from south to north. Climate diagrams (Figure 2) from four locations in northern Alberta and Ft. Smith in the Northwest territories are representative of the regional climate.

According to the climate classification of Hamet-Ahti et al. (1974) most of the study sites are located in the southern boreal. The extreme northern sites may be considered as marginally southern boreal to middle boreal. As climate is one of the main determinants of plant species distribution, there may be vegetational differences between northern study sites and southern study sites. However, neither field observations nor laboratory analysis of the data reveal any significant vegetational differences amongst the study sites which could be attributed to climate.

2.2 Geology and Physiography

The study region (Fig. 1) was last glaciated during the Wisconsin age (11,400 B.P.) when the Laurentide ice sheet advanced from the northeast (Lichti-Federovich 1970). A

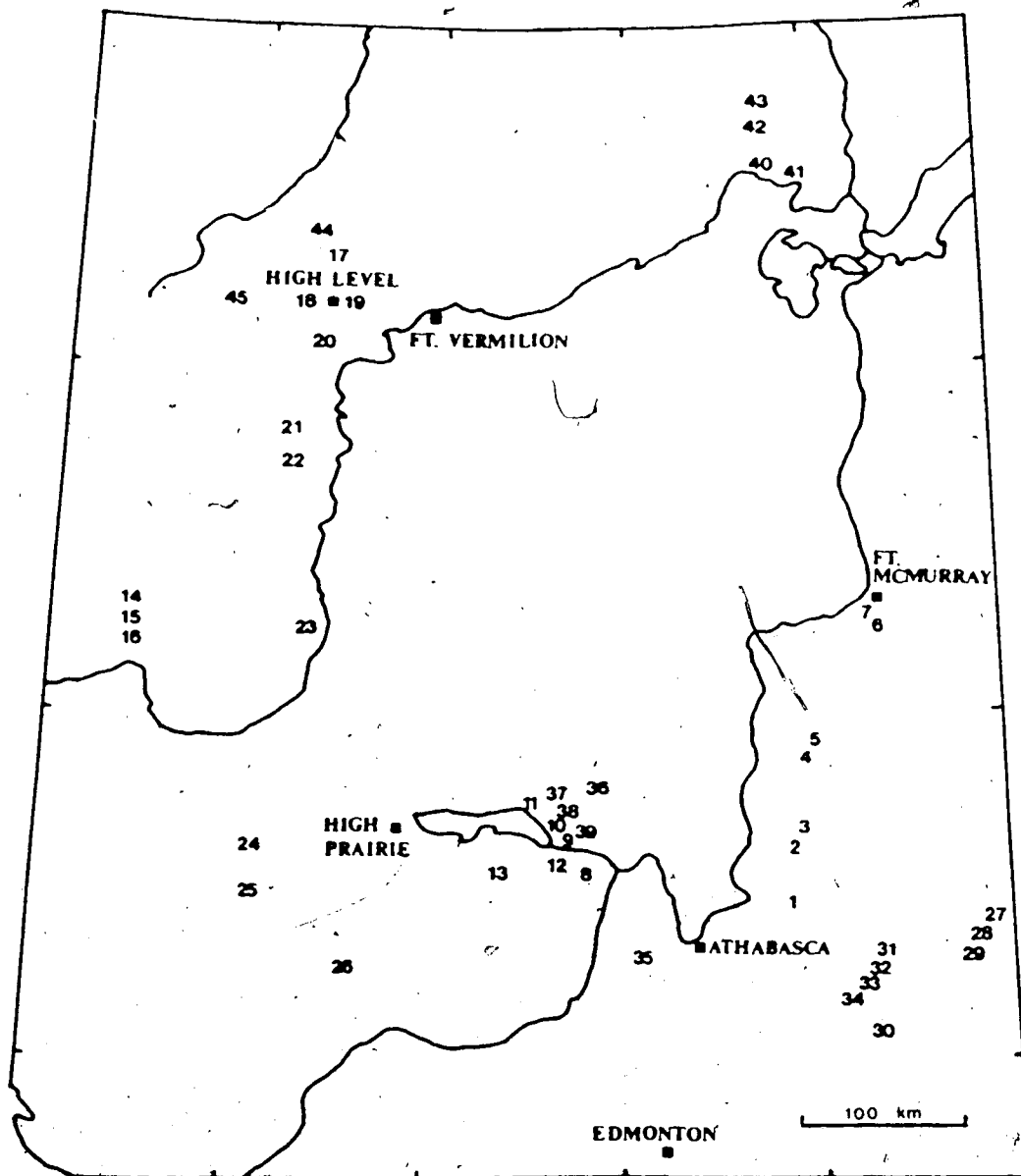
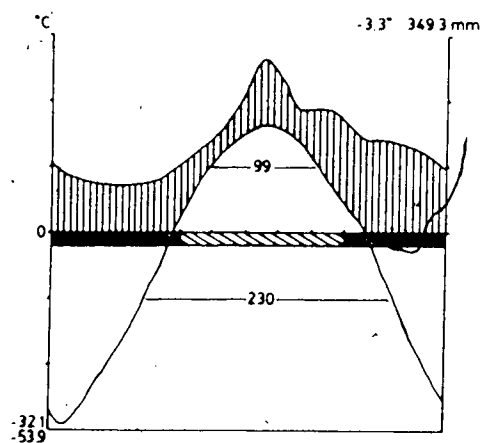


Figure 1. Locations of stands.

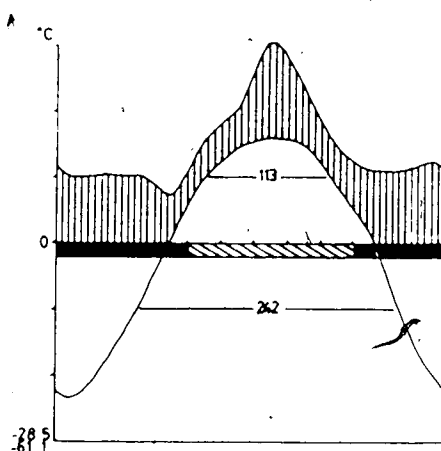
Figure 2. Climate diagrams (after Walter and Lieth 1967) of five stations located in northern Alberta and southwestern Northwest Territories. Data from Environment Canada 1980a and 1980b.

Key: abscissa = months of the year, January to December;
ordinate = one unit equals 10°C or 20mm precipitation;
a = station name; b = altitude (m); c = number of years
of observation (where two figures are given, the first
indicates temperature and the second precipitation);
d = mean annual temperature ($^{\circ}\text{C}$); e = mean annual
precipitation (mm); f = mean daily minimum temperature;
during the coldest month; g = absolute minimum temperature;
h = curve of mean monthly temperature; i = curve of mean
monthly precipitation; j = humid period; k = months with
mean daily minimum below 0°C (black); l = months with
absolute minimum below 0°C (diagonal shading); m = number
days with mean temperature above $+10^{\circ}\text{C}$; n = number of days
with mean temperature above -10°C .

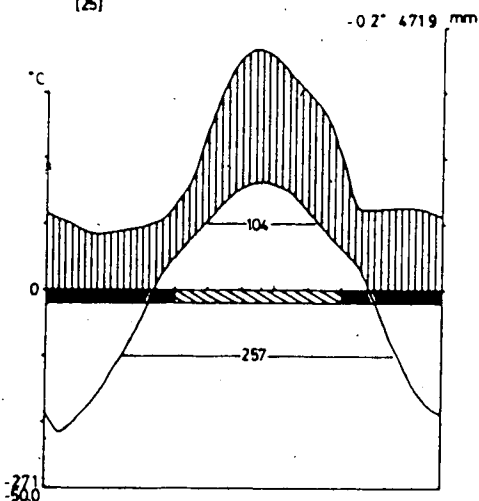
FT SMITH A (203m) 60°02'N 111°56'W
[25]



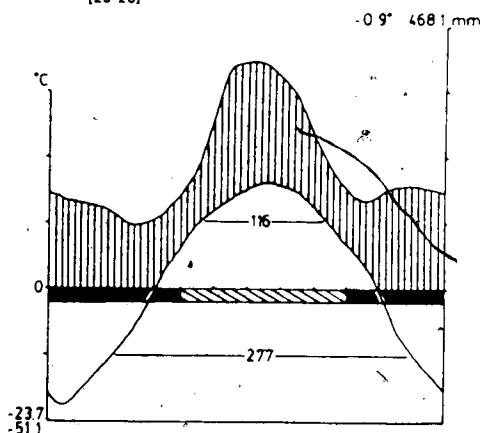
FT VERMILION CBA (279m) 58°23'N 116°02'W
[30]



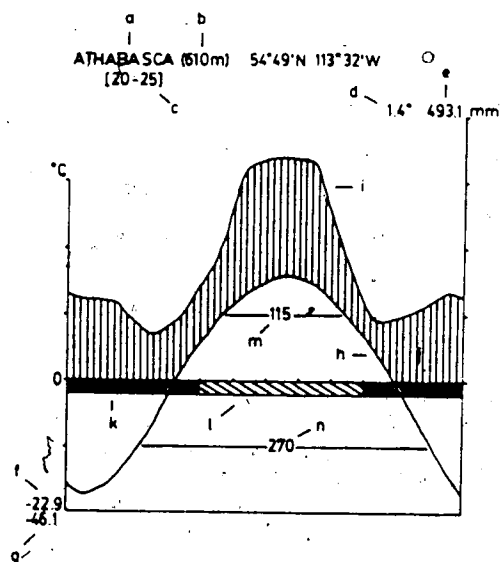
FT MURRAY A (369) 56°39'N 111°13'W
[25]



HIGH PRAIRIE (594m) 55°22'N 116°52'W
[25-20]



ATHABASCA (610m) 54°49'N 113°32'W
[20-25]



number of extensive, short-lived proglacial lakes, which formed along the retreating ice front, have resulted in large areas of the region being capped with glacio-lacustrine deposits. Modification of the landscape is occurring at the present time by infilling of depressions and lakes by organic materials.

Most of the study region is underlain by shales and sandstones deposited during the late Cretaceous (Kjarsgaard 1972, St-Onge 1972, Scheelar et al. 1972, Bayrock 1960, Odynsky et al. 1952). The predominant parent materials are till and lacustro-till deposits with gravelly outwash and shoreline materials important in local areas. Surficial deposits are unconsolidated materials consisting of (1) till, (2) lake deposits of silt and clay and (3) glacial outwash which is composed of lake and wind deposits of sand and sand/gravel.

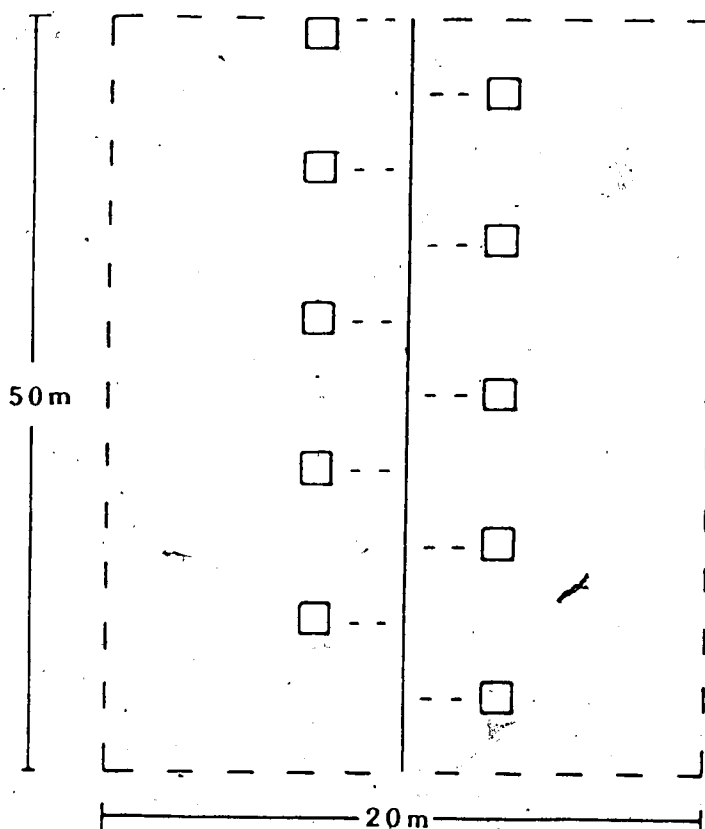
3. Methods

3.1 Field Methods

Preliminary selection of mixedwood forest stands was made using black-and-white airphotos and Alberta Forest Cover Type maps (scale 1:126,720). Criteria for preliminary site selection were designed to obtain a wide range of age-classes throughout the Boreal Mixedwood Ecoregion of Alberta. Final selection involved ground-truthing to locate sites which were: (1) dominated by any one or combination of *Picea glauca* or *Populus tremuloides*, (2) relatively undisturbed by man, (3) relatively uniform in the spatial distribution of plant species over a 1-2 hectare area, and (4) located on sites with less than 10° slope angles.

Within each stand one 20 x 50 m macroplot was centrally located. In stands which had an apparent slope the macroplot was oriented perpendicular to the slope, i.e. parallel with the contour. Plot boundaries were established by running a band chain out 50 m and pacing 10 m in opposite directions at both ends of the chain.

Species cover estimates, except for tree species, were made using 1 m² quadrats spaced at 5 m intervals along the chain and 5 m perpendicular from the chain in an alternating pattern (Fig. 3). Tree species cover was assessed over the entire macroplot. Percent cover was estimated by vertically projecting the ground area covered by a species, disregarding openings in the foliage (Daubenmire 1959).



1/10 HECTARE PLOT METHOD

Figure 3. Diagram of the 1/10 Hectare Plot Method.

