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ABSTRACT

When trees fall to a horizontal position on the forest floor and then slowly decay, lichens, bryophytes, bracket fungi and other wood-decomposing organisms gradually colonize the decaying wood and, eventually, are replaced by herbs and tree seedlings. This directional change was quantitatively investigated in 27 plots in Eastern Canada.

Sampling was done by microquadrats placed randomly or systematically or in a combination of both sampling modes on the central portion of logs. Four scales for the estimation of cover were compared. The effects of microquadrat shapes on values of ecological diversity were tested. Some parameters related to the degree of succession were investigated. Seasonal changes of the pH of the log substrate as well the effect of different sizes of wood particles in suspension on the pH were measured.

For one plot the author had access to records from logs which had been tagged since 1926. It was possible, therefore, to relate most logs present in that plot to a time sequence. In all other plots, change in species composition was investigated along gradients of communities. Change in plant assemblages on logs at different stages of decay was studied and interpreted from a succession point of view. Other community parameters including species richness, degree of succession, growth-forms or life-forms have been emphasized.

Vegetational change on logs was found to be dependent on forest structure. Plant assemblages on logs in early

stages of decay often had low ecological diversity values. Peak diversity occurred on logs prior to the latest stages of decay, then declined as litter accumulation made the habitat unfavourable for most bryophytes and lichens.

Most hepatics and mosses growing on decaying logs in the Northern Hardwood Forests seem to favor wet and mesic stands whereas most lichens seem to have a preference for dry habitats. In the coniferous forests, however, lichens favor open habitats close to the upper limits of the timberline whereas hepatics and mosses prefer cool, humid subalpine forests.

Résumé

En forêt, lorsqu'un arbre passe de la position verticale à l'horizontale et que le processus de décomposition du bois commence, des lichens, des bryophytes, des champignons et d'autres organismes envahissent tour à tour le bois et le décomposent lentement. Le cycle est complété par l'apparition d'humus et la colonisation par des plantes herbacées ou ligneuses. Cette succession a été étudiée quantitativement pour 27 stations dans l'est du Canada.

L'échantillonnage a été fait par l'entremise de carrés d'essais (quadrats) placés au hasard ou de façon systématique au centre des troncs pourrissants. Quatre échelles pour l'estimation de ~~la~~ couverture ont été comparées pour leur précision. L'influence de la forme du quadrat sur la diversité écologique a été étudiée. Divers degrés de succession ont été reconnus. L'influence du ph des troncs pourrissants sur la succession a également été analysée.

Dans un cas l'auteur a eu accès à des documents historiques importants où la localisation des troncs pourrissants d'une région avait été enregistrée depuis 1926. Il a donc été possible d'étudier le phénomène de la succession en fonction du temps. Dans toutes les autres stations des changements dans la composition de la végétation ont été analysés en fonction d'un ou de plusieurs gradients écologiques. Enfin d'autres paramètres comme la richesse en espèces, les degrés de succession, les formes biologiques, etc. ont été étudiés.

L'auteur croît que les changements dans la composition de la végétation des troncs pourrissants dépendent de la structure d'une forêt. Les troncs d'arbres dans leur première phase de décomposition n'ont qu'une faible diversité écologique. Cette diversité devient maximale juste avant la phase terminale de décomposition des troncs alors que cette diversité diminue suite à l'accumulation d'une litière organique sur les troncs.

En général, les hépatiques et les mousses poussant sur les troncs pourrissants dans les forêts décidues du nord semblent préférer les stations mésiques alors que les lichens semblent préférer les stations sèches. Dans les forêts boréales de conifères, cependant, les lichens se trouvent surtout sur les troncs disposés dans les lieux ouverts et en altitude alors que les hépatiques et les mousses préfèrent les troncs localisés dans les habitats frais et humides des forêts subalpines.

CHAPTER I

GENERAL INTRODUCTION

1. Introduction

During the life cycle of a forest ecosystem, trees die and their trunks change position from upright to horizontal. On the forest floor the logs decompose and their elements are recycled. The change in position of the log and its decomposition causes a succession of species on the log as well as inside the trunk. Schuster (1949) concluded from his study that succession on decaying logs "is one of the few obvious distinct successions that can be treated without much subjectivity" (Schuster, 1949, p. 666).

Studies of succession on and in decomposing logs are numerous, and only the more pertinent papers of plant succession on decaying logs will be reviewed here.

Raschendorfer (1946) found that succession of cryptogams on decaying wood differed markedly in regions with a humid climate and relatively small fluctuations in air humidity from that of regions which had a dry season during the year. She also noted that in very humid forests hepatics were of considerable importance on rotten boles whereas in less humid forests lichens and mosses were more abundant.

Ştefureac (1969) distinguished four successional stages on trees related to substrate characteristics:

1. Epiphytes - corticolous stage
2. Epixylic stage

3. Saprolignicolous stage

4. Humicolous - terricolous stage

Each stage had a characteristic combination of species and succession from stage one to four was assumed to be mostly unidirectional. He also indicated that in the cool humid alpine climate of the Carpatians, certain logs required about 30 years to decompose. Frey (1959), on the other hand, reported that in a dry continental climate from a valley in the Central Alps practically no apparent change in log decomposition and no major shift in species composition was observed during that same period.

Cain and Sharp (1938) investigated succession of bryophytes on logs in the fir forests of Eastern Tennessee. Sharp (1939) summarized these observations in the following way. From a corticolous *Frullania asagrayana* stage, succession proceeded in either of two directions: (1) logs deposited close to wet rocks on steep slopes were colonized, after they lost their bark, by the *Anastrophyllum michauxii* union; (2) logs present in other habitats were colonized by the *Nowellia curvifolia* union. When logs disintegrated, the *Anastrophyllum michauxii* union could be replaced directly by the *Hylocomnium splendens* union. This last community, probably the "climax union" for the forest floor, was observed also in less wet habitats on logs which were in their final stage of decay. Succession from the *Nowellia curvifolia* union however was not so direct. A seral community, the *Dicranum fuscescens* union, established itself on partially decayed logs and later, when

these logs were in an advanced stage of decay, the *Hylocomium splendens* union finally established itself.

Norris (1964) compared bryophyte communities in parts of the Smoky Mountains (Tennessee/North Carolina) with those in the Adirondack Mountains (New York State). The habitats on decaying wood were carefully studied and, in general, good agreement with Cain and Sharp's (1938) results was apparent. Norris noted a gradual succession of plants on fallen logs until the wood was completely broken down. Three events had prime importance on directional vegetational change. These were loss of bark, decay of the outer wood cylinder and final incorporation of the completely humified wood into the organic layer. From his descriptions of the decaying wood habitat it is evident that a simple successional diagram with clearly distinguishable seral and climax unions seems unlikely for most habitats because the cryptogam vegetation as well as the log habitat are of considerable complexity.

Jovet and Jovet (1944) described from the Savoyen Alps stages of succession in relation to wood decay. They distinguished three substrate types: wood not decomposed, wood spongy, and wood spongy and turned into humus. On each of these substrates they recognized that four successional stages could occur: a pioneer stage, two intermediate stages, and a mature stage. Pioneer stages occurred on all three substrates and the species composition on each substrate was different. It can be concluded, therefore, that these differences noted by Jovet and Jovet (1944) were caused directly by factors of

the substrate. These authors also found that fewer floristic differences occurred after the pioneer stage. Substrate types were, therefore, less important as succession progressed and the authors proposed a scheme showing a unidirectional change towards the final plant community of the forest floor.

Lambert and Maycock (1968) investigated lichens in hardwood forests of Eastern Canada and presented valuable information on the log substratum. They reported that the presence of logs was most important in dry, dry-mesic, wet-mesic, and wet habitats, while the presence of rocks and tree bases were of less or equal importance to the presence of logs in mesic habitats. Conifer logs, as substratum for lichens, appeared important in areas close to the extremes of the moisture gradient. They noted a marked decline of lichens such as *Cladonia chlorophaea*, *C. fimbriata*, *C. squamosa* and *C. bacillaris* in mesic stands. Especially noteworthy was the fact that lichens present on logs in wet forests were found to be somewhat similar in their substrate preference to those found in dry forests.

Mosses and hepatics, not considered by Lambert and Maycock (1968) are, however, important components on logs in aquatic, wet and moist habitats. Forest stands in those habitats are sometimes dominated by *Acer rubrum*. Cain and Penfound (1938) described such forests from Long Island, N.Y. and it can be concluded that trees and shrubs present in that area show floristic affinities to the Coastal Plain Flora of southeastern America. In the Long Island forests and in similar habitats

mosses and hepatics do not show such restricted distribution and, are with the exception of a few species such as *Lophocolea bidentata*, *Hypnum curvifolium*, *Plagiothecium micans*, etc., quite typical of northern temperate decidous forests. It is apparent that in the rather moderate macroclimate of the Coastal Plain, bryophytes have, in general, a rather wide ecological amplitude (Walter, 1970). Only a few mosses on logs have a narrow amplitude and show a substrate preference for wood (e.g. *Lophocolea bidentata*, *Climacium americanum*, *Entodon cladorrhizans*, etc.).

These studies, and many others, seem to indicate that succession of cryptogams on decaying logs is a common feature in undisturbed forests. The overriding importance of microclimatic and substrate factors on the direction of succession of bryophytes and lichens is probably the same on a world-wide basis.

2. Statement of problem

Ouellet and LeBlanc (1967), after a preliminary study of succession on decaying logs on Mont Saint-Hilaire, concluded that a more detailed analysis of plant communities on logs was possible and would probably reveal some interesting aspects of the ecology of these cryptogams; that is one of the reasons why this research was initiated.

The aim of this thesis is to examine, describe and quantify some plant assemblages of bryophytes, lichens and sporophores of polypores on fallen trunks in several forests of Eastern Canada. Community parameters including ecological

diversity, species richness, degree of succession, growth-forms or life-forms are emphasized. The kind of log and stage of decay will be determined. The possibility to relate species frequencies on logs of certain decay stages to succession will be investigated. The log-diameter which depends on sample numbers per unit area will be related to structure of forests.

This study is restricted to horizontal logs located along an intuitively chosen elevational gradient.

The presence of tree seedlings on decaying logs is an important factor in the regeneration of some "primeval" forests (Eichrodt, 1969) and have, in certain areas, a strong impact on the structure of naturally regenerating forests (Sernander, 1936; Hillgarter, 1971). Therefore, species composition of seedlings on decaying logs was also investigated and related to the successive stages in the breakdown of wood.

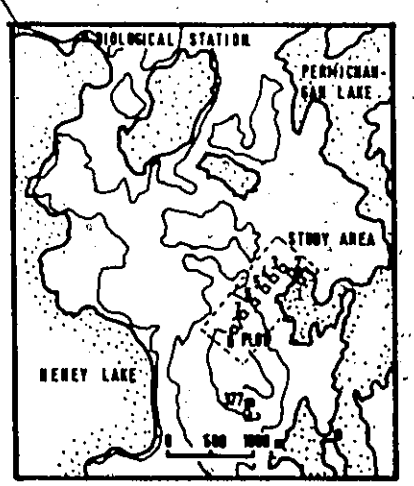
Our study, made over a fairly wide area in Eastern Canada, is perhaps the first of its kind and affords a better understanding of floristic as well as ecological relationships of cryptogams.

This study of cryptogams in a dynamic situation expands on the information already obtained in an experimental investigation on competition between cryptogams (Muhle, 1968).

3. Location and description of study areas

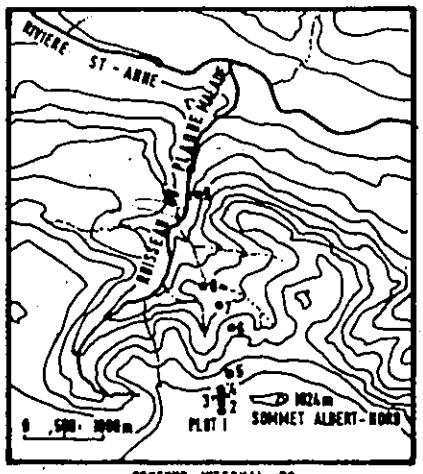
The locations of the investigated sites are given in Fig. 1. They are (1) Petawawa (Petawawa Forest Experiment Station) (2) Mont Saint-Hilaire (Field Station of McGill University, Montréal) (3) Heney Lake (Biological Station of

Figure 1. Location of study areas and sampling plots.



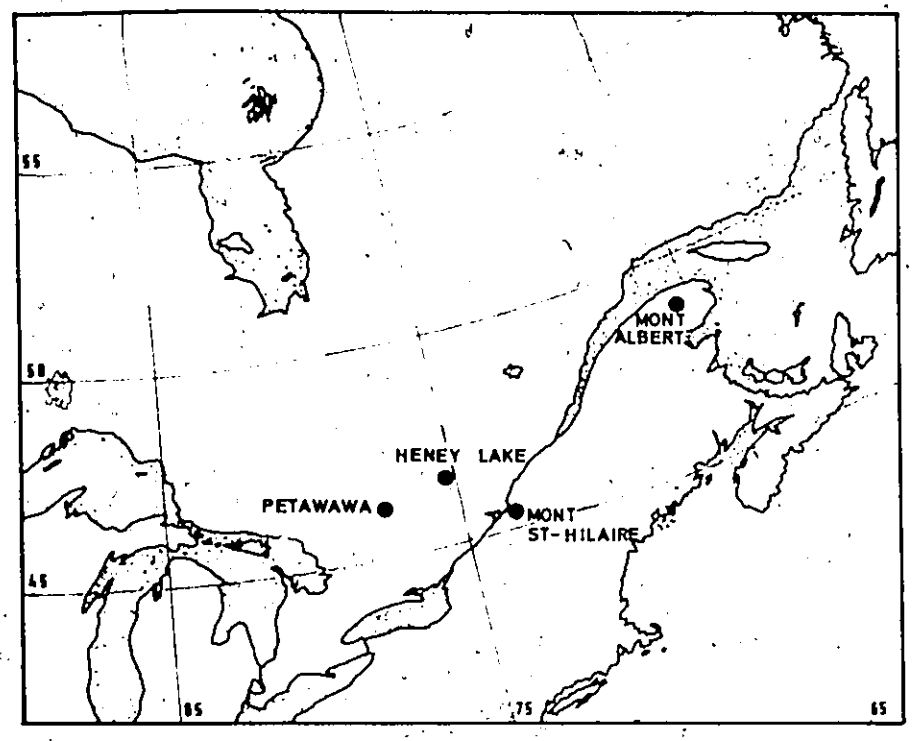
CONTOUR INTERVAL 76 m

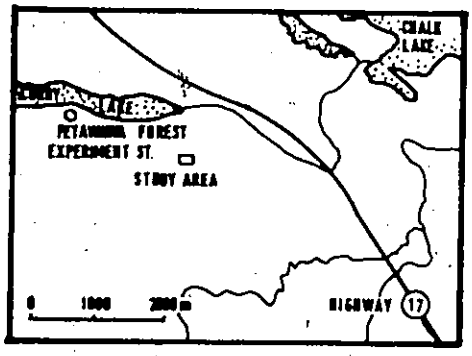
HENEY LAKE



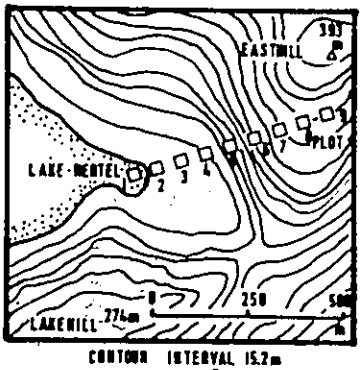
CONTOUR INTERVAL 76m

MONT ALBERT





PETAWAWA



CONTOUR INTERVAL 15.2m

MONT ST-HILAIRE

the University of Ottawa) (4) Mont Albert (Parc de la Gaspésie).

a) Petawawa:

The study area is located at the Petawawa Forest Experiment Station, Chalk River, Ontario. The area has an irregular topography varying from lowlands flats to a strongly rolling type of upland terrain. Gillespie, Wicklund and Mathews (1964) recognize two physiographic divisions for this area: The eastern lowland section and the upland section. The study area is located in the latter. The plot is located in a well-preserved area which was and is under close supervision of the Canadian Forestry Service. It is a permanent sampling plot in which no silvicultural treatments are planned. The micro-topographic differentiation (Lyford and MacLean, 1966) is rather indistinct in this plot as a result of agricultural use prior to 1900.

b) Mont Saint-Hilaire:

Mont Saint-Hilaire is one of the eight Monteregian Hills in the St. Lawrence Valley of Southern Québec. It is situated 20 miles northeast of Montréal. The mountain appears as a solid rock mass in the plain, rising rather abruptly to approximately 300 m above the valley. Almost in the center of this igneous rock mass there is a sizable depression filled in part by a lake. The outer slopes of the mountain are quite steep whereas the inner slopes, facing the lake, are more gentle. These inner slopes act as watersheds for small rivulets which drain into the central basin to form Lake Hertel.

The boggy ground close to the lake with its intermittent streams and mud flats has a number of gravel mounds, sometimes called blow-down mounds, which may be the result of soil uplifting due to windfall of trees. In the spring of 1969 it was observed that most logs in this area, especially those which had been deposited on mud flats, were partly covered with water. It seems probable that the hydrology of this area has changed since the end of the last century because a concrete dam was build around 1890 at the only outlet of Lake Hertel (Maycock, 1961).

The swampy area and the adjacent mesic hardwood stands on the flat areas close to the lake show considerable differentiation in their micro-relief. Blow-down mounds are frequently encountered there, especially in the area in which the moist depressions show no open water in the summer.

The lower part of the steep slopes (20^{o}-40^{o}) is generally covered with rubble of different sizes. These surface materials have not yet stabilized since some logs along the contour lines show considerable accumulation of soil and rocks on the side facing the slope. Parts of the slope also show boulders and ridges of basaltic rocks, and in the central part, a ridge of limestone is exposed. The uppermost part of the slope is not as steep as the lower part and the mineral-soil cover is continuous. Blow-down mounds from uprooted trees are numerous and indicate mechanical disturbance of the soil surface by the roots of fallen trees.

c) Heney Lake:

The second area is located in the Laurentian Highlands of South-eastern Québec. The region is characterized by many lakes, forest-covered hills and plateaus. Agriculture has been established on the sandy soils in the valleys. The transect close to Lake Parmichangan is located on relatively undisturbed crown land. The remote forests do not show any recent signs of exploitation; though it is probable that logging operations for giant white pines occurredin the late 19th century (Hughson and Bond, 1965). The slope investigated has open rocks over most parts of the transect. This substrate increases in frequency uphill where extensive rock ridges are encountered. On the sandy soils of the lower slopes one can find frequent blow-down mounds due to uplifting by wind-thrown trees. Close to the lakeshore, mudflats with intermittent streams are encountered. The somewhat irregular location of the three lowermost quadrats is in response to those topographic features.

d) Mont Albert:

The most northeastern extension of the Appalachian physiographic province of Eastern America is found in Québec. The mountains reach their greatest heights in the Gaspé peninsula where Mont Albert is situated. Two important streams, Grande Cascapedia and Petite Cascapedia, flow from the flanks of Mont Albert towards the Baie des Chaleurs while Rivière Ste-Anne drains towards the St. Lawrence.

The most striking topographical feature of Mont Albert

is the flattened summit. The area of the summit is about 3.5 km by 1 to 2 km. Along the northern part there is a series of small, shallow, sometimes swampy, ponds which never dry out. The mountain flanks have a number of amphitheatre-like cirques evidently formed by small local glaciers (Alcock, 1927).

4. Geology

The Petawawa and the Heney Lake region are both situated within the Precambrian Shield whereas Mont Albert and Mont Saint-Hilaire are of volcanic origin.

a) Petawawa:

The northern gently sloping parts of Algonquin Park lie within the Precambrian Canadian Shield. Most of the area is underlain by pink granitic gneisses. A few outcrops of amphibolite, greenville-type metasedimentary gneisses and pegmatite occur (Gadd, 1963) in this area. Most of these rocks are covered with glacial deposits. The texture of the soils is mostly loamy sand with pebbly layers and, occasionally, a hardpan. They were deposited as deltaic gravels and sands by the Champlain Sea and are of a non-calcareous nature (Moore, 1972). The study area is located in this sandy area and does not show rock outcrops.

b) Mont Saint-Hilaire:

Mont Saint-Hilaire, like all the Monteregian Hills, is thought to be composed of intrusive igneous rocks probably formed at the beginning of the Tertiary (Currie, 1970). Two main areas of igneous rocks can be distinguished on this mountain. In the western parts, essexite is the dominant rock

whereas in the eastern part syenitic rocks are found more frequently. Limestone inclusions appear here and there as small outcrops in the eastern section. During the Pleistocene the mountain was glaciated and as a result the soil was removed over large areas.

c) Heney Lake:

Heney Lake is also situated within the Precambrian Canadian Shield. It is placed in the Archaen as a subsection where sedimentary rocks and derived matamorphics such as argillite, slate, arkose, quarzite, greywacke and conglomerate rocks occur (Atlas du Canada, 1970-72). Clays were deposited in the area probably by the Champlain Sea (Coleman, 1922). The soil cover is thickest at the hill bases and in the valleys whereas uphill glacial drift material has resulted in a discontinuous soil cover. Rocks are exposed from lakeshore to hilltops, where they attain their greatest importance. Localized crystalline calcareous outcrops of the Precambrian Greenville Series occur (Wilson, 1926) as well as gneisses which seem to be locally rich in ore judging from several short-term mining attempts throughout the area (Sabina, 1964).

d) Mont Albert:

The mountain top consists of serpentinized peridotite. The serpentine is surrounded by amphibolite which projects above the plateau level in the North Summit area. The lower part of the mountain consists of volcanic rocks which are probably locally rich in minerals judging from the bryophyte communities growing in contact with them. These volcanic and

sedimentary rocks are attributed by Alcock (1927) to the Ordovician but are placed by Mattinson (1964) in the Cambro-Ordovician since there is no sharp demarcation between Cambrian and Ordovician rocks.

5. Soils

The soils of all four study areas are mainly podzolic. In the Petawawa and Heney Lake area they may be classified as Brunisols on mineral rich substrates or as Humo-ferric podzols on poorer sandy substrates (Hills, 1960). The soils of Mont Saint-Hilaire are probably similar but seem to reflect the peculiar mineral composition of the bedrock (Webber and Jellema, 1965). Since soils, to some extent, reflect the mineralogical characteristics of the bedrock and, to a certain degree, influence the composition of minerals in the humus and in the plants (Duvigneaud et al. 1970; Klausing, 1956) it should be mentioned that on Mont Saint-Hilaire elements like Zr, Zn, Nb, Rb and Ca show an increase along a transect from lakeshore to hilltop whereas potassium decreases (Webber and Jellema, 1965).

The soils of Mont Albert are different from these three areas where the forest soils are podzolic with considerable thick litter horizons. Close to the krummholz at the tree-line, as well as in certain topographic situations on the lower slopes, paludification results in a continuous peat cover or in local peaty mounds. Certain soils covering the amphibolite rocks of the alpine tundra are similar to Nano-Podzols (Dahl, 1956). The poorly structured B horizon over

the serpentine, however, makes it difficult to place these soils in any previously described soil type.

6. Macroclimate

A series of standardized climatic diagrams from Walter and Lieth (1960-1967) show the general trend in climate from west to east for the areas investigated (Fig. 2).

a) Petawawa:

The climate of the Petawawa Forest Reserve is continental with cold winters and hot summers. It is influenced by the Great Lakes and is therefore, in general, milder than the climate of the upland section of Algonquin Park. The local mean annual precipitation is 788.4 mm based on a ten-year period (Clements, 1971). However, the precipitation of the general climatic area, indicated as "Haliburton slopes" in Brown, McKay and Champman (1968), varies between 710 and 1020 mm.

b) Mont Saint-Hilaire:

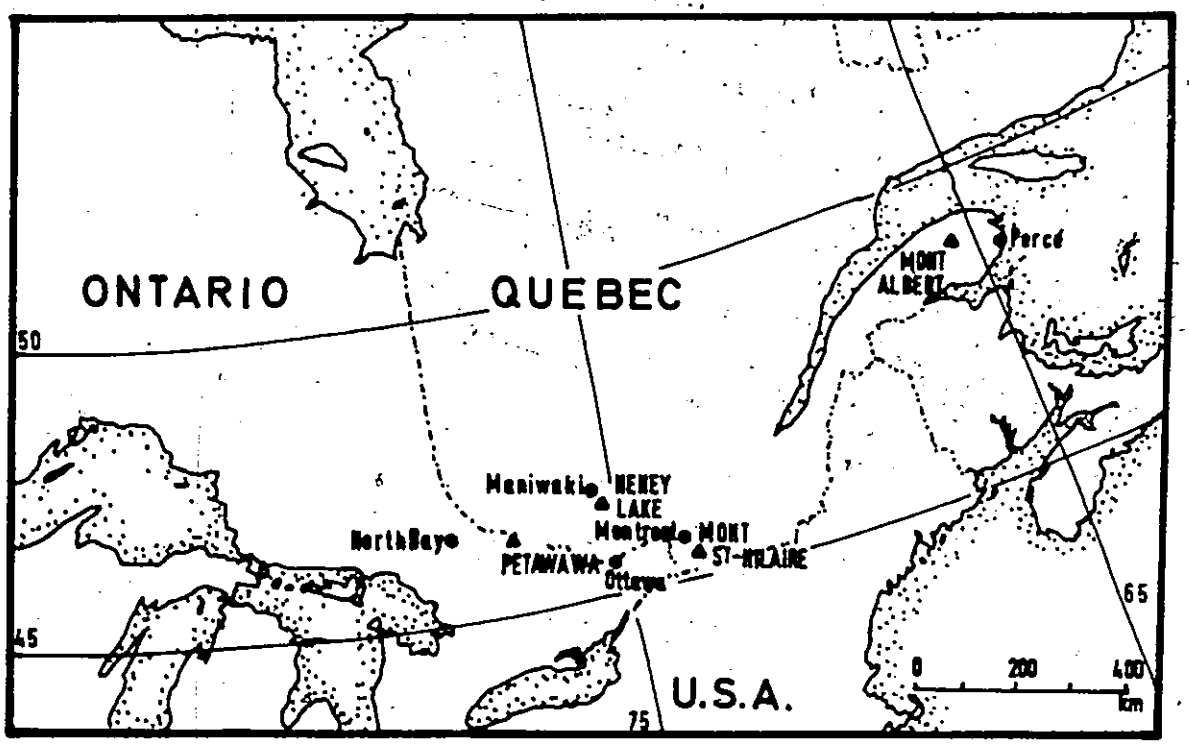
The climate of the St. Lawrence and Ottawa River plain is in general subcontinental as is evident from stations in Ottawa and Montréal (Fig. 2). Mont Saint-Hilaire is exposed on the plain and its climate can be expected to differ somewhat from that from the plain stations. While temperature measurements over a five year period at Mont Saint-Hilaire show sufficient agreement with those obtained over a 75-year period for Montréal, extrapolation of precipitation data is not justified (Rouse, 1965).

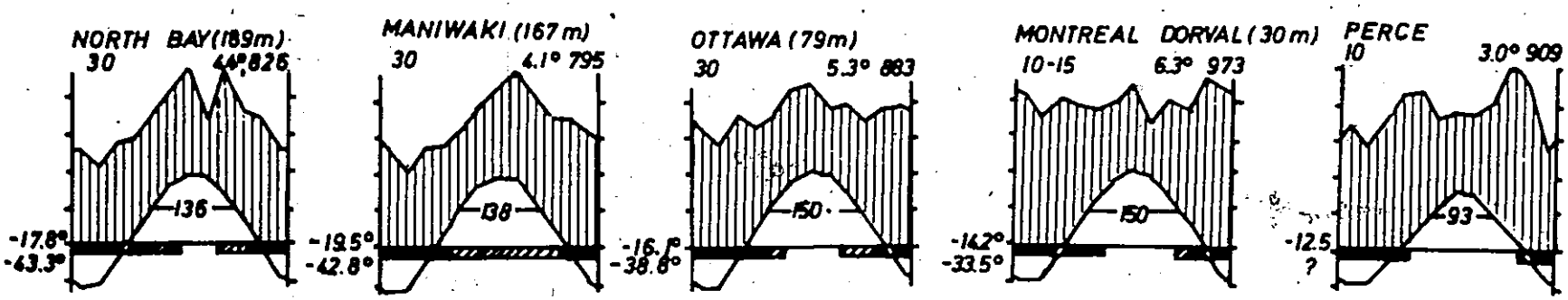
c) Heney Lake:

The climate of the region, as shown by the data from nearby

Figure 2. Meteorological stations relevant for study areas and climatic diagrams (Walter and Lieth, 1960-67) Abscissa: months from January to December; black bar: months with mean daily minimum below 0°C; hatched bar: months with absolute minimum below 0°C; Ordinate: one interval equals 10°C or 20 mm precipitation; upper curve: mean monthly precipitation; lower curve: mean monthly temperature; number below this curve: mean duration of frost-free period in days.

Top of the diagram from left to right: Station, elevation of station; below station; years of meteorological observations; in case of Montreal temperature was recorded for 10 years, precipitation for 15, hence the double number (10-15); in the right-hand corner: mean yearly temperature in C°, mean yearly precipitation in mm. numbers on the left side outside the diagram: upper number is the mean of minima of the coldest month; the lower number is the absolute temperature minimum recorded; vertically hatched area: relative humid season of the year.