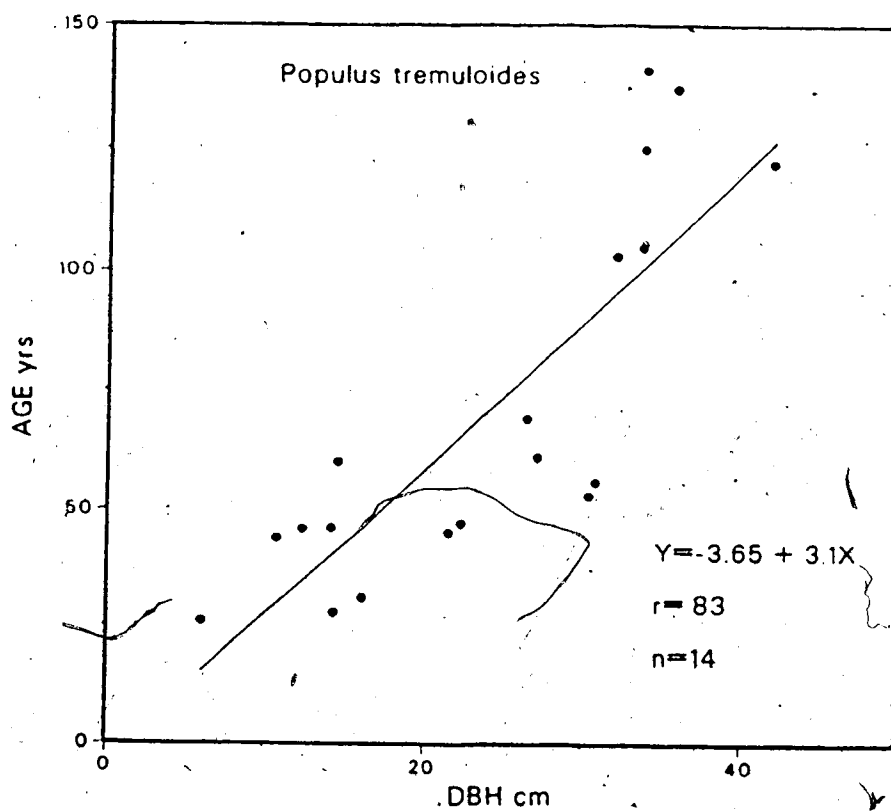
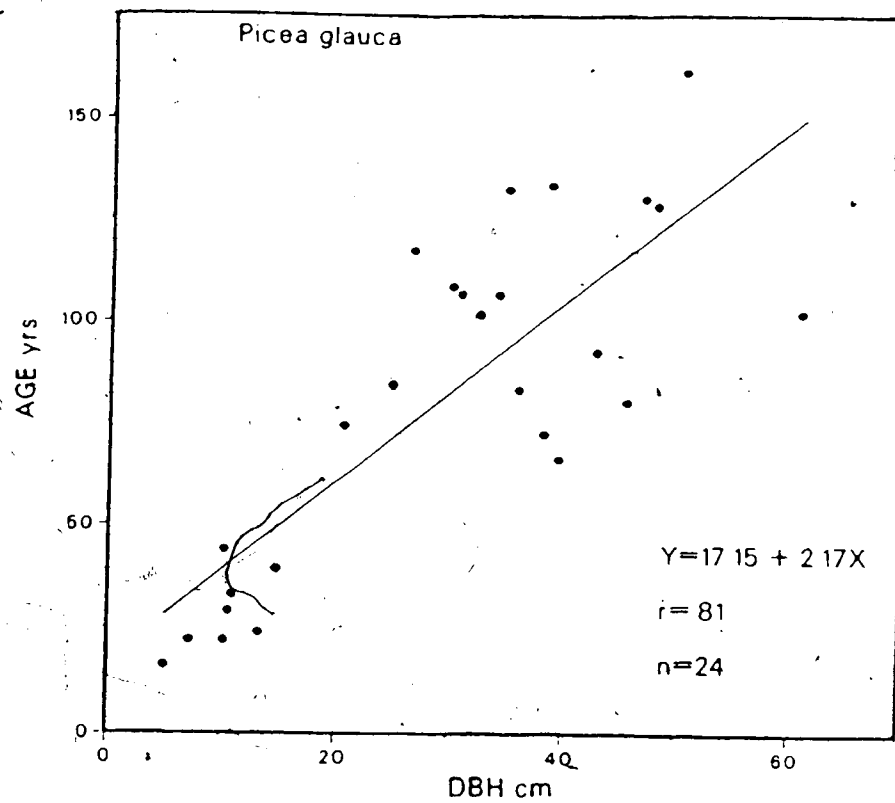
Cover estimates were made for each species using a nine-point cover scale: R (rare), + (<1%), 1 (1-5%), 2 (6-15%), 3 (16-25%), 4 (26-50%), 5 (51-75%), 6 (76-95%), 7 (96-100%). Cover-class mid-points were used to compute mean cover values.

The macroplot was used as a sampling unit to obtain: (1) tree cover estimates, (2) tree basal area estimates, (3) tree ages, and (4) information on community structure. Basal area of all trees was recorded by species for living and dead individuals, at five points at 10 m-intervals along the band chain, using the variable-radius method (Bitterlich 1948; see Mueller-Dombois 1974). Two or three trees were cored in each stand to obtain a stand origin date; cores were taken ca. 25 cm above tree base. The oldest core counted was taken as an estimate of stand age. When datable cores could not be obtained stand-age was estimated from dbh (diameter at 1.4 m above ground) using linear regression lines for *Picea glauca* and *Populus tremuloides* (Fig. 4). The problem of obtaining datable cores lies primarily with *P. tremuloides* and only occasionally with *P. glauca*.

Stand drainage was assessed using a 7-point system: 1-very rapid, 2-rapid, 3-well, 4-fresh, 5-impeded, 6-poor, and 7-stagnant. Stand moisture was assessed using a 7-point scale: 1-xeric, 2-xero-mesic, 3-mesic, 4-hygro-mesic, 5-hygric, 6-hygro-hydric and 7-hydric.

A soil pit was centrally located in the stand and a profile description made following the nomenclature of The

Figure 4. Linear regression estimate of tree age from
DBH in Picea glauca and Populus tremuloides.



Canadian System of Soil Classification (Canada Soil Survey Committee 1978).

3.2 Laboratory Analyses

3.2.1 Synthetic Moisture Index

The moisture regime of each site was also evaluated using a weighted Synthetic Moisture Index (SMI) (after Rowe 1956). A SMI value was derived for each stand using the following formula:

$$SMI = \left(\sum_{i=1}^N (SIV \times SC) / N \right) \times 100$$

where, SIV = species indicator value, SC = species cover and N = number of species.

Each species was subjectively assigned to a moisture class with an associated indicator value, i.e. Dry - 1, Fresh - 2, Moist - 4, Very Moist - 8 and Wet - 16 (see Appendix II). Species preferring wet habitats generally have a narrower ecological amplitude than species in drier habitats. Thus, using the preceding geometric scale, species with wet values are given greater weight in calculating the index. Rare species and ubiquitous species are omitted when evaluating a stand's SMI.

3.2.2 Classification

To discover associations and structure in the data, a cluster analysis (CLUSTAN) and a two-way indicator species analysis (TWINSpan) were conducted using the Clustan 1C

(Wishart 1978) and TWINSpan (Hill 1979b) computer packages, respectively.

Cluster analysis is a numerical procedure which sorts individuals into groups based on some similarity criterion. In this study, a similarity matrix was computed for the 45 stands based on error sum of squares of individual stands. Cluster fusions were made using Ward's method (error sum of squares) (Ward 1963) which is a sequential, agglomerative, hierarchic and non-overlapping classification method (Sneath and Sokal 1973).

Two-way indicator species analysis (TWINSpan) is a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals (plots) and attributes (species) (Hill 1979b). TWINSpan is a polythetic divisive method of classification in which the plots are classified first and species are classified second, using the classification of the plots as a basis.

3.2.3 Ordination

Stands were ordinated using Detrended Correspondence Analysis (DECORANA), a detrended form of reciprocal averaging developed by Hill (1979a). Gauch (1977) recommended reciprocal averaging as the ordination of first choice when gaining familiarity with a data set where underlying environmental gradients are not obvious. Ordinations were based on mean species cover values. Only the following default options of DECORANA were invoked to

Analyze the data: the data were not transformed, rare species were not down-weighted, axes were not re-scaled, twenty-six segments were used in detrending subsequent axes with respect to the first axis, and the default rescaling threshold was used.

3.2.4 Canopy Preference Analysis

To assess the degree of "preference" of a species for an evergreen or deciduous canopy, I developed a Canopy Preference Index (CPI).

$$CPI = \sum_{i=1}^N (ETC/TTC \times S_i) / \sum_{i=1}^N S_i,$$

where, ETC = evergreen tree cover/stand, TTC = total tree cover/stand, S_i = species cover in stand i , and N = number of stands, i.e. five stands with highest cover of S . Mean cover data for each of five stands where the cover of the species was highest were examined in relation to the percent cover of evergreen and deciduous species cover in the tree canopy. Five stands were considered to be sufficient to obtain a reasonable estimate of a species' cover preference. A high CPI value indicates preference for an evergreen canopy while a low CPI value indicates preference for a deciduous canopy.

3.2.5 Dominance-Diversity Analysis

Dominance-diversity curves (Whittaker 1965) were constructed for each stand and were compared in terms of (1) species sequences, and (2) shape. Simpson's Index of

Dominance Concentration (C ; Simpson 1949) and the Shannon-Weaver Index of Diversity (H' ; Shannon and Weaver 1949) were calculated for each stand based on cover estimates for all vascular species.

Both Simpson's and Shannon-Weaver are equitability indices. They are measures of the variation in the proportions among species. The Simpson index is most sensitive to numbers of abundant species and gives little weight to rare species. Shannon-Weaver is more sensitive to rare species and thus is more adversely affected by sampling error.

The variety of species or species richness was calculated as the sum of species recorded in the 20 x 50 m macroplot. Species per square meter was calculated as the mean number of species present in the 10-1m² quadrats.

To determine the heterogeneity or degree of patchiness within each stand a Heterogeneity Index (HI) was calculated as follows:

$$HI = 100 \times (\text{Sum of SCV}(\%) / \text{Number of Species})$$

where, SCV, the species coefficient of variation, is the standard error:mean ratio for a species present in the 10-1m² quadrats. The higher the HI value the more patchy the stand.

4. Results

4.1 Soils

The soils of the study region have been surveyed either at the reconnaissance level (Kjearsgaard 1972, Scheelar et al. 1972, Reeder and Odynsky 1969), to soil series, or at the exploratory level (Wynnyk et al. 1963, Lindsay et al. 1962, 1960, 1957, Odynsky et al. 1952), to soil subgroup. Soils in this study were classified to great group or subgroup levels (Table 1).

Gray Luvisols, on fine-textured clays, silty clays or loams, were found at 37 sites. Eleven of these sites had Orthic Gray Luvisols and three sites had Gleyed Gray Luvisols. Thirty-one of the 37 Gray Luvisols were on well to moderately well-drained sites. Three sites had Luvic Gleysols, two sites had Brunisols, one of which was a Dystric Brunisol, one site had a Ferro-humic Podzol and one site had a Gleyed Regosol.

4.2 Classification

The cluster analysis dendrogram (Fig. 5) has two major clusters. The first cluster is composed of 25 stands and has two recognizable subclusters. Stands in the first subcluster are dominated by either *Picea glauca* or *P. glauca* and *Populus tremuloides*. There are only two stands, Nos. 22 and 26, in the second subcluster (Group 1A), and *P. glauca* is co-dominant with *Pinus banksiana* in Stand 22 and with *Pinus*

TABLE 1. STAND CHARACTERISTICS.

Soil Type: GL (Gray Luvisol), LG (Luvic Gleysol), GGL (Gleyed Gray Luvisol), GL (Gleyed Luvisol), B (Brunisolic), OGL (Orthic Gray Luvisol), DB (Dystic Brunisolic), GR (Gleyed Regosol), FHP (ferro-humic Podzol); Soil Texture Class: C (Clay), SC (Silty-Clay), CL (Clay-Loam), SL (Sandy-Clay), L (Loam), SIL (Silty-Loam), SL (Sandy-Loam), S (Sand); Drainage Class: R (Rapid), W (Well), F (Fresh), I (Impeded); Moisture Class: XM (Xero-Mesic), M (Mesic), HM (Hygro-Mesic).

Stand	Soil Type	Soil Texture ¹	Drainage Class	Moisture Class	Aspect (°)	Slope Angle (°)	Synthetic Moisture Index	Stand Age
1	GL	C	F	HM	90	3	546	83
2	GL	SIL/SL	W	M	90	5	452	45
3	LG	SIC	W	HM	0	0	544	66
4	GGL	SIC	I	HM	270	4	504	141
5	GL	SL	W	M	45	10	593	161
6	GL	SIC	F	HM	340	1	552	47
7	GL	SIC	F	M	135	2	458	105
8	GGL	SCL	W	M	0	0	529	69
9	LG	C	I	HM	0	0	718	92
10	B	LS	F	M	180	3	576	56
11	GL	C	W	M	270	3	531	55
12	GL	SIC	W	XM	25	3	873	11
13	LG	SIC	I	HM	270	2	528	117
14	GL	SC	F	M	270	2	423	100
15	GGL	SC	F	M	360	1	565	122
16	GL	SC	I	M	45	3	---	165
17	GL	L	W	M	315	2	365	85
18	GL	C	W	M	360	1	421	60
19	GL	SIC	I	M	0	0	498	80
20	GL	CL	F	M	0	0	496	31
21	GL	C	F	M	270	2	582	61
22	GL	SIC	I	M	0	0	---	38
23	GL	C	R	M	0	0	403	106
24	GL	C	F	M	0	0	561	28
25	GL	SIC	W	M	45	4	505	128
26	GL	C	I	M	0	0	---	13
27	OGL	L	W	M	200	1	473	33
28	GL	-	F	M	180	1	533	136 ²
29	OGL	SIL	I	M	160	1	---	99 ²
30	GGL	L	F	M	340	2	343	107 ²
31	OGL	C	-	-	180	7	547	102
32	OGL	SL	F	M	180	2	513	112
33	OGL	SL	F	M	180	4	543	132 ²
34	GL	C	F	M	20	5	378	46
35	GL	SC	F	M	270	0	572	120 ²
36	OGL	C	-	M	135	2	582	173
37	OGL	C	I	M	45	2	652	108
38	OGL	C	W	M	90	-	567	46
39	OGL	C	F	M	90	4	452	82 ²
40	DB	SIL	W	M	360	3	273	75 ²
41	-	-	F	M	135	3	525	92 ²
42	GR	S	R	XM	0	0	306	65 ²
43	FHP	SL	W	M	360	-	386	106
44	OGL	C	F	M	360	2	515	89 ²
45	OGL	C	F	M	90	3	538	99 ²

²Soil texture is based on hand texturing of materials from the top 30 cm of the soil profile.

³Estimates from Picea glauca or Populus tremuloides regression lines (see Figure 4).

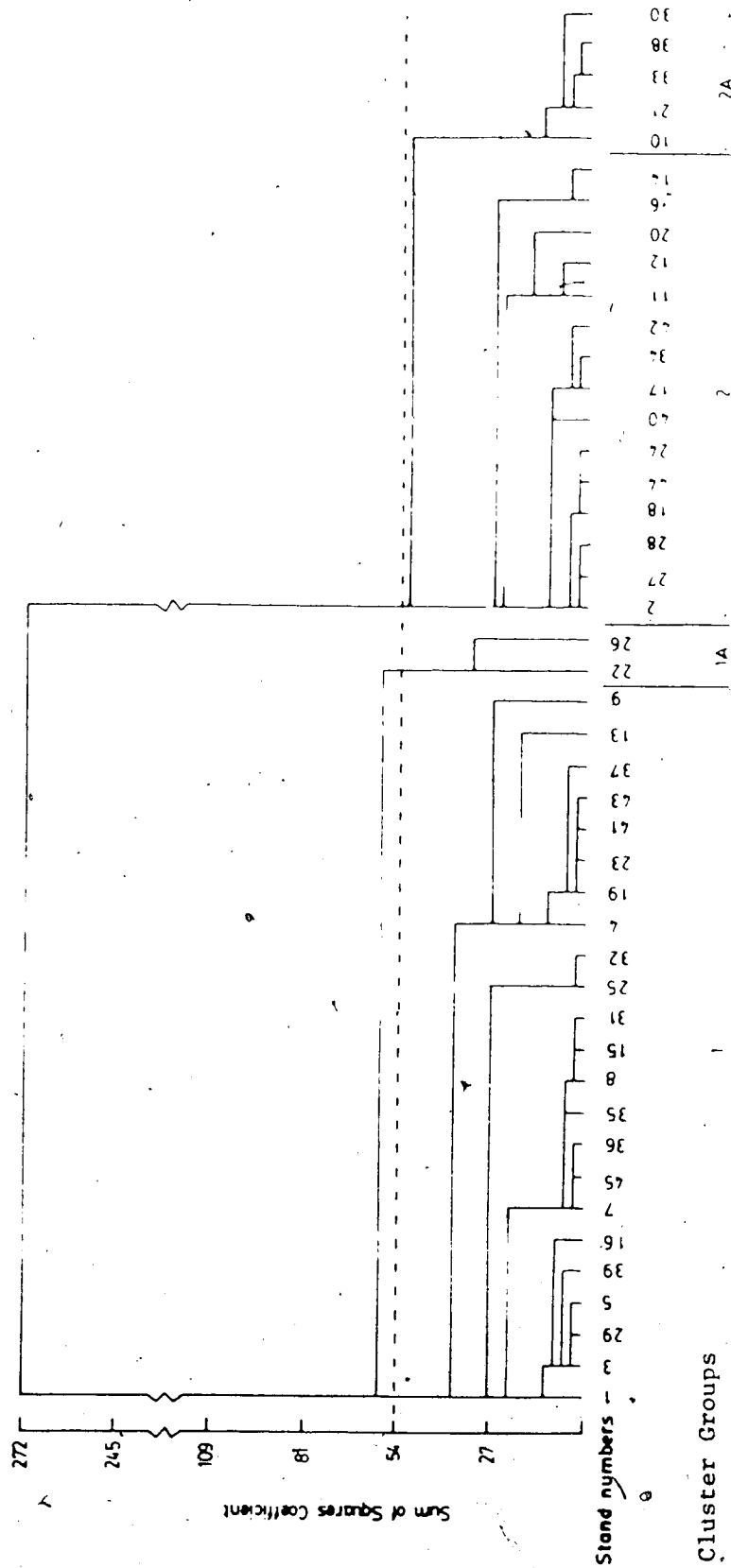


Figure 5. Cluster dendrogram derived from Ward's (1963) method of cluster analysis using quantitative data from the 45 study sites. The broken line indicates where cluster groups were recognized.

contorta in Stand 26.

The second cluster is composed of 20 stands and has two recognizable subclusters. The first subcluster, containing 16 stands, is dominated by *Populus tremuloides* while the second subcluster is co-dominated by *P. tremuloides* and *P. balsamifera*.

Initial trial runs with DECORANA indicated that Stands 16, 22 and 26 are outliers. Removal of these three stands from the data gave a less clumped distribution of stands on the DECORANA-XY ordination (Fig. 7). Only these three stands had *P. banksiana* or *P. contorta* present as co-dominants in the tree layer. Therefore, based on CLUSTAN results, which segregated Stands 22 and 26 as a cluster, and DECORANA results, which suggested Stands 16, 22 and 26 were outliers, these three stands have been excluded from further analysis.

TWINSPAN segregates stands into four major groups (Fig. 8). *P. tremuloides* and *P. glauca* are co-dominant and *Abies balsamea* is present as a sub-dominant tree or transgressive in Group 1 and Group 1a. *A. balsamea* is generally absent from Group 2 where *P. tremuloides* and *P. glauca* are again co-dominant. *P. glauca* and *A. balsamea* are largely absent from Group 3 in which *P. tremuloides* is dominant.

Characteristic understory species in Group 3 include: *Amelanchier alnifolia*, *Rubus idaeus*, *Symphoricarpos albus*, *Vicia americana* and *Aster conspicuus*. Group 4 contains three *P. tremuloides*-dominated stands located in northern Alberta. Stand Nos. 40 and 42 are in Wood Buffalo National Park while

Stand No. 18 is situated north of High Level (Fig. 1). Stands in Group 4 are distinguished from stands in Group 3 by the absence of such species as *Lonicera involucrata*, *Rubus idaeus*, *Aralia nudicaulis*, *Mertensia paniculata* and *Calamagrostis canadensis*.

4.3 Product-Moment Correlations

A product-moment correlation matrix was constructed for the most common plant species and vegetation variables (Table 2) within the 42 stands. Significant r values are described below.

Stand age is positively correlated with evergreen canopy cover, bryophyte cover and pteridophyte cover, and negatively correlated with shrub cover and graminoid cover. Species positively correlated with stand age include *Picea glauca*, *Mitella nuda* and *Lycopodium annotinum*. *Populus tremuloides* and *Rosa acicularis* are negatively correlated with stand age.

In order of decreasing r values, evergreen canopy cover is: (1) significantly positively correlated with bryophyte cover, immature tree cover, understory evergreen and wintergreen species, *Ledum groenlandicum*, *Linnaea borealis* and *Mitella nuda*; and (2) significantly negatively correlated with shrub cover, graminoid cover, *Rosa acicularis*, *Viburnum edule*, *Calamagrostis canadensis*, *Aster ciliolatus*, *Aster conspicuus*, *Epilobium angustifolium*, *Fragaria virginiana*, and *Lathyrus ochroleucus*.

Table 2 (cont'd)

28	<i>Viburnum edule</i>	27	28	29	30	31	32	33	34	35	36	37	38	39
29	<i>Vaccinium vitis-idaea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
30	<i>Lycopodium annotinum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
31	<i>Calamagrostis canadensis</i>	47**	-	-	-	-	-	-	-	-	-	-	-	-
32	<i>Achillea millefolium</i>	-	36*	-	-	-	-	-	-	-	-	-	-	-
33	<i>Aster ciliolatus</i>	-	-	-	-	37*	-	-	-	-	-	-	-	-
34	<i>Aster conspicuus</i>	43**	49**	-	-	-	33*	-	-	-	-	-	-	-
35	<i>Epilobium angustifolium</i>	-	51**	-	-	38*	-	31*	37*	55**	-	-	-	-
36	<i>Fragaria virginiana</i>	-	43**	-	-	-	32*	-	-	-	-	-	-	-
37	<i>Goodyera repens</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
38	<i>Lathyrus ochroleucus</i>	-	-	-	-	-	-	-	-	-	52**	-	-	-
39	<i>Linnaea borealis</i>	37*	-	34*	-	-	-	-	-	-	-	-	-	-
40	<i>Mitella nuda</i>	-	-	-	-	-	37*	-	-	-	-	-	-	-
41	<i>Pyrola asarifolia</i>	-	-	-	-	-	-	-	-	-	-	-	96*	-
42	<i>Orthilia secunda</i>	-	-	-	-	-	-	-	35*	-	30*	-	40**	-
43	<i>Rubus pubescens</i>	-	62**	-	-	-	-	-	33*	-	-	-	-	-
44	<i>Trientalis borealis</i>	-	-	-	-	-	42**	-	-	-	-	-	-	-
45	<i>Viola renifolia</i>	40**	54**	-	-	-	-	-	72**	-	44**	-	42**	-
46	<i>Cornus canadensis</i>	-	-	40**	-	-	-	-	-	-	-	-	-	61**
47	<i>Maianthemum canadense</i>	36*	36*	-	-	-	-	-	31*	-	35*	-	-	-
48	<i>Mertensia paniculata</i>	34*	34*	-	-	-	36*	-	31*	-	38*	-	-	-
49	<i>Petasites palmatus</i>	30*	30*	-	-	-	-	-	-	35*	40**	-	63**	-

Table 2 (cont'd)

41	<i>Pyrola asarifolia</i>	40	41	42	43	44	45	46	47	48
42	<i>Orthilia secunda</i>	-	31*	-	-	-	-	-	-	-
43	<i>Rubus pubescens</i>	44**	-	-	-	-	-	-	-	-
44	<i>Trientalis borealis</i>	-	-	-	-	-	-	-	-	-
45	<i>Viola renifolia</i>	-	-	-	44**	-	-	-	-	-
46	<i>Cornus canadensis</i>	41**	-	-	39*	-	-	-	-	-
47	<i>Maianthemum canadense</i>	-	47**	-	39*	-	30*	-	-	-
48	<i>Mertensia paniculata</i>	51**	-	-	51**	-	45**	-	-	-
49	<i>Petasites palmatus</i>	-	31*	-	41**	-	33*	38*	-	35*

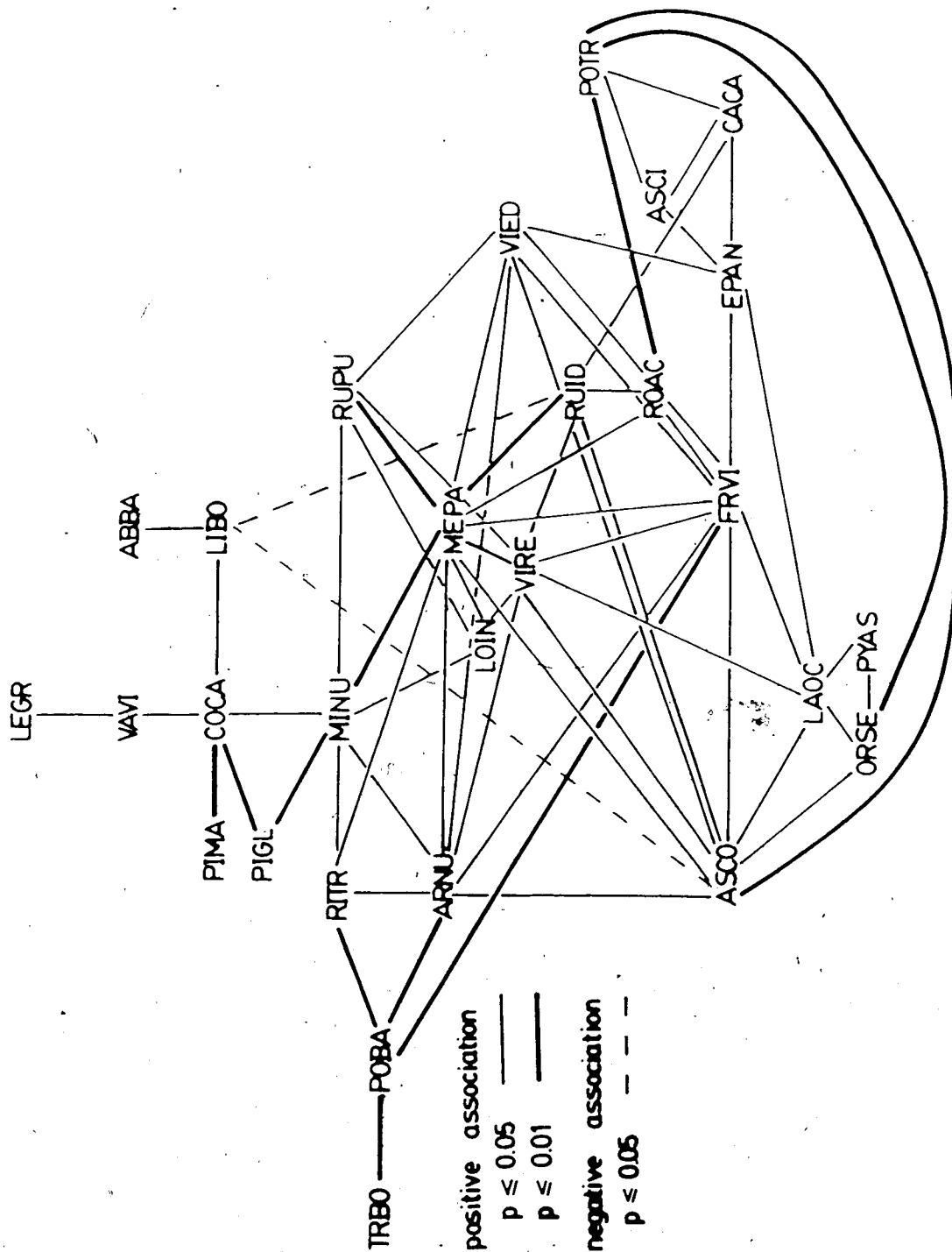
* indicates $P < 0.05$. ** indicates $P < 0.01$.
 † Trees < 2.5 cm dbh and/or < 2 m tall were used to estimate immature tree cover.

A plexus diagram (after McIntosh 1957) (Fig. 6) was constructed to show interrelationships amongst species having significant ($P > 0.95$ or $P > 0.99$) positive or negative product-moment correlations with one another. The arrangement of species on Figure 6 suggests a number of overlapping clusters of correlated species. The foremost species cluster, centered around *Mertensia paniculata*, includes *Viola renifolia*, *Rubus pubescens*, *Viburnum edule*, *Rubus idaeus*, *Fragaria virginiana*, *Ribes triste*, *Aster conspicuus*, *Lonicera involucrata* and *Aralia nudicaulis*. A second species cluster, centered around *Populus tremuloides*, includes *Aster ciliolatus*, *Calamagrostis canadensis*, *Rosa acicularis*, *Lathyrus ochroleucus*, *Orthilia secunda* and *Aster conspicuus*. A third species cluster, centered around *Cornus canadensis*, includes *Picea glauca*, *P. mariana*, *Linnaea borealis* and *Vaccinium vitis-idaea*. *Ledum groenlandicum* is correlated with *Vaccinium vitis-idaea* alone. *Pyrola asarifolia* and *Orthilia secunda* are correlated with each other and with *Lathyrus ochroleucus*.

DECORANA output shows XY-axis loci for species as well as for stands. However, there was no interpretable pattern of species interrelationships based on the DECORANA output.

Figure 6. Plexus diagram of significant associations amongst important vascular plant species.

ABBA	<u>Abies balsamea</u>
ARNU	<u>Aralia nudicaulis</u>
ASCI	<u>Aster ciliolatus</u>
ASCO	<u>Aster conspicuus</u>
CACA	<u>Calamagrostis canadensis</u>
COCA	<u>Cornus canadensis</u>
EPAN	<u>Epilobium angustifolium</u>
FRVI	<u>Fragaria virginiana</u>
LAOC	<u>Lathyrus ochroleucus</u>
LEGR	<u>Ledum groenlandicum</u>
LIBO	<u>Linnaea borealis</u>
LOIN	<u>Lonicera involucrata</u>
MEPA	<u>Mertensia paniculata</u>
MINU	<u>Mitella nuda</u>
ORSE	<u>Orthilia secunda</u>
PIGL	<u>Picea glauca</u>
PIMA	<u>Picea mariana</u>
POBA	<u>Populus balsamifera</u>
POTR	<u>Populus tremuloides</u>
PYAS	<u>Pyrola asarifolia</u>
RITR	<u>Ribes triste</u>
ROAC	<u>Rosa acicularis</u>
RUID	<u>Rubus idaeus</u>
RUPU	<u>Rubus pubescens</u>
TRBO	<u>Trientalis borealis</u>
VAVI	<u>Vaccinium vitis-idaea</u>
VED	<u>Viburnum edule</u>
VIRE	<u>Viola renifolia</u>



4.4 Ordination

4.4.1 Detrended Correspondence Analysis (DECORANA)

The first two ordination axes respectively accounted for 50% and 13% of the variance in the data. Locations of the stands on the ordination are shown in Figure 7 and the distribution of the CLUSTAN and TWINSpan group clusters are shown in Figure 8. The DECORANA-XY coordinates are listed in Appendix 1.

4.4.2 Response Patterns of Community Attributes

The clearest pattern on the ordination field is displayed by evergreen canopy cover in each stand (Fig. 9). Increasing evergreen canopy cover, bryophyte cover and the percent of total understory cover that is wintergreen or evergreen (Fig. 9) are strongly correlated with the first ordination axis. Stand age (Fig. 9), though significantly correlated with increasing evergreen canopy cover (Table 3), shows no clear pattern when mapped on the XY ordination field. Slope angle, slope aspect, drainage, stand moisture, thickness of humus layer, and Synthetic Moisture Index (SMI) values (Table 1) showed no interpretable pattern on the ordination.