ONTARIO
QUEBEC
U.S.A.
50
45
65
75
Maniwaki
NORTH BAY
PETAWAWA
Ottawa
MONT ST-HILAIRE
Perce
MONT ALBERT
0
200
400
km


NORTH BAY (189m)
30
44°826
136
-17.8°
-43.3°
MANIWAKI (167m)
30
4.1° 795
138
-19.5°
-42.8°
OTTAWA (79m)
30
5.3° 883
150
-16.°
-38.6°
MONTREAL DORVAL (30m)
10-15
6.3° 973
150
-14.2°
-33.5°
PERCE
10
3.0° 909
93
-12.5
?

Maniwaki (Fig. 2) is essentially similar to that of the Petawawa area except that there is a longer period with an absolute minimum below 0°C. The temperate influence of the Great Lakes on the macroclimate is, therefore, diminishing to the north.

d) Mont Albert:

Very little is known about the climate of central Gaspé where Mont Albert is one of several mountains of nearly equal elevation in a mountain range called Shickshocks. Most of the meteorological stations of the peninsula are situated on the shore and show a frostfree season of 120 to 140 days (Meteorol. Branch, Dept. Transp., Toronto, 1959). The growing season inland at higher elevations, however, is considerably less than 100 days. Whereas on the Atlantic side of the peninsula, at Percé, the annual precipitation shows values which exceed 800 mm, the north side of the Shickshocks (e.g. Cap-Chat) is drier due to rain shadow effects (Blanchard, 1960). The Shickshocks themselves, however, probably receive more than 1200 mm of rain (Blanchard, 1960) due to precipitation from rising clouds. The main wind directions in winter are from the north and northwest, whereas in summer southeastern winds are most frequent followed by northwestern winds (Atlas of Canada, 1957).

7. Microclimate

Bryophytes and lichens seem to be very sensitive to microclimatic factors. Therefore, a brief review of the topoclimates of the transects investigated will be given. Since in

the Petawawa area no transect was studied the microclimate of that area will not be reviewed.

a) Mont Saint-Hilaire:

The transect on Easthill is located in a south-western exposure. Since in the northern Hardwood region one can expect the southern slopes to be drier and warmer than the northern slopes (Geiger, 1965), logs under the dense forest cover could face a drier microclimate than those on the more shaded northern exposures. Since Lakehill on the south of Mont Saint-Hilaire provides at least shade for the lower quadrats of the transect and since the inner slopes of the mountain facing the lake are relatively protected from wind, the microclimatic extremes generally observed on southern versus northern exposures are probably less pronounced. Logs on the open lakeshore and on the steep slopes will receive, however, higher amounts of radiation than those on the forest floor in the multilayered mesic forest (Rouse et al., 1969).

b) Heney Lake:

The topoclimate of the Heney Lake transect on northeastern exposure is in part different from that of Mont Saint-Hilaire. The lowermost quadrats of both transects have probably similar microclimate. However, logs in the open exposed pine forests on the hilltop receive more radiation during summer than those under the dense decidous forest cover on top of Easthill at Mont Saint-Hilaire (Rouse, 1965).

c) Mont Albert:

When one moves eastwards towards the ocean, areas close

to the considerably higher mountain tops are often in contact with clouds and are, therefore, no longer in a relatively dry environment. Since this difference is important for cryptogams (i.e. oceanic vs. continental, Barkman, 1958) a detailed review will be presented.

The microclimate of the transect in northern exposure can best be described in two sections: (1) the winter climate and (2) the summer climate.

(1) In winter direct and indirect effects from winds on the cryptogams are of considerable importance close to the treeline (Savile, 1972). Direct mechanical effects from wind can be expected from drifting ice crystals which slowly abrade every exposed surface either on the top of mounds in the tundra or on logs and trees close to the treeline (Aulitzky, 1961). The spatial patterns of plant assemblages caused by the above-mentioned factors are well known from alpine habitats and from alpine tundra (Dahl, 1956). Cryptogams which are buried under snowbanks in winter are not only protected from direct mechanical effects but also from the even more important freeze-drying forces of the winds (Aulitzky, 1961). In the lee parts of the mountain, snow accumulates behind clusters of trees or mounds of peat. If these snow banks are above a certain size and especially if they are located on a northern exposure, they cover the vegetation for a rather long period of time and will favor "snowbed vegetation" (Gjaerevoll, 1956). In subalpine forests environmental gradients are not as steep. In forests of similar densities the winter microclimate of logs

will not change as drastically as that of the treeline and the krummholz communities.

(2) In summer the microclimate of such an altitudinal gradient is quite different. Geiger (1965) compared temperatures of peak (1447 m) slope (1008 m) and valley (645 m) at Grosse Arber in the Bavarian Forest. Of these sites the valley stations were the coldest and wettest at night but the warmest and driest during the day. The slope stations were the warmest at night while during the daytime the temperature was dependent on altitude. The daytime temperatures were highest in the valley and lowest on top of the mountain. The peak station showed the smallest variation between day and night temperatures. The mountain peak had the driest microclimate at night and moistest during the warmer parts of the day.

Similar microclimatic relations may be found on Mont Albert during parts of the summer. However, owing to its geographical position certain differences can be expected. Especially the movement of cold air masses from higher latitudes as well as the ascent of warm humid air from southerly directions may modify this picture considerably (Larsen, 1971).

When one leaves the krummholz and proceeds downhill on the northern side of the mountain, direct solar radiation can be expected to decrease (Dirmhirn, 1951). Radiation affecting log surfaces could be reduced even more since the krummholz and the boreal forests can be expected to have albedos which differ by a factor of 4 to 6 (Turner and Tranquillini, 1961).

There is, therefore, a drastic change in radiation conditions when one moves from the alpine tundra to the base of the mountain. Logs decomposing under the densely interwoven krummholz layer will receive less radiation than those remaining upright. Radiation in subalpine forests in a northern exposure is even more reduced providing northern slopes with a cool humid environment.

On the unforested rocky plateau the climatic conditions may be close to those of an arid continental arctic fellfield (Scoggan, 1950). The rocky serpentine tundra evidently persists on soil with very low water capacity. However, precipitation effectiveness close to the treeline is considerably different from that of the alpine tundra. Aerodynamic factors of the vegetation surface, e.g. roughness factors of the mostly decumbent shrubby alpine tundra versus the dwarf krummholz and the subalpine forests (Kung, 1961) cause probably differences in fog drip (Byers, 1953). Plants and epiphytes, especially in the krummholz zone, can be expected to receive more "precipitation" from fog than those of the treeless alpine tundra (Baumgartner, 1958; Ellenberg, 1959). Measurements of precipitation from fog with catchment nets (Grunow, 1955) showed that the amount of precipitation exceeded that obtained with ordinary rain gauges by 100%. Since the frequent *Alectoria* spp. and *Usnea* spp. in the subalpine forests can be considered to function as "catchment nets" these results have some relevance.

8. Vegetation

The Petawawa, Heney Lake and Mont Saint-Hilaire area are all situated in the Great Lakes - St. Lawrence Region (Rowe, 1972). Though the general vegetation is somewhat similar, there are regional floristic differences. The general Petawawa area shows affinities to western areas (Moore, 1972). In the Heney Lake area some northern elements can be found whereas on Mont Saint-Hilaire a number of southern plants are present (Maycock, 1961). Mont Albert's flora is essentially boreal and, therefore, floristically different from the other three regions. There are, however, in the Petawawa area, the Heney Lake region and around Mont Saint-Hilaire azonal plant communities (Walter, 1970) which harbour cryptogams and cormophytes of general boreal distribution.

a) Petawawa:

Most of the area around the Petawawa Forest Experiment Station is covered by a mixed forest less than 100 years old. The woods contain a mixture of coniferous and decidous trees such as *Pinus strobus*, *Pinus resinosa*, *Abies balsamea*, *Picea glauca*, *Tsuga canadensis*, *Populus balsamifera*, *Populus tremuloides*, *Acer rubrum* and *Betula papyrifera*. According to Braun (1950) this forest would belong to Helmlock-White Pine-Northern hardwood forests. Rowe (1972) classified the regional forests as belonging to the Algonquin-Pontiac Section of the Great Lakes - St. Lawrence Forest Region. The hardwood deciduous species are most frequent on the finer textured soils of the mesic sites on southern exposures whereas the dry sites

or sand deposits overlying shallow bedrock are occupied by pines (Lambert and Maycock, 1968). Fires and selective lumbering, especially since 1800, have resulted in a reduction of the once abundant stands of red and white pines.

b) Mont Saint-Hilaire:

According to Dansereau (1959) the climatic climax of the St. Lawrence Lowland is the Maple Forest (*Aceretum sacchari laurentianum*). This forest is dominated by *Acer saccharum*, *Fagus grandifolia* and *Tilia americana*. The virtual absence of conifers from the forests below 300 m was emphasized by Dansereau (1959). Also Rowe (1972) noted the predominantly decidous character of the Upper St. Lawrence Section of the Great Lakes-St. Lawrence Forest Region. The forests of Mont Saint-Hilaire differ floristically from the regional forests. Well drained dry areas and wet habitats provide suitable niches for conifers and trees of southern prevalence such as *Carya ovata*, *Carya cordiformis*, *Quercus alba* and *Quercus bicolor*. Maycock (1961), therefore, noted in his taxonomic treatment of higher plants of this mountain, the transitional aspects between southern and northern floristic elements. The composition of the various climatic and edaphic climax communities led him to include the vegetation of the mountain in the Northern Conifer-Hardwood Zone.

c) Heney Lake:

The study area lies within the Middle Ottawa Section of the Great Lakes - St. Lawrence Forest Region (Rowe, 1972). The mesic sites are usually occupied by decidous trees whereas

the dry sites or those with poor drainage conditions are dominated by conifers. Therefore, some elements of the boreal forest which become dominant a few hundred miles north are intricately mixed with elements of southern forests (Hills, 1962).

d) Mont Albert:

The Gaspé peninsula is covered mostly by the boreal forest, described by Grandtner (1966) in his hierarchial system as the *Abieto-Piceetea marianae*. The south shore of the peninsula as well as certain valleys of the north shore along the St. Lawrence harbour maple forests where yellow birch (*Betula alleghaniensis*) is also present (Dansereau, 1959). The central parts of the peninsula are dominated by *Abies balsamea*, *Picea mariana* and *Picea glauca* often in combination with *Betula papyrifera*. On the lower slopes, sometimes on southern exposures, one also encounters *Pinus strobus* and *Betula alleghaniensis*. *Thuja occidentalis* may occur in pure clumps in rich fens or mixed with fir and spruce as large trees along the main rivers.

The boreal forest is less dense just below the summit of Mont Albert. This subalpine forest is relatively open and trees are reduced in size. In this area, especially close to ravines, tall herb communities with *Heracleum lanatum* can be found. These wet open habitats can be considered as being natural meadows and are floristically very rich (Scoggan, 1950).

Above this zone a truly alpine krummholz is encountered. On the amphibolite of the North Summit this krummholz is found at a higher altitude than the tundra of the serpentine plateau.

This area harbours ponds along with boggy and swampy habitats. Most of the tableland, however, is a rather dry alpine heath with dwarf shrubs. It should be mentioned that the floristically more interesting species for which Mont Albert is famous are present either in more mesic habitats or in open rocky habitats where there is little competition from other plants (Dansereau and Raymond, 1948).

CHAPTER II

METHODS

1. Sampling techniques

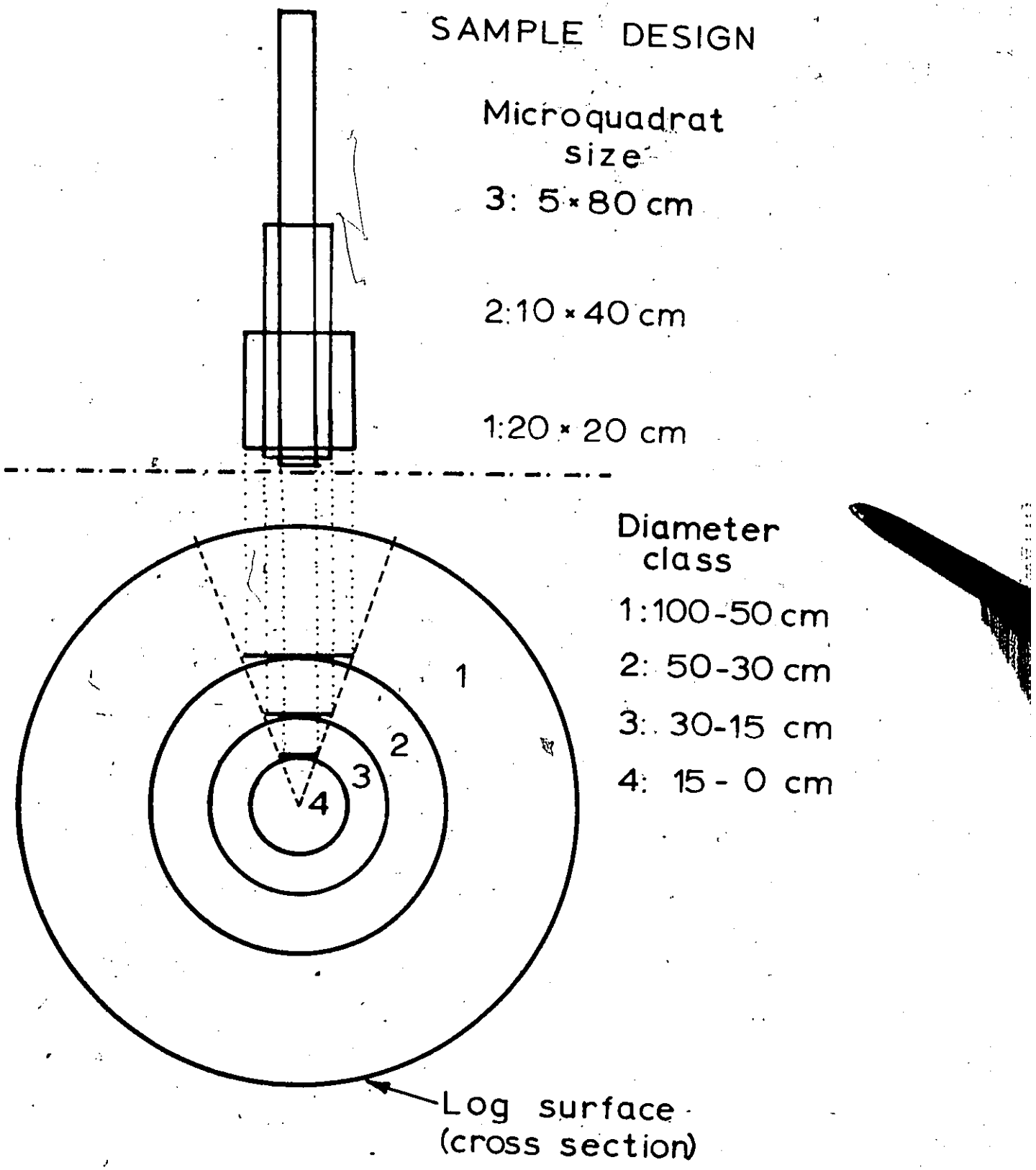
Since microclimatic factors have overriding importance on photosynthesis of cryptogams, it was decided that sampling along a moisture gradient, as measured by change of evaporation from wet lakeshore to dry hilltop or along an elevational gradient from boreal to arctic-alpine climate, would be most rewarding.

a) Microquadrat sample design:

The vegetation of each log was analyzed by microquadrats (LeBlanc, 1963). This technique was preferred because quantitative aspects of plant assemblages can be determined. Preliminary results obtained from random sampling with microquadrats of different sizes and shapes indicated that marked discontinuities in species composition existed when quadrats extended over the sides of the logs. Therefore, it was decided to sample only the central area of the upper surface, that is, that area forming an angle of 20° from both sides of the perpendicular axis of a log. This decision, however, made it necessary to use microquadrats of different shapes (Fig. 3) in order to maintain a constant area.

In the Mont Saint-Hilaire area, where the author started his investigations, three microquadrat sizes were utilized: 1) 20 x 20 cm; 2) 10 x 40 cm; 3) 5 x 80 cm. Microquadrat size 1 was used to sample logs having diameter classes of 100 to 50 cm; microquadrat size 2 for logs measuring 50 to 30 cm;

Figure 3. Sample design of microquadrats for logs of different diameters (see also Fig. 9).


SAMPLE DESIGN
Microquadrat size
3: 5 × 80 cm
2: 10 × 40 cm
1: 20 × 20 cm
Diameter class
1: 100-50 cm
2: 50-30 cm
3: 30-15 cm
4: 15 - 0 cm
1
2
3
4
Log surface (cross section)

and microquadrat site 3 for logs having a diameter of 30 to 15 cm. Data for logs whose diameter measured less than 15 cm were not recorded for this area.

In the Heney Lake area, in the Petawawa plot, and in the Mont Albert transect the sample design was slightly changed to include logs of smaller diameters (Fig. 14, p. 60).

b) Transect sampling:

In the Petawawa area a single rectangular plot (18 m x 45 m) was sampled. The plot is situated in the southern corner of the permanent sampling plot no. 2 (P.S.P. 2) of the Petawawa Forest Experiment Station (Fig. 1).

On Easthill of Mont Saint-Hilaire (Fig. 1) a transect of nine quadrats (plots) located at regular intervals along an elevational gradient was made. At every 30.5 m (100 feet) all logs within a 30.5 x 30.5 m quadrat were sampled.

In the Heney Lake area a transect similar to the one made on Mont Saint-Hilaire was sampled. The quadrats close to the lakeshore were arranged in such a way as to have them in a position where contour lines cross the plot at approximately right angles. Locating of plots close to the lakeshore in such a way ensures, in most cases, the presence of a uniform forest community within a plot.

In the boreal forests of Mont Albert, for reasons of logistics, plots were not arranged in a straight line as was the case with the other transects. The quadrats in these more uniform forests were also smaller, i.e., 232 m^2 (50 x 50 feet). They were placed at preselected spots ten meters

from a hiking trail where there were no apparent disturbances.

c) Sampling strategies within plots:

The sampling procedure within plots of the four study areas can be reduced to basically three strategies (Cochran, 1963): (1) restricted random microquadrat sampling (Mont Saint-Hilaire), (2) unrestricted random microquadrat sampling (Petawawa), (3) systematic microquadrat sampling (Heney Lake, Mont Albert).

(1) In the Mont Saint-Hilaire area locating of the samples on the logs within one quadrat was done by the "random walk" technique. Starting from the center of the plot one traveled a preselected random distance in a random direction and the part of the log present at the shortest distance to the endpoint of the walk was sampled. The diameter was measured or simply assessed in cases where logs were in advanced stages of decay, and the appropriate microquadrat placed on the log (Fig. 3). The random walk procedure was then repeated from the position on the log just sampled until all logs within the plot had been sampled at least one time. When the limit of the plot was reached during a particular walk the procedure was stopped and a new random walk started from the center of the plot. Because with this sampling strategy a tendency of oversampling towards the center of the sides of the plot was encountered, the technique was considered as being a "restricted random sampling".

(2) In the Petawawa plot all logs present were mapped and numbers assigned to all microquadrat positions on each log.

Then these numbers were written on small cards of identical size, placed in a plastic bag, and drawn out one at a time after they had been thoroughly mixed. The procedure was repeated until all logs had been sampled at least one time. The sampling was without replacement, which means that a card was not replaced since this might allow the same unit to enter the sample more than once. The sampling procedure within the plot was considered as being an "unrestricted random sampling".

(3) In the Heney Lake area and on Mont Albert all microquadrat positions on all logs within plots were sampled. The sampling strategy was therefore considered as being "systematic sampling".

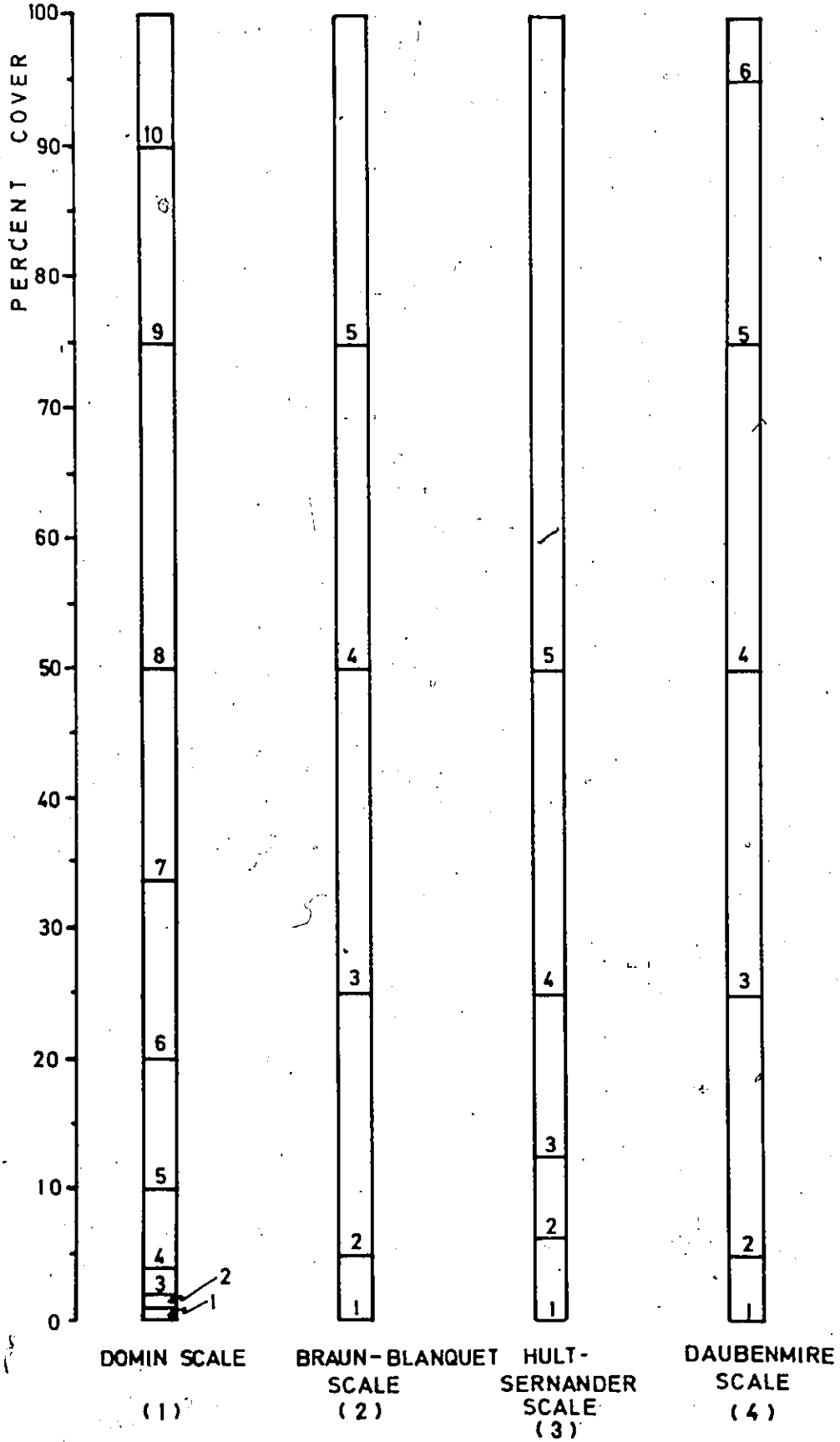
2. Estimated or calculated values

a) Degree of cover:

Quadrat sampling techniques are often employed in studies of cryptogams (Hale, 1955; LeBlanc, 1963). The degree of cover of each species or the presence/absence are often recorded in phytosociological studies. If it is easy to tally presence/absence, it is not always so simple to estimate cover, especially when plots of different sizes are analyzed. Because a sampling error is unavoidable in estimating cover, a preliminary investigation was initiated to find out how accurate "estimation" was. This is important when sampling of the same logs is to be repeated in the future.

Four frequently used scales (Fig. 4) for the estimation of cover are those of: (1) Domin (in Shimwell, 1971),

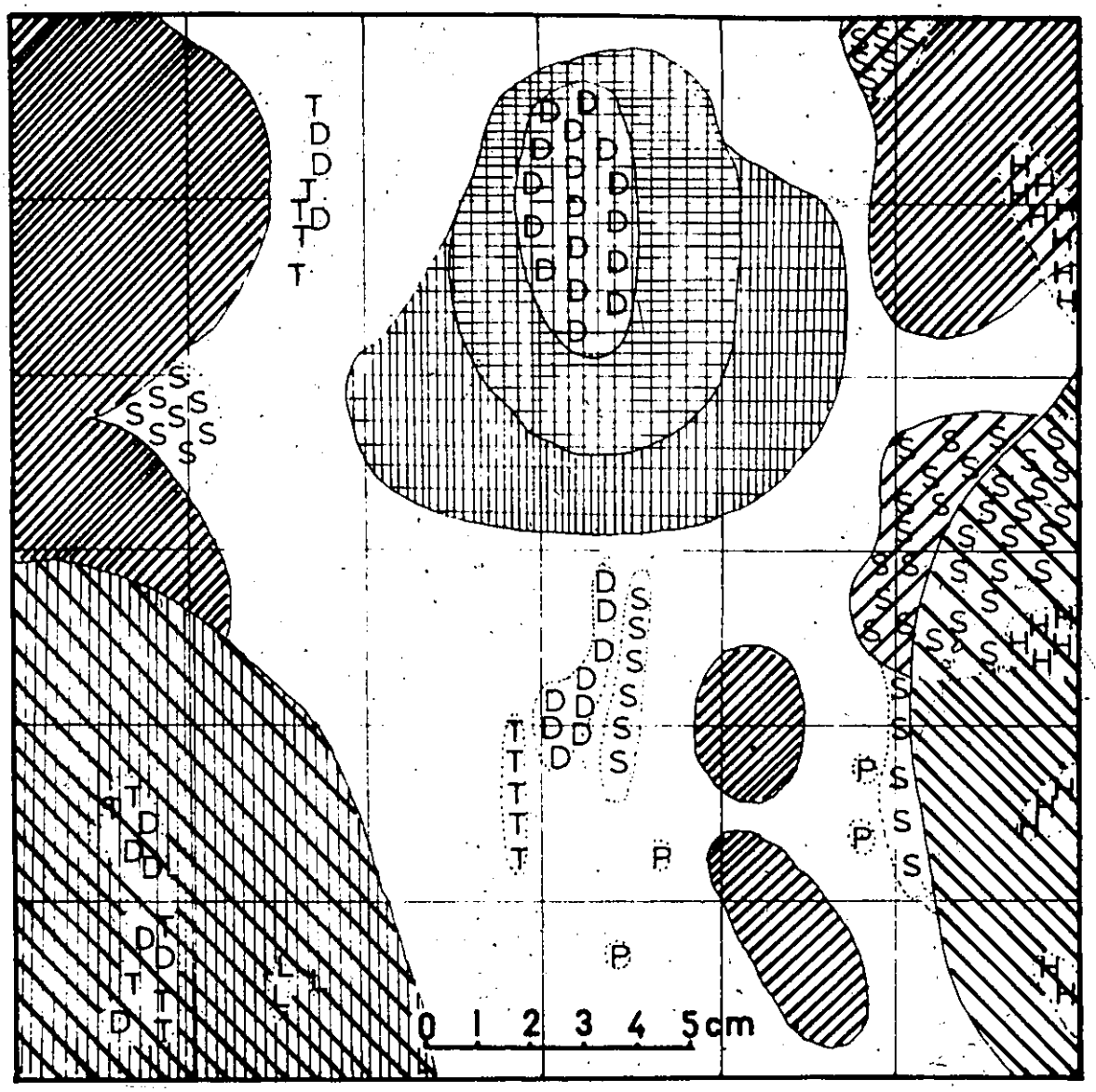
Figure 4. Comparision of four scales often used for the estimation of cover.


PERCENT COVER
100
90
80
70
60
50
40
30
20
10
0
10
9
8
7
6
5
4
3
2
1
5
4
3
2
1
5
4
3
2
1
6
5
4
3
2
1
DOMIN SCALE
(1)
BRAUN-BLANQUET SCALE
(2)
HULT-SERNANDER SCALE
(3)
DAUBENMIRE SCALE
(4)

(2) Braun-Blanquet (1928), (3) Hult-Sermander (in Sernander, 1898) and (4) Daubenmire (1959). Generalized diagrams (Figs. 5 and 6) representing the vegetation of seven 20 x 20 cm microquadrats were shown to four ecologists who were asked to estimate independently the degree of cover of different species combinations by using the four scales. In Fig. 5 nine plant-units are illustrated. They represent the vegetation of a microquadrat where plant combinations are either dominant (100% cover), codominant (50% cover) or present as single plants. Fig. 6 represents six microquadrats where cover had to be estimated for two synthetic units only (Hutchings and Holmgren, 1959) but present in divers combinations. The surface occupied by various species or groups of species were planimetrically measured and the exact values obtained were compared with the average cover values estimated by the four test-persons.

In Tables 1 and 2 cover values estimated by four persons are actually compared for accuracy, on a percent basis, with the exactly measured areas shown in Figs. 5 and 6 . The inaccuracy of scale 1 for the estimation of cover in microquadrat studies is quite evident from the data cited in Tables 1 and 2 . Scale 4 is rated second in inaccuracy, whereas scales 2 and 3 are almost identical in their percentage accuracy with respect to microquadrat data. It seems that small ranges in cover classes are responsible for the differences demonstrated. In scale 3 cover class 5 (50-100%) is rather wide. Therefore it was decided to use scale 2 in these

Figure 5. Schematic representation of the vegetation of a microquadrat (20 x 20 cm) used for the estimation and measurement of cover.



a b c

P Ptilidium pulcherrimum

J Jamesoniella autumnalis

C Cephalozia media

N Nowellia curvifolia

a - deminant b - codominant c - single plants

c

S Cladonia sp. (squamules)

D Dicranum flagellare

T Tetraphis pellucida

L Lophocolea heteroph.

H Heterophyllium haldanianum

Figure 6. Schematic representation of the vegetation of six simplified microquadrats (20 x 20 cm) used for the estimation and measurement of cover.

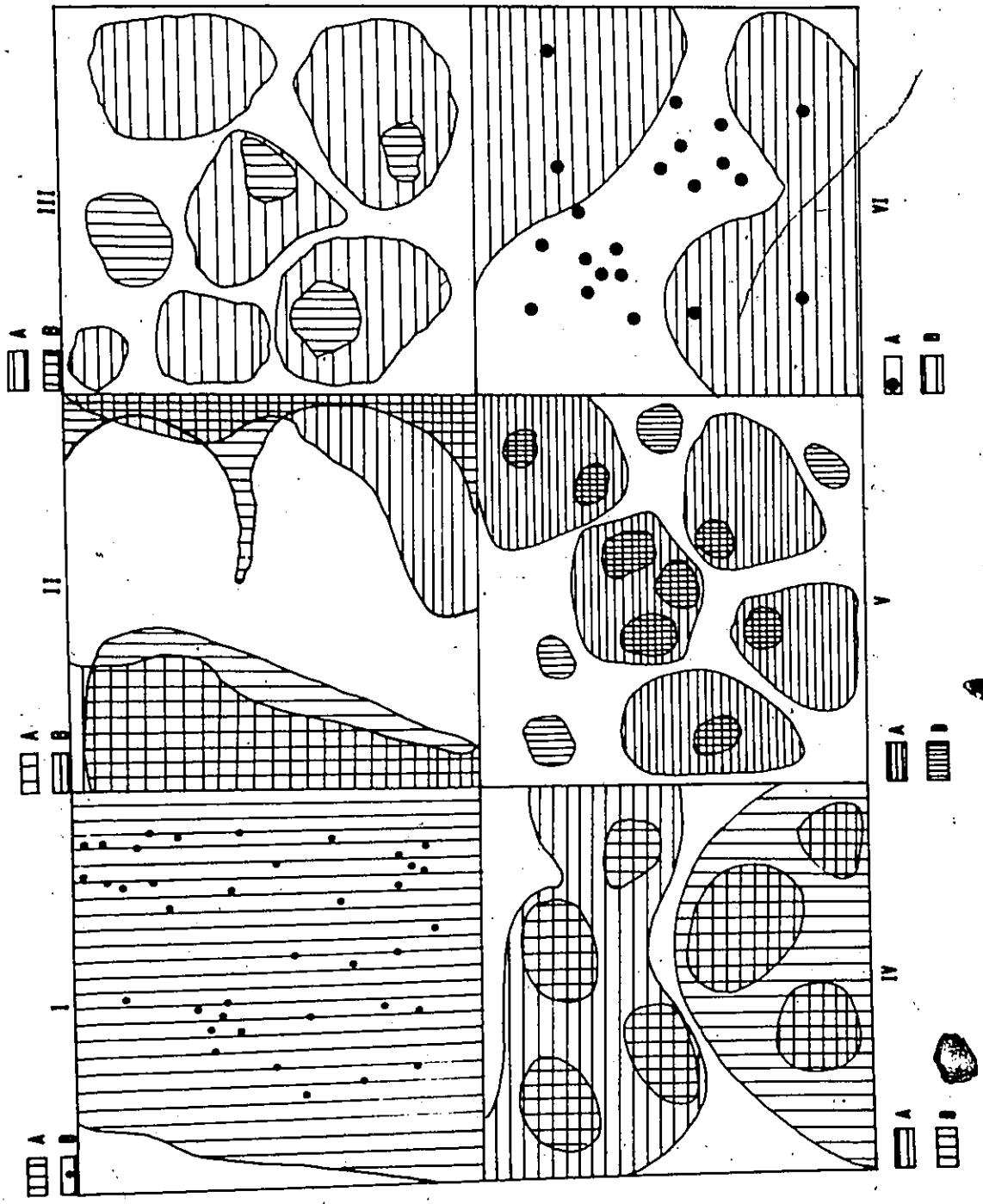

III
A
B
VI
A
B
II
A
B
V
A
B
I
A
B
IV
A
B

Table 1

Percentage accuracy of cover averages estimated by four persons for the vegetation of microquadrat 1 in Fig. 5.

Microquadrat area symbol Fig. 5	Number of symbol in Fig. 7	Scale 1	Scale 2	Scale 3	Scale 4
P	1	50	75	50	50
J	2	75	50	75	50
C	3	50	75	100	100
N	4	0	25	0	25
S	5	0	25	25	0
D	6	25	50	25	50
T	7	50	75	75	75
L	8	50	100	100	100
H	9	0	50	75	75
	Mean	33.3	58.3	58.3	58.3

Table 2

Percentage accuracy of the cover average estimated by four persons for the vegetation of microquadrats 1-6 in Fig. 6.

Microquadrat number in Fig. 6		Number of quadrat in Fig. 8	Scale 1	Scale 2	Scale 3	Scale 4
I	A	1	25	100	100	75
	B	2	75	75	75	100
II	A	3	75	75	75	100
	B	4	50	50	50	25
III	A	5	75	0	75	25
	B	6	25	100	100	75
IV	A	7	50	50	75	50
	B	8	25	25	25	25
V	A	9	0	75	25	75
	B	10	0	25	0	25
VI	A	11	25	25	50	0
	B	12	100	50	50	0
		Mean	43.8	54.2	58.3	47.9

studies. It has to be made clear that the data have importance for studies where small areas are investigated and where plants are growing together, especially when they differ in height by a factor of 1 to 100 or less.

The author realizes that Tables 1 and 2 represent result data and could have been incorporated in the result section. Since they refer mainly to the methods used in the four study areas they have been placed for practical purposes, in this part of the thesis. The same remark holds true for the other experiments described in relation to hydrogen ion concentration, ecological diversity, and degree of succession.

In Figs. 7 and 8 the cover percentages measured with a planimeter, are compared with those estimated by four persons. The figures show that at low percentage cover, estimates are generally too high whereas at high percentage cover, they are too low. Between the 20 and 60 percent cover figure the measurements estimated scatter pretty well around the real values. Estimates from scales 2, 3 and 4 show no consistent pattern in their deviation from the measured values. Estimates from scale 1, however, tend to follow the real value rather closely.

The microquadrat technique for the estimation of cover is quite suitable for cryptogam studies and yields reproducible results of fair accuracy. Precision usually increases with experience in sampling (Greig-Smith, 1964). It is thought that the generally green-brown color difference (plant-log) and the numerous combinations of shapes and sizes of

Figure 7. Exact cover percentage compared with the average cover estimates made by four persons using four different scales for analyzing microquadrat 1 (Fig. 5); (see Table 5 for reference of number of quadrat).

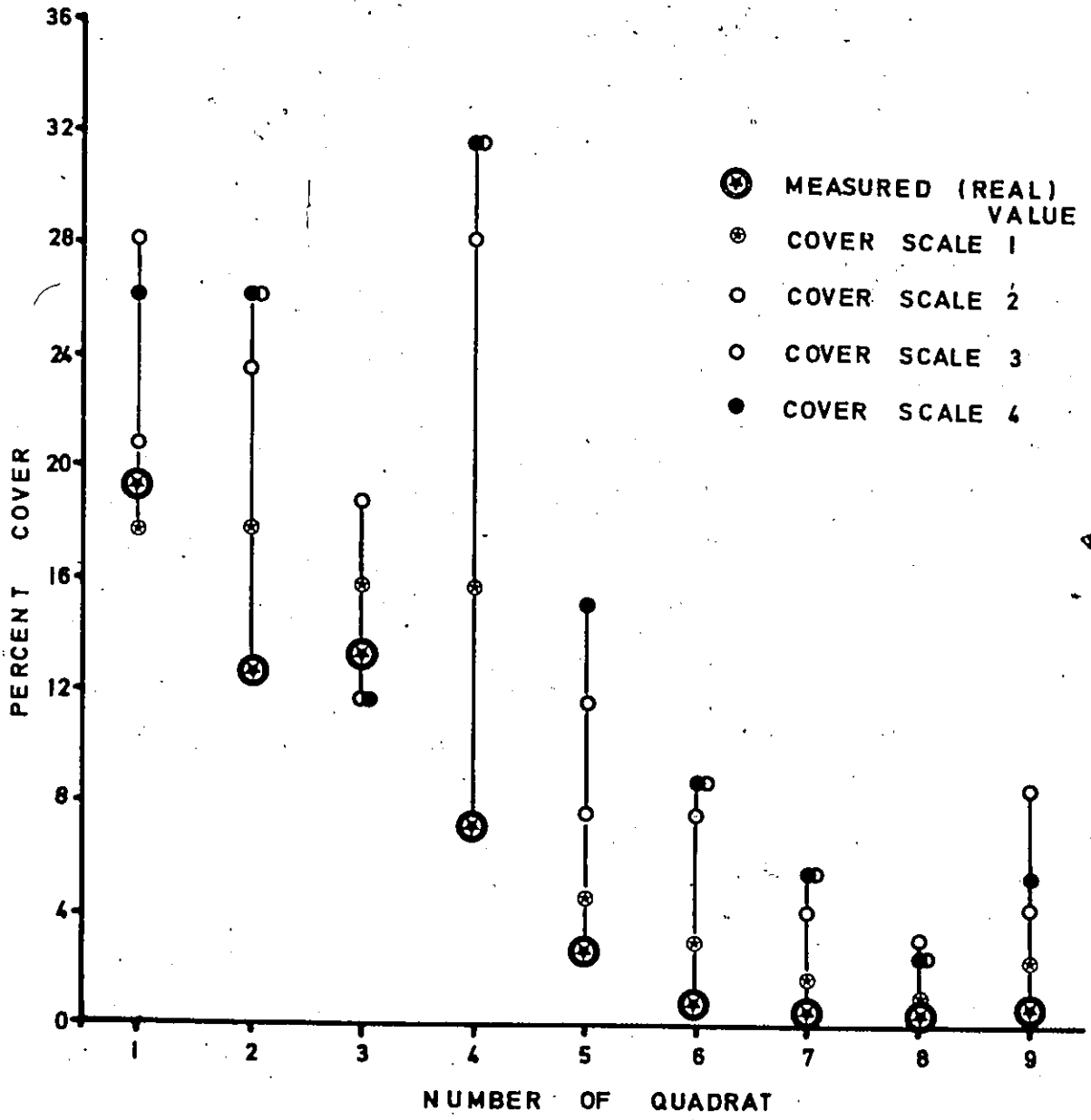
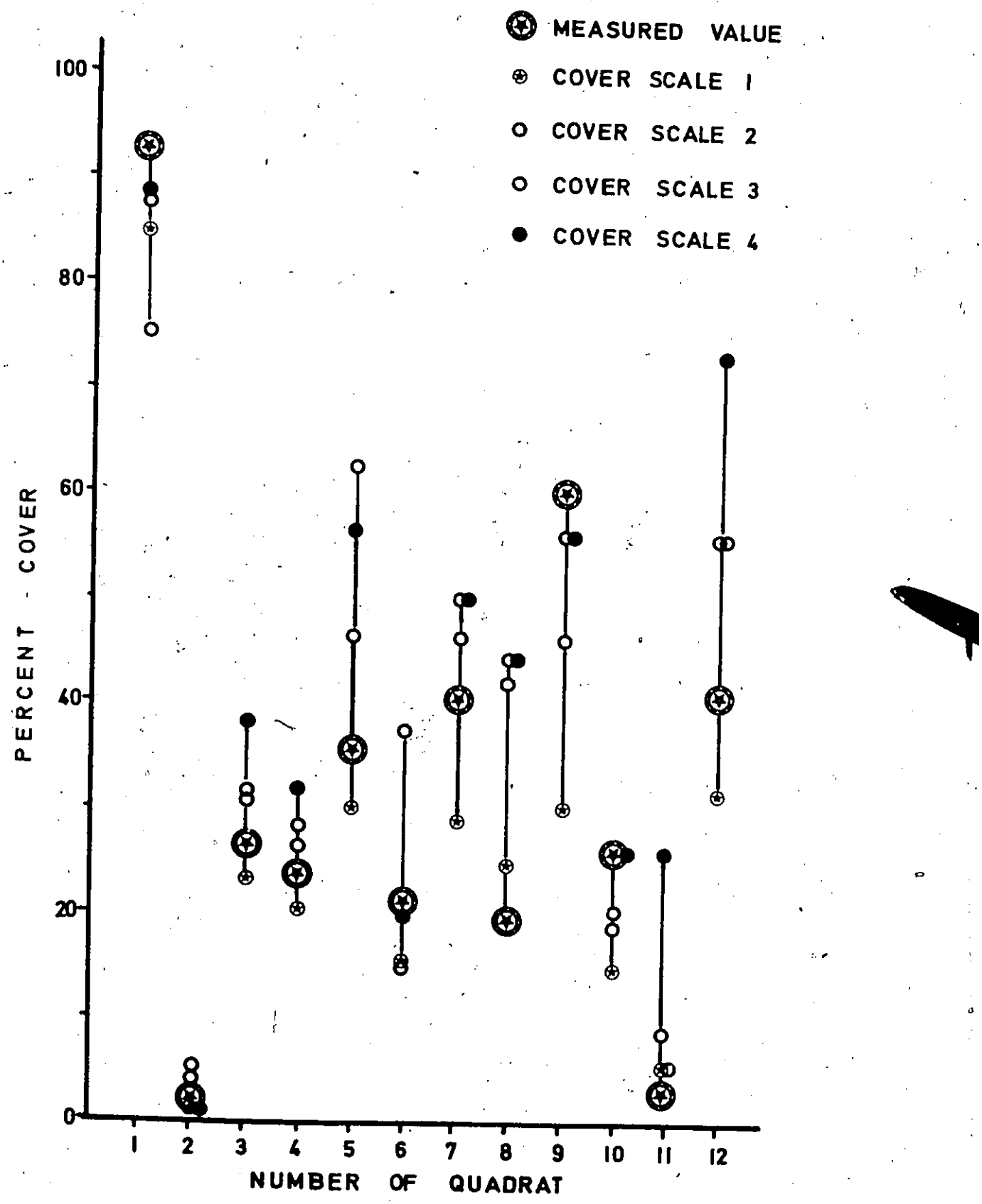

36
32
28
24
20
16
12
8
4
0
PERCENT COVER
1
2
3
4
5
6
7
8
9
NUMBER OF QUADRAT
MEASURED (REAL) VALUE
COVER SCALE 1
COVER SCALE 2
COVER SCALE 3
COVER SCALE 4

Figure 8. Exact cover percentage compared with the average cover estimates made by four persons using four different scales for analyzing microquadrat 1 to 6 (Fig. 6). (See Table 6 for reference of number of quadrat).


MEASURED VALUE
COVER SCALE 1
COVER SCALE 2
COVER SCALE 3
COVER SCALE 4
PERCENT - COVER
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10
11
12
NUMBER OF QUADRAT

cryptogams that the investigator had to face in the field, made the processes associated with cover estimation far more complex than one might assume from the simplified picture presented here. The tendency of overestimation at low cover values and underestimation of high cover values was common to all scales.

It was finally decided to use scale 2 which has the following range:

1. indicates that a species covered an area between 1 and 5% of the microquadrat,
2. indicates that a species covered an area between 5 and 25% of the microquadrat,
3. indicates that a species covered an area between 25 and 50% of the microquadrat,
4. indicates that a species covered an area between 50 and 75% of the microquadrat,
5. indicates that a species covered an area between 75 and 100% of the microquadrat.

Reproducibility of estimates with this scale, judging from the percent accuracy, is fair although averages from midpoints of cover classes from scale 1 are better than those of scale 2.

b) Growth-forms:

In a preliminary survey, qualitative differences in growth-forms of plants were observed along an elevational gradient on Mont Saint-Hilaire. Therefore, it was decided to examine the growth-forms of bryophytes, lichens and cormophytes (vascular cryptogams and phanerogams).

(i). Bryophytes:

Evidence from an earlier experimental study (Muhle, 1968) showed that orthotropic forms had to be separated from plagiotropic forms. In the orthotropic forms a distinction was made between cushions with numerous terminal shoots per surface area and turfs with few shoots per surface area. The following guideline was useful for the distinction between turf and cushion; when the distance of the central shoot in relation to the closest neighbouring shoot of a colony of a given species was more than one third of the total height (dead bases included) of the central shoot, the whole entity was assigned to turf; when this distance was less than one third, the colony of certain species was recorded as cushion. This somewhat rigid separation was necessary because on logs of different ages a mosaic of cryptogams of all sizes and ages can be expected.

Three size classes were estimated: bryophytes in size-class 1 ranged from 1 mm or less to 10 mm (height of erect plants or thallus diameter of appressed growing species); size-class 2 extended from 10 mm to 20 mm; plants larger than 20 mm were placed in size-class 3.

(ii) Lichens:

For the lichens the four classical growth-form types were identified: crustose, squamulose, foliose and fruticose.

Two size classes were distinguished. Lichens in size-class 1 ranged from 1 mm to 10 mm while species larger than 10 mm were placed in size-class 2. Again the size refers to

the height of erect plants or thallus diameter of appressed growing species.

(iii) Cormophytes:

Seedlings were classified as trees, shrubs or herbs. When young plants were larger than 1 m in the case of trees, 0.5 m in the case of shrubs or 0.05 m in the case of herbs, they were recorded as trees, shrubs or herbs.

c) Raunkiaerian life-forms:

The diversity in growth-forms encountered on Mont Saint-Hilaire showed a distinctive pattern along an elevational gradient. In the Petawawa study a more detailed analysis was attempted through the application of Raunkiaer's system of plant life-forms. The key provided by Ellenberg and Müller-Dombois (1966) was followed for the cormophytes. The key used for the thallophytes is slightly modified and adapted for those cryptogams encountered on logs according to the following scheme:

1 Plants with chlorophyll, or at least with access to photosynthates

2 Plants in close contact with humus, litter or the outer wood cylinder of decaying wood

3 Dense (cushion-like) to open (turf-like) erect plants

THALLO-CHAMAEPHYTES

3 Flat-matted, appressed plants

THALLO-HEMICRYPTOPHYTES

2 Plants attached to the surface of dead or living bark

THALLO-EPIPHYTES

1 Plants without chlorophyll

THALLO-SAPROPHYTES

Subdivisions of these groups were distinguished and are listed with an example in the Petawawa section. For the division of major groups, growth characters similar to those used for growth-forms were applied.

d) Stage of decay:

The decay stages commonly used in wood science are (Society of American Foresters, 1944):

1. The invasion phase or hidden stage,
2. The early phase or the incipient stage,
3. The typical phase or the advanced stage,
4. The final stage.

This is the scheme that was used with slight modifications. These were compiled from the work of Arnborg (1942), Raschendorfer (1946) and Peck (1954). The author of this thesis added characters of the trunk and roots which could be recognized in the field. For each log studied the condition of the bark, roots and twigs, especially for those logs which had been blown over while still in living condition was recorded. Dead trees, when standing upright for some time, lose their bark and twigs totally or partly before falling to the horizontal position. In this case, the estimation of the stage of decay in a certain microquadrat was based on the condition of the outer wood cylinder only. Since these trees frequently break at the base or since their roots decay in the ground, they have only a small impact on the soil surface. This difference was used to separate them from wind-uprooted logs which always show prominent mounds at their former tree base (see also Fig. 37, p. 174).

A description of the decay stages distinguished in this study is found in Tables 3 and 4.

e) Hydrogen ion concentration:

Water infiltrated in wood and in equilibrium with chemical composition of the wood has a certain pH which, in the outer wood cylinder especially close to the surface, influences plants growing on logs. Since in most cases, it is not possible to obtain these solutions from the wood one has to resort to another technique. One way to proceed is to measure the pH in some sort of wood-water suspension. This usually means that the wood has to be broken up and its natural moisture content increased by addition of deionized water. Since in any wood-water suspension not only the free diffusing hydrogen ions affect the hydrogen ion activity but this ion activity is also affected by the hydrogen ions absorbed at the wood particles and also affected by substances in colloidal state, then as a result, one usually observes a "suspension effect" (Schlichting et al., 1966). One way to reduce the impact of the suspension effect, which usually results in unstable potentials, is to measure the pH in a pasty wood-water suspension (H_2O-pH, Steubing, 1965). The pasty condition of the suspension is generally considered to be a fair compromise between physicochemical measurement requirements and a proximity to natural moisture conditions (Ellenberg, 1958). Another way to minimize the suspension effect is to exchange the hydrogen ions absorbed at the particles with N-KCl in the following way (Schlichting et al., 1966):

$$H_x \cdot \text{wood} + yK^+ \rightleftharpoons H_{x-z} \cdot K_z \cdot \text{wood} + zH^+ + y\text{-}zK^+$$

Table 3

Stages of decay in relation to bark characteristics and the conditions of the outer wood cylinder

Stage of decay	Bark	Outer wood cylinder of trunk	
	Bark remained on tree when trunk fell (when bark lost see next columns and Table 4)	Macroscopic and mechanical properties	Microscopic and chemical characters
1	Bark intact without insect holes	Wood solid, bark, when present, firmly attached to wood	Most outer wood tissue without hyphae, blue stain locally present
2	Bark with insect holes and surface desquamating	Wood solid, signs of animal activity, phloem-mining animals loosen the bark	Wood with hyphae
3	Bark partly lost, breaking into pieces	Application of weak manual pressure on outer surface leaves mark in the soft rotten wood	Advanced development of hyphae, large areas discolored
4	Bark mostly lost	Wood breading into pieces, turning into a brown charcoal-like mass or broken down into a spongy fibrous condition	Most wood with discolorations, some areas only weakly stained by Phloroglucin-HCl

Table 3 cont.

Stage of decay	Bark	Outer wood cylinder of trunk	
5	Same as 4	Log broken into pieces, completely rotten	Wood structure totally destroyed, Phloroglucin-HCl negative.

Table 4

Stages of decay in relation to state of twigs, roots and log surface

Stage of decay	Twigs	Root	Material accumulated on log surface
1	All twigs present, smaller twigs sometimes with attached needles	Uprooted soil as "root plate" (Sernander, 1936) present	No material
2	Smallest twigs broken	Soil of the outer parts of the "root plate" gone	Needles and other organic material in cracks and depressions on outer surface
3	Most twigs without bark, smaller twigs broken off	All uplifted soil eroded, smaller roots broken off or decomposed	Needles and other organic fractions (bud scales, small twigs, leaves, etc.) cover the log
4	Only bases of the bigger twigs left	Thicker parts of the main root system left	Same as 3
5	No twigs left	Rarely hardwood core left at main root base	As 3 but with decayed layer of humus-like material

Hydrogen ions are exchanged on the particles and result in a generally lower pH. The suspension effect is not observed by this method and the KCl-pH is, therefore, considered in soil science a reproducible value largely independent of seasonal changes (Schlichting et al., 1966).

Among the ecological factors of the cryptogam substrate, the pH of the outer wood cylinder is usually considered to have good indicator value (Brodo, 1973).

To determine the pH, wood samples were collected from the upper part of logs. The thickness of each wood sample was one to three mm; however, when a log was covered by humus the sample could be as thick as six mm. This material was kept in sterile bags. For all these procedures, material was ground to very fine particles and the fluid/solid ratio was kept approximately 1:1 by volume. With this ratio the suspension was generally found to have a pasty consistency. All pH measurements were done with an Ingold glass electrode. Other electrode types failed to yield reproducible results. Standardizations were done with test buffers over the measured range before, during (in some cases) and after the measurements. The material was kept for 12 hours in suspension and was stirred carefully three to four times.

(i) Effect of particle size:

When measuring the hydrogen ion activity the type of bark-water suspension can modify the pH to a certain degree (Culberson, 1955). Therefore, it was decided to investigate the effect of particle sizes of decayed wood on the hydrogen ion activity of the wood-water mixture.

Birch wood homogeneously decayed (decay stage 3) from Petawawa was exposed to different grinding methods which yielded five sets of samples of different sizes. After the pH had been measured, the samples were dried and the actual size of fifty randomly selected particles per set were measured.

All samples investigated had the same volume. To make sure that possible effects of different particle sizes on the glass electrode were not masked by other factors (e.g. differential separation of particles of certain sizes) the N-KCl method was tried together with the water suspension method (Steubing, 1965).

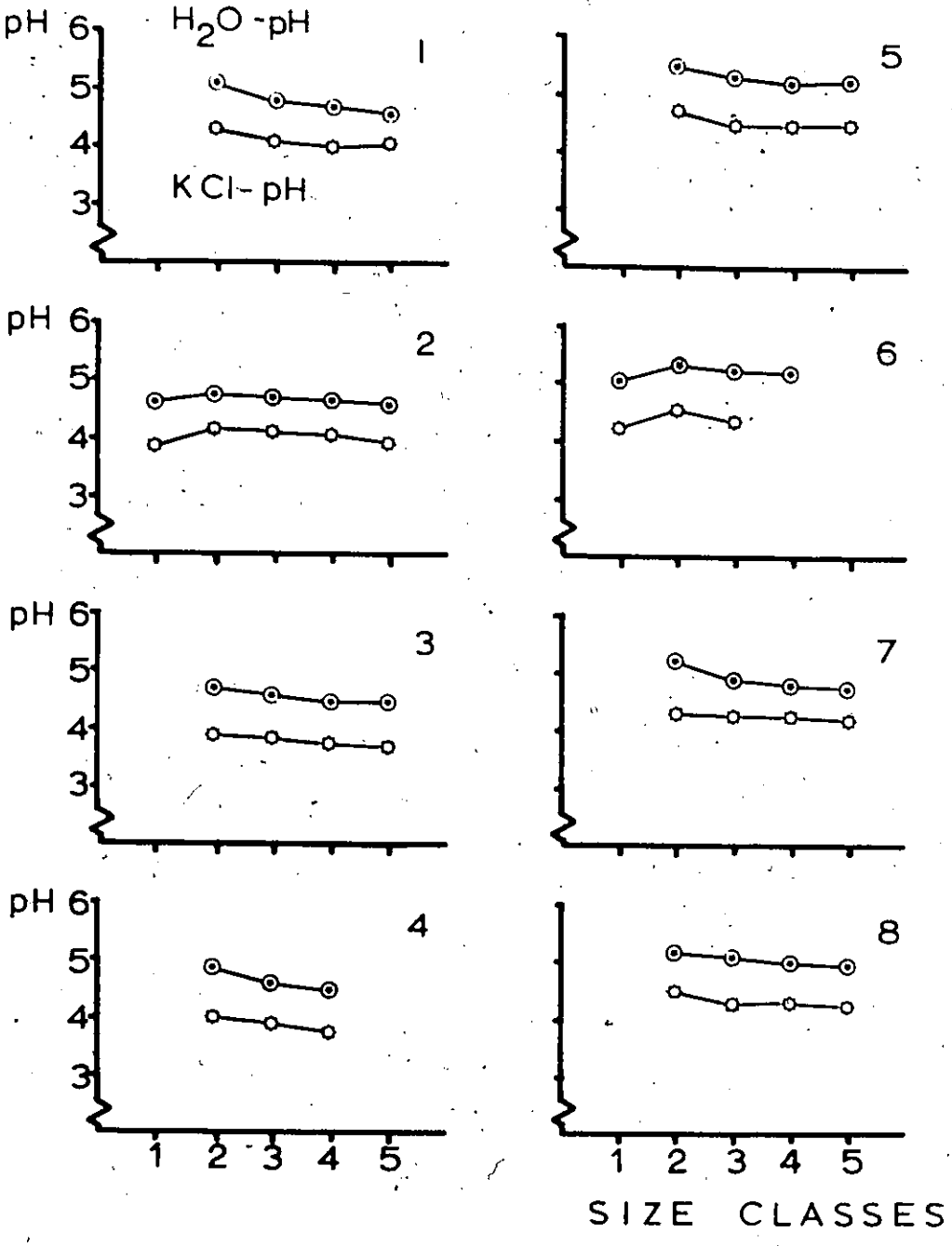
In Fig. 9 data are presented for eight samples (1-8, in Fig. 9) which were ground into five size classes. Means of the antilogs of the pH values of these eight samples were not calculated since this procedure would assume that the hydrogen ion activity is comparable (Rypacek, 1966). Hydrogen ion concentration of wood suspended in water and pH of wood suspended in N-KCl are shown with different symbols. It is a consistent observation that from size classes 2 to 5, the pH decreases. Wood pieces in size class 1, obtained only for two samples, yielded a lower pH than those of size class 2.