Based on the percent of evergreen canopy cover, as mapped on the DECORANA-XY ordination field, stands have been separated into three groups. Stands in Group 1 have less than 10% evergreen canopy cover, stands in Group 2 have

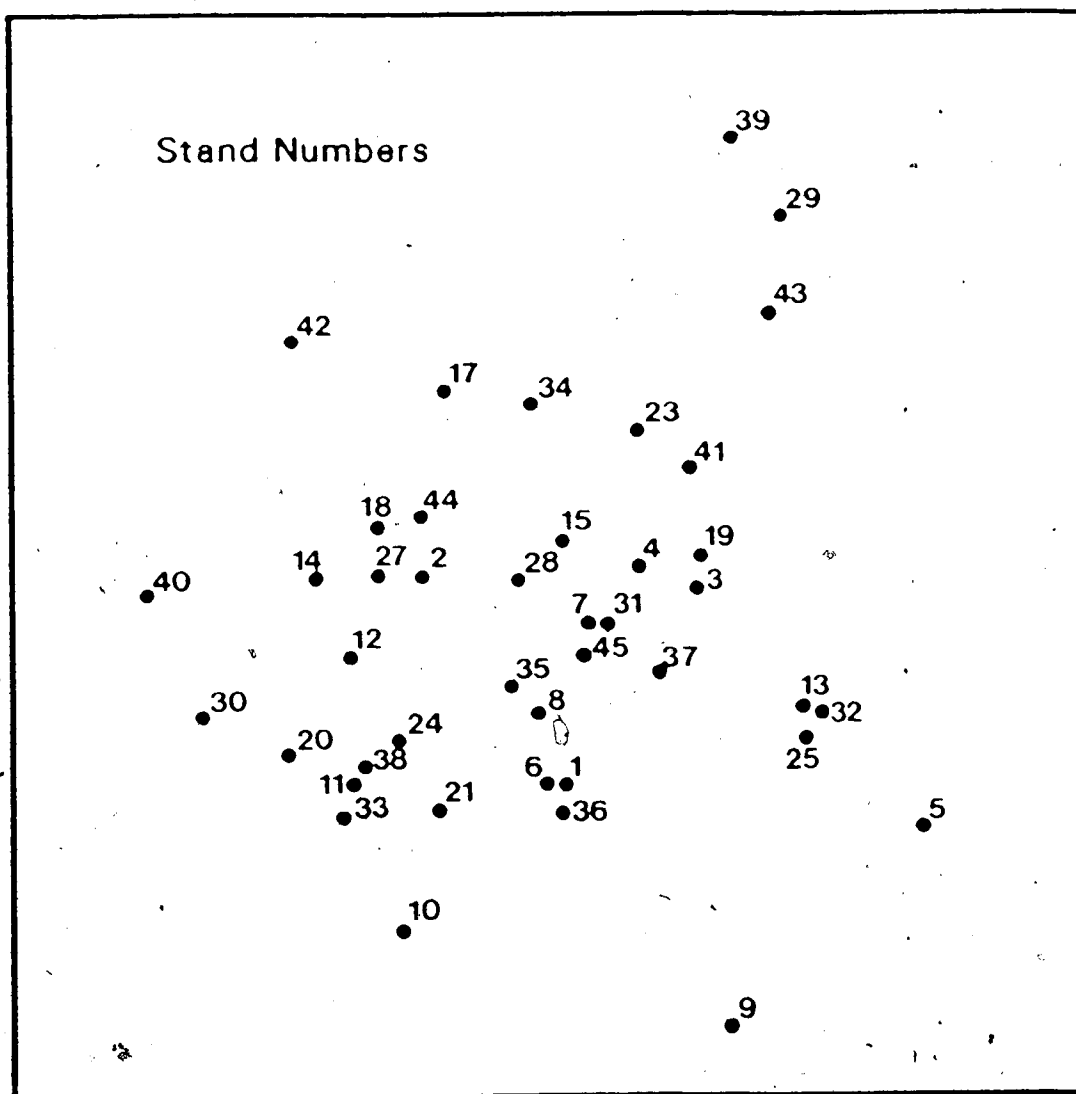


Figure 7. Locations of stands on the DECORANA-XY ordination.

Figure 8. Locations of CLUSTAN and TWINSpan cluster groups on the DECORANA-XY ordination.

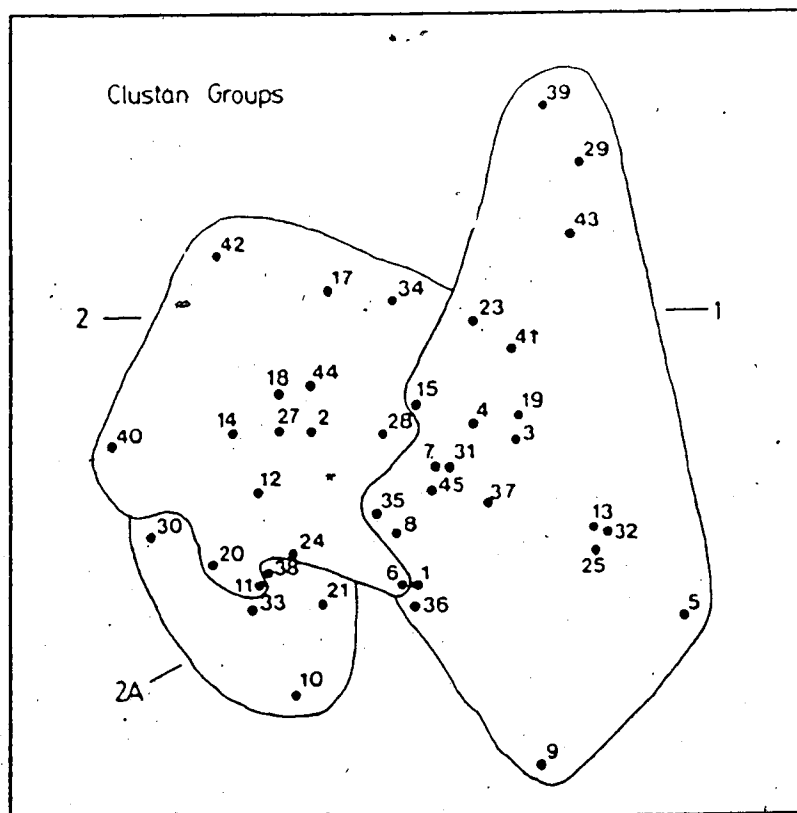
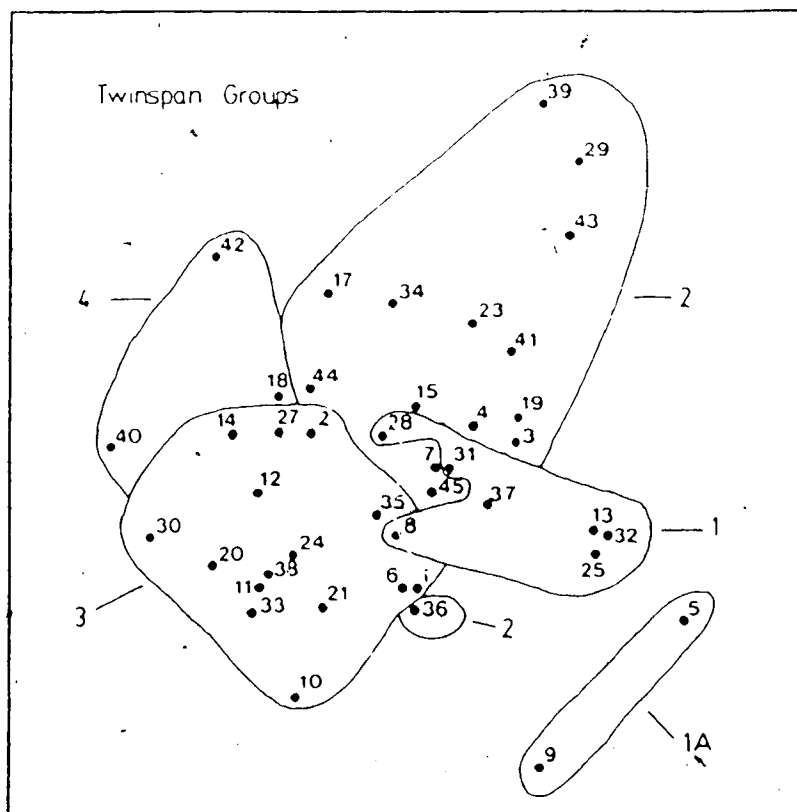


Figure 9. Patterns of community attributes on the DECORANA-XY ordination.

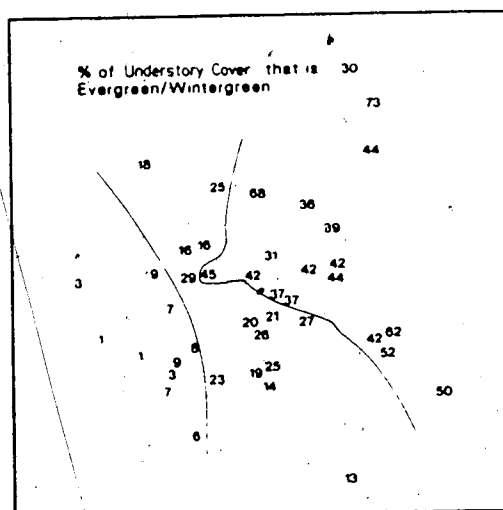
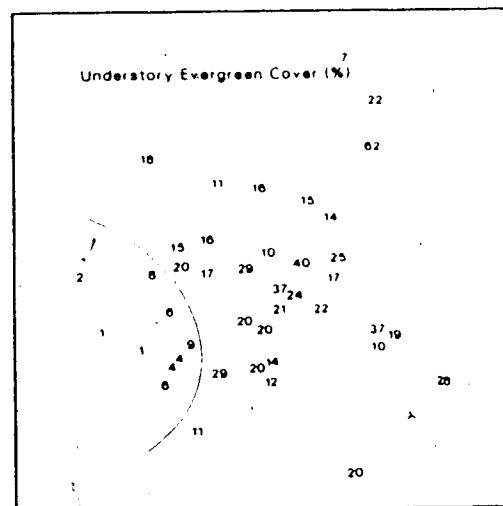
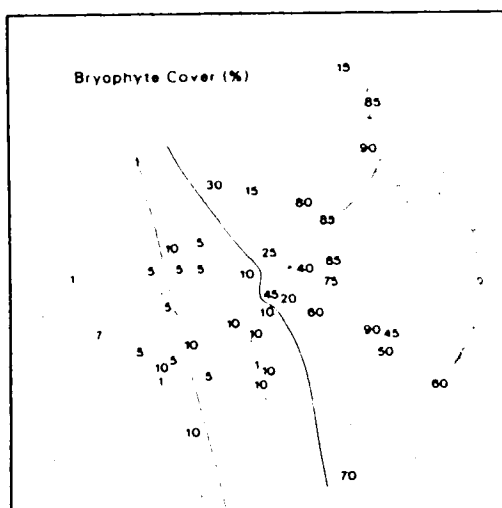
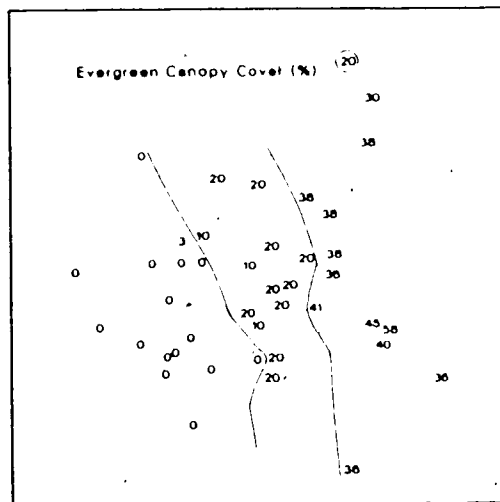
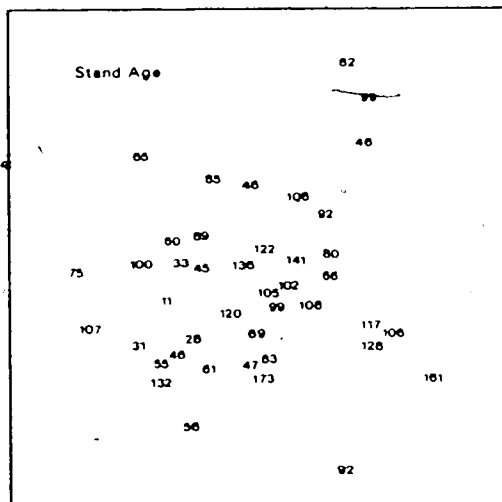


Table 3. Means of selected community attributes Stand groups are based on evergreen canopy cover (%) as mapped on the DECORANA-XY ordination field.

	Evergreen Canopy Cover (%)	Stand Age	Bryophyte cover (%)	Total Vascular Cover (%)	Deciduous Shrub Cover (%)
Group 1 (n=16)	0.7±0.5 ¹	64±8	5.6±1.0	133.9±9.7	39.0±3.9
Group 2 (n=13)	17.7±1.2	105±9 ^a	18.5±3.6	111.1±7.2	22.3±3.3
Group 3 (n=13)	37.0±8	101±8 ^a	69.2±6.2	91.4±11.0	12.4±2.3
	Total Herb Cover (%)	Deciduous Herb Cover (%)	Understory Evergreen Cover (%)	% of Total Understory that is Evergreen	Species Richness
Group 1 (n=16)	50.7±6.3 ^a	39.6±5.8	9.9±1.9	15.6±3.2	31.2±1.4 ^a
Group 2 (n=13)	44.5±5.9 ^a	24.8±3.9 ^b	20.8±2.6 ^b	31.0±4.0	28.6±1.6 ^a
Group 3 (n=13)	37.1±8.7 ^a	17.7±6.8 ^b	22.9±3.9 ^b	42.9±3.9	23.8±1.5
	Shrub Species Richness	Shrub Species Richness/1m ²	Forb Species Richness	Forb Species Richness/1m ²	Shannon-Weiner Index of Diversity (H')
Group 1 (n=16)	8.4±0.6 ^a	3.8±0.2	20.1±0.9 ^a	10.1±0.6 ^a	2.522±0.082 ^a
Group 2 (n=13)	6.5±0.7 ^{ab}	3.0±0.3 ^b	18.7±0.8 ^{ab}	8.9±0.8 ^{ab}	2.472±0.115 ^{ab}
Group 3 (n=13)	5.0±0.4 ^b	2.3±0.2 ^b	15.6±1.1 ^b	7.0±0.7 ^b	2.150±0.112 ^b
	H' Understory Only	Simpson's Index of Dominance (C)	C Understory Only	Synthetic Moisture Index	Species Structure Angles (°)
Group 1 (n=16)	2.703±0.075 ^a	0.143±0.017 ^a	0.013±0.011 ^a	5.0±0.35 ^a	4.2±0.3 ^a
Group 2 (n=13)	2.594±0.092 ^{ab}	0.138±0.019 ^a	0.109±0.012 ^a	5.1±0.20 ^a	4.9±0.4 ^{ab}
Group 3 (n=13)	2.390±0.084 ^b	0.202±0.029 ^a	0.202±0.013 ^a	5.3±0.25 ^a	5.9±0.9 ^b
	Heterogeneity Index				
Group 1 (n=16)	57.2±1.2 ^a				
Group 2 (n=13)	60.4±2.0 ^{ad}				
Group 3 (n=13)	62.2±2.0 ^d				

¹All means ± s.e.m. having a common superscript letter are not significantly different at p<0.05 using Duncan's Multiple Range Test.

10-20% evergreen canopy cover, and stands in Group 3 have more than 20% evergreen canopy cover (Fig. 9). Group 1 stands have the lowest heterogeneity, as indicated by the coefficient of variation and are significantly younger than stands in either Group 2 or Group 3 (Table 3). Group 3 stands have the lowest species richness. Though Group 3 has a significantly higher evergreen canopy cover than Group 2, the ages of the stands within these two Groups are not significantly different.