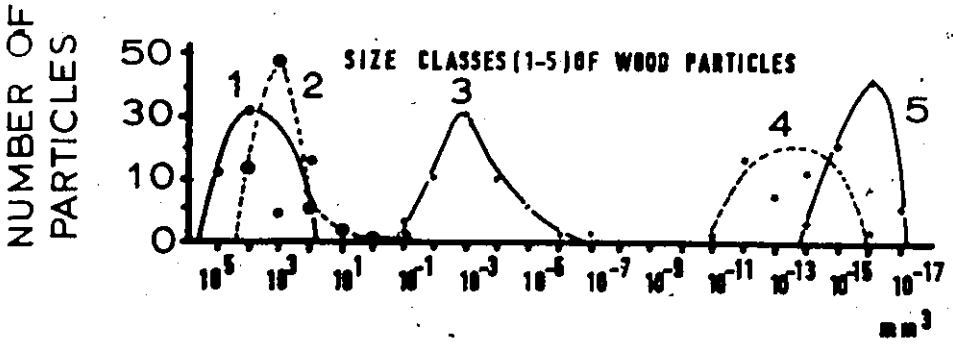
In the following experiments dealing with the effects of site and season, all wood was ground to size classes 4 to 5. The same procedure was repeated for wood sampled in the Petawawa plot.

(ii) Effect of site on the log:

Since the log substrate may be either chemically homo-

Figure 9. Effects of different size classes on H_2O-pH and KCl-pH. Size distribution of 50 randomly selected particles given below.


pH 6
5
4
3
H_2O -pH
KCl- pH
1
2
3
4
5
6
7
8
1 2 3 4 5
SIZE CLASSES


NUMBER OF PARTICLES
50
30
10
0
SIZE CLASSES (1-5) OF WOOD PARTICLES
1
2
3
4
5
10^{5} 10^{3} 10^{1} 10^{-1} 10^{-3} 10^{-5} 10^{-7} 10^{-9} 10^{-11} 10^{-13} 10^{-15} 10^{-17}
m^3

geneous or heterogeneous as a result of microbial activity, a sampling study was necessary. Variation in pH measurements is possible in space and/or in time. Therefore a log from Kingsmere in the Gatineau Park was studied with respect to spatial variation in pH from a number of samples scattered evenly over the whole log and kept separate in sterilized plastic bags. In the lab these individual samples

1 2 3 4 5 6 7 8

were partitioned in the following manner:

1: $x_{11}\ x_{12}\ x_{13}\ x_{14}\ x_{15}\ x_{16}\ x_{17}\ x_{18}$

2: $x_{21}\ x_{22}\ x_{23}\ x_{24}\ x_{25}\ x_{26}\ x_{27}\ x_{28}$

3: $x_{31}\ x_{32}\ x_{33}\ x_{34}\ x_{35}\ x_{36}\ x_{37}\ x_{38}$

4: $x_{41}\ x_{42}\ x_{43}\ x_{44}\ x_{45}\ x_{46}\ x_{47}\ x_{48}$

5: $x_{51}\ x_{52}\ x_{53}\ x_{54}\ x_{55}\ x_{56}\ x_{57}\ x_{58}$

6: $x_{61}\ x_{62}\ x_{63}\ x_{64}\ x_{65}\ x_{66}\ x_{67}\ x_{68}$

7: $x_{71}\ x_{72}\ x_{73}\ x_{74}\ x_{75}\ x_{76}\ x_{77}\ x_{78}$

8: $x_{81}\ x_{82}\ x_{83}\ x_{84}\ x_{85}\ x_{86}\ x_{87}\ x_{88}$

Then they were recombined in a sequential manner leaving the first column ($x_{11}\ x_{21}\ x_{31}\ \cdots\ x_{81}$) subsamples unmixed. The sample indicated as x_{11} is illustrated in Fig. 10 by a large symbol, whereas the other samples in the first column are represented by small dots. For the second column, the large symbol in Fig. 10 stands for the combination of $x_{12} + x_{22}$; the rest of the subsamples in that column were measured separate and are indicated with small dots in Fig. 10. In

the third column the subsamples $x_{13} + x_{23} + x_{33}$ were recombined leaving the other five subsamples uncombined. The procedure was repeated up to the last column starting with x_{18} where all subsamples were recombined.

In Fig. 10 the data for two sets of experiments are shown. In the upper part of this Figure, only the recombined subsamples are pictured.

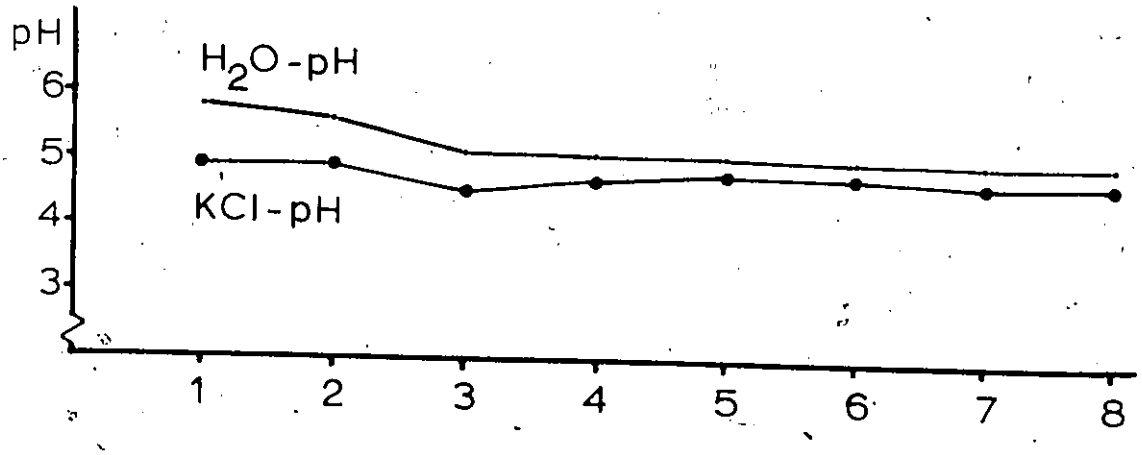
The approach followed, explained on the previous page, is sequential in nature. Therefore, in a strict sense, no combined sample for sample number one exists; it was nevertheless indicated as a big dot in the lower part of Fig. 10 since it was, in all other respects, comparable to the combined samples. Since for all subsamples and combined samples a separate measurement of material was prepared in the same fashion, one could formulate the hypothesis that with the decreasing importance of a local part of a sample the pH approaches asymtotically a certain value. It is evident that from sample number 6 on, the big dots show only little deviation from a pH of 6.3. Similar data for different wood are found in the upper part of Fig. 10 . From sample number 4 on, the pH values measured in H_2O as well as in N-KCl change only slightly.

(iii) Seasonal changes of pH on a log:

Seasonal changes in pH (H_2O) values in soils are well documented (Ellenberg, 1950). Very little is known, however, of their effects in the field on cryptogams in general, as well as on changes in the outer wood cylinder of the log. In

Figure 10. Cumulative H_2O-pH and KCl-pH (above) and comparison of H_2O-pH of sequentially combined samples below (big dots, except number one for reasons given on p. 51) versus subsamples (small dots).

CUMULATIVE pH



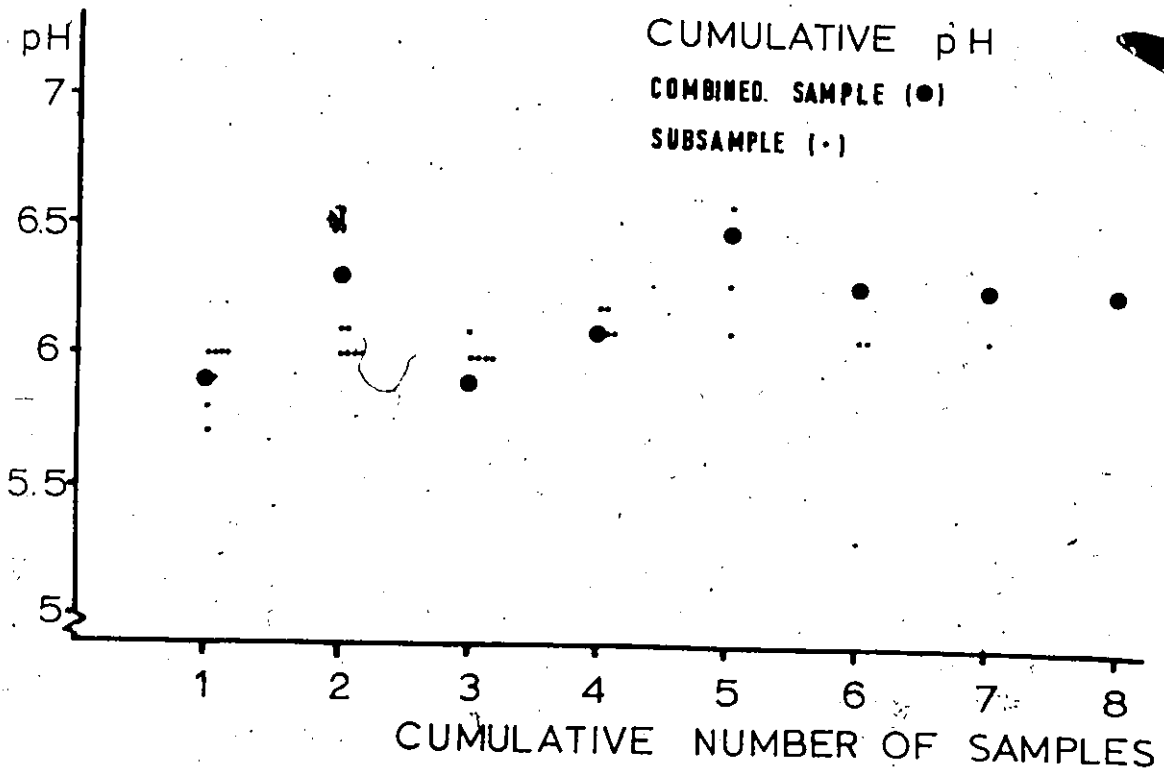


Fig. 11 the change of pH on a log during one summer is given. It is obvious that in certain parts of this particular pine log little fluctuation can be observed, whereas in other parts the pH changes seem to be more pronounced. In those instances where the curves representing H_2O-pH and KCl-pH are not parallel, the samples were probably not identical due to phloem remnants with mining beetles and larvae in it left here and there on the log after the bark had broken off. After the second sampling in the field, the phloem effect was recognized and compensated for through appropriate sampling. Even when the above-mentioned restriction was taken into consideration, it is probable that some of the pH changes were affected by hydrological factors of the substrate.

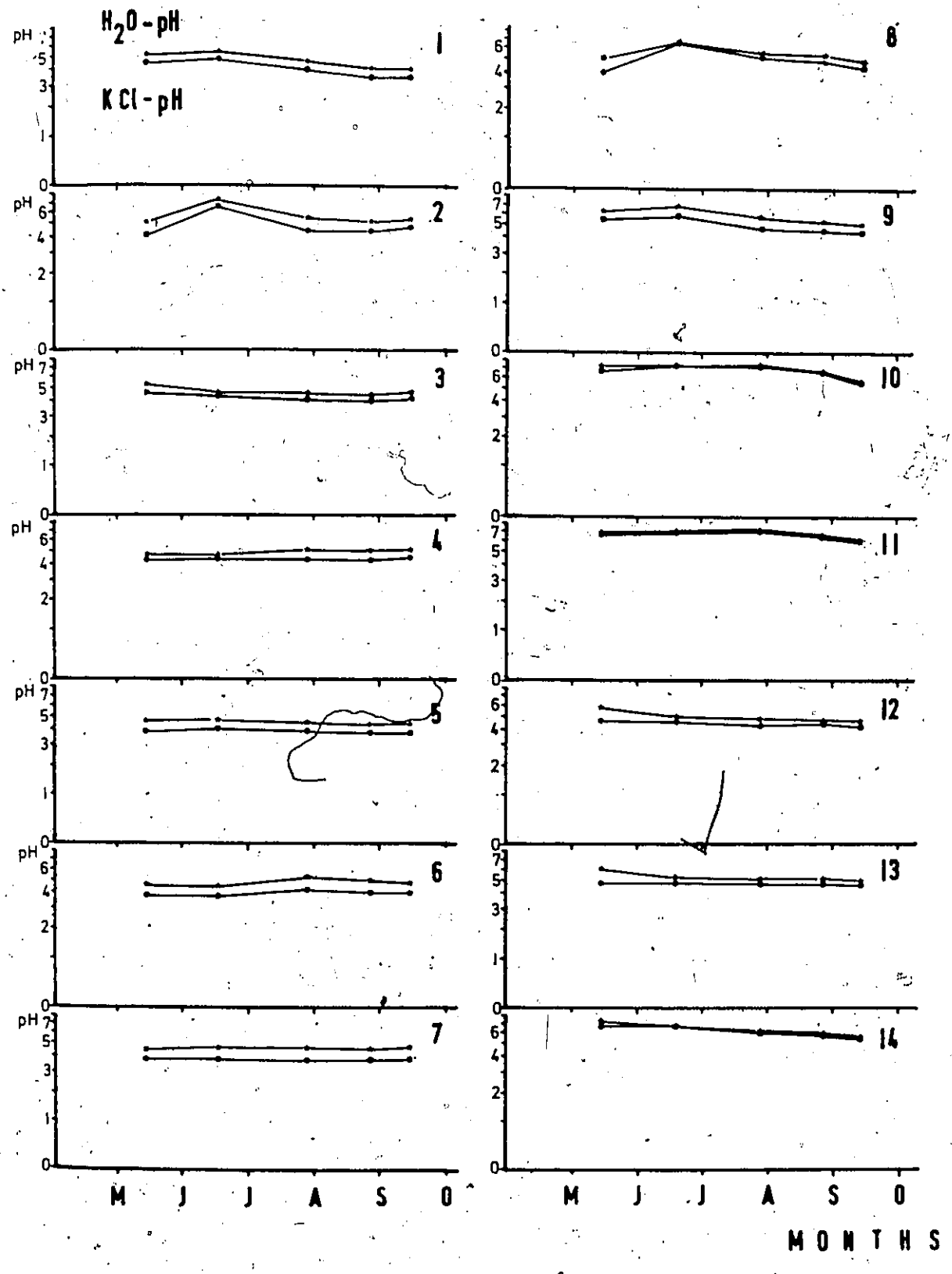
The sampling studies in relation to pH suggest that a representative pH measurement exists for a certain log. Seasonal variations, although important when pH samples are taken at different times, are of little importance for logs present in dry and mesic sites.

f) Ecological diversity:

Ecological diversity as defined by Pielou (1969) relates both the number of species present in a certain sample and the manner by which individuals are apportioned among species within a sample.

Within the broad concept of diversity, basically three types of indices may be distinguished. The first type is based essentially on number of species or on some other measure of species abundance (Margaleff, 1958). The second

Figure 11. Seasonal H_2O-pH and KCl-pH change on 14 positions on a single log (from Gatineau Park).


H_2O - pH
KCl - pH
pH
1
2
3
4
5
6
7
8
9
10
11
12
13
14
M J J A S O
M O N T H S

type of index requires also some measurement of species number but, in addition, one has to assume the existence of hypothetical distributions of species abundance (e.g. Williams, 1964). The third type of diversity measurements are based on formulas used in the information theory (Margaleff, 1958). It relates both number of species present in a sample and the way they are alloted among species within that sample. Pielou (1966a, 1966b, 1967, 1969) discussed the proper use of the third type indices. She recommended the use of the formula given below in cases when "a particular collection is treated as an entity to be studied for its own sake" (Pielou, 1967, p. 167). Ecological diversity was calculated according to the following formula (Pielou, 1967).

$$H = \frac{1}{N}\left[\log N\,! - \sum_{i=1}^{s} \log Ni\,!\right]$$

In this formula H stands for the diversity per individual. When the base of the logarithm in the formula is 2, H is expressed as bits of information. N is collection of individuals belonging to s species with Ni individuals in the ith species $\left[i = 1, 2, 3, \ldots, s\ ;\ \sum_{i=1}^{s} Ni = N;\ ! = \text{factorial}\right]$.

Since "species diversity" is a rather ambiguous term (Hurlbert, 1971), the term ecological diversity is preferred for diversity values calculated with the above-mentioned formula. This formula is used for diversity calculations in the Petawawa section.

To be able to calculate diversity values one must deal with reasonably well distinguishable entities or countable

individuals. Since for many cryptogams the concept of an individual cannot be applied easily, a measure of relative importance (cover, biomass, etc.) is sometimes used in the calculation procedure (Whittaker, 1965).

(i) "Cover-diversity" compared with "terminal-shoot-diversity":

To the knowledge of the author no comparision has been made in the past for microquadrat sampling with respect to diversity values (number of individuals vs. degree of cover). Therefore, a sampling study was made on cryptogam communities whose members have terminal shoots distinct enough to be counted.

For this part of the diversity study a log with well developed cryptogam cover was systematically sampled with microquadrat size 1 (Fig. 3) and with cover scale 2. Then this representative part of the log was sampled, but this time the terminal shoots were counted. For both series diversity values were calculated. The counts of individual shoots were used directly in one case, whereas in the other the cover data were transformed into square centimeters based on midpoints of cover classes. Since many types of mosses do not have easily countable individuals in many cases (it is almost impossible, for morphological reasons, to trace individuals back through their dead branching systems) one has to rely on cover if diversity values are to be calculated. In some cases, however, terminal shoots are easy to distinguish and some data for such plant assemblages were collected and were used to compare diversity calculated from cover values

with diversity values based on counts of individual shoots. From Fig. 12 it is evident that the diversity values based on counts of "individuals" are lower than those calculated from cover data. Both sets, however, show a similar trend. Therefore it seems to be justified to use midpoints of cover-values for the calculation of diversity values.

(ii) Systematic vs. random sampling

For this part of the study a log was sampled with micro-quadrat size 1, first systematically and then randomly to compare these sampling modes in relation to diversity values. For this study a log with an obvious environmental discontinuity was chosen: half of the log still being covered by bark while the rest being exposed wood. For this part (ii) as well as the third (iii) a sequential calculating approach for the diversity values was followed (Pielou, 1969). Therefore, the abscissa in Fig. 13 has to be labeled "cumulative sample number". It is evident from this figure that levelling off exists for both random sampling procedure (cumulative sample number 18) and systematic sampling (cumulative sample number 9). It is, however, noteworthy, that the systematic sampling does not level off on bark in such clear fashion as it does on wood.

(iii) Microquadrat shape and cover-diversity:

To find out the effect of different quadrat shapes on the ecological information obtained through systematic sampling, the same log was resampled with microquadrat types 1 to 4. The microquadrat sample design for this study is presented in Fig. 14. The same sample design is used also in

Figure 12. Comparison of diversity values calculated from counts of individuals and from average cover (mid-points of cover classes, scale 2 in Fig. 4) for three species.

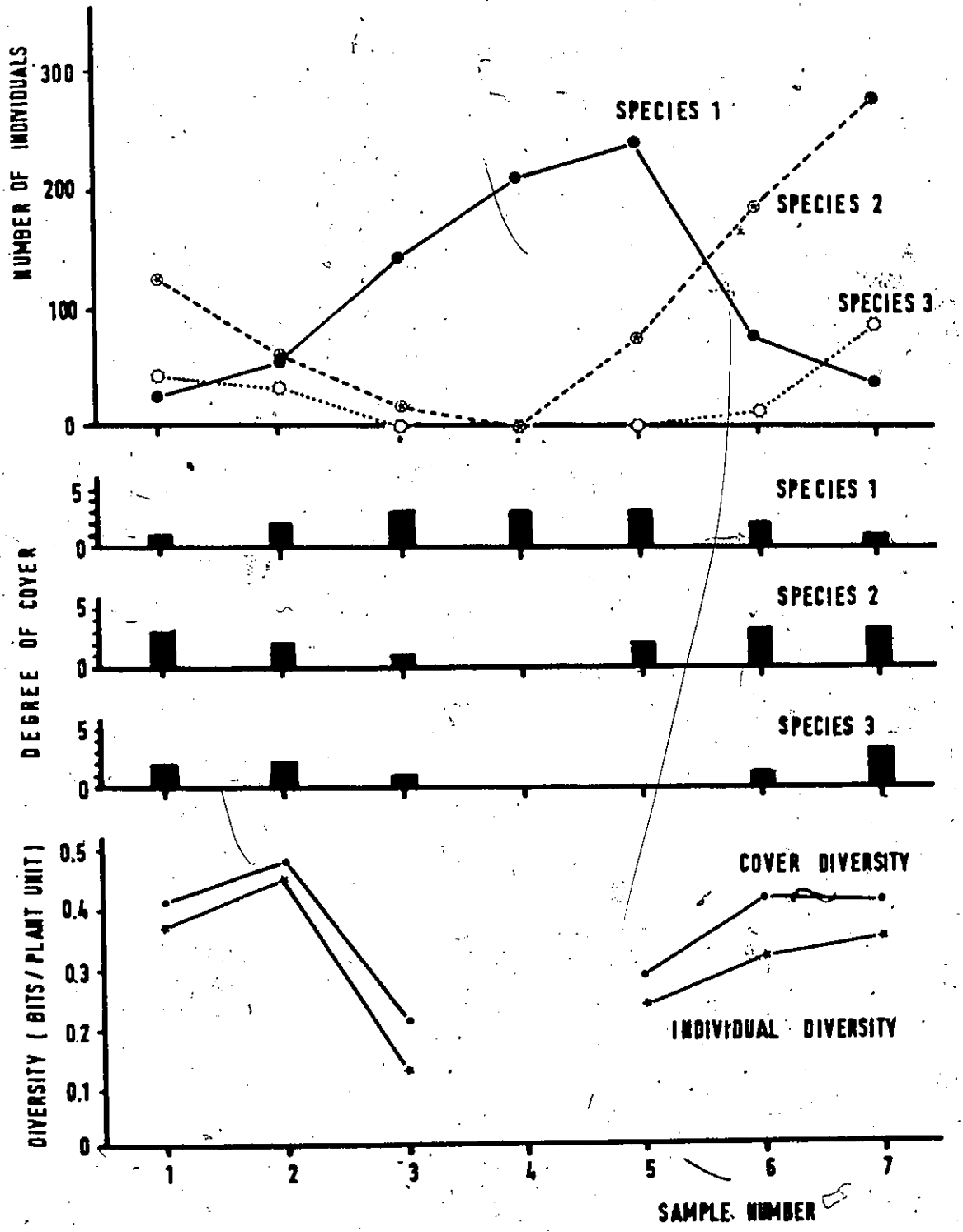

NUMBER OF INDIVIDUALS
300
200
100
0
SPECIES 1
SPECIES 2
SPECIES 3
DEGREE OF COVER
5
0
SPECIES 1
SPECIES 2
SPECIES 3
DIVERSITY (BITS / PLANT UNIT)
0.5
0.4
0.3
0.2
0.1
0
COVER DIVERSITY
INDIVIDUAL DIVERSITY
1
2
3
4
5
6
7
SAMPLE NUMBER

Figure 13. Diversity of plant assemblages on a log with a wood bark discontinuity based on systematic and random samples.

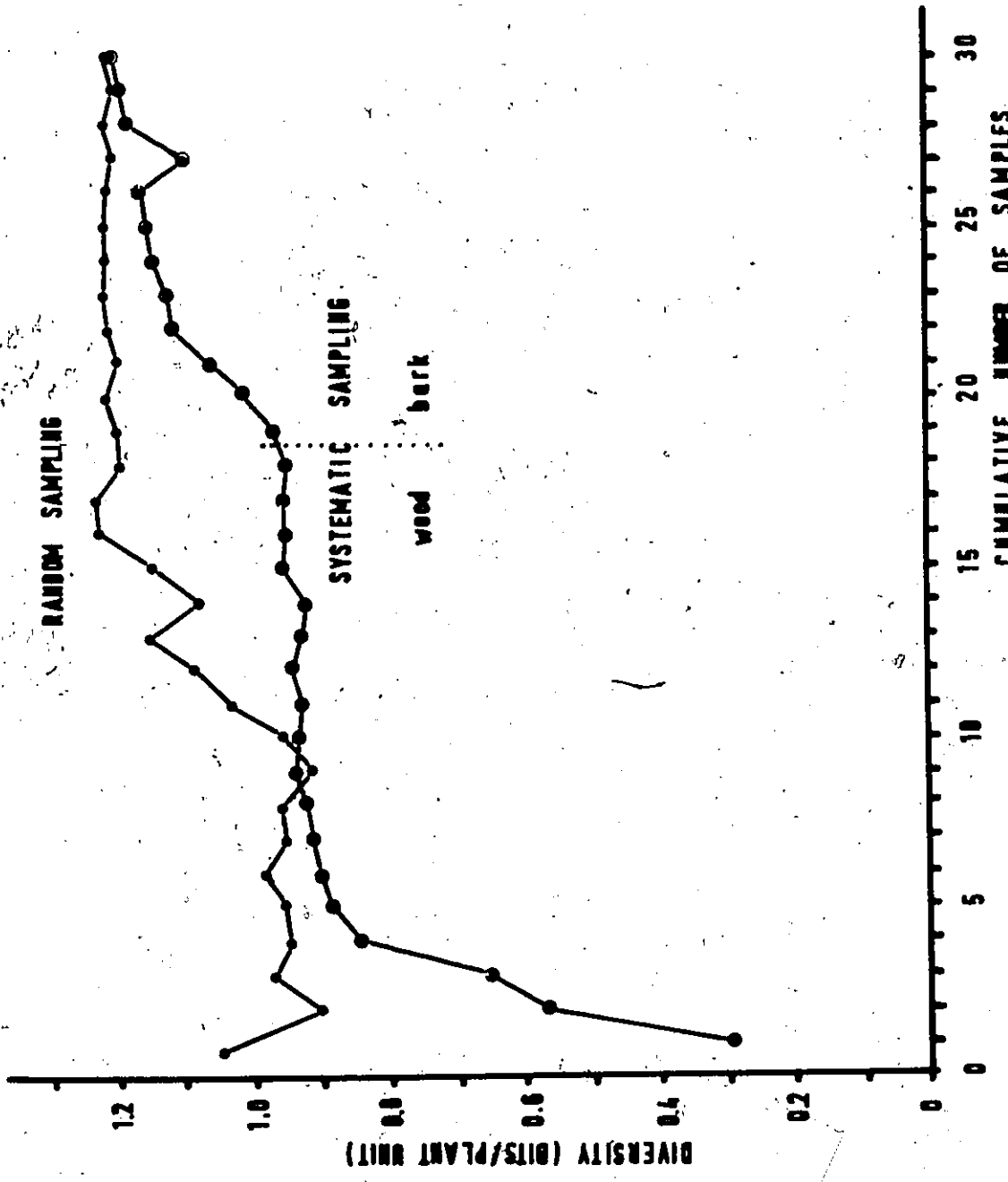
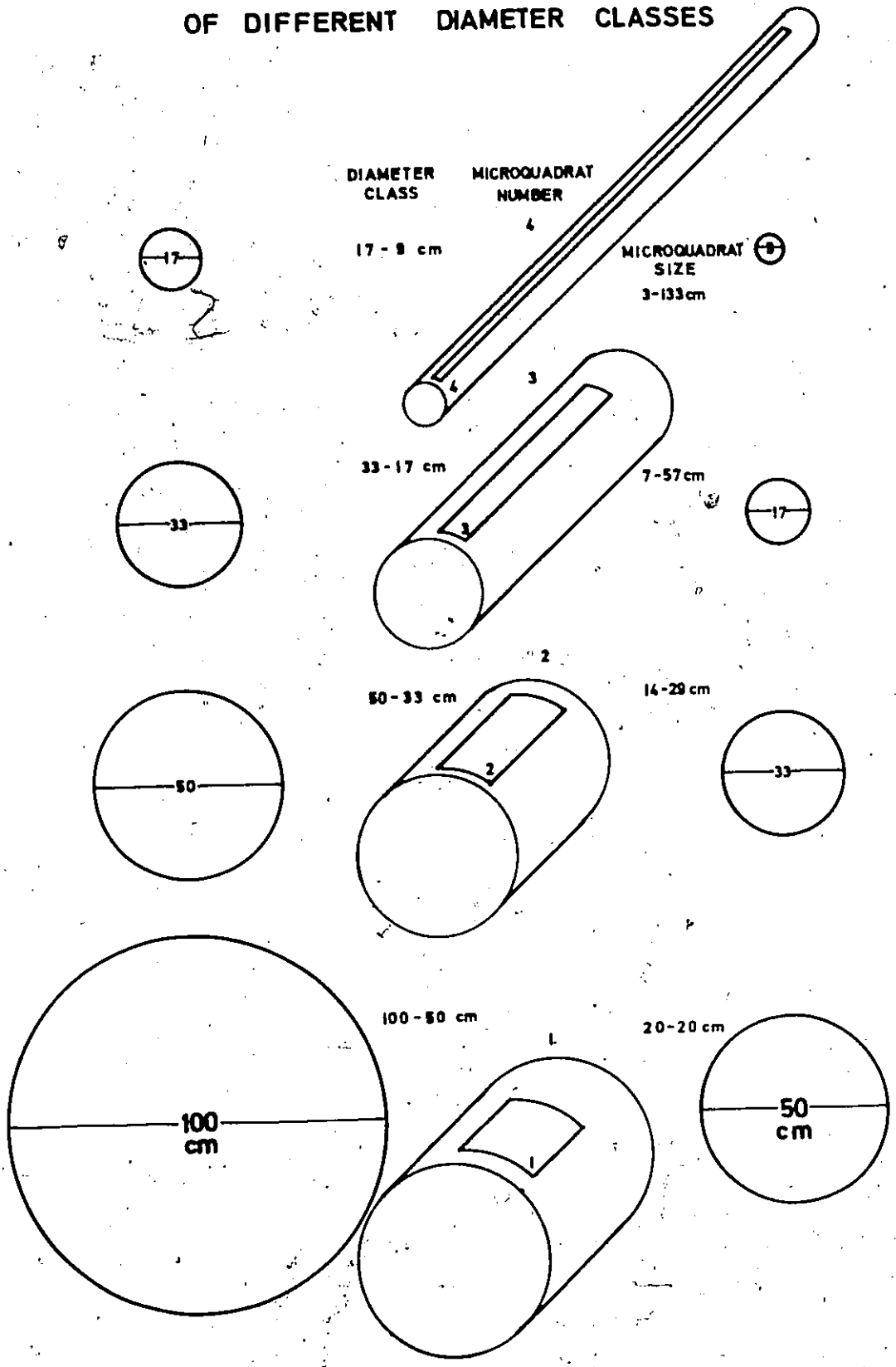

RANDOM SAMPLING
SYSTEMATIC SAMPLING
wood
bark
DIVERSITY (BITS/PLANT UNIT)
1.2
1.0
0.8
0.6
0.4
0.2
0
0
5
10
15
20
25
30
CUMULATIVE NUMBER OF SAMPLES

Figure 14. Microquadrat sample design for logs in the Petawawa area, Heney Lake and Mont Albert transect (for sample design of Mont Saint-Hilaire, see Fig. 3).