The three evergreen canopy groups (Fig. 9) do not coincide with either CLUSTAN or TWINSpan groups (Fig. 8). The most significant difference, between the CLUSTAN groups and the evergreen canopy groups, is that evergreen canopy Group 2 is composed of a mixture of stands from CLUSTAN Groups 1 and 2. This difference can be attributed to differences inherent to ordination (e.g. DECORANA) and classification (e.g. CLUSTAN) techniques. Classification attempts to segregate discrete groups of stands, whereas ordination attempts to arrange stands along a continuum or gradient.

Based on bryophyte cover (Fig. 9) stands were separated into groups. Stands in Group 1 have <10% bryophyte cover while stands in Group 2 have >20% cover. The understory evergreen cover ordination field (Fig. 9) has been divided into two groups. Stands in Group 1 have <10% understory evergreen cover while Group 2 stands have >20% cover. Three groups were recognized on the ordination field depicting

percent of understory cover that is evergreen/wintergreen (Fig. 9). Group 1 stands have <10% cover, Group 2 stands have 10-30% cover and Group 3 stands have >30% cover.

There is no significant correlation of soil moisture regime, expressed as a weighted Synthetic Moisture Index (after Rowe 1956), with evergreen canopy cover.

4.4.3 Response Patterns of Species

Figure 10 shows the tree species response pattern mapped on the DECORANA-XY ordination. Figure 11 shows the response patterns of 12 important understory vascular plant species on the DECORANA-XY ordination. Table 4 shows the response of tree species to increasing evergreen canopy cover as determined from the DECORANA-XY ordination. *P. tremuloides* and *P. balsamifera* attain their highest mean cover in Group 1 stands (with <5% evergreen canopy cover). Table 5 indicates the response of selected understory species to increasing evergreen canopy cover as determined from the DECORANA-XY ordination.

Epilobium angustifolium, *Aralia nudicaulis*, *Rosa acicularis*, *Rubus idaeus* and *Lonicera dioica* attained their highest mean cover in Group 1 stands. *Cornus canadensis*, *Maianthemum canadense*, *Mertensia paniculata*, *Mitella nuda*, *Ribes triste*, and *Rubus pubescens* attained their highest mean cover in Group 2 stands. *Linnaea borealis* attained its highest mean cover in stands with >20% evergreen cover (Group 3).

Figure 10. Response patterns of tree species on the DECORANA-XY ordination.

0 = Absent	
1 = .1%	Cover
2 = 1-4.9%	
3 = 5-14.9%	
4 = 15-24.9%	
5 = 25-34.9%	
6 = >35%	

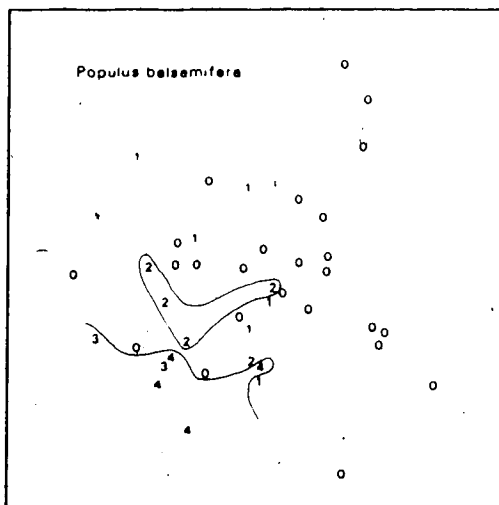
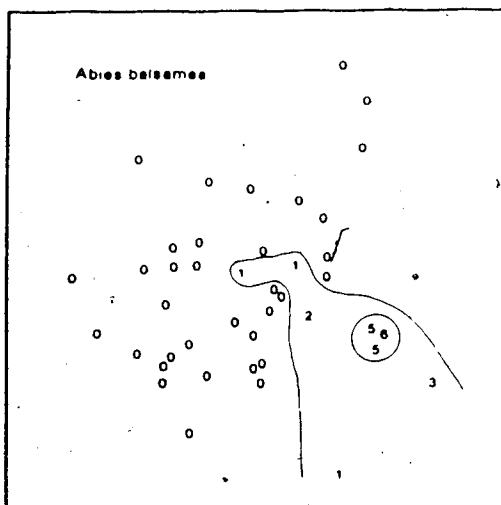
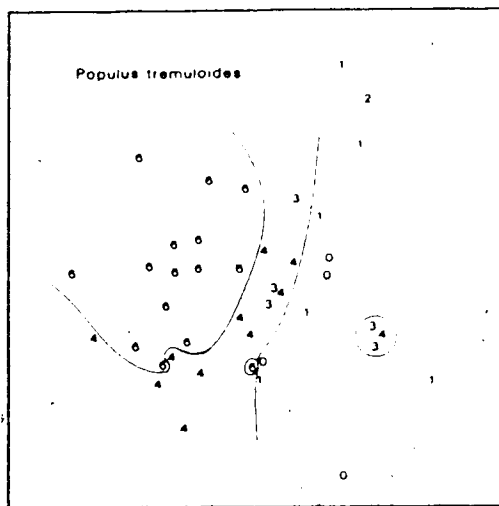
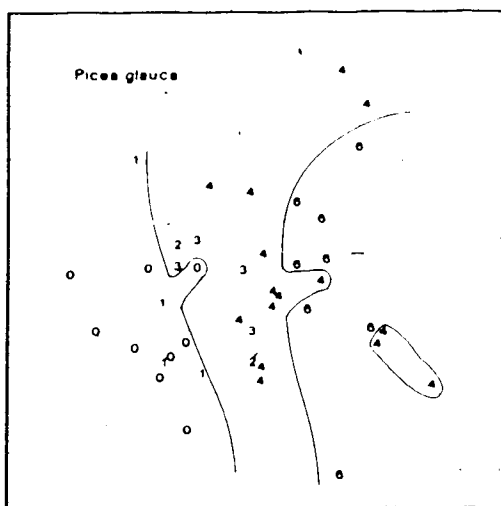
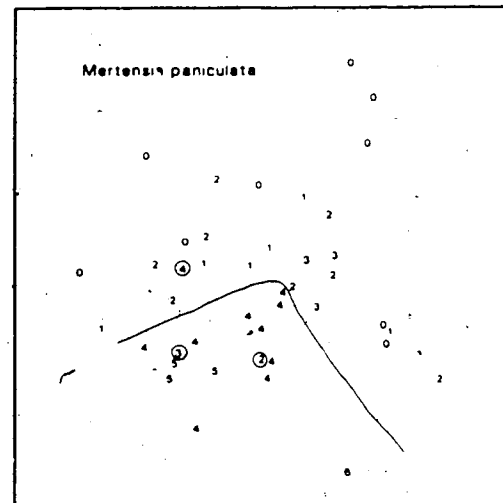
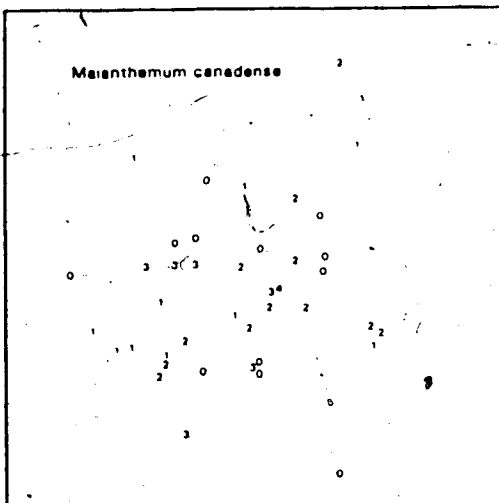
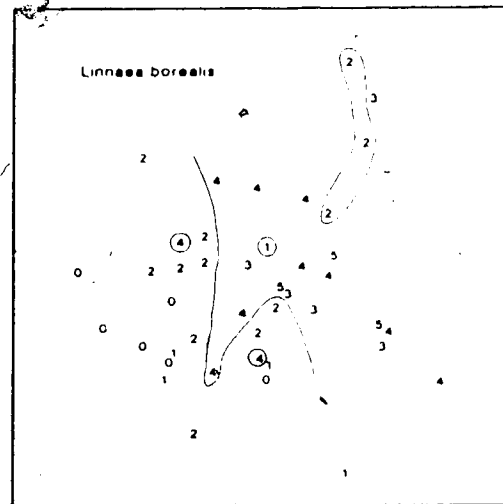
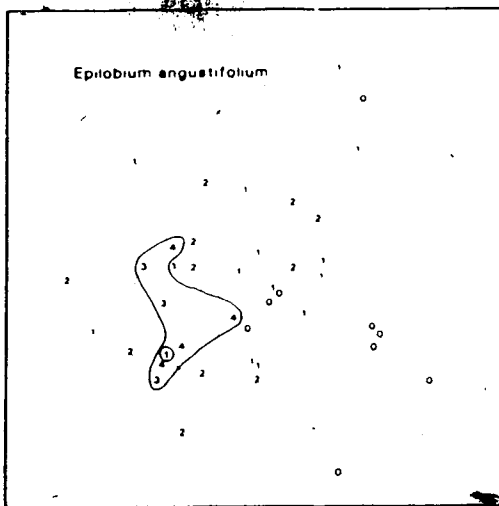
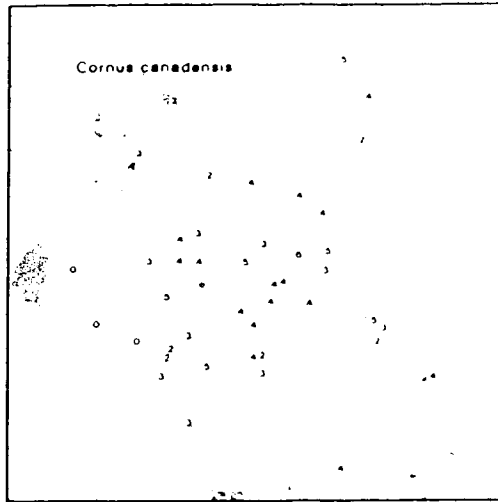
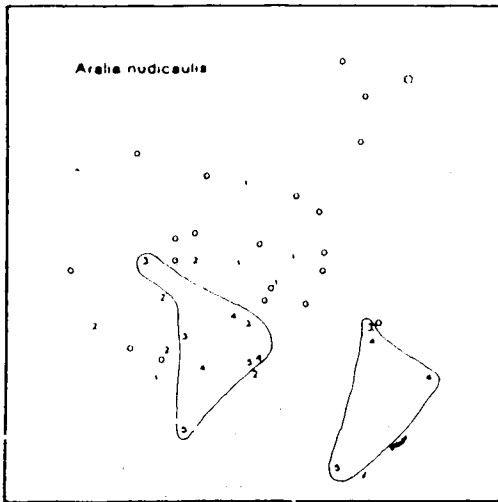


Figure 11. Response patterns of selected understory species on the DECORANA-XY ordination.

0 = Absent	
1 = <1%	Cover
2 = 1-2.9%	
3 = 3-4.9%	
4 = 5-9.9%	
5 = 10-14.9%	
6 = ≥15%	



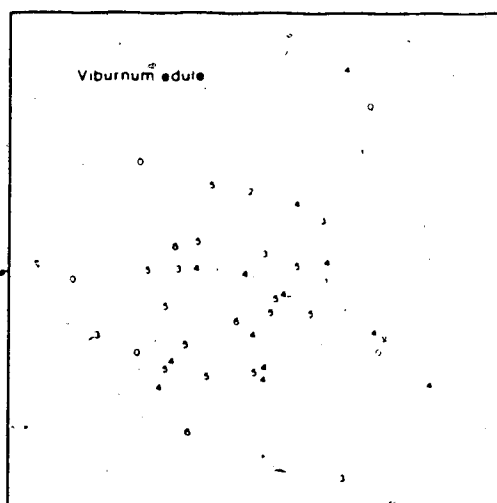
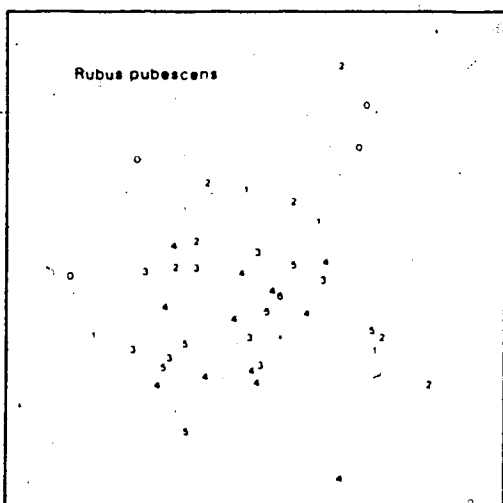
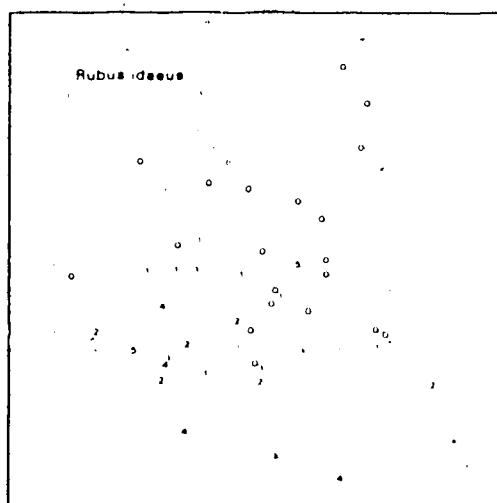
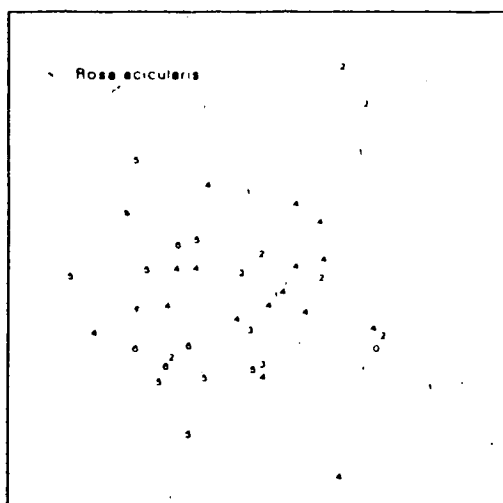
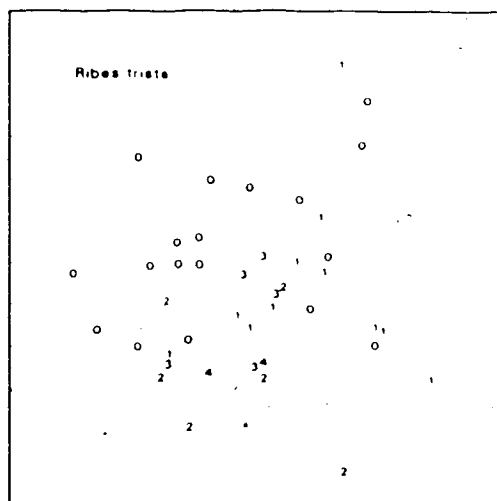
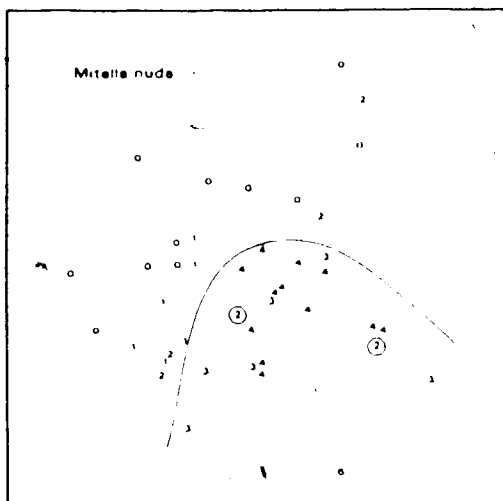


Table 4 Mean cover of tree species. Stand groups are based on evergreen canopy cover as mapped on the DECORANA-XY ordination field.

	<i>Picea glauca</i>	<i>Populus tremuloides</i>	<i>Populus balsamifera</i>	<i>Abies balsamea</i>
GROUP 1 (n=16)	0.8±0.5	35.4±3.8	8.1±2.4	0.0
GROUP 2 (n=13)	19.2±2.0	21.5±3.7	0.4±2.5	0.1±0.1
GROUP 3 (n=13)	29.8±2.6	4.6±1.7	0.0	8.8±3.8

All means ± s.e.m. are significantly different at P<0.05 using Duncan's Multiple Range Test.

Table 5. Mean cover of selected understory plant species. Stand groups are based on evergreen canopy cover (%) as mapped on the DECORANA-XY ordination field.

	<i>Epilobium angustifolium</i>	<i>Aralia nudicaulis</i>	<i>Rosa acicularis</i>	<i>Rubus idaeus</i>	<i>Lonicera dioica</i>
GROUP 1 (n=16)	2.9±0.4 ^a	3.5±0.6 ^a	12.4±0.7	2.0±0.4 ^a	0.7±0.2 ^a
GROUP 2 (n=13)	1.1±0.4 ^a	1.7±0.4 ^a	5.5±0.5 ^a	1.2±0.5 ^a	0.6±0.3 ^a
GROUP 3 (n=13)	0.3±0.2 ^a	2.6±0.6 ^a	3.6±0.5 ^a	0.8±0.4 ^a	0.4±0.2 ^a
	<i>Viburnum edule</i>	<i>Cornus canadensis</i>	<i>Malanthemum canadense</i>	<i>Mertensia paniculata</i>	<i>Mitella nuda</i>
GROUP 1 (n=16)	9.1±1.6 ^a	4.3±0.4	1.3±0.3 ^a	4.4±0.5 ^a	1.0±0.3
GROUP 2 (n=13)	8.5±1.2 ^a	7.4±0.6 ^a	1.6±0.4 ^a	4.6±0.5 ^a	5.4±0.5 ^a
GROUP 3 (n=13)	3.9±0.9	6.5±0.5 ^a	1.0±0.3	2.9±0.7 ^a	4.8±0.7 ^a
	<i>Ribes triste</i>	<i>Rubus pubescens</i>	<i>Lilnaea borealis</i>		
GROUP 1 (n=16)	1.2±0.3 ^a	5.0±0.5 ^a	2.1±0.4 ^c		
GROUP 2 (n=13)	1.9±0.4 ^a	6.7±0.6 ^a	4.6±0.6 ^c		
GROUP 3 (n=13)	0.3±0.2	4.1±0.6 ^a	5.8±0.6		

All means ± s.d.m. having a common superscript letter are significantly different at P<0.05 using Duncan's Multiple Range Test.

Cover of *Epilobium angustifolium* and *Rosa acicularis* decreased significantly when evergreen canopy cover increased from Group 1 to Group 2. *Cornus canadensis*, *Linnaea borealis* and *Mitella nuda* cover increased significantly when evergreen cover increased from Group 1 to Group 2. Cover of the above species did not significantly change with further increases in evergreen canopy cover. *Ribes triste*, *Maianthemum canadense* and *Viburnum edule* showed a significant cover decrease when evergreen cover increased from Group 2 to more than Group 3. Changes in cover of *Mertensia paniculata*, *Lonicera dioica*, *Rubus idaeus* and *Rubus pubescens* were not significantly correlated with changes in evergreen canopy cover.

4.5 Species Canopy Preference

Table 6 shows the Canopy Preference Index (CPI) rankings of some important understory vascular plant species.

Linnaea borealis, *Vaccinium vitis-idaea* and *Ledum groenlandicum* exhibit a strong preference for an evergreen canopy. *Mitella nuda*, *Goodyera repens* and *Cornus canadensis* appear to favour an evergreen canopy but also do well under a mixed evergreen-deciduous canopy. Species which appear to be indifferent to canopy type include: *Lonicera involucrata*, *Mertensia paniculata*, *Rubus pubescens*, *Aralia nudicaulis*, *Petasites palmatus* and *Pyrola asarifolia*. *Maianthemum canadense*, *Viburnum edule*, *Orthilia secunda* and *Ribes triste*

Table 6. Canopy Preference Index¹ (CPI) of some important vascular plant species of mixedwood forests. A high CPI indicates a preference for an evergreen canopy while a low CPI indicates a preference for a deciduous canopy.

Species	CPI	Leaf Growth Form ²
<i>Linnaea borealis</i>	0.780	E
<i>Vaccinium vitis-idaea</i>	0.772	E
<i>Mitella nuda</i>	0.739	E
<i>Ledum groenlandicum</i>	0.689	E
<i>Goodyera repens</i>	0.654	W
<i>Cornus canadensis</i>	0.565	W/S
<i>Lonicera involucrata</i>	0.451	S
<i>Mertensia paniculata</i>	0.382	S
<i>Rubus pubescens</i>	0.344	S
<i>Aralia nudicaulis</i>	0.344	S
<i>Petasites palmatus</i>	0.331	S
<i>Pyrola asarifolia</i>	0.286	W
<i>Maianthemum canadense</i>	0.244	S
<i>Aster ciliolatus</i>	0.222	S/W
<i>Viburnum edule</i>	0.217	S
<i>Orthilia secunda</i>	0.182	W
<i>Rubus idaeus</i>	0.177	S
<i>Ribes triste</i>	0.173	S
<i>Epilobium angustifolium</i>	0.115	S
<i>Lathyrus ochroleucus</i>	0.108	S
<i>Fragaria virginiana</i>	0.101	S/W
<i>Calamagrostis canadensis</i>	0.074	S
<i>Viola renifolia</i>	0.050	S
<i>Rosa acicularis</i>	0.011	S
<i>Aster conspicuus</i>	0.000	S

$$^1 \text{CPI} = \frac{\sum_{i=1}^N (\text{ETC}/\text{TTC} \times S_i)}{\sum_{i=1}^N S_i},$$

where, ETC = evergreen tree cover/stand,

TTC = total tree cover/stand, S = species cover in stand i, and N = number of stands, i.e. five stands with highest cover of S.

²E = evergreen, W = wintergreen, S = summergreen.

show a preference for a deciduous canopy, but do reasonably well under a mixed canopy. The remaining nine species strongly prefer a deciduous canopy.

From inspection of the vegetation data and Table 6 it appears that understory evergreen plants have a strong preference for an evergreen canopy. Wintergreen plants are divided in canopy preference; *Cornus canadensis* and *Goodyera repens* favour an evergreen canopy; *Pyrola asarifolia* is indifferent to canopy type, and *Fragaria virginiana* and *Aster ciliolatus* prefer a deciduous canopy. None of the summergreen plants prefers an evergreen canopy.

There are a number of exceptions to these general trends of species canopy preference. *Viburnum edule* reached its maximum cover in Stand 5, an evergreen-dominated stand (36% cover) in which deciduous canopy cover (0.05%) was negligible. Stand 5 was a mature *Picea glauca* community with *Abies balsamea* present in the understory. The community was diverse with a series of gap-phases present.

Rubus idaeus, *Mertensia paniculata* and *Aralia nudicaulis* attained their highest cover in Stand 9 where evergreen canopy cover was high (36%) and deciduous canopy cover absent. Stand 9 was a mature *Picea glauca* community developed on a Luvic Gleysol with a well-developed medium shrub layer dominated by *Rubus idaeus*, a well-developed forb layer dominated by *Mertensia paniculata*, *Circaea alpina* and *Mitella nuda*, and a well-developed bryoid layer consisting largely of *Mnium* species. Thus, it appears that other site

factors, such as high soil moisture, were as important as canopy cover in influencing the development of understory vegetation in Stand 9.

4.6 Dominance-Diversity Analysis

Using low to high evergreen canopy cover as a successional gradient, stands may be segregated into three groups (Fig. 9). Following Purchase and La Roi (1983), a comparison of species structure curves was made along this successional gradient to see if "slope angle" changes in a directional manner. Comparison of the mean slope angle of the dominance-diversity curves amongst the three groups reveals a trend of increasing slope angle with evergreen canopy cover (Fig. 12). Thus, the slopes of the dominance-diversity curves gradually steepen as succession proceeds. This indicates that the mean difference in percent cover between adjoining species in the species sequence increases during succession, i.e. the dominance hierarchy becomes more pronounced.

Kendall's Tau was used to test the null hypothesis of independence between evergreen canopy cover and the ratio of understory evergreen/wintergreen: herbaceous understory species cover (EW:H). The resulting positive rank correlation ($T=0.34$) between evergreen canopy cover and EW:H is significant at the $P<0.01$ level. Hence, evergreen/wintergreen understory species become significantly more important than deciduous understory

species as evergreen canopy cover increases.

There is no significant $P < 0.05$ trend of increasing species dominance from group 1 to 3, as expressed by Simpson's Index of Dominance Concentration (C), with evergreen canopy cover (Table 3). The Shannon-Weaver Index of Diversity (H') indicates that species diversity gradually decreases as evergreen canopy cover increases (Table 6).

The Heterogeneity Index (HI) increases significantly ($P < 0.05$) with evergreen cover (Table 3). Thus, as evergreen cover increases the distribution of understory vegetation becomes more patchy..

A representative sample of four dominance-diversity curves covering the spectrum of curves from the 42 analyzed stands is shown in Figure 12. One dominance-diversity curve was selected from each of the three evergreen canopy groups as delineated on the DECORANA-XY ordination. The fourth dominance-diversity curve was drawn to show the variation that exists within evergreen dominated communities.

Stand 11 (Plate 1) was selected to represent a community with a deciduous canopy and is shown as curve 1 in Figure 11. Stand 35 (Plate 2) was chosen to represent a community having a mixed evergreen-deciduous canopy and is represented by curve 2 in Figure 12. Stand 25 (Plates 3 and 4) was selected to represent a community having an evergreen-dominated canopy and is shown as curve 3 in Figure 12.

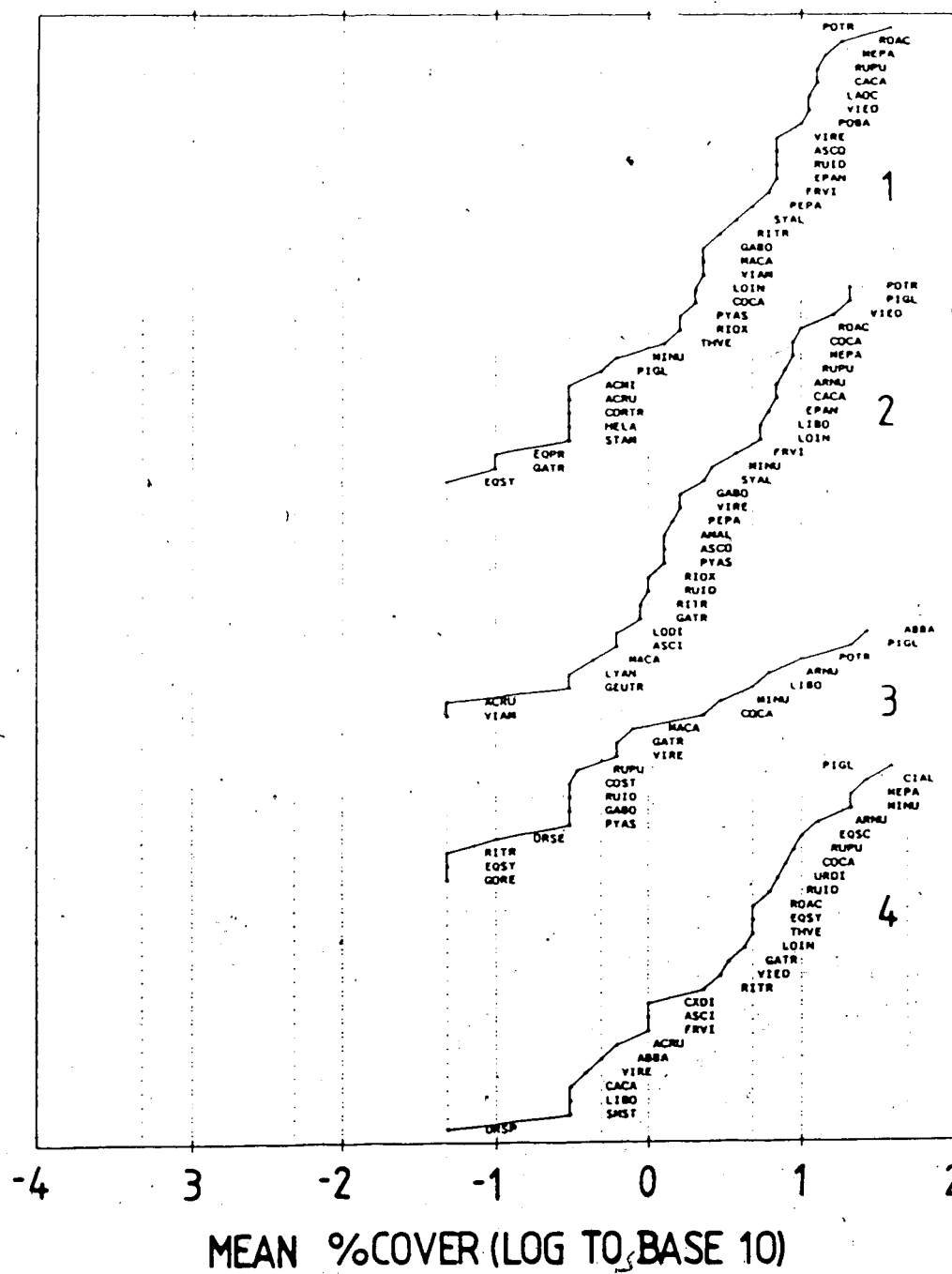


Figure 12. Dominance-diversity curves for selected sites.

Plate 1.

Stand 11 is a 55-year old stand that has a tree layer dominated by *Populus tremuloides* (46% cover); scattered individuals of *Picea glauca* (0.05% cover) are present in the sub-canopy. *Rosa acicularis* and *Viburnum edule* are dominant in the medium shrub layer. Prominent medium and tall herbs include *Calamagrostis canadensis*, *Mertensia paniculata* and *Lathyrus ochroleucus*. The low herb layer is not well developed. Bryophyte cover is 10% and angiosperm cover is 50%.

Plate 2.

Stand 35 is a 120-year old stand with *Populus tremuloides* (20% cover) and *Picea glauca* (20% cover) co-dominant in the tree layer. The medium shrub layer and herb layers are similar in species composition to Stand 11. The percent covers of the medium shrub, tall, medium and low herb layers are less than half of the cover of these same layers in Stand 11. Understory evergreen and wintergreen species are more prominent here than in Stand 11. Bryophyte cover is 10% and angiosperm detritus cover is 10%.