MICROQUADRAT SAMPLE DESIGN FOR LOGS OF DIFFERENT DIAMETER CLASSES



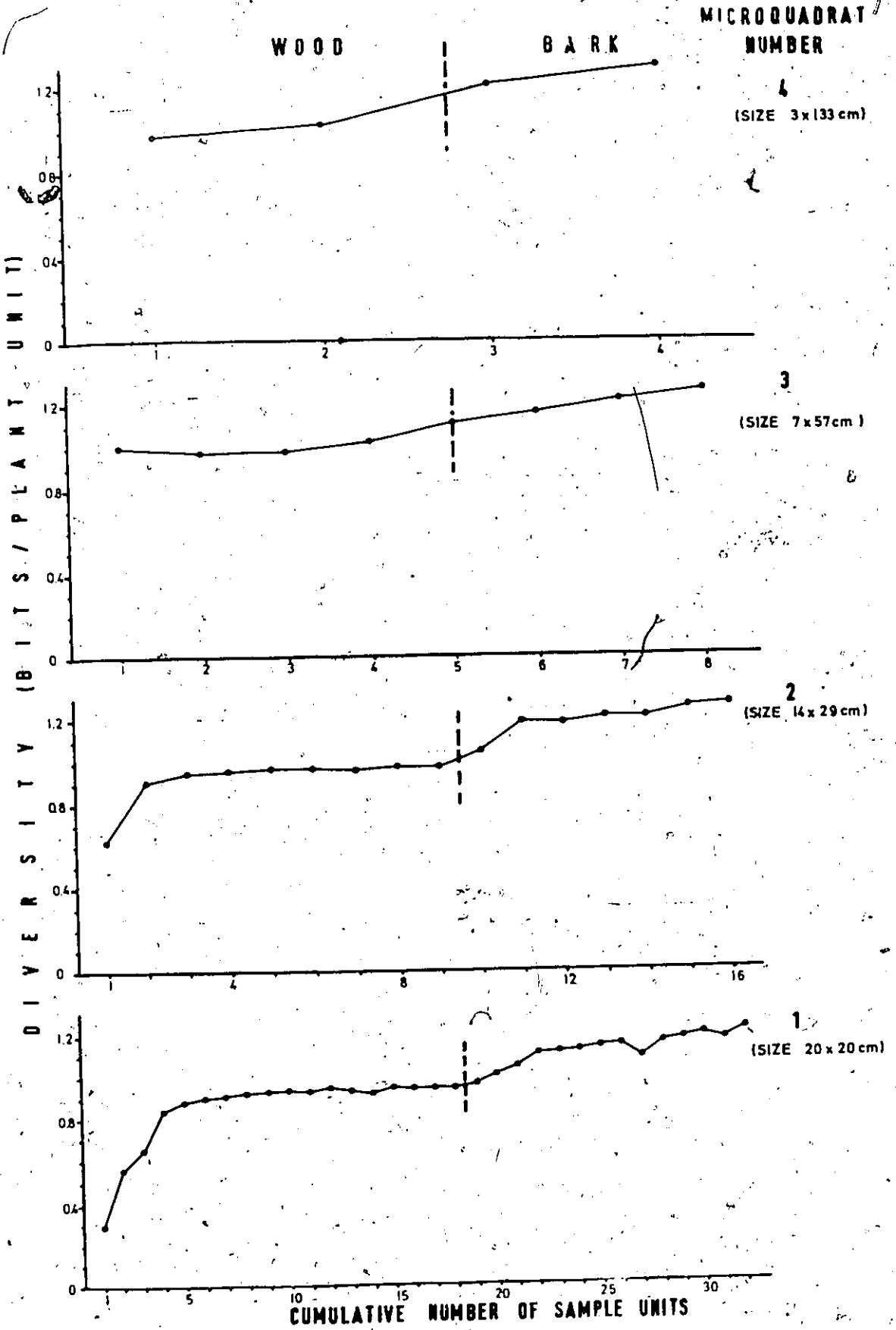
the Petawawa area, Heney Lake area and on Mont Albert. From Fig. 15 it is apparent that although a much smaller segment of the log was sampled a similar diversity value was obtained. With a more rectangular quadrat levelling off of diversity values is more difficult to demonstrate and, therefore, a less clear distinction between diversity values will be obtained from plant assemblages growing on different substrates.

It seems justified to use midpoints of cover classes for the calculation of diversity values. For a representative sequence of plant assemblages, diversity values obtained from cover estimates are similar to values based from shoot counts. When a random sampling procedure is used on a log covered with a clear mosaic of plants, more samples than usually used in systematic sampling are necessary to obtain a levelling off of cumulative diversity values. From the study of diversity values in relation to different shapes of microquadrats it is evident that the composite samples still show the presence of two distinct regions (wood vs. bark) of probably different pattern intensities. Since the absolute diversity values do not drop with increasing rectangular quadrat shapes, the microquadrat technique is rather insensitive to variations in small scale mosaics.

g) Species richness:

Hurlbert (1971) discussed "species diversity" and found the present use of the term to be ambiguous. The author, therefore, restricted himself to species richness which can be calculated easily and which represents one aspect of diversity. No attempt was made to calculate the second aspect,

Figure 15. Comparison of diversity values calculated from systematic samples of microquadrats of different shapes.


WOOD
BARK
MICROQUADRAT NUMBER
4
(SIZE 3 x 133 cm)
3
(SIZE 7 x 57 cm)
2
(SIZE 14 x 29 cm)
1
(SIZE 20 x 20 cm)
DIVERSITY (BITS/PLANT UNIT)
CUMULATIVE NUMBER OF SAMPLE UNITS

ie. the evenness or equitability component (Hill, 1973).

Species richness was calculated as number of species per quadrat (plot). In the Heney Lake and Mont Albert chapters species richness is expressed as number of species per growth-form or per major taxonomic units for logs of certain stages of decay and/or positions on the gradient.

Since species richness was calculated per unit area, it is clear from the sampling design that only Mont Saint-Hilaire and Heney Lake are strictly comparable. In those two areas the plot size was the same, whereas on Mont Albert and in the Petawawa area different plot sizes were used.

h) Degree of succession:

In succession studies authors usually survey direct vegetation changes only over relatively short time spans (e.g. Bornkamm, 1961; Brodo, 1968; Ares, 1972). When, as in the case for the Petawawa plot, a considerably longer period of time of successional change is investigated, some indication of the successional state of certain plant assemblages is necessary.

The successional stage is indicated with an index established by Numata (1969, 1970). The index is defined by Numata (1970) as:

$$DS = \frac{lf \cdot d}{n} \cdot v$$

where DS stands for degree of successions, lf is the lifespan of the constituents in years, d is a dominance measure, n is the number of sample species and v is the ground cover ratio.

This index will be used in the Petawawa chapter only

since here some information on the life span of the constituents could be obtained.

When values of this index are calculated from microquadrat data (e.g. Petawawa plot) one has to know what influence a mosaic of different successional stages within each microquadrat could have on this value. This small scale mosaic, sometimes encountered on unstable surface of logs, results in "overlap" between successional stages when a formalized microquadrat sample design is used.

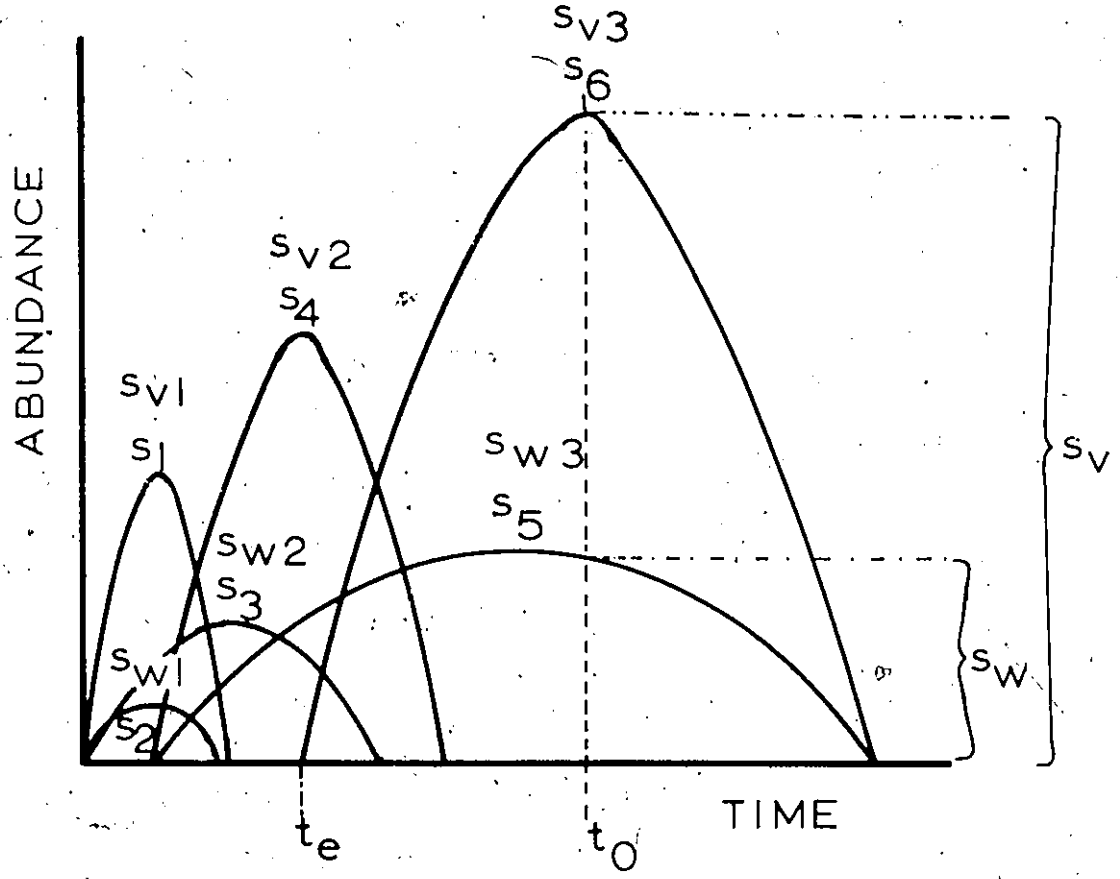
To investigate the effects of overlap on degree of succession a synthetic series of curves was created. The curves stand for individual populations and were kept in such a form that they can be described in rather simple arithmetic terms. In this "quasi-simulation" three identical series of curves were graphically composed in such a way that various degrees of overlap occur.

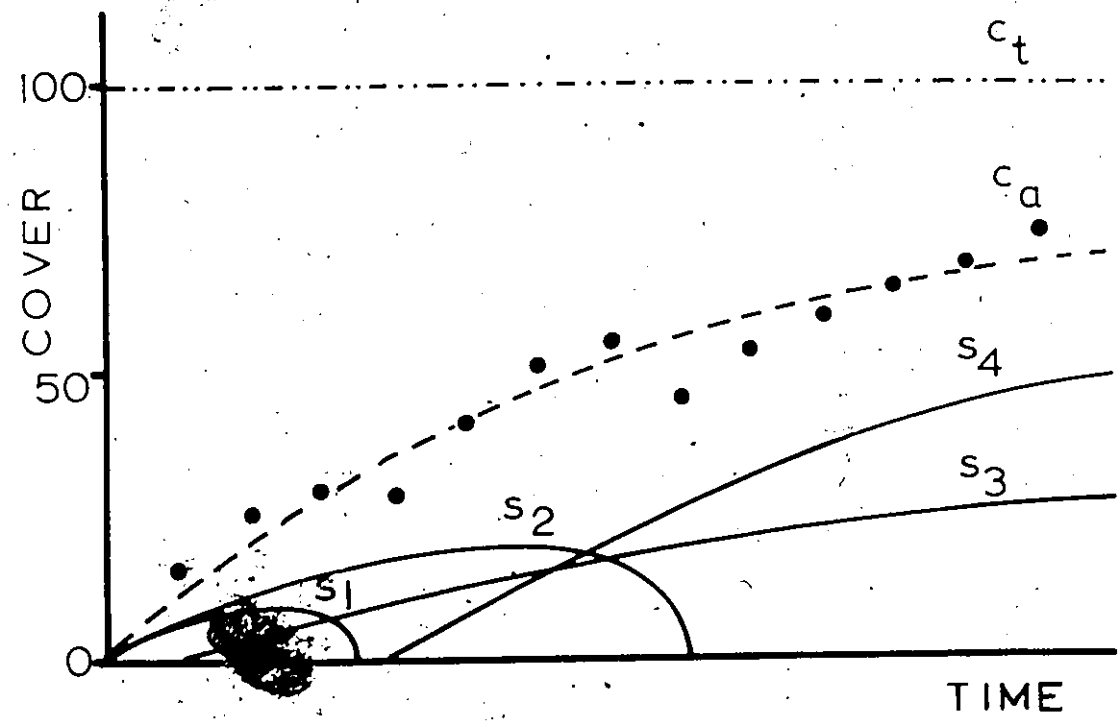
Before the data of overlap of the three series of curves standing for abundance changes of 18 populations can be presented, the formula for DS (Numata, 1970) has to be defined by the author of this thesis for the simulation study.

The formula has evidently three major components: (1) the competitional component (c) = d/n; (2) the relative openess component (ro) = v; (3) the lifespan component (ls) = lf.

(1) If there are N individuals belonging to s species and the number of individuals for the respective species are N_1 N_2 N_3 ... N_m then, under consideration of unidirectional change, abundance relations existing between populations of individuals such as in Fig. 16 may be proposed. For the sake

Figure 16. Graphic display of two synthetic succession sequences (species = s_1 s_2 s_3 s_4 s_5; vigorous species = s_{v1} s_{v2} s_{v3}; weak species = s_{w1} s_{w2} s_{w3}; t_0 = point of time of maximum abundance; t_e = time of establishment of a particular species; c_a = actual sum of cover; c_t = total possible cover).


ABUNDANCE
s_{v3}
s_6
s_{v2}
s_4
s_{v1}
s_1
s_{w3}
s_5
s_{w2}
s_3
s_{w1}
s_2
s_v
s_w
t_e
t_0
TIME


c_t
100
c_a
COVER
50
s_4
s_3
s_2
s_1
0
TIME

of simplicity symmetric sinusoid abundance curves are considered in the upper part of Fig. 16 although in nature assymmetric curves like the ones in the lower part of the same figure seem to be more common (e.g. Kellman, 1969; Odum, 1971). Out of the total $[s_1\ s_2\ s_3 \ldots s_m]$ certain vigorous species $[s_v\ s_{v1}\ s_{v2}\ s_{v3} \ldots s_{vm}]$ (e.g. $s_1\ s_4\ s_6$ in Fig. 16) may become dominant whereas other species $[s_w\ s_{w1}\ s_{w2}\ s_{w3} \ldots s_{wm}]$ are relatively "weak" (small cover producers, e.g. $s_2\ s_3\ s_5$ in Fig. 16) and remain subdominant. The competitional component (c) is, therefore, defined by the sum of the quotient $\left[c_{t_0} = \sum_{i=1}^{m} \frac{s_{vm}}{s_{wm}}\right]$ at a certain time t_0 of the successional sequence as shown in the upper part of Fig. 16.

(2) The actual area covered by all populations at a definite point of time is called c, and is defined as c_a (see lower part of Fig. 16) by the sum of a certain abundance measurement (e.g. cover) of all species encountered $\left[c_a = \sum_{i=1}^{m} s_i\right]$. Overlap of cover of two different populations which ought to be divided between the two populations in question is not considered. The total plant available space is called c_t and the relation to c_a is pictured with an example in the lower part of Fig. 16. The quotient between the two $[ro = c_t/c_a]$ is called the relative openness component.

(3) The "life span" lf of a population is defined for the sinusoid case $[lf = 2\ (t_e + t_0)]$ where $t_e = 0$ and is the point of time when the population became established and t_0 is the time point of maximum abundance (see upper part of Fig. 16 for t_e, t_0). The life span component is defined by the following quotient $\left[ls = \sum_{i=1}^{m} \frac{lf_i}{d}\right]$ where d is the number of species

at a specific point in time, lf_i are the life spans of particular s, $[s_1\ s_2\ s_3 \cdots s_m]$ occurring at a definite time in the successional sequence.

The formula for DS may, therefore, be simply expressed as DS = c · ro · ls, where c is the competitional component, ro is the relative openess component, and ls the life span component. This definition was used to calculate the values of DS from the three series (I, II, III) of identical curves standing for the cyclical development of assemblages of populations (Barkman, 1958; Moravec, 1969).

The data from the simulation study are presented in Fig. 17. The line for the changes in DS was freely fitted to the scattered points to show the main tendency. It is evident that increasing overlap of the different series gives rise to less abrupt changes in D S.

The degree of succession seems quite a suitable quantitative index when some information on the life span of the populations can be obtained. Since this was the case only in the permanent sampling plot for the Petawawa data the D S could only be applied for that plot. Secondly, it is important to note that overlap of different stages is rare. If, however, the overlap is irregular or wide, one can predict a scatter diagram without a clear tendency for a change in D S. This limits somewhat the general use of the D S in succession studies with quadrat sampling.

3. Data of organization

a) Preliminary table:

For the arrangement of the data matrix one has to keep

Figure 17. Synthetic successional sequence for demonstration of overlap between three identical series (I, II, III); the 18 sinusoid curves with a series stand for change of abundance of individual populations (e.g. Whittaker, 1970).

SERIES III
SERIES II
SERIES I
TIME
RELATIVE SPECIES-ABUNDANCE
DEGREE OF SUCCESSION

in mind that a species-relevé table is a two-way table having relevés in columns and species in rows (Table 5). A relevé is a term used within the Zürich-Montpellier tradition for a record of a sample from an area with uniform vegetation. The uniformity sometimes objectively quantified (e.g. Dahl, 1956) is, in most cases, subjectively assessed. The author used this effective field technique for the tree stratum only. The term relevé (record of a stand of vegetation) is used also for the cryptogam stratum although a quadrat sample design is not generally used in the above-mentioned field technique.

The information from all quadrats of the transects was incorporated into a preliminary table (Table 6) listing the coverage data for all microquadrats. Certain quantitative aspects (e.g. species richness, average percent cover, frequency, and average percent frequency) were summarized using this kind of table.

b) Table sorting technique:

The basic aim of the table sorting technique is to group those relevés together which have in common a particular group of species and vice versa to group those species together which are typical for certain groups of relevés. Cattell (1952) pointed out that such a data processing technique represents a simultaneous computation of Q-type analysis and of R-type analysis. The technique has been described in detail by Ellenberg (1956), Becking (1957) and critically evaluated by Moore et al. (1970). They concluded that this table sorting technique was preferable for general surveys,

TABLE 5

Two way species relevé table

M:	1	2	3	. . . . .	N	
S						
1	x_{11}	x_{21}	x_{31}	. . . . .	x_{N_1}	z_1
2	x_{12}	x_{22}	x_{32}	. . . . .	x_{N_2}	z_2
3	x_{13}	x_{23}	x_{33}	. . . . .	x_{N_3}	z_3
.	.	.	.		.	.
.	.	.	.		.	.
.	.	.	.		.	.
.	.	.	.		.	.
.	.	.	.		.	.
.	.	.	.		.	.
m	x_{1m}	x_{2m}	x_{3m}	. . . . .	x_{N_m}	z_m
						$\bar{R}$
	y_1	y_2	y_3	. . . . .	y_m	:C

S : Number of species

M : Number of microquadrat

R : Number of species per row

C : Number of species by column

TABLE 6

Preliminary table

A'	B'	A: 16	16	14	15	19	12	17	13	20	17	14	18	10	11	13	18	20	03	02
		B: 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
20	1	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x
21	2		x		x	x	x	x	x	x		x	x	x			x		x	x	
10	3	x	x	x	x	x	x		x		x			x	x			x	x		
22	4	x	x	x		x	x	x		x	x	x				x					x
11	5	x	x	x	x	x		x	x		x			x	x						
12	6	x	x	x	x	x	x	x	x		x				x						
6	7	x			x	x	x	x	x						x			x	x		
7	8	x			x	x	x		x						x			x	x		
8	9		x		x	x	x	x	x						x			x			
23	10	x	x	x	x	x				x					x					x	
2	11	x		x	x			x				x							x		x
13	12		x	x						x	x		x	x		x					
14	13		x	x				x		x	x		x	x							
1	14	x			x			x				x							x		x
3	15	x						x				x							x		x
4	16	x			x							x		x					x		
9	17	x			x	x	x		x											x	
15	18			x						x	x				x	x	x				
16	19		x	x						x	x		x				x				
24	20		x	x			x					x					x		x		
26	21		x				x					x					x		x		
18	22			x						x			x				x				
5	23							x				x									
17	24						x			x			x								
19	25									x			x				x				
25	26	x	x																	x	
27	27						x		x			x									
29	28							x			x										
28	29																				
30	30								x												

A : Number of column in differentiated table

B : Number of column in preliminary table

A': Number of row in differentiated table

B': Number of row in preliminary table

especially when combined with a description of vegetation. Groenewoud (1965) in comparing certain ordination and classification techniques found that the differential species-group method, as he called the sorting technique, is quite suitable for an initial description of vegetation.

When Ellenberg's (1956) suggestions are taken into consideration, this technique can be quite efficiently used. Based on Ellenberg's (1956) description, Češka and Roemer (1971) have published all 20 steps necessary to obtain a differentiated table (Table 7).

In the light of recent suggestions in relation to data processing of similar data matrices (Austin, 1972; Lambert, 1972; Yarranton et al. 1972), it seems evident that there are certain matrices which cannot satisfactorily be handled by the above sorting technique. When "weakly structured data" (Češka and Roemer, 1971) are processed, it seems unlikely that replicate runs from the same data will yield a similar sequence in rows and columns (Lambert, 1972).

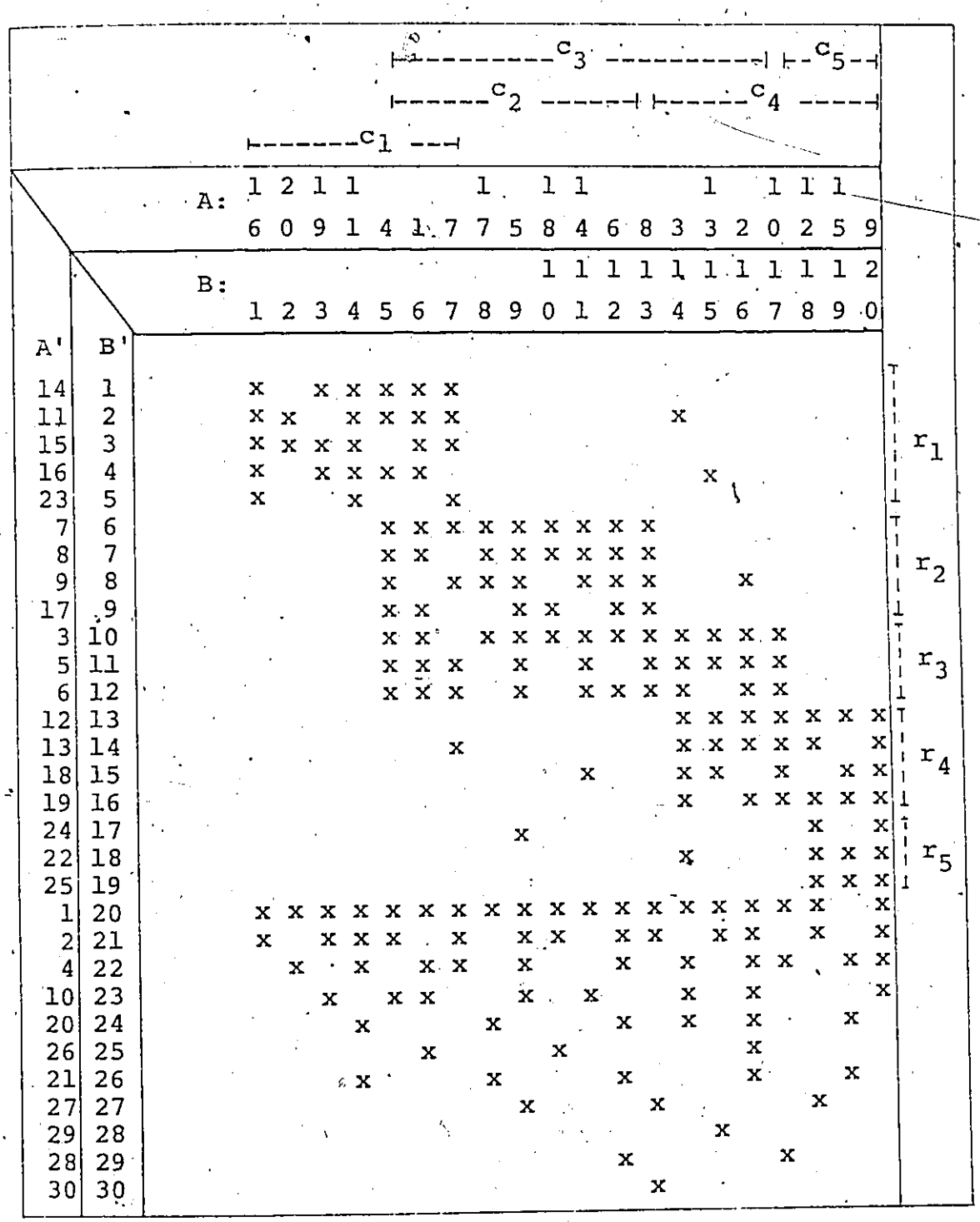
Since in this study a coenocline, a sequence of communities, was chosen, the chance of getting "weakly structured data" from transect data is rather remote. Rewriting of one of the differentiated tables resulted in nearly identical sequences in rows as well as in columns.

c) Nomenclature of groups:

When the preliminary table (Table 6) is differentiated (Table 7) certain groups are apparent. They may be called "ecological groups" (Ellenberg, 1956) when the members of

Table 7

Differentiated table



A: Number of column in preliminary table

B: Number of column in differentiated table

A': Number of row in preliminary table

B': Number of row in differentiated table

c_1 - c_5, r_1 - r_5 : Ecological groups

the groups have a similar ecological performance (Bazukis, 1969). When these differential species groups (Shimwell, 1971) originate from a table based on data from a restricted area only, as is the case in the Petawawa study, the term "phytosociological units" is preferred (e.g. Fig. 25, p. 105). If the time relationships of these units can be demonstrated, the units are called "successional groups" (e.g. Fig. 24, p. 101).

d) Data synthesis of transect data:

In the Mont Saint-Hilaire study the most frequent species were taken into account to differentiate the ecological series (Shimwell, 1971). The sporadic occurrence of rare species was not used to delineate species groups because of the dynamic state of the vegetation on logs. Therefore in the differentiated table (Fig. 29, p.121) only those species which were present in 20 percent or more of the microquadrats analyzed were included in each large quadrat (plot) along the gradient. However, species present in less than 20 percent of the microquadrats are indicated for all plots. On the basis of these presence or absence data species-relevé groups were obtained. They present major communities along an ecocline. An ecocline is in the sense of Whittaker (1970) a gradation of ecosystems along an environmental gradient of communities and the complex gradient of environmental conditions. The term coenocline is used when a sequence of communities is considered in relation to environmental gradients.

The associations based on the above-mentioned species

groups are named according to the rules of Bach et al. (1962). The author hesitates, at this stage, to present from successional data a hierarchical system of plant community classification, according to the Zürich-Montpellier tradition. When more is known about the dynamic status of certain species groups this may well be possible.

It has to be pointed out at this stage that in cases where a coenocline is selected for investigation, the columns of the preliminary table do not have to be rearranged since they represent positions on the gradient. The same is true when data for a stage of decay appear in the columns. For the data organization in the rows the term "frequency" is applied in the phytosociological sense as introduced by Raunkiaer (1913) and as used by De Vries (1949). "This method consists of a certain number of sample areas of a determined size spread as uniformly as possible over the field, the species present in the sample being recorded. Finally, it is calculated in how many per hundred of these sample plots each species is present. These figures calculated to 100 are called frequency percentages (F%)" (De Vries, 1949, p. 51). It is evident that this definition of frequency holds true for the systematically sampled transects at Heney Lake and Mont Albert. In the Mont Saint-Hilaire transect and in the Petawawa plot "frequency of a species, determined by a particular size of sample area, is the chance of finding the species within the sample area in any one trial" (Greig-Smith, 1964, p. 9). Since any species which

covered parts of a microquadrat was recorded, the correct term of this frequency value would be "coverage frequency" (Daubenmire, 1968).

Both types of frequency data may be subjected to the table sorting techniques mentioned above. In the Heney Lake Table 22, the sum of the frequencies per column and group was divided by the number of taxons within that same group. In this way a number for each of the groups was obtained. The calculation procedure for the Petawawa data left the groups intact. The frequencies per row and group of a certain taxon was divided by the number of columns. In the Heney Lake study the average percent frequency was indicated directly whereas the frequency value in the Mont Saint-Hilaire study was transformed to the following constancy classes (Shimwell, 1971):

I	:	0 - 10%	occurrence in microquadrat/plot
II	:	11 - 25%	" " " "
III	:	26 - 50%	" " " "
IV	:	51 - 75%	" " " "
V	:	76 - 100%	" " " "

The Petawawa data were also transformed into the same constancy classes. Since these frequency values represent group constancy classes they are indicated by arabic numerals.

Constancy is not used as a synthetic concept here (Daubenmire, 1968) but a step in data synthesis from a differentiated table. In the Zürich-Montpellier tradition constancy classes are based on relevés of irregular size

and form but the use of constancy classes is not restricted to records in two-way tables (Ellenberg, 1956).

For Mont Albert percent frequency is given for all microquadrats sampled on logs of certain stage of decay within one plot (quadrat). Only the thin twigs of the birches in the tundra have no microquadrat frequency since they were too small. Percent frequency in this quadrat indicates frequency per number of dead twigs.

The approach followed in the Petawawa section is basically an indirect gradient analysis (Whittaker, 1967). The gradient to be analyzed in a number of plant assemblages is time. Here the data were arranged according to the method illustrated in Tables 6 and 7 . In the Mont Saint-Hilaire, Heney Lake and Mont Albert chapters, coenoclines were investigated and, therefore, microquadrat data in the columns were arranged as an average per position on the gradient or per stage of decay. The procedure outlined in Tables 6 and 7 corresponds only to arranging the averages (e.g. average percent frequency, constancy, etc.) within the rows. One can therefore consider the approach in the above-mentioned three sections as a form of direct gradient analysis (Whittaker, 1967).

4. Taxonomy and nomenclature

An ecological study incorporating such diverse groups as bryophytes, lichens, bracket fungi and cormophytes would be impossible without the advice and help from many specialists. Besides the contribution made by the scientists mentioned in the Acknowledgements, the author learned a great

deal from Dr. H. Jahn (Polyporaceae), Dr. h.c. O. Klement (Lichenes), Dr. F. Koppe (Musci, Hepaticae), Prof. Dr. H. Gams (alpine Hepaticae and Musci) in summer courses and in communications over the years.

Cryptogams could be identified sometimes to the genus only and/or tentatively to the species. This difficulty points to the fact that in many cases cryptogams are poorly developed on a dynamically changing log substrate where impoverished plants often occur.

a) Lichens:

To deal effectively with an enormous amount of material which needed microscopic and chemical treatments, the author had to adopt a pragmatic approach. Those plants whose morphological differences are generally accepted and whose coverage could be estimated in the field were considered "operational taxonomic units" (O.T.U.) (Sokal and Sneath, 1967; Vandermeer, 1972). When a subsequent laboratory determination revealed that the collected material represented more than one species, the percent cover originally estimated was divided equally among the species present. In those cases where that could not be done, the collected material was placed in a broad taxonomic category (e.g. *Cladonia chlorophaea* s.l.). One has to be aware that in ecological studies certain intrinsic taxonomic errors are sometimes unavoidable especially when dealing with problems such as squamulose modifications of *Cladonia* species or with sterile crustose forms. From the ecological point of view

the author would favor creating a special taxonomic category for those forms (Lichenes imperfecte cogniti). Such a tradition is often observed in the field of mycology (e.g. Gäumann, 1964).

The author used certain chemical techniques for lichen identification (Hale, 1967). Spot tests with KOH (15%) and Steiner's (1955) PD-reagent used directly on the specimen in the field were very helpful.

In the laboratory the following tests were applied:

(1) PD as an alcoholic solution of p-phenylene diamine was always prepared prior to use; this solution is specific for aldehyde groups on both depsides and depsidones.

(2) A 15% solution was used for the K test; this solution is generally less specific for the same substances that react as PD+ and sometimes the test is indecisive (Hale, 1967).

(3) For the C test a freshly prepared calcium hypoclorite solution was used; the test is positive for lichen acids which have a m-hydroxy configuration.

(4) Application of the above-mentioned KOH solution followed by the application of calcium hypoclorite is called the KC test; the test is positive for some orcinol depsidones (Hale, 1967).

(5) The filter paper technique of Santesson (1967) was used for extraction of lichen substances. A thallus fragment was placed on a Whatman filter paper No. 1 and the substances were extracted from the lichen with acetone which was added slowly in order for a zone of substance to be eluted in a

circle around the fragments. The detection of color is easy and accurate when using this method.

(6) Microcrystal tests were performed only in a few cases. The test, for example, with G.A.o -T.* for atranorin or for norstictic acid was especially useful. In some cases the author had problems with microcrystal tests with material which evidently contained more than one lichen substance. Since these problem specimens formed less than one percent of the collected cryptogamic material, the author did not apply the TLC techniques (Culberson, 1972).

The reliability of the reagents were checked in some cases on lichens of known chemical composition (e.g. *Lecidea scalaris*, C+). All chemicals were added with disposable micropipettes on thallus fragments removed from the packet and placed on a slide. The color change was observed under the dissecting microscope. Sometimes the color change on the thallus fragments were difficult to demonstrate. Therefore, the above-mentioned chemicals were applied to extracts of lichen substances.

For the nomenclature of lichens the list by Hale and Culberson (1970) was followed except in the case of the genus *Cladonia* for which Thomson's (1967) treatment was adopted.

b) Fungi:

It was decided to investigate fromthe wood-decaying fungi only the sporophores of the Polyporaceae except the resupinate species (Poria, sensu Lowe, 1966).

Observations of specimens were made on thin sections cut

* glycerin - alcohol-o-toluidine, 2:2:1 by volume.

freehand with a razor blade and mounted in 95% alcohol. Then a two percent KOH solution was applied to the material to swell it to the size on which taxonomic descriptions are generally based (e.g. Overholts, 1967). The generic concept followed is that of Donk (1933). Since this monograph does not give all specific names encountered in the present study, Smith's (in Overholts, 1967) and Jahn's (1963) lists were adopted. In cases where synonyms were ambiguous, Overholts' (1967) names were retained.

c) Algae:

Algae on logs were frequently encountered in the wetter sites of Mont Saint-Hilaire. They are not treated in this thesis since a majority of forms could be identified only tentatively. These plants seem, however, to have ecological importance in wet and mesic sites where they can interact with moss protonemata.

d) Mosses:

For the nomenclature of mosses the list by Crum, Steere and Anderson (1973) was followed. For the species concept within the *Mniaceae*, Koponen's (1968a, 1968b, 1971a, 1971b) and Iwatsuki's et al. (1972) views were adopted. *Rhizomnium appalachiensis* to be published soon by Koponen was accepted since the author was able to distinguish it from *Rhizomnium punctatum* s.str. Koponen's (1971c) view on *Rhythidiadelphus calvescens* was also adopted. Ireland's (1969) monograph on *Plagiothecium* was used with the nomenclatural changes suggested by Iwatsuki (1970). The changes in generic names as a

result of Smith's (1971) revision of the *Polytrichaceae* were adopted.

Attempts were made to identify taxonomic forms of mosses which differ from typical plants in their asexual diaspore production and, in most cases, were named in the tradition of Mönkemeyer (1927). This differentiation of forms is especially important for analysis of diaspore production strategies of moss populations growing along certain resource gradients (Whittaker, 1972).

e) Hepatics:

For the liverworts, Schuster's nomenclature (1966, 1969) was followed. For those taxa not yet covered by Schuster's flora, Müller's (1951-58) nomenclature was used. Grolle's (1965) views on *Harpanthus* were accepted and Williams' (1969) provisional list of Gaspé hepatics was consulted.

d) Cormophytes:

For the vascular plants the Flore Laurentienne by Frère Marie-Victorin (1964) was followed. In the section on Mont Albert, Scoggan's (1950) flora was used and the nomenclature adopted. Dansereau and Raymond's (1948) paper was consulted for names of certain forms.

When the determination of a log to the genus level was not possible in the field, a relatively undecayed wood sample was collected and identified in the laboratory with the help of keys provided by Hale (1952) and Tsoumis (1968). When wood with a relatively intact structure could not be found, a piece of the decayed material was collected. In

the laboratory this was macerated (Nultsch and Grahle, 1968) so that its coniferous or deciduous nature could be determined.

CHAPTER III

RESULTS

The results in this chapter are presented in four sections.

Section 1 deals with Petawawa. Because of the existance of a unique historical record, it was possible to investigate this area with various quantitative methods. The "successional state" will be indicated as degrees of succession and the diversity relationships that exist between individual populations will be expressed for plant assemblages on logs of certain stages of decay. Changes in the plant component on logs with progress of decay will be analyzed by the application of the Raunkiaerian life-form system. Results of an investigation of pH-values of the outer wood cylinder in particular stages of decay will also be analyzed.

In Section 2, dealing with Mont Saint-Hilaire, the author will show how some plant communities vary on logs along a coenocline in the Northern Hardwood Region. This section will also contain a study on growth-forms and their relative importance over the investigated transect as well as their relation to particular stages of decay.

In the third Section results of a study of a gradient analysis of communities at Heney Lake will be presented and changes in species richness per growth-form will be analyzed.

Finally, Section 4 will yield results of a study made in the boreal forests of Mont Albert, Gaspé, where changes of plant assemblages on logs along a coenocline, from an alpine

tundra to a boreal forest, have been investigated.

1. Petawawa

The aim of this section is a detailed account of plant succession on decaying logs. The unique historical record available at Petawawa permits a quantitative approach to succession. Therefore the concepts of degree of succession (Numata, 1969; 1970) and of ecological diversity (Pielou, 1969) will be applied to the vegetational change of plants on decaying logs. Plant associations in the Zürich-Montpellier tradition (Shimwell, 1971) will not be distinguished in this chapter. The floristic inventory of this plot, however, corresponds in a wide sense to that of the *Cladonio-Ptilietum* described in the Mont Saint-Hilaire chapter (see page 121).

a) Stand history and description:

In 1916, the former Dominion Forestry Branch initiated forestry research around Petawawa. A permanent research station was founded and permanent sampling plots were established (Howe, 1926). In 1926 permanent sampling plots(P.S.P. 2) was mapped to show the location of all those trees having a diameter at breast height (d.b.h.) greater than 1.27 cm. Every 5 years (10 for 1946 to 1956) the plot was re-examined and all dead trees were recorded. New individuals established after 1926 were listed but not mapped for this plot. When the plot was young, natural thinning took place. Death exceeded ingrowth and the initial high stem densities of the trees which had colonized the burnt-over land were reduced.

Table 8 provided by the Petawawa Forest Experiment Station shows some silvicultural characteristics of the plot examined.

In 1959 white pine (*Pinus strobus*) accounted for 67% of the basal area of the trees in P.S.P. 2 while red pine (*Pinus resinosa*) was codominant with 26%. The remaining 7% included white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), large-tooth aspen (*Populus grandidentata*), red maple (*Acer rubrum*), canoe birch (*Betula papyrifera*) and beech (*Fagus grandifolia*).

The forest site type of the area was described by Ilvessalo (1929) as a *Vaccinium-Gaultheria-type*. This is similar to the *Oryzopsis-Maianthemum-type* of Kujala (1945). The following description is from the observations of J. Fraser (Sept. 1950) provided by the Petawawa Forest Experiment Station. "The plot is on general, somewhat irregular northwest slope, and is supposed to be a mai.-cor. site-type.* However the western end of the plot must be on a different site-type as shown by the soil data. It is more moist, but the difference doesn't appear in the main stand growth. The lack of vegetation on the N-eastern part of the plot is outstanding and is due in part to the density of crown cover. The high shrub layer is patchy; the hazel occur in patches, apparently where natural openings have occurred in the canopy, and under this *Corylus* the reproduction is scarcer than usual (Author's note: cover of hazel

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* mai.-cor. site-type: *Maianthemum - Corylus site-type*

Table 8

Per hectare data of trees (8.9 cm d.b.h. or larger) of permanent sampling plot no. 2 (P.S.P. 2, species listed on p. 86, based on per acre data)

Year and item	Number of stems	Basal area m^2	Average d.b.h. cm	Total volume m^3
1926	1,787	40.10	42.00	263.2
1959	830	47.34	66.47	475.2
Total yield		47.34		475.2
Mortality	974	16.95	37.07	123.1
Average annual mortality		0.49		3.7
Increment 1926-59		6.62		212.0
Total wood production		64.30		598.2

was nearly continuous in 1970). The main 'noticeable' reproduction is Mr**, which averages about 2' in height. However Pw** is more numerous, but very small, suppressed, and growing poorly. The number of Pw indicated reasonable germination, but its size indicates anything but good survival beyond 3-5 years".

b) Distribution of logs:

The distribution of logs as they occurred in 1967 - corrected in 1970 - is shown in Fig. 18. Since 1967 a few additional logs moved to the forest floor. These new logs are pictured in Fig. 19. It is evident that a forest has a definite rate of log deposition. Not only a "birth rate" but also a "death rate" for logs could be observed. In 1970 some logs were completely rotten although they were detectable in 1967. In some cases however a few traces of wood could still be located.

A certain clustering of logs occurred in the southern and northern corner. The middle part of the plot did not yield such high amounts of dead wood material.

The location of standing dead trees, stumps and logs that were sampled is shown in Fig. 20.

On some of the big stumps, charcoal was encountered presumably left by the fire that had destroyed these forests at the end of the last century. This shows also that decay-resistant white pine stumps can persist more than 70 years in a stand.

** (Mr = *Acer rubrum*; Pw = *Pinus strobus*;)

Figure 18. Location of logs and trees in 1967 (corrected in 1970).

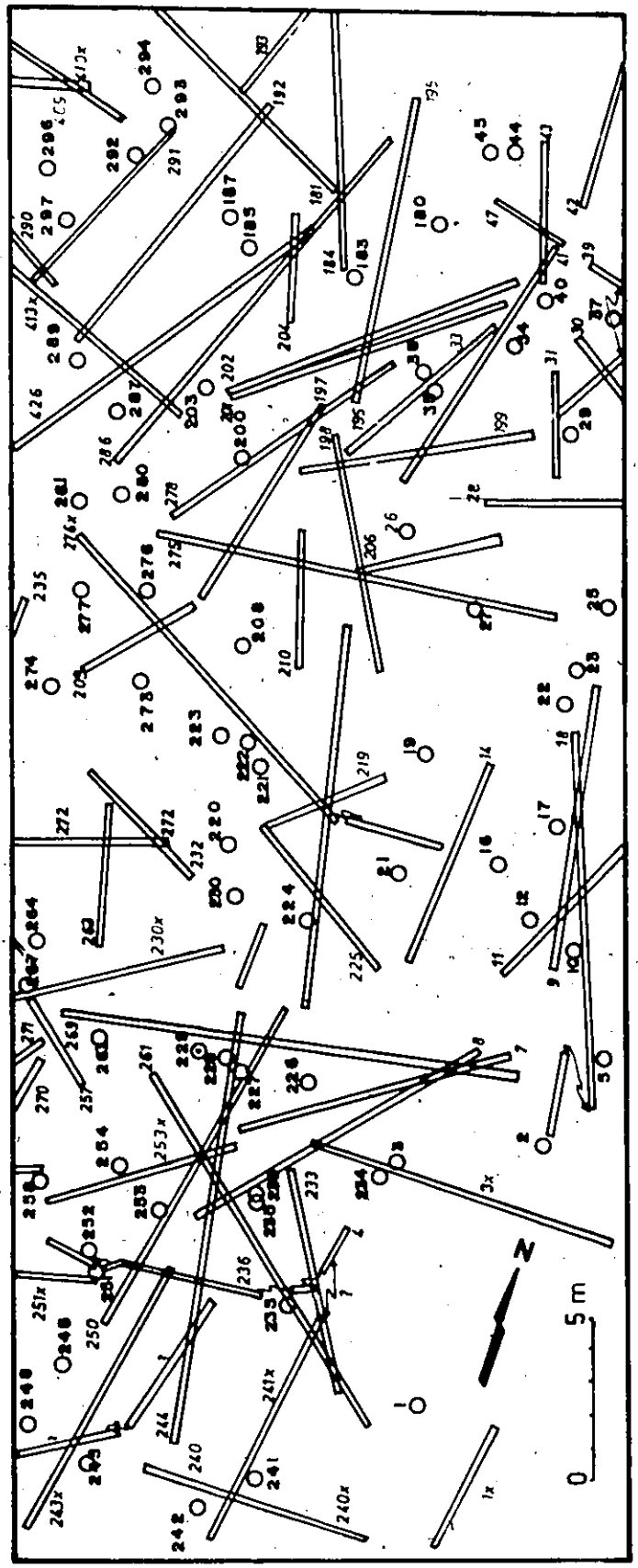

LOCATION OF LOGS AND TREES IN 1967 (CORRECTED 1970)
N
0
5m

Figure 19. Location of stumps and logs which were deposited between 1967-1970 or otherwise changed from 1967 to 1970.

LOCATION OF STUMPS(○) AND NEW(1967-70) OR OTHERWISE CHANGED LOGS IN 1970

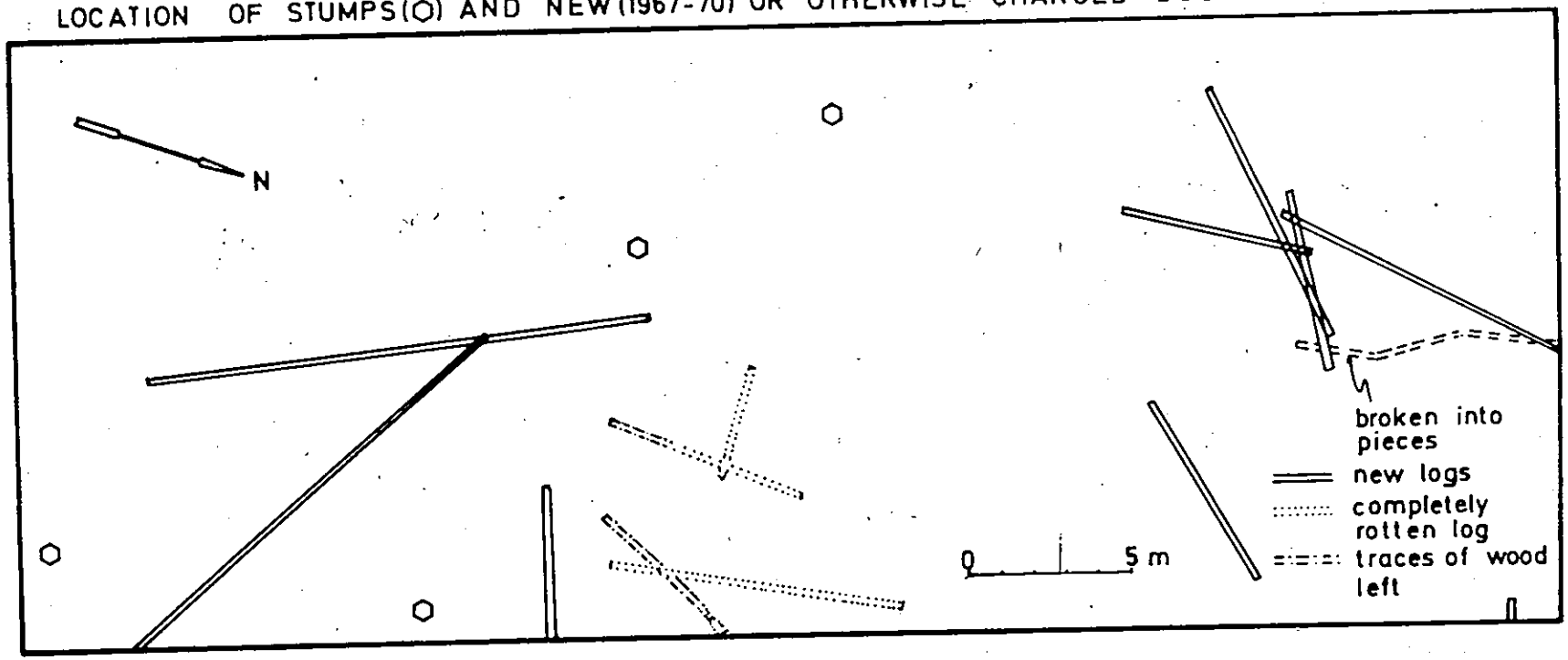
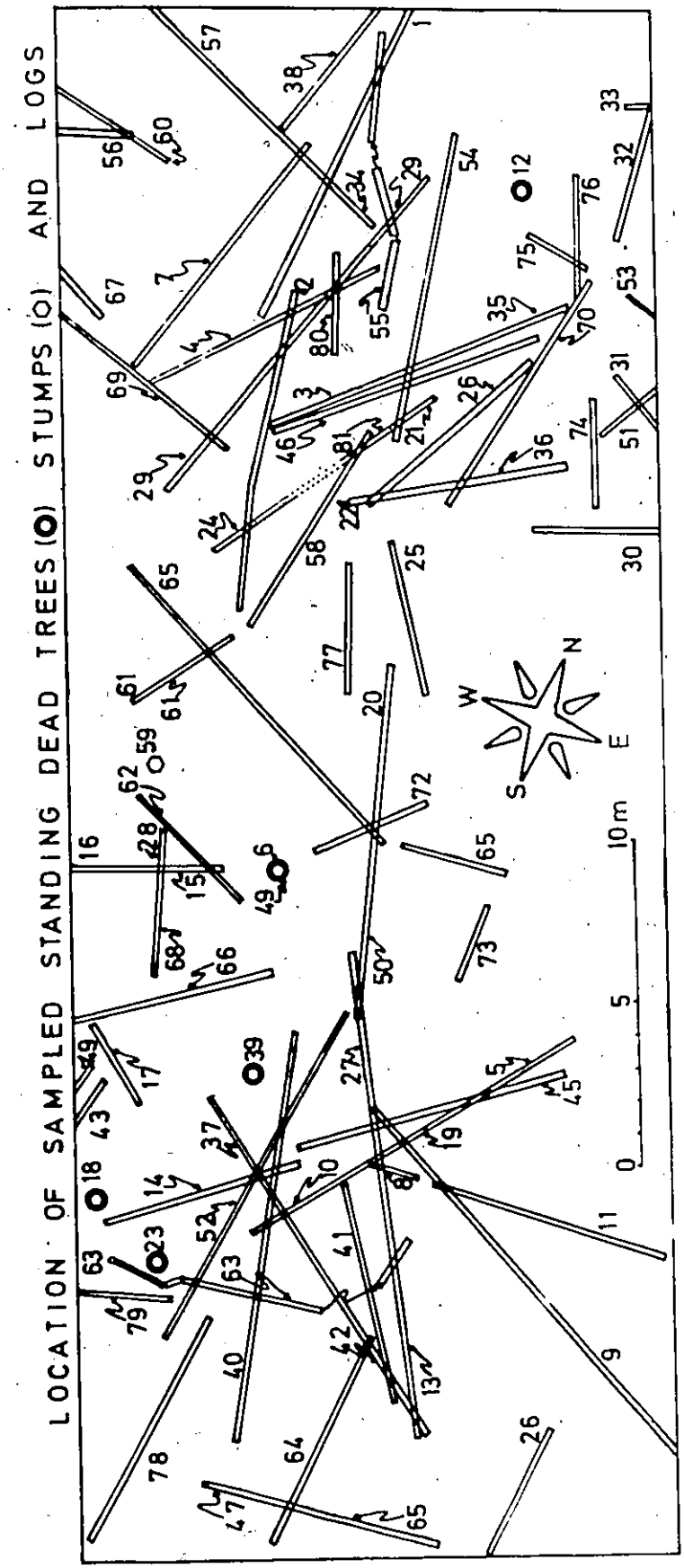


Figure 20. Location of sampled standing dead trees, stumps and horizontal logs.


LOCATION OF SAMPLED STANDING DEAD TREES (O) STUMPS (O) AND LOGS
N
W
E
S
0
5
10 m

c) Stage of decay:

As a result of natural thinning trees die within a forest ecosystem. Figure 21 illustrates this process in the form of a stereogram. Trees with the thinnest d.b.h. grown before 1926 are now more or less in decay stage 1 to 3. Within the following time intervals from 1966 to 1970, from 1941 to 1946 and from 1936 to 1941 trees with the outer wood cylinder in the most advanced stage of decay are not those with the smallest d.b.h. For the periods 1921 to 1926, 1926 to 1931, 1931 to 1936, and 1946 to 1956 there is, however, a trend showing that trees with the smallest biomass are also the most decayed.

The pH of the outer surfaces of the log deposited at various times is pictured in Fig. 22. The youngest and the oldest logs show the least variation in pH. These logs of varying decay stages deposited approximately between 1931 and 1956 have large variations in their surface pH. The widest ranges in pH occur from 1941 to 1946. Logs in decay stage 3 contribute most to these variations. Logs in decay stage 5 show a tendency towards higher pH values whereas logs in decay stage 1 are more acid.

The relationships between ecological diversity, decay stage and time of deposition are illustrated in Fig. 23. It is evident from Fig. 23 that peak diversity does not coincide with decay stage five. However certain vegetation assemblages with relatively high diversity values can be observed on wood in an advanced stage of decay. The epiphytic stage from

Figure 21. Relationships between diameter breast height, stage of decay and time interval when tree was recorded dead.

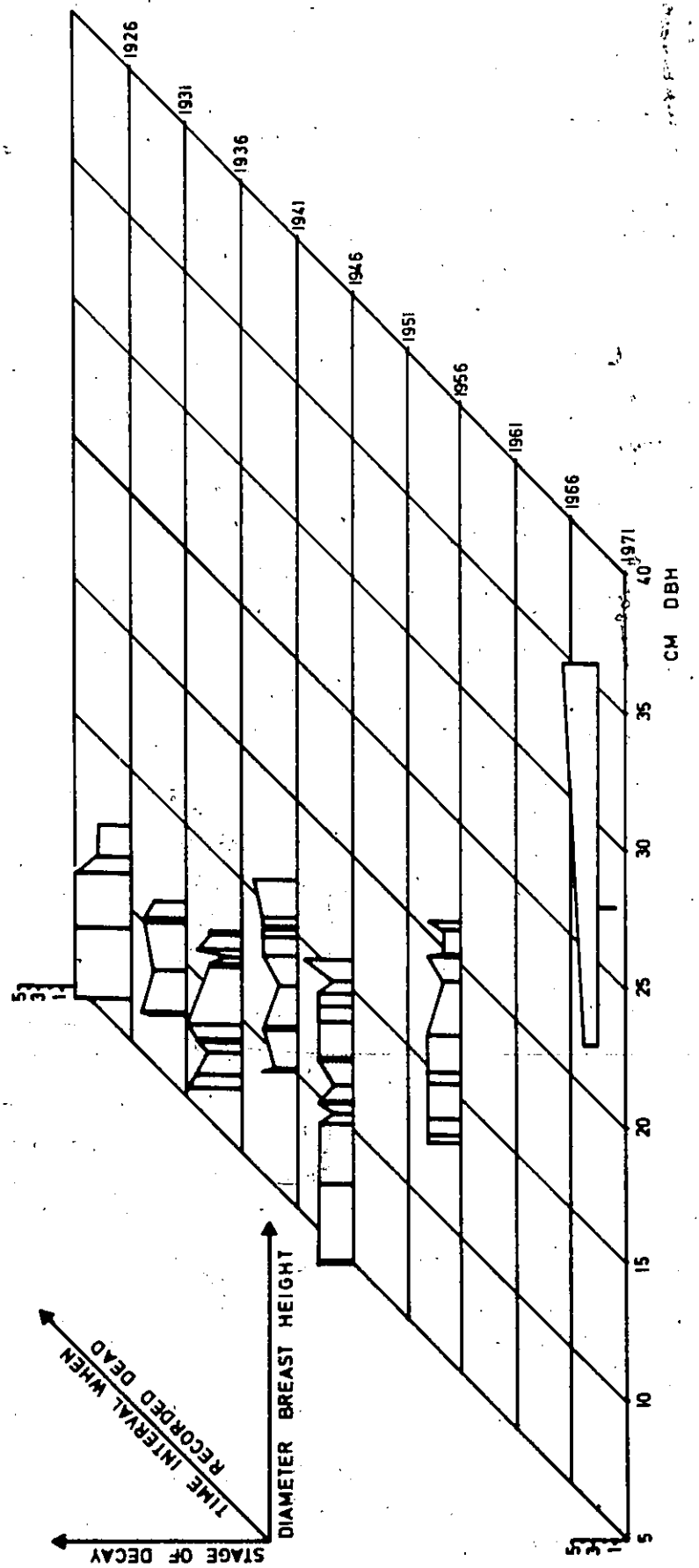

1926
1931
1936
1941
1946
1951
1956
1961
1966
1971
5
10
15
20
25
30
35
40
CM DBH
5
3
1
DIAMETER BREAST HEIGHT
TIME INTERVAL WHEN RECORDED DEAD
STAGE OF DECAY

Table 22. Relationships of concentration of hydrogen ions of the log surface, the stage of decay and time interval when the tree was recorded dead.