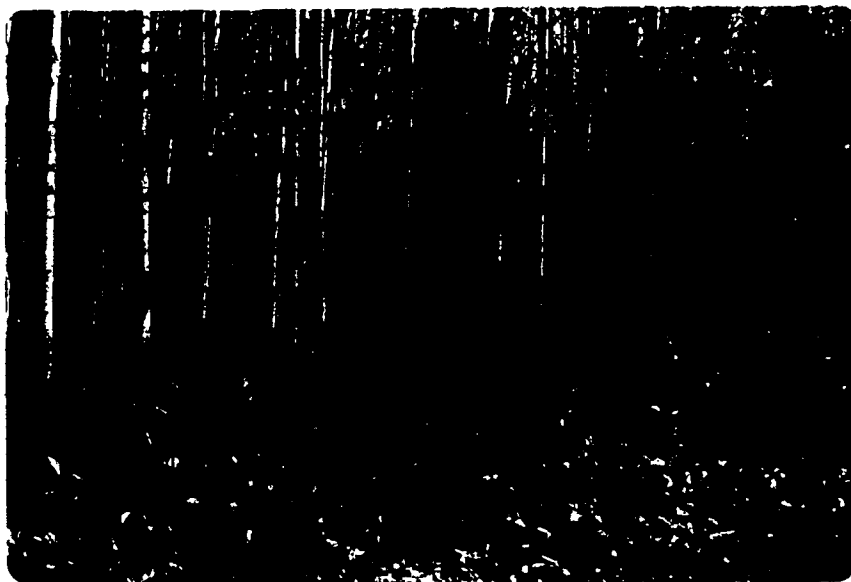
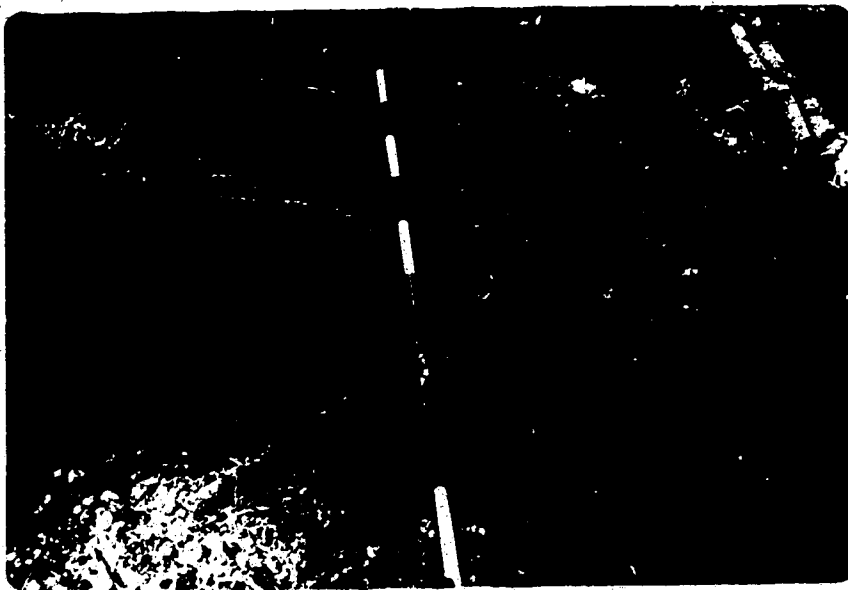


Plate 3.

Stand 25 is a 128-year old stand which has a primary tree cover dominated by *Picea glauca* (20% cover) with *Populus tremuloides* (10% cover) present as a sub-dominant. A second tree layer consisting of *Abies balsamea* (20% cover) is well-developed. The species structure and species composition in Stand 25 differ greatly from Stand 35 (Plate 2) though both stands are almost the the same age.

Plate 4.

The vascular understory, in Stand 25, is poorly developed under the highly evergreen canopy cover. Shrubs are virtually absent, *Aralia nudicaulis* is prominent as occasional individuals in the medium herb layer. The moderately well-developed low herb layer consists of *Viola renifolia* and the evergreens, *Mitella nuda* and *Linnaea borealis*. The well developed bryophyte carpet (50% cover) is predominantly *Hylocomium splendens* with occasional small clumps of *Ptilium crista-castrensis*. Angiosperm detritus cover is 50%.



Curve 1, Stand 11, has a lognormal species distribution with few species having high cover, many species having intermediate cover, and few species having low cover. Curve 2, Stand 35, has a modified lognormal distribution. The upper part of the curve is truncated where POTR (*Populus tremuloides*) and PIGL (*Picea glauca*) share dominance. There are fewer species in the upper portion of curve 2 than in curve 1, otherwise both curves have similar shapes. Curve 3, Stand 25, lies somewhere between a lognormal distribution and a geometric distribution. Curve 3 has few species with abundant or intermediate cover, and, compared to curves 1 and 2, fewer species of low abundance.

Species composition of Stands 11 and 35 (curves 1 and 2) are similar but the two species rankings differ. Evergreen/wintergreen species, such as *Cornus canadensis*, *Linnaea borealis* and *Mitella nuda* are more important, and summergreen species, such as *Lathyrus ochroleucus*, *Aster conspicuus* and *Calamagrostis canadensis*, are less important in Stand 11 than in Stand 35. Species composition and species rankings in Stand 25 (curve 3) are markedly different from Stands 11 and 35. Stand 25 has 19 vascular plant species compared to 34 and 32 species in Stands 11 and 35. Evergreen/wintergreen species are more important and summergreen species are less important in Stand 25 than the other two stands.

Stand 9, curve 4 in Figure 12, has an entirely evergreen canopy yet the species structure curve lies

between curves 2 and 3 in terms of shape and species composition. Stand 9 has 29 species, a well-developed herb layer and a poorly developed shrub layer. Both summergreen and evergreen/wintergreen understory species have high cover in this stand.

Stand 9 was selected to show variation in curve structure for stands dominated by evergreen cover. Stand 11, curve 3, is representative of evergreen stands on well-drained sites with Luvisolic soils while Stand 9 is located on a poorly drained site underlain by a Luvic Gleysol. The differences in understory structure and composition between Stand 11 and Stand 9 can be attributed to site differences, in particular soil moisture.

5. Discussion

5.1 Succession

The major assumption of this thesis is that the 42 study sites investigated reflect the developmental changes that would occur if it were possible to sample one site over a 173 year period. Early development (over the first 25 years) is largely unknown due to the virtual absence of study sites in this age-class. Similarly, site changes which occur after 173 years are unknown.

Frequent forest fires, well-documented in the Boreal Forest Region (Lutz 1956, Heinselman 1973, Viereck 1973, Rowe and Scotter 1975), preclude very long disturbance-free periods. Short disturbance-free periods were found to be the case in this thesis research as only one stand, of the 42 stands surveyed, was older than 141 years. The boreal forest biome may be said to exhibit a "pulse stability" (*sensu* Odum 1969) where plant communities in it have adapted to a particular fire frequency and intensity over an evolutionary time scale. Sousa (1984) states that it is this evolutionary interaction of disturbance, predation and competition which accounts for most of the spatial pattern and organization of communities. However, site disturbance history is known only from the few clues, including fire scars, fire margins and charcoal in the soil profile, gleaned from present day sites.

From the research reported in this thesis it is concluded that the single most important factor influencing succession in *Populus tremuloides*-*Picea glauca* mixedwood forest understories in northern Alberta is the shift in tree canopy dominance from *Populus tremuloides* to *Picea glauca*. Ordination of stands on the DECORANA-XY field supports this conclusion; the X-axis accounts for the majority (50%) of the variance in the vegetation data and the ordering of stands along the X-axis is strongly correlated ($r=0.88$, $P<0.01$) with evergreen canopy cover.

Upland sites in the boreal forest region are often favourable for the establishment and development of both *Populus tremuloides* and *Picea glauca*. The degree to which one or both species becomes established depends largely on site disturbance history. If both species are relatively successful in regenerating after fire, the rapidly-growing *Populus tremuloides* will dominate the canopy until the slower-growing, longer-lived, *Picea glauca* catches up. Once *Picea glauca* begins to exert its dominance, changes in the community occur which are related to a functional shift from a summergreen- to an evergreen-dominated canopy.

One of the most prominent consequent effects of the development of an evergreen canopy is the dramatic rise in cover of terrestrial bryophytes. Other workers studying the mixedwood boreal forest have also made this observation (Dix and Swan 1971, Rowe 1956, Moss 1953). Tamm (1955, 1964) found that moss carpets under trees are supplied with nutrients

contained in canopy wash and that feather mosses also have a requirement for shade provided by an evergreen canopy. In this study it was found that bryophyte cover increases markedly in northern Alberta mixedwood forests once evergreen canopy cover reaches approximately 20%. Other important correlations with increasing evergreen canopy cover demonstrated in this research are: increasing stand age, a decline in total understory plant cover, a decline in understory vascular species richness, a decrease in summergreen shrub and summergreen herb cover, and an increase in understory evergreen (including wintergreen) cover.

Evergreen understory vascular cover and bryophyte cover increase as evergreen canopy cover increases to approximately 10-20%. Once evergreen canopy attains 10-20% cover and bryophyte cover is >10%, evergreen vascular understory cover does not significantly increase. However, unlike deciduous shrub and summergreen herb species, understory vascular evergreen species maintain their constant high cover in stands having very high bryophyte and evergreen canopy cover. Thus, species cover shifts from a predominantly summergreen understory in the early stages to an understory co-dominated by summergreen and evergreen species in the later stages. If terrestrial bryophyte cover is included with vascular evergreen species cover, then the understory is overwhelmingly evergreen in the later stages of succession.

Understory evergreen cover is significantly, positively correlated with evergreen canopy cover ($r=0.50$, $P<0.01$) while understory summergreen cover is significantly, negatively correlated with evergreen canopy cover ($r=-0.54$, $P<0.01$). Understory evergreen cover is not significantly correlated with stand age, while understory summergreen cover is significantly, negatively correlated with stand age ($r=-0.30$, $P<0.05$).

When similar-aged stands are compared, those with evergreen canopies generally have the highest understory evergreen cover. However, Stand 2 which has a particularly high deciduous canopy cover (62%) also has a high percent of total understory that is evergreen/wintergreen (45%). *Cornus canadensis*, a wintergreen, is the most prominent understory species with 10% cover. The high evergreen understory cover is probably related to the high deciduous canopy cover and the comparatively thick (13 cm) humus layer. Separate comparisons of understory evergreen cover among deciduous-dominated stands and evergreen-dominated stands indicated no stand age-related differences in either group. Therefore, it is concluded that differences in evergreenness type are more important than stand age *per se* in controlling the development of the understory over the age range of stands investigated.

Chabot and Hicks (1980) have recently reviewed a number of hypotheses relating to leaf life-span. They concluded that since there is a variety of leaf cycles and a variety

of anatomical and morphological structures that relate to leaf life-span no single hypothesis can be invoked to explain evergreenness. However, they stated that "leaf life-span seems to relate most closely to carbon gain."

The following is a list of some advantages and disadvantages evergreen leaves have compared to summergreen leaves in a cold boreal climate.

Advantages:

1. Evergreen leaves may act as year round storage organs for carbon and nutrients (Chapin et al. 1980, Reader 1978).
2. Evergreen leaves have longer periods of photosynthetic productivity than summergreen leaves.
3. Leaves with longer life spans may also be less susceptible to herbivory (Rhoades and Cates 1976, Bryant et al. 1983).
4. Evergreen leaves have lower light and nutrient requirements than summergreen leaves (Mooney 1972)
5. Evergreen leaves may permit greater carbon gain per unit of nutrient used than summergreen leaves (Schulze et al. 1977).

Disadvantages:

1. Evergreen leaves have a slower rate of growth than summergreen leaves.
2. Leaves with longer leaf life-spans have lower rates of photosynthesis (Larcher 1983).
3. Evergreen leaves, if lost, are more expensive to

replace than summergreen leaves (Mooney 1972).

Van Cleve and Viereck (1981), working in Alaska, have shown that as the moss cover develops, decomposition slows and organic matter accumulates on the forest floor. The result is a lower C:N ratio and a less favourable nutrient environment for plants. Small (1972) has found that evergreen species are more efficient users of nutrients than summergreen species. Thus evergreen species have an advantage on nutrient-limited sites. Experimental work needs to be done to assess changes in the nutrient environment, in the mixedwood boreal forest understory, and the possible consequent effects this has for species of varying leaf life-span.

5.2 Diversity

Of the three initial hypotheses, based on Odum's (1969) ecosystem model regarding species richness (R), species diversity (H') and spatial heterogeneity, the first two do not appear to hold for the vascular phytocoenotic component of the *Populus tremuloides*-*Picea glauca* mixedwood forest ecosystem in northern Alberta. R and H' were highest during early stages of succession, when shade tolerant and shade intolerant species were present, and gradually declined as succession proceeded and shade intolerant species were eliminated. Dominance (C), a measure of species equitability, was lowest during the early stages of succession and highest in the mature stages. However spatial

heterogeneity, as measured by the heterogeneity index (HI), indicates that *Populus tremuloides*-*Picea glauca* forests in northern Alberta do in fact, become more heterogeneous (or more complex) as succession proceeds.

Bormann and Likens (1979), working in mesophytic forests in the eastern U.S., found that diversity increases rapidly in the early stages of succession and then gradually drops after 10-15 years. As noted earlier in this thesis, few stands younger than 30 years were investigated, thus diversity characteristics of the earliest stages of succession in *Populus tremuloides*-*Picea glauca* forests remain unknown. However, the decreasing diversity found during late succession corresponds to the Bormann and Likens model. The effects of evergreen canopy on understory diversity in the boreal forest of central Saskatchewan have been noted by Dix and Swan (1971) and by other workers elsewhere (Auclair and Goff 1971, Glenn-Lewin 1976). Glenn-Lewin (1976) found percent conifer to be the best single variable for predicting total species richness and which agrees with the results from this work.

The dominance-diversity curves in this study were lognormal during early succession and gradually became geometric as species were removed in late succession. These findings contrast with work done in pine forests of northern Alberta (Purchase and La Roi 1983), and old-field ecosystems in Illinois (Bazzaz 1975) where species structure curves are geometric in early succession and, as species are added,

become progressively lognormal. Carleton (1982), working in pine forests in Ontario, also found species richness and diversity to increase along a successional gradient.

Frequency of disturbance, i.e. fire, is so high in the Boreal Forest region that there has been very little opportunity for species to have evolved in, or become adapted to, a stable, disturbance-free forest. This may explain why there are so few species in mature evergreen-dominated communities. An alternative explanation for decreased species richness in late successional communities may be related to the changes in the light regime which result from changes in evergreen canopy cover. Not only are there changes in light quality and quantity but seasonal fluctuations in the light regime are lower under an evergreen canopy than under a deciduous canopy (M. Ross pers. comm.). Alaback (1982) has hypothesized that understory development in Sitka spruce-western hemlock forests of southeast Alaska is a response to changes in the light environment created by changes in tree canopy cover.

Understory summergreen species rankings on the species structure curves (Fig. 11) decrease along the successional gradient while rankings of understory evergreen species increase. This shift from summergreen to evergreen species on the species structure curve may be related to changes in the light regime. The relationship of understory boreal forest plants to light, including the minimum light threshold levels for plant growth and reproduction, remains

largely unknown.

5.3 Species Composition

The species compositions of deciduous- and evergreen-dominated stands are not vastly different from one another. Although several summergreen and wintergreen understory species present in deciduous stands are absent from evergreen-dominated stands, very few species occur only in the latter. Dix and Swan (1971) who surveyed a wide range of boreal forest community types in Saskatchewan found approximately one-half of the understory taxa to be specific to a particular canopy type. However, Carleton and Maycock (1981) in Ontario found less than one-third of understory species showing any specificity to canopy type. Carleton and Maycock attribute this lack of specificity of understory to overstory, to the nature of regeneration after forest fires. Regeneration of boreal forest species occurs largely from underground root stocks and as seeds from a persistent seed bank or from wind-blown immigration.

It is difficult, without knowing the site history, to attribute structural or compositional differences among stands to either (1) the passage of time, or (2) to differences in stand life history, particularly the frequency and intensity of past disturbances. *Abies balsamea* is the only vascular species which appears able to invade and become established under a well-developed evergreen canopy. The virtual lack of recruitment of new species

during succession has been reported and commented upon by numerous workers in the boreal forest (Rowe 1956, Dix and Swan 1971, Carleton and Maycock 1978). In one *Picea glauca*-dominated stand, *P. glauca* seedlings were noted, indicating the possibility of a self-perpetuating community given a sufficient fire-free period.