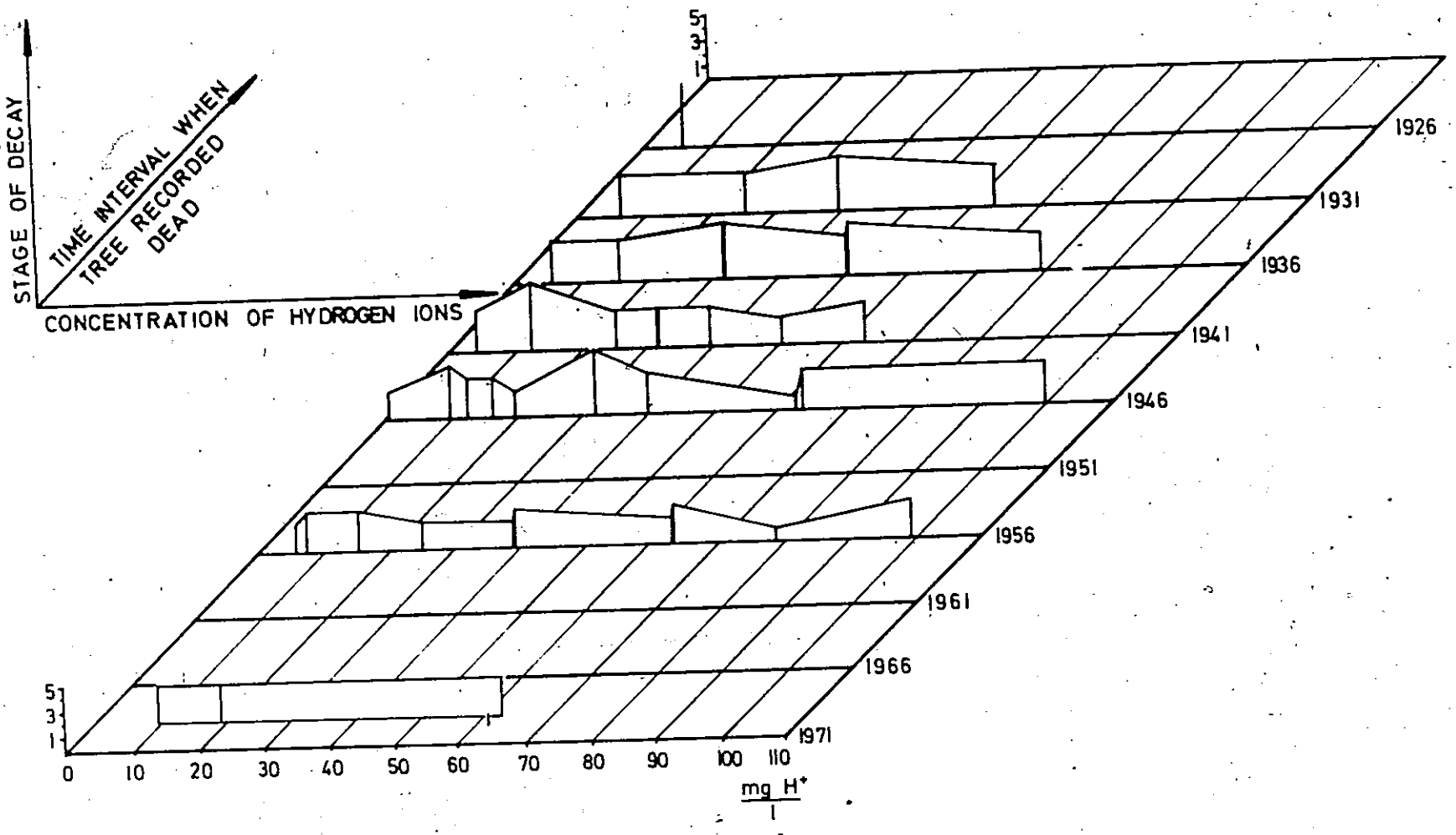
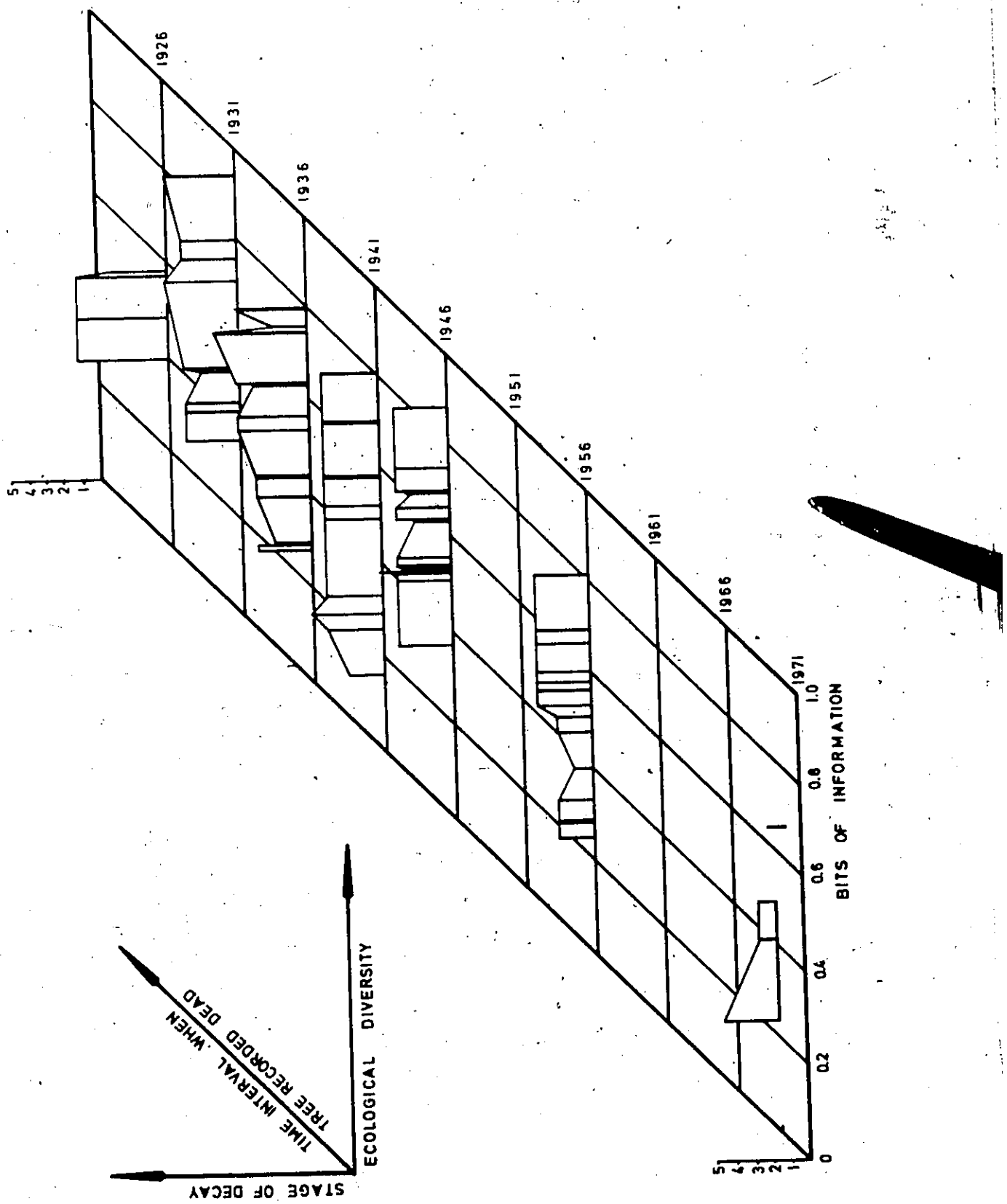

STAGE OF DECAY
TIME INTERVAL WHEN TREE RECORDED DEAD
CONCENTRATION OF HYDROGEN IONS
5
3
1
1926
1931
1936
1941
1946
1951
1956
1961
1966
1971
0
10
20
30
40
50
60
70
80
90
100
110
mg H+
l

Figure 23. Relationships between ecological diversity, stage of decay and time interval when tree was recorded dead.


1926
1931
1936
1941
1946
1951
1956
1961
1966
1971
5
4
3
2
1
0
0.2
0.4
0.6
0.8
1.0
BITS OF INFORMATION
ECOLOGICAL DIVERSITY
TIME INTERVAL WHEN TREE RECORDED DEAD
STAGE OF DECAY

1966 to 1971 has a rather low diversity value. In the period 1956 to 1966 there is a slow increase in variation of diversity to a relative high value in 1946 to 1956. From then on a few logs in decay stages 2, 3 and 4 exhibit considerable low diversity values up to 1931. Vegetation assemblages in decay stages 3 and 4 reach peak diversities. In 1926 those high diversity values for logs in decay stage 5 are no longer encountered and probably they become similar to those of the forest floor.

d) Successional Groups:

In a differentiated table (Ellenberg, 1956) 15 successional groups could be separated. The rows arranged in the fashion mentioned above allowed a distinction of 18 vegetation units in the columns. The results of this step in data synthesis are shown in Table 9.

Group I lists the epiphytes present on logs. These plants originated from former communities of the middle trunk. These communities are only fragmentarily developed in this stand due to substrate factors such as frequent desquamation of the flaky pine bark. In groups 2 and 3 epiphytes on the log close to the former treebase are listed. Mosses, hepatics and lichens in groups 4 to 9, typical for more or less decayed wood, show much wider ecological amplitude than those in 1 to 3. In groups 10 to 12 the mosses listed are evidently well adapted to needle litter and are also characteristic for the forest floor. In groups 13, 14 and 15 cormophytes indicate that either a suitable subsoil has developed on top of the log and/or

Table 9

Differentiated table showing successional groups (1-14) in rows and vegetation units (1-18) as constancy classes (1-5) in columns

Successional Groups		Phytosociological units and ecological groups 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
1	Crustose lichen (Indet. sterile)	5 3
	Neckera pennata	3 2 2
2	Bacidia chlorococca	2 5
	Bacidia cf. beckhausii	4
	Cetraria oakesiana	2 3
	Hypogymnia physodes	2 2
	Catillaria cf. micrococca	2 2
	Lepraria incana	3
	Coriolus hirsutus	2
3	Parmeliopsis ambigua	4
	Ochrolechia sp.	2 4
	Cetraria pinastri	3
	Parmelia sulcata	3 2
	Polystictus cinnamomeus (=Coltricia cinnamomea)	3 2
4	Ptilidium pulcherrimum	4 5 5 4 5 5 5 5 5 5 5 5 4 4 3
	Cladonia coniocraea	3 3 2 4 3 4 3 5 4 3 3 5 4 3 2
	Cladonia sp. (squamules)	4 3 4 3 5 4 5 4 3 5 5 3 4 3 4 3 4
	Dicranum flagellare	2 5 4 4 5 4 5 5 4 3 4 3 4 3 5
5	Jamesoniella autumnalis	2 4 4 3 3 3 4 3
	Tetraphis pellucida	2 4 3 2 4 3 5 2 3
	Odontoschisma denudatum	2 2 2 2
	Herzogiella turfacea (=Sharpiella turfacea)	2 3

Table 9 cont.

Successional Groups		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
6	*Lophocolea heterophylla*						2				5	5	5	5	5			2	
	Nowellia curvifolia						2		2	3	3	3	4	3					
	Cephalozia media							3		3	3		3		3			2	3
7	*Cladonia squamosa*										4	5							
	Cladonia chlorophaea										5	2						2	
	Cladonia cristatella		2				4		3		2	4			2			2	
	Cladonia rangiferina											4							
	Cladonia botrytes						4					2							
	Cladonia cenotea						2					2							
8	*Hypnum pallescens f. reptile*	5		2								4	5	3			2		
	Micarea prasina						3		3		2			3					
9	*Hypnum imponens*									3				3		3	2		
	Heterophyllium haldanianum (*Callicladium haldanianum*)													4		3	2		
	Dicranum fuscescens	2		2						2	2	2							
	Leucobryum glaucum									2									
	Amblystegium serpens													2					
	Brotherella recurvans						3												
10	*Dicranum montanum*			2	3									2			3		
	Pohlia nutans						2										2		
	Polytrichastrum ohioense						3										2		
	Lepidozia reptans																2		
11	*Brachythecium sp.*	3						2			2	3		2		3		3	
	Pleurozium schreberi	3										3		2			2	4	
	Dicranum scoparium													2				3	

Table 9 cont.

Successional Groups		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	Herb Layer:																		
12	*Maianthemum canadense*									2					4	5	5	4	5
	Trientalis borealis									2					5	3	3	5	5
	Gaultheria procumbens													2	3	3	3	3	4
	Linnaea borealis														3	3	2	3	3
	Aster cf. *macrophyllus*														3		2		2
	Vaccinium myrtilloides														3				2
	Chimaphila umbellata														3		2	3	
	Vaccinium angustifolium																2		2
	Mitchella repens																		2
	Clintonia borealis																		2
	Shrub Layer (seedlings)																		
															3	2	3	3	3
13	*Corylus cornuta*																		2
	Cornus stolonifera																2		
	Lonicera canadensis																		
	Tree Layer (seedlings)																		
															4	4		4	5
14	*Pinus strobus*														3			3	4
	Acer saccharum																		2
	Picea glauca																	3	
	Betula sp.																		

that penetration of the wood matrix is possible for these plants.

e) Degree of succession:

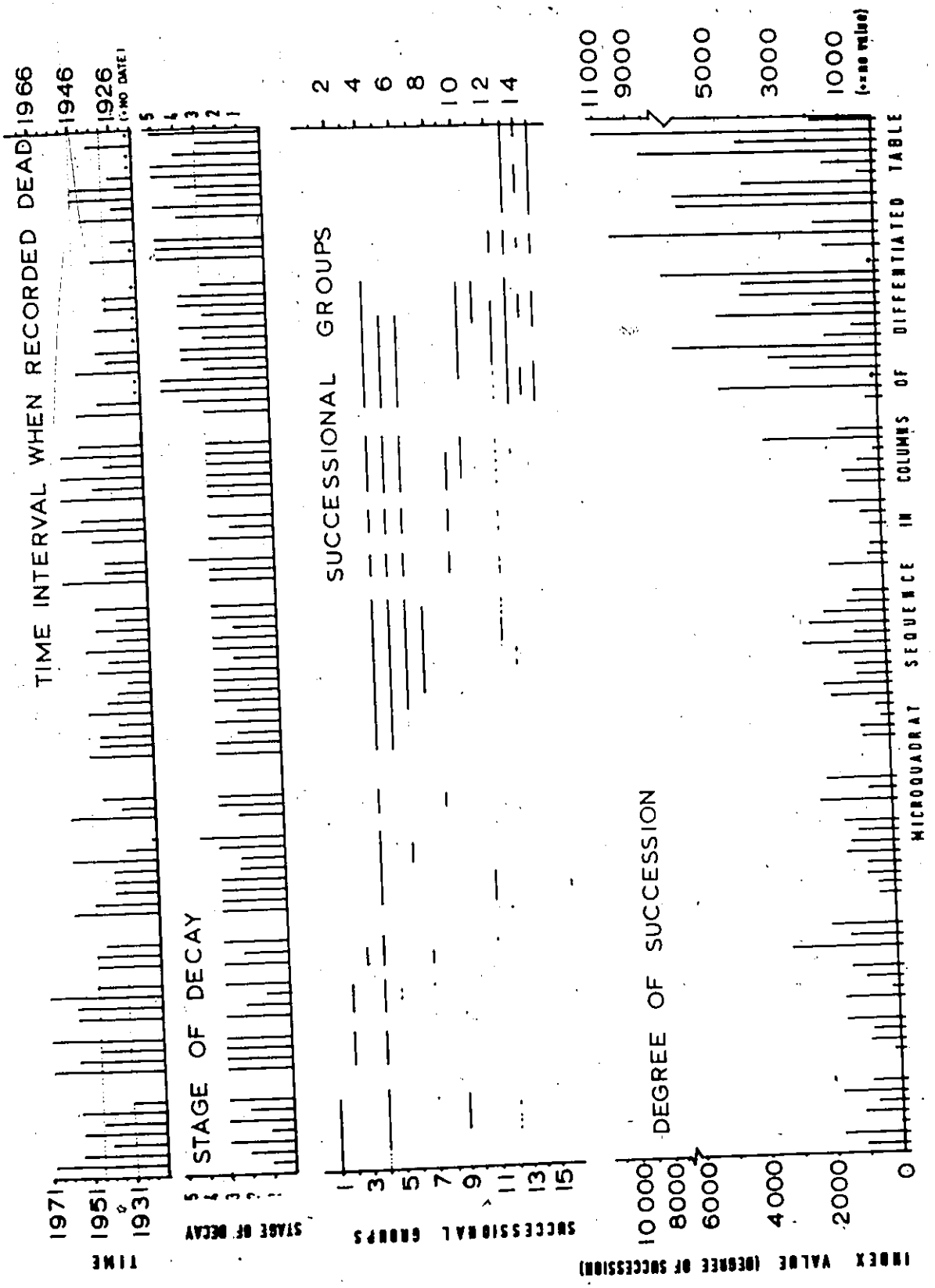
The successional state of these successional groups is indicated in Fig. 24 by the degree of succession. To calculate this index information on the life spans of the constituents is necessary. The life spans of some bryophytes and lichens of successional groups could be determined since the approximate age of the log on which they thrived is known. The life spans of herbs, shrubs and trees had to be set at arbitrary values selected from the literature (Altman and Dittmer, 1972).

A scale of relative structural stability may be set to show better certain trends in the degree of succession:

Degree of succession 1 - 1000; highly unstable
" " " 1000 - 2000; unstable
" " " 2000 - 4000; stable
" " " 4000 - 11000; highly stable

Considering this scale it is evident from Fig. 24 that highly unstable stages occur in all combinations of successional groups. Unstable vegetation assemblages are present in all successional groups dominated by cryptogams (1 to 12). Certain relatively stable communities may, however, be locally developed. The highest values of degree of succession are evidently achieved on logs when phanerogams become established. These highly stable vegetation assemblages may represent a local cyclical pattern (Kershaw, 1964) of a larger vegetation unit.

Figure 24. Degree of succession in relation to successional groups, stage of decay and time interval when the tree was recorded dead.


TIME INTERVAL WHEN RECORDED DEAD
1966
1946
1926
(=NO DATE)
TIME
1971
1951
1931
STAGE OF DECAY
5
4
3
2
1
SUCCESSIONAL GROUPS
2
4
6
8
10
12
14
SUCCESSIONAL ERRORS
1
3
5
7
9
11
13
15
DEGREE OF SUCCESSION
11000
9000
5000
3000
1000
(=no value)
10000
8000
6000
4000
2000
0
INDEX VALUE (DEGREE OF SUCCESSION)
MICROQUADRAT SEQUENCE IN COLUMNS OF DIFFERENTIATED TABLE

f) Raunkiaerian life-forms:

Raunkiaer (1907, 1934) chose, as the basis for his life-form characterization, the structural adaptation of plants to survive the unfavourable season. In the cormophytes, the important character is the position of the buds on the plant. In the nonvascular cryptogams, it is the structural arrangement (see growth characters in Table 10) of the tissues with highest metabolic activity and those parts of the plants which produce or carry diaspores. In Table 10 sections and subsections of the life-forms encountered in this work are listed.

The numbers of vegetation units in Table 9 correspond to phytosociological units in Fig. 25. This figure shows the relationships of the sum of average cover in a certain phytosociological unit (1-18, see Table 9 , p. 97) for subsections of life-forms. The average cover was calculated as sum of cover (midpoints of cover classes in cm^2) per phytosociological unit divided by the number of columns within a phytosociological unit. These values were added for respective life-form subsections.

Thallo-epiphytes occur on logs with phytosociological units 1 and 2. In units 3, 4 and 5 thallo-saprophytes, thallo-hemicryptophytes and thallo-chamaephytes occur mixed with thallo-epiphytes which become gradually less important from units 6 to 12. Rarely certain thallo-epiphytes persist with a high average cover (phytosociological units 12 and 14). This is evidently a result of microhabitat patchiness. Certain decay-resistant bark pieces remain on a log especially around

Table 10

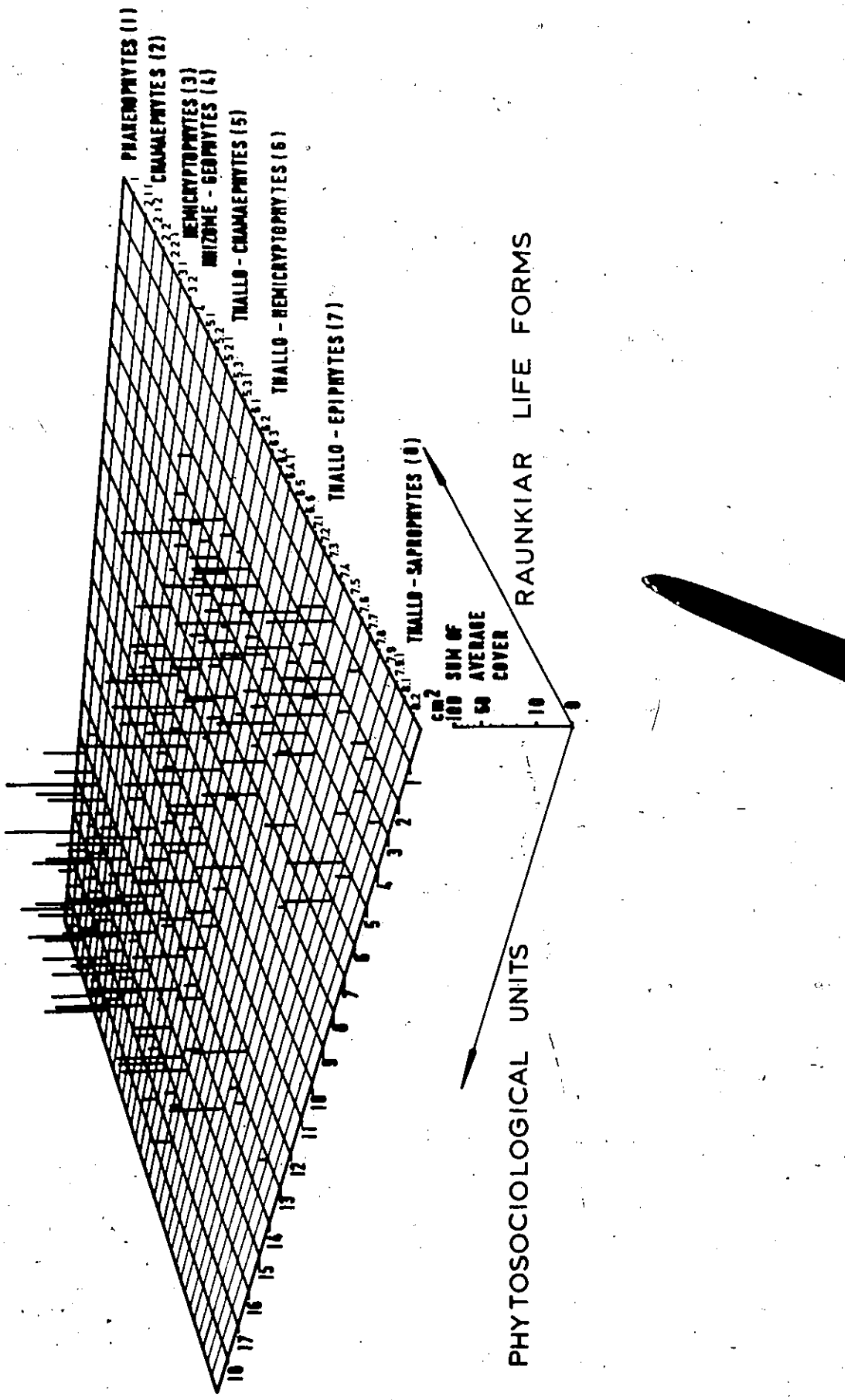
RAUNKIAERIAN PLANT LIFE-FORMS

LIFE-FORM	GROWTH CHARACTERS	EXAMPLE
1. Phanerophytes		*Pinus strobus*
2. Chamaephytes	2.1 Chamaephytes, frutescent	*Vaccinium myrtilloides*
	2.2 " , suffrutescent	*Chimaphila umbellata*
	2.2.1. " , reptant	*Linnaea borealis*
3. Hemicryptophytes	3.1 Hemicryptophytes, semi-rosette	*Tiarella cordifolia*
	3.2 " , reptant	*Agrostis alba*
4. Geophytes	4. Rhizome-geophytes	*Clintonia borealis*
5. Thallo-chamaephytes	5.1 Fruticose lichens	*Cladonia squamosa*
	5.2 Turfs (mosses)	*Polytrichastrum ohioense*
	5.2.1. Turfs with asexual diaspores	*Tetraphis pellucida*
	5.3 Cushions (mosses)	*Leucobryum glaucum*
	5.3.1. Cushions with asexual diaspores	*Dicranum flagellare*
6. Thallo-hemicrypto-phytes	6.1 Foliose lichens	*Hypogymnia physodes*
	6.2 Squamulose lichens	*Lecidea scalaris*
	6.3 Crustose lichens	*Bacidia chlorococca*
	6.4 Appressed mats (hepatics)	*Ptilidium pulcherrimum*
	6.4.1 " " with asexual diaspores	*Odontoschisma denudatum*
	6.5 Closed appressed mats (mosses)	*Hypnum pallescens*
	6.6 Open mats (mosses)	*Amblystegium serpens*

Table 10 cont.

LIFE-FORM	GROWTH CHARACTERS	EXAMPLE
7. Thallo-epiphytes	7.1 Fruticose lichens	*Evernia mesomorpha*
	7.2 Foliose lichens	*Parmelia sulcata*
	7.3 Squamulose lichens	*Cladonia* sp., primary thallus of Section *Microphyllae*
	7.4 Crustose lichens	*Lecanora chlarona*
	7.5 Appressed mat (hepatics)	*Frullania eboracensis*
	7.6 Closed appressed mats (mosses)	*Platygyrium repens*
	7.7 Open mats (mosses)	*Leskeella nervosa*
	7.8 Turfs (mosses)	*Rhizomnium punctatum*
	7.9 Cushions (mosses)	*Ulota crispa*
	7.9.1 Cushions with asexual diaspores	*Orthotrichum obtusifolium*
8. Thallo-saprophytes	8.1 Sporophytes stipitate	*Polystictus cinnamomeus*
	8.2 Sporophytes sessile	*Coriolus hirsutus*

Figure 25. Sections and subsections of Raunkiaerian life-forms in relation to sum of average cover and phytosociological units.