5.4 Snow and Temperature Patterns

There is evidence to suggest that depth of snow cover affects overwintering of evergreen species. Cover of the evergreen-dwarf shrub *Arctostaphylos uva-ursi* is significantly positively correlated with depth of snow cover and significantly negatively correlated with cover of *Pinus banksiana* (R. Hastings pers. comm.). Whether this effect is due to increased soil moisture recharge in the spring or ameliorated winter temperatures, or both, is presently not known. Havas and Kubin (1983) have found similar results in an old spruce forest in Finland. They have shown that successful growth of *Vaccinium myrtillus* is dependent on snow cover and that *Vaccinium vitis-idaea* dominates hummocks which have only a thin snow cover. Observations on *Cornus canadensis* in Alberta suggest that increasing depth of snow pack may increase the frequency of flowering and, hence, the number of leaves per individual (G.H. La Roi pers. comm.). Fertile individuals of *Cornus canadensis* produce six leaves while non-fertile individuals produce only four leaves. Snow may influence the development of other understory evergreen

species but little on this topic is known and further research is required.

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Appendix I. DECORANA X-Axis and Y-Axis Coordinates

Stand No.	X-Axis	Y-Axis	Stand No.	X-Axis	Y-Axis
1	183	72	24	111	85
2	121	34	25	295	85
3	244	130	27	102	134
4	218	136	28	165	132
5	347	59	29	284	240
6	178	72	30	24	92
7	198	119	31	202	119
8	173	93	32	300	93
9	260	0	33	86	62
10	112	29	34	171	184
11	92	74	35	161	101
12	90	110	36	183	64
13	293	94	37	228	106
14	74	133	38	95	76
15	184	144	39	261	263
17	132	188	40	0	128
18	102	148	41	241	165
19	246	139	42	84	203
20	62	181	43	279	211
21	129	65	44	121	151
23	218	176	45	193	110

Appendix II. Species Cover (%) by Stand. (cont'd)

Species/Stand	Species Cover														
<i>Amelanchier alnifolia</i> (SIV=2)															
1-15	0.05	0.30	0.00	0.00	0.00	1.60	0.00	30	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	1.30	0.00	5.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.35
17-45	0.00	0.00	0.00	0.00	1.30	0.30	0.00	1.05	0.00	18.70	0.00	0.00	0.00	0.00	0.00
<i>Cornus stolonifera</i> (SIV=8)															
1-15	4.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	13.30	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.30	0.35	30	6.60	0.00	0.00	4.30	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Ledum groenlandicum</i> (SIV=8)															
1-15	0.00	0.35	0.00	0.00	0.00	1.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	11.30	0.00	0.00	0.00	39.10	0.00	0.00	4.90	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lonicera dioica</i> (SIV=4)															
1-15	0.00	10	0.40	0.00	0.00	1.60	0.00	5.05	0.00	1.30	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	3.30	1.00	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.85
17-45	0.00	0.00	1.00	0.00	0.60	0.35	1.00	2.60	0.00	0.00	0.40	0.00	0.00	0.00	0.00
<i>Lonicera involucrata</i> (SIV=8)															
1-15	4.05	1.00	2.30	0.00	0.00	2.30	3.00	1.90	4.10	6.80	2.00	1.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	2.00	0.30	0.00	0.00	5.40	0.00	11.60	1.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Prunus pennsylvanica</i> (SIV=2)															
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.80	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.30
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Ribes glandulosum</i> (SIV=8)															
1-15	0.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Ribes hirtellum</i>															
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Ribes lacustre</i> (SIV=8)															
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Ribes oxycanthoides</i> (SIV=4)															
1-15	1.80	0.00	55	0.00	0.00	0.00	0.00	35	65	0.00	35	1.60	0.00	0.00	0.00
16-30	0.00	0.00	0.05	0.30	0.00	2.20	0.00	0.05	1.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	1.60	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
<i>Ribes triste</i> (SIV=8)															
1-15	8.20	0.00	30	40	30	4.25	2.95	60	2.30	2.30	3.00	2.00	65	0.00	2.95
16-30	0.00	0.00	0.00	0.00	0.00	0.00	5.60	0.00	0.00	0.00	0.00	0.00	3.15	0.00	90
17-45	1.65	0.05	1.00	0.00	0.00	0.90	1.90	0.00	35	0.00	15	0.00	0.00	0.00	30

Appendix II. Species Cover (%) by Stand. (cont'd)

Species/Stand	Species Cover																			
<i>Rosa acicularis</i> (SIV=4)																				
1-15	3.70	8.90	2.45	6.30	0.05	11.10	7.30	4.90	5.00	11.00	17.80	8.35	5.30	11.60	1.45					
16-30	0.00	9.30	16.00	6.35	40.80	13.60	1.30	6.60	15.40	0.00	2.90	7.50	4.20	1.55	5.10					
17-45	95	1.95	11.30	35	9.80	7.60	5.00	2.50	2.65	14.00	8.60	3.90	0.05	12.35	9.75					
<i>Rubus idaeus</i> (SIV=8)																				
1-15	0.05	30	0.00	0.00	2.70	0.00	0.00	0.00	6.30	5.60	6.70	5.90	0.00	80	0.00					
16-30	0.05	0.00	0.00	0.00	11.00	35	0.00	0.00	1.05	30	0.00	0.30	0.00	0.00	1.25					
17-45	30	0.00	1.20	0.00	1.00	2.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
<i>Shepherdia canadensis</i> (SIV=1)																				
1-15	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	10					
16-30	0.00	12.60	6.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.40	0.00	2.95	0.00					
<i>Symphoricarpos albus</i> (SIV=2)																				
1-15	70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.20	3.60	0.00	0.00	0.00	0.00					
16-30	0.00	0.00	1.00	0.00	11.30	0.00	0.00	0.00	1.30	0.00	0.00	1.00	0.00	0.00	75					
17-45	0.00	0.00	1.60	0.00	2.30	0.00	0.00	0.00	0.00	0.00	0.00	.65	0.00	30	0.00					
<i>Viburnum edule</i> (SIV=4)																				
1-15	4.95	9.00	.60	10.60	6.10	9.90	12.70	9.00	3.00	22.20	10.90	11.00	7.60	14.10	4.40					
16-30	1.00	2.30	16.45	5.60	0.00	12.40	0.00	6.30	13.90	0.00	0.00	4.35	7.90	0.00	3.85					
17-45	9.00	2.15	8.30	1.30	17.00	8.80	10.30	9.55	5.55	0.00	3.75	0.00	50	12.10	11.30					
<i>Viburnum opulus</i> (SIV=4)																				
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
16-30	0.00	0.00	0.00	0.00	0.00	6.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
<i>Salix bebbiana</i> (SIV=8)																				
1-15	0.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
16-30	0.00	0.00	4.05	0.00	3.80	0.00	0.05	0.00	0.00	0.00	35	4.00	0.00	0.00	0.00					
17-45	0.00	0.00	4.05	.30	0.00	0.00	.30	0.00	0.00	3.00	0.00	1.00	0.00	0.00	0.00					
<i>Salix glauca</i>																				
1-15	3.80	0.00	9.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
<i>Salix prolixa</i>																				
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00					
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
<i>Salix pseudomonticola</i>																				
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30	0.00	0.00	0.00					
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
<i>Salix pyrifolia</i> (SIV=16)																				
1-15	0.00	0.00	0.00	0.00	0.00	3.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					

Appendix II. Species Cover (%) by Stand. (cont'd)

Species/Stand	Species Cover														
<i>Calypso bulbosa</i> (SIV=4)	1-15	0.00	0.00	0.00	0.00	35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Circaea alpina</i> (SIV=8)	1-15	0.00	0.00	0.00	0.00	70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Coptis trifolia</i>	1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Coralorrhiza trifida</i> (SIV=2)	1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cornus canadensis</i> (SIV=4)	1-15	1.00	9.60	4.35	20.60	2.20	7.90	8.65	9.60	7.60	4.90	2.00	5.60	14.60	2.55
	16-30	5.35	2.65	7.20	10.05	0.00	10.90	14.30	7.90	3.25	2.30	10.20	6.20	10.60	5.25
	17-45	9.60	3.45	3.20	6.20	8.60	3.60	5.50	1.90	30	0.00	6.10	3.25	6.60	3.85
<i>Delphinium glaucum</i> (SIV=8)	1-15	30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Disperum trachycarpum</i> (SIV=2)	1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Epilobium angustifolium</i> (SIV=4)	1-15	0.05	2.45	0.05	1.40	0.00	1.00	30	0.00	0.00	1.05	6.60	4.20	0.00	3.60
	16-30	0.00	2.00	7.60	0.95	2.30	2.20	95	1.00	7.20	0.00	90	10	40	0.00
	17-45	0.00	0.00	3.90	7.75	6.20	2.80	35	35	35	2.85	1.00	65	05	2.40
<i>Fragaria vesca</i> (SIV=4)	1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Fragaria virginiana</i> (SIV=4)	1-15	35	2.50	70	0.00	30	5.00	1.20	1.30	1.00	2.30	5.90	0.00	0.00	2.10
	16-30	0.00	0.00	3.10	0.05	0.00	2.20	05	0.00	0.90	0.00	40	05	1.00	45
	17-45	1.40	35	3.85	0.00	3.90	1.00	1.20	20	0.00	2.95	40	20	0.00	0.00
<i>Gallium boreale</i> (SIV=4)	1-15	15	35	65	1.05	0.00	75	95	1.85	0.00	5.00	2.20	2.35	0.00	1.25
	16-30	0.00	30	3.00	65	1.95	0.00	0.00	0.00	60	30	0.00	1.85	40	0.00
	17-45	0.00	0.00	2.35	0.00	1.65	1.95	2.45	60	0.00	0.00	0.00	1.00	0.00	20

Appendix II. Species Cover (%) by Stand. (cont'd)

Species/Stand	Species Cover														
<i>Galium triflorum</i>	15	0.00	0.00	0.00	0.05	0.05	1.30	1.85	3.55	3.20	10	30	0.00	0.00	0.00
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	30	0.00	0.00	0.00	0.90	0.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Geocaulon lividum</i> (SIV=8)															
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Geum macrophyllum</i> (SIV=4)															
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Geum triflorum</i>															
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Goodyera repens</i> (SIV=2)															
1-15	0.00	0.00	0.00	0.45	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Habenaria hyperborea</i> (SIV=8)															
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Habenaria obtusata</i> (SIV=8)															
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heracleum lanatum</i> (SIV=8)															
1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lathyrus ochroleucus</i> (SIV=2)															
1-15	0.05	1.65	4.60	0.00	1.00	1.00	1.00	30	0.00	2.60	11.30	95	0.00	6.20	1.10
16-30	0.00	0.00	1.35	1.35	0.90	1.00	1.00	1.00	1.60	0.00	0.00	2.65	1.45	15	10
17-45	0.00	1.85	35	0.00	0.00	0.65	10	0.00	0.00	2.90	0.00	3.65	0.00	10	40
<i>Linnaea borealis</i> (SIV=4)															
1-15	90	2.10	7.20	8.60	8.80	6.25	13.35	2.30	30	1.00	0.00	0.00	14.30	1.65	20
16-30	3.30	6.80	7.90	10.00	0.00	5.95	7.30	6.25	2.90	4.90	1.90	2.65	3.70	3.15	0.00
17-45	4.30	5.50	35	7.10	5.65	0.00	4.30	35	2.70	0.00	2.15	2.40	1.70	2.70	2.40
<i>Malanthemum canadense</i> (SIV=4)															
1-15	0.00	3.35	0.00	1.35	2.20	3.60	4.60	2.65	0.00	3.50	2.20	40	2.50	3.95	0.00
16-30	0.00	0.00	0.00	0.00	0.05	0.00	0.00	1.90	1.30	80	0.00	3.10	2.15	20	65
17-45	5.85	1.55	2.60	85	45	0.00	1.50	70	1.10	0.00	0.00	40	25	0.00	1.25

Appendix II. Species Cover (%) by Stand. (cont'd)

Species/Stand	Species Cover															
<i>Mertensia paniculata</i> (SIV=4)	1-15	7.05	10	1.00	3.95	1.60	1.90	9.45	5.90	20.60	9.00	14.80	1.75	0.00	1.30	35
16-30	0.00	1.05	0.00	4.30	6.30	10.30	0.00	0.00	3.30	7.20	0.00	30	5.50	0.95	0.00	65
17-45	1.80	90	11.00	0.00	8.60	9.00	3.95	3.85	0.00	0.00	2.65	0.00	0.00	0.00	1.65	7.60
<i>Mitella nuda</i> (SIV=8)	1-15	7.50	35	5.10	7.90	3.95	4.15	7.20	7.20	19.80	3.95	60	10	7.20	0.00	5.30
16-30	0.00	0.00	0.00	3.55	3.30	3.95	0.00	0.00	0.00	70	3.85	35	0.00	7.90	1.65	0.00
17-45	7.90	5.50	1.60	0.00	2.80	6.50	7.90	1.65	0.00	0.00	2.45	0.00	0.00	0.00	0.05	4.50
<i>Moneses uniflora</i> (SIV=8)	1-15	0.00	0.00	0.00	0.00	0.05	0.00	40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00
<i>Pedicularis groenlandicum</i>	1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites palmatus</i> (SIV=4)	1-15	0.00	30	1.95	5.10	0.00	70	1.75	90	0.00	0.00	4.70	1.00	0.00	1.00	60
16-30	0.00	0.00	0.00	0.00	0.00	0.00	1.95	0.00	1.00	95	0.00	1.60	40	1.25	0.05	10
17-45	95	30	2.45	1.50	1.50	90	60	10	0.00	0.00	0.00	0.00	0.00	0.40	65	0.00
<i>Pyrola asarifolia</i> (SIV=2)	1-15	0.00	1.40	0.05	1.60	1.60	60	2.90	90	0.00	30	1.70	0.00	1.00	1.95	15
16-30	0.00	90	0.00	1.30	30	2.60	30	30	30	0.05	30	0.00	3.20	30	0.00	40
17-45	1.35	30	1.20	0.05	1.25	65	1.60	15	2.20	90	1.10	2.00	35	20	70	70
<i>Orthilia secunda</i> (SIV=2)	1-15	0.00	0.05	0.05	1.30	35	0.05	10	0.00	0.00	60	0.00	0.00	0.00	2.25	30
16-30	1.00	95	0.00	0.65	0.00	0.00	0.00	0.00	0.00	0.00	10	0.00	1.65	0.00	0.00	0.00
17-45	0.05	0.05	1.35	0.00	0.00	0.00	0.00	0.05	0.00	0.00	90	15	30	15	0.05	10
<i>Pyrola chlorantha</i> (SIV=1)	1-15	0.00	0.00	0.00	10	30	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
16-30	0.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00
<i>Rubus arcticus</i> (SIV=16)	1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	75
16-30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Rubus pedatus</i>	1-15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16-30	9.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17-45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Rubus pubescens</i> (SIV=4)	1-15	4.50	3.20	4.70	11.40	2.90	6.80	7.30	3.80	9.30	12.10	13.40	8.60	12.10	5.30	3.00
16-30	0.00	2.00	6.25	8.90	3.30	5.10	0.05	1.35	11.00	35	30	2.30	6.50	0.00	0.00	65
17-45	15.10	1.35	7.00	0.05	7.90	5.55	6.50	4.50	1.00	0.00	0.00	75	0.00	1.35	13.80	80