PHANEROPHYTES (1)
CHAMAEPHYTES (2)
HEMICRYPTOPHYTES (3)
MIXOME - GEOPHYTES (4)
THALLO - CHAMAEPHYTES (5)
THALLO - HEMICRYPTOPHYTES (6)
THALLO - EPIPHYTES (7)
THALLO - SAPROPHYTES (8)
SUM OF AVERAGE COVER
cm²
100
50
10
0
RAUNKIAR LIFE FORMS
PHYTOSOCIOLOGICAL UNITS

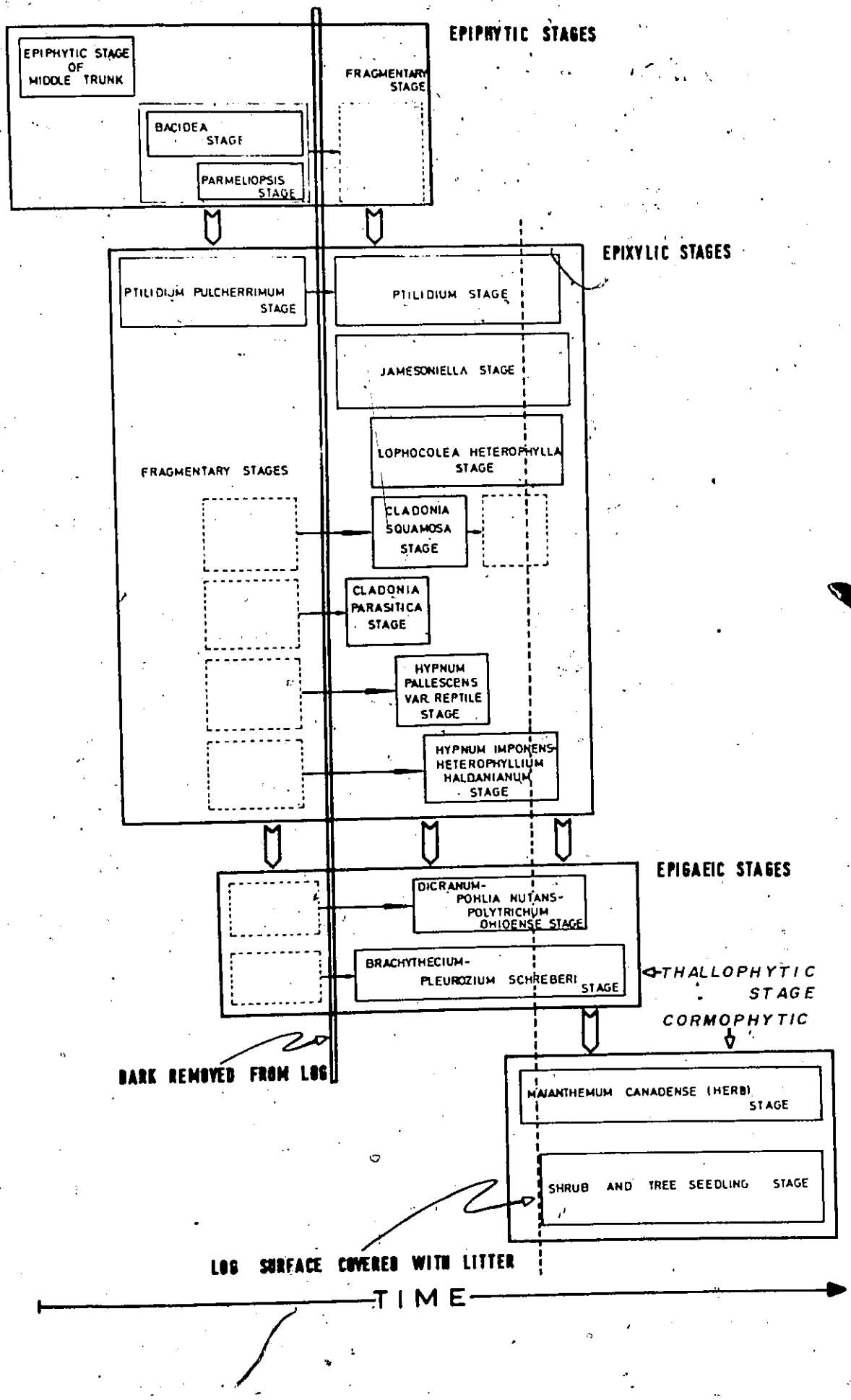
knots. They provide a more or less constant topographic surface where adaptable epiphytes may persist even when most wood is in an advanced stage of decay. In phytosociological unit 13 the first chamaephytes appear. In unit 14, finally, they are accompanied by geophytes, hemicryptophytes and phanerophytes.

g) Successional scheme:

A tentative synopsis of vegetational change in P.S.P. 2 (permanent sampling plot 2) is presented in Fig. 26. On the horizontal axis of this diagram, from left to right, a relative time scale may be imagined. The vertical axis from top to bottom of Fig. 26 indicates the change in the plant component during the investigated time period. The whole sequence is thought to take from 50 to 70 years approximately and is fairly representative for young pine stands in similar environments and with similar history. During this sequence two important processes for cryptogam succession occur; the first is bark removal and the second is litter deposition. These are indicated in the scheme with different types of line since bark removal is a rather steep environmental change (double solid line) and litter deposition a more gradual process (broken line).

Three prominent series of stages are distinguished: epiphytic, epixylic and epigaeic. The epigaeic stages are divided in thallophytic and cormophytic stages. Directional changes can occur as indicated by open arrows on bark, wood and on litter. The stages which correspond mostly to the phy-

Figure 26. Scheme of substrate changes and subsequent vegetational change from epiphytic through epixylic to epigaeic stages.


EPIPHYTIC STAGES
EPIPHYTIC STAGE OF MIDDLE TRUNK
FRAGMENTARY STAGE
BACIDEA STAGE
PARMELIOPSIS STAGE
EPIXYLIC STAGES
PTILIDIUM PULCHERRIMUM STAGE
PTILIDIUM STAGE
JAMESONIELLA STAGE
LOPHOCOLEA HETEROPHYLLA STAGE
FRAGMENTARY STAGES
CLADONIA SQUAMOSA STAGE
CLADONIA PARASITICA STAGE
HYPNUM PALLESCENS VAR REPTILE STAGE
HYPNUM IMPONENS-HETEROPHYLLIUM HALDANIANUM STAGE
EPIGAEIC STAGES
DICRANUM-POHLIA NUTANS-POLYTRICHUM OHIOENSE STAGE
BRACHYTHECIUM-PLEUROZIUM SCHREBERI STAGE
THALLOPHYTIC STAGE
CORMOPHYTIC
BARK REMOVED FROM LOG
MIANTHEMUM CANADENSE (HERB) STAGE
SHRUB AND TREE SEEDLING STAGE
LOG SURFACE COVERED WITH LITTER
TIME

tosociological units in Table 9 (p. 97) may show optimal development on one substrate whereas on the other substrate they may occur only fragmentarily. This is especially true for the *Bacidia* and *Parmeliopsis* stages of the treebase, the *Cladonia* and *Hypnum* stages on wood and the *Dicranum* and *Brachythecium* stages on wood and litter. Some stages like the *Ptilidium* stage occur on bark as well as on wood. The *Jamesoniella* stage and the *Lophocolea* stage are present mainly on wood. All of these three hepatic stages may grow also on litter covered logs, but here they do not persist when litter accumulation exceeds litter decomposition. However, some species in certain genera like *Dicranum*, *Brachythecium* or *Pleurozium* may resist the intermittent fall of needles and still be present on the soil when all wood is completely rotten.

h) Discussion and conclusions:

The change in spatial distribution of plants on logs in relation to time shown in this study is especially relevant for the understanding of cryptogam succession on decaying logs.

With the index degree of succession it seems possible to predict stability of successional plant assemblages. It is clear that the controlling factors for this sequential change are, to a certain degree, connected to the heterotrophic decomposition cycle of terrestrial systems. Thus a food chain stability in the sense of Leigh (1965) may not exist at all for decomposing logs. However, a certain structural stability of those dependent plant assemblages as shown with the degree of succession may exist for different seral stages. Since a

number of variables in this index have to be set at a probable value it is evident that degree of succession describes a potential with a certain probability rather than a deterministic relationship between variables.

For a more or less even-aged forest, log deposition and decomposition on the forest floor is clearly a time-dependent process. Since only logs with a certain range in d.b.h. will be produced by a forest of a particular age structure, it seems difficult to assess the direct time relations of the stage of decay of logs of different sizes. To obtain more information about the time relations of decay of wood one would have to try to reconstruct the invasion pattern of decay fungi by sectioning logs (Shigo, 1965) as well as by trying to determine the exact date of death by dendrochronological methods. Since in permanent sampling plots sampling of the inner parts of trees and logs is usually impossible for phytopathological reasons, the problem of time relations of stages of decay seems intractable to the author. However, inspection of the outer wood cylinder gave some important information. Logs pass rather quickly through stage 1 (1 to 3 years) and stage 2 (3 to 15 years) and may more or less stabilize locally in stage 3 for more than 50 years. Direct progression from stages 1 to 3 and thus bypassing stage 2 evidently exists but similar changes do not seem to occur for other combinations of stages.

Under the environmental stresses of the rather dry pine forests, the ecological diversity of epiphytic and some epi-

xylic stages is frequently low. This is thought to be a reflection of cyclic recolonization phases of the rather unstable substrate as well as a result of environmental vigor. The fact that the diversity of the final stages is lower than the diversity of the later sequential stages is noteworthy. It is thought to be caused, at least in part, by different pattern intensities (Kershaw, 1970) of cryptogams vs. cormophytes. This also indicates that there are areas on logs where more diverse plant assemblages find a stable topographic microhabitat.

Due to its dependance on the heterotrophic cycle, succession on logs is basically allogenic (Tansley, 1929). However, certain autogenic components may also exist. Most covered logs accumulate raw humus as well as their own decomposition products, especially when certain growth-forms are present. These moss covered areas seem to provide a much more suitable microhabitat for certain wood decomposing organisms than does bare wood. The regularly observed pattern in the decomposition of the outer wood cylinder seems to be influenced by the moss cover. This argument may however be circular: mosses may preferentially establish themselves on spongy wood rather than on solid wood. For the time being we may assume a feedback mechanism between moss cover, its moisture relations and decomposition of the outer wood cylinder.

The successional groups obtained suggest that vegetational change follows a marked stage-wise pattern. Only a few rare species do not show a clear affinity to the time-dependent

groups. In other words, the probability for the frequent species to find a suitable substrate is about equal for all members of the group. If a disparity in the establishment of plants of a group manifests itself, it is attributed to change in substrates. These disparities pictured in the successional scheme (Fig. 26) are poorly understood since plant dispersal, plant establishment and chemical and physical factors are intimately interrelated.

The main trends in vegetational change can be clearly recognized. With accumulation of raw humus and increasing porosity of the log, thallo-saprophytes, thallo-epiphytes, thallo-hemicryptophytes and thallo-chamaephytes become less important and the establishment of cormophytic life-forms can take place.

2. Mont Saint-Hilaire

The Petawawa section dealt with a nearly even-aged coniferous forest where some factual knowledge from the past could be related to plant succession on logs. In this section, however, such a detailed record is not available and it was decided to investigate logs along a coenocline (a sequence of communities in relation to environmental gradients, Whittaker, 1970) from lakeshore forest to hill top forest. Emphasis is placed on plant communities occurring on logs and their phytosociological associations in the sense of Braun-Blanquet (1964) as they occur along the gradient of evaporational stress (MacHattie and McCormack, 1961). Change in species composition within a definite plot on logs at various stages of decay is also examined.

a) Plant communities along the transect:

A transect was run from Lake Hertel (Fig. 1) up Easthill to the dry hilltop. Sampling of plant communities was done at nine positions on the gradient. At some positions where discontinuities were evident, two to three relevés were made where the area was uniform. A total of 16 relevés were made along the transect. The results for the tree and shrub layers are summarized in the form of a differentiated table (Table 11).

(i) Lakeshore and wet forests (plots 1, 2, and 3):

The first plot was located partly in the lake close to the lakeshore and did not show any woody species. Plot 2 was in the periodically inundated area where the forest is quite open and shrubs, such as *Myrica gale*, *Cornus stolonifera*, or

Table 11

Coverage of trees and shrubs along the Mont Saint-Hilaire transect

Quadrat (plot) Subplot)	1	2		3			4			5			6	7	8	9
		2a	2b	3a	3b	3c	4a	4b	4c	5a	5b	5c				
Tree Layer I 25-10 m																
Acer saccharum							2	2				2	2			
Betula alleghaniensis								1	2	2		2	3			3
Tsuga canadensis							3	2		3						
Quercus rubra								3		2		1				3
Fagus grandifolia								1	2				2			
Tilia americana									2					3		
Pinus resinosa								1								2
Pinus strobus																
Populus grandidentata																
Tree Layer II 10-5 m																
Acer rubrum	3	2		1												
Alnus rugosa			2	2									2		1	
Abies balsamea		1		1											1	2
Betula alleghaniensis		1	3													
Fraxinus americana				1	3	3	1									
Tsuga canadensis				2		1	1	1	4							2
Acer spicatum					2	2	3	1					2			3
Fagus grandifolia					1		2									
Acer saccharum							1			2	3	1				
Ostrya virginiana							1	1		1						
Tilia americana								2		1						
Ulmus americana										1						
Acer pensylvanicum														2	3	
Quercus rubra														2		
Betula papyrifera														2		
Populus grandidentata															2	
Thuja occidentalis															1	
Pinus strobus																

Table 11 cont.

Quadrat (plot)	1	2		3			4			5			6	7	8	9
		2a	2b	3a	3b	3c	4a	4b	4c	5a	5b	5c				
Shrub Layer I 5-1 m																
Alnus rugosa			3			2										
Ulmus rubra			2													
Acer rubrum				1	2											
Cornus stolonifera				2												
Viburnum alnifolium							1									
Acer pensylvanicum							1	2	1							1
Acer spicatum									1	1		1				
Fagus grandifolia									1			1	2			
Acer saccharum										2	1		1		1	3
Tilia americana											2	2				
Amelanchier sanguinea													1		2	
Quercus rubra													1			
Betula alleghaniensis													1			
Ostrya virginiana																1
Shrub Layer II 1-0.1 m																
Myrica gale		4	2													
Salix nigra		1		1												
Alnus rugosa		1														
Cornus stolonifera		1	2	1							1				3	
Cornus alternifolia									1	1						
Fraxinus americana									1				1	1		
Viburnum acerifolium									1	1						
Corylus cornuta										1		1	1	1	1	1
Fagus grandifolia										1	1	1				
Tsuga canadensis										3			1			
Ribes cynosbati										1	3					
Acer saccharum										2		2		1		
Diervilla lonicera										1						1
Lonicera canadensis											1					
Ribes lacustre											2	1				
Rubus subgen. *Rubus*											1					
Cornus rugosa												2	1	1		

Table 11 cont.

Quadrat (plot)	1	2		3			4			5			6	7	8	9
Subplot		2a	2b	3a	3b	3c	4a	4b	4c	5a	5b	5c				
Amelanchier laevis												1	1	1	1	
Viburnum trilobum														2		
Lonicera dioica														1	1	
Prunus pensylvanica														1		1
Pinus strobus														1		
Pinus resinosa														1		
Thuja occidentalis															1	
Crataegus sp.																1
Dirca palustris																1
Carya cordiformis																1
Populus grandidentata																1

small trees, such as *Alnus rugosa* are most important. Some of the big hardwood forest logs encountered here were probably not of local origin or might have lived here if habitat factors such as water level, were different than they are today. *Acer rubrum*, *Fraxinus americana*, *Abies balsamea* and *Tsuga canadensis* may be locally dominant in adjacent elevated areas.

(ii) Mesic forests (plots 4, 5, and 6):

In the mesic stands *Acer saccharum* and *Fagus grandifolia* grow in company with species which extend into the dry mesic part of the gradient such as *Betula lutea* and *Corylus cornuta*. On the lower slopes *Tsuga canadensis* is locally dominant on thin soil covered with rocks whereas *Acer spicatum* in subplot 5b is most important on evidently stabilized shaded screes.

(iii) Xeric forests (plots 7, 8, and 9):

On the upper slopes *Pinus resinosa* in plot 7, *Quercus rubra* in plot 8 form pure clumps. In plot 9 some mesic hardwood species such as *Fagus grandifolia* and *Acer saccharum* dominate again but a group of small woody species e.g. *Carya cordiformis*, *Dirca palustris* and *Crataegus* sp. differentiate this forest from all the others.

b) Quantitative aspects of plant assemblages on rotten logs:

An overall view of the major floristic changes on logs along the transect is given in Fig. 27, which shows the total number of species for each stage of decay at each position on the gradient.

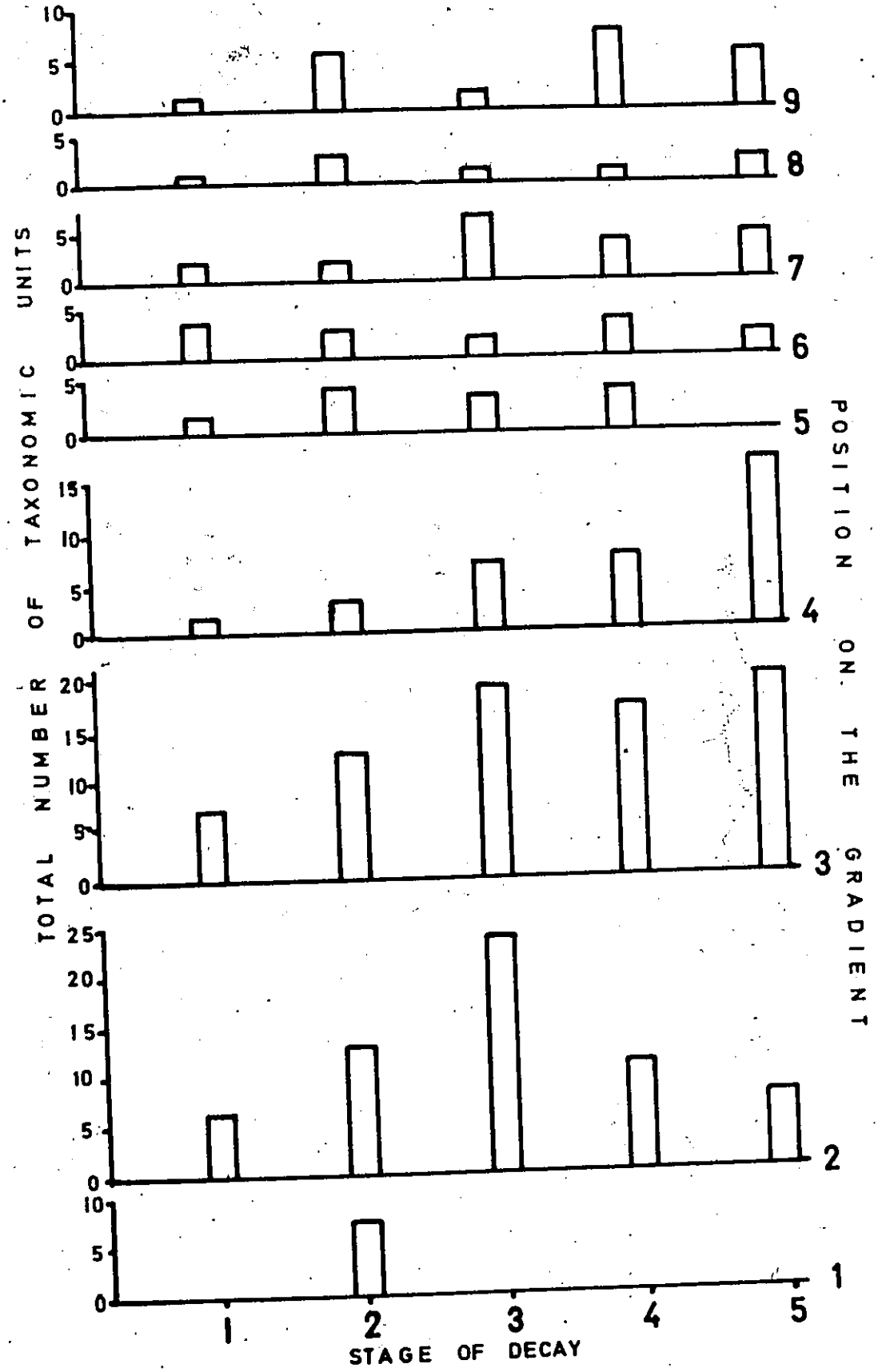
(i) Total number of species:

All logs encountered in plot 1 (position 1 on the gradient (Fig. 27) are in decay stage 2. Only hydrophytic mosses and lichens establish themselves on these logs. Close to the lakeshore (e.g. position 2) logs are not in permanent contact with water; as a result wood can break down completely and the cryptogams are found on logs in all stages of decay. Species number rises from 10 in stage 1 to over 40 in stage 3 and then declines for logs in stages 4 and 5. The gradual increase in plot 3 from decay stages 1 to 3 is similar to that in the wet plot 2. In decay stages 4 and 5, however, the decline in species number is only slight in quadrat 3 and an increase can be noted for plot 4. When one proceeds from the mesic hardwoods to the drier slopes, species richness in plots 5 to 9 is generally less high than that found in the wet and mesic parts (plots 1 to 4) of the transect. Species richness in plot 5 is eight, in plot 6 it is as low as seven and in plot 7 it increases to 14. In the dry-mesic parts of the transect the highest species numbers are six species in plot 8 (stage 5) and 16 species for plot 9 (stage 4).

(ii) Specific numbers of species:

To show which major taxonomic group contributes most to the change in species richness, the number of sporophore-forming polypores, lichens, hepatics, mosses, herbs and tree seedlings was calculated for each stage of decay and for the positions on the gradient. The results are summarized in Fig. 28 .

Figure 27. Total number of taxonomic units in relation to stages of decay (1 to 5) and positions on the gradient (1 to 9).


TOTAL NUMBER OF TAXONOMIC UNITS
POSITION ON THE GRADIENT
STAGE OF DECAY
1
2
3
4
5
9
8
7
6
5
4
3
2
1

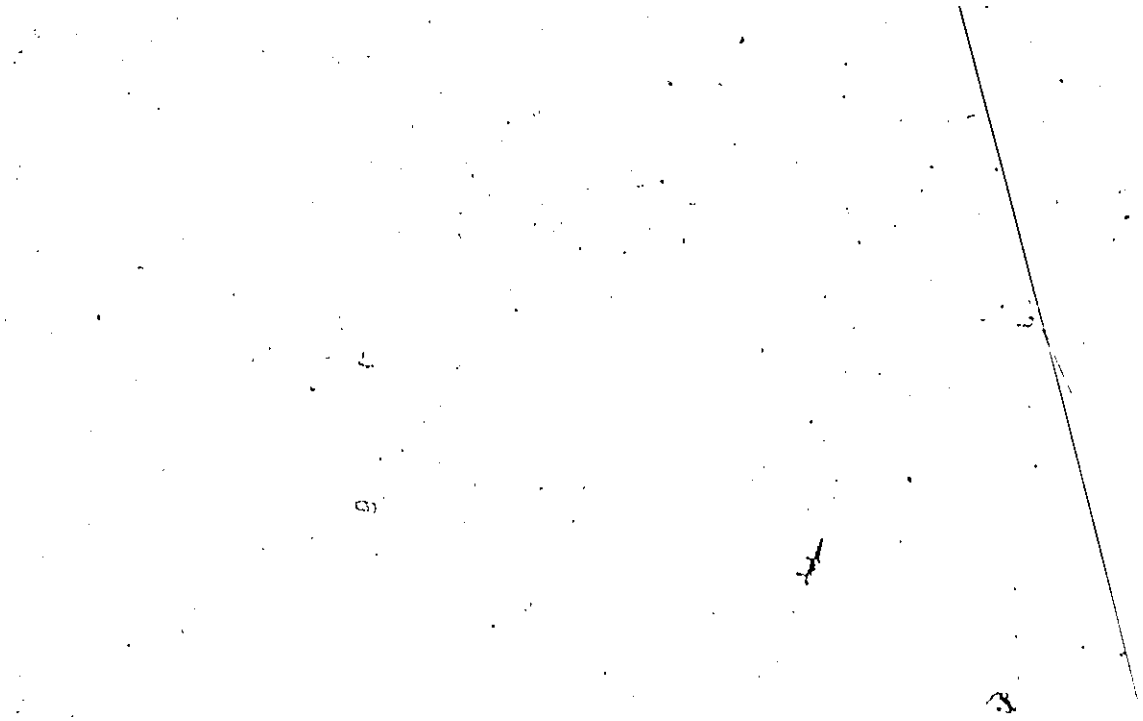
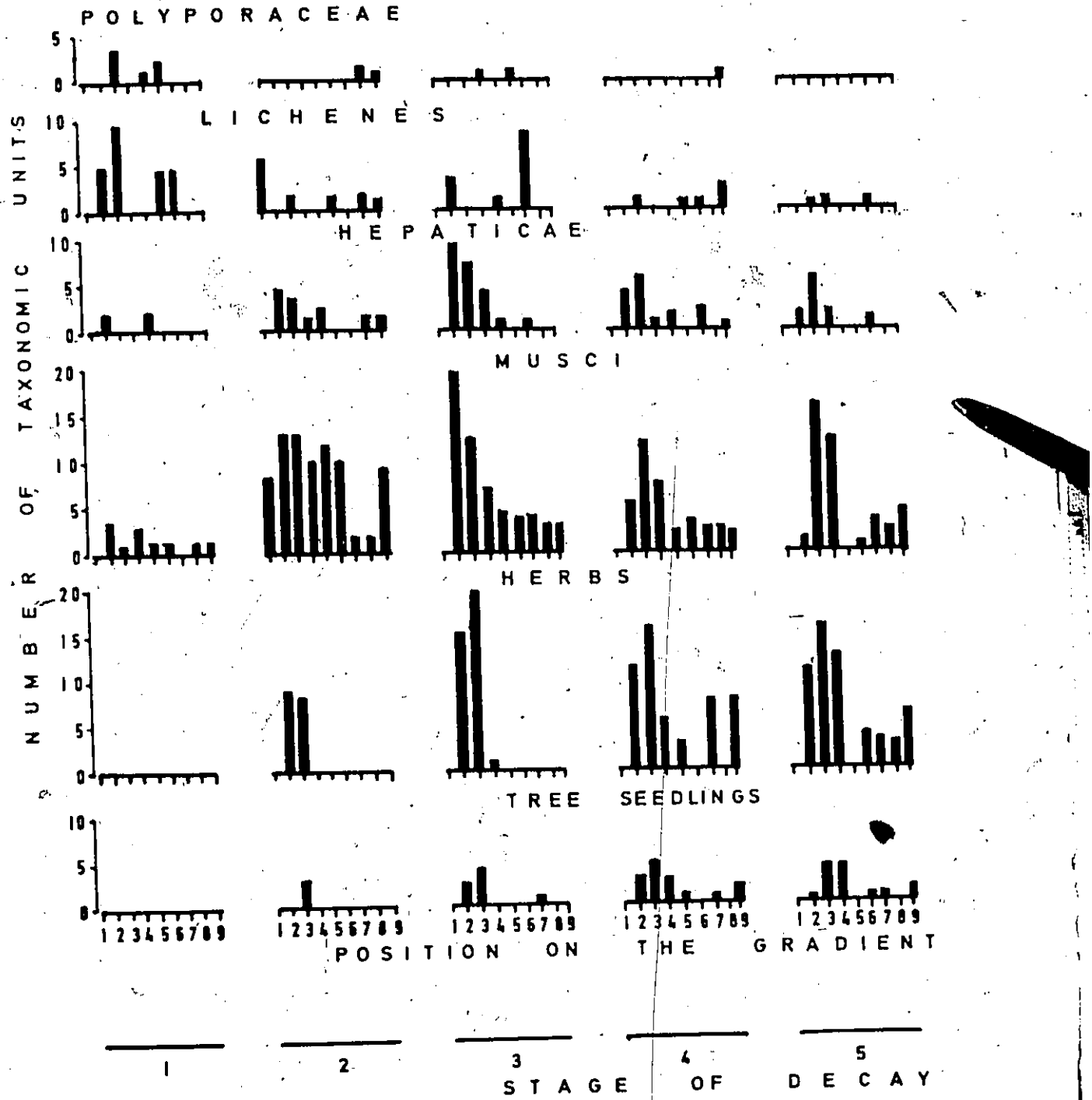


Figure 28. Number of species for major taxonomic groups in relation to positions on the gradient (1 to 9) and stages of decay (1 to 5).


POLYPORACEAE
LICHENES
HEPATICAE
MUSCI
HERBS
TREE SEEDLINGS
NUMBER OF TAXONOMIC UNITS
POSITION ON THE GRADIENT
STAGE OF DECAY
1
2
3
4
5

Sporophore-forming bracket fungi and lichens achieve their greatest importance in the early stages of decay whereas tree seedlings and herbs are most abundant on wood in the more advanced stages of decay. The wetter parts of the transects show consistently higher species numbers for hepatics and mosses. They increase from stages 1 to 3 and decrease in stages 4 and 5. On the drier slopes species number shows a tendency to increase from stages 1 to 5. Only position 9 in stage 2 is an exception. A similar tendency in the increase of species with the progress of decay may be found also for the tree seedlings.

c) Phytosociological associations:

Since the statement of the number of species is not sufficient for the demonstration of floristic changes, the species composition will be analysed here in two ways. First, major changes in species composition are considered for those species which were present in 20% or more of the microquadrats studied in any one of the nine large quadrats without regard to stage of decay. The second aspect, discussed in the next chapter, is the vegetational change in each quadrat in relation to breakdown of wood.

Major changes in species composition are summarized in the form of a differentiated table (Table 7, p. 73). On the basis of presence and absence data six major cryptogam associations are distinguished and shown in Fig. 29.

(i) Wet habitat associations:

Leptodictyum sp., *Campylium polygamum* and *Bryum pseudo-*

Figure 29. Major cryptogamic communities based on those species which were present in 20 percent or more of the microquadrats analyzed in each large quadrat (position on the gradient).

LEPTODICTYETUM									
LEPTODICTYUM RIPARIUM	●	•							
LEPTODICTYUM cf TRICHOP.	•								
PHYCOPHYTA (filaments)	●								
CAMPYLIUM POLYGAMUM	●	•							
PLATYGYRIUM REPENS	●	•	•						•
BRYUM PSEUDOTRIQUETRUM	•	•							
CHILOSCYPHO - CLIMACIETUM									
CHILOSCYPHUS PALLESC.		•	•						
CLIMACIUM DENDROIDES		•							
HYPNUM LINDBERGII		•							
MYRICA GALE		•							
SIUM SUAVE		•							
BRYHNIETUM									
BRYHNIA NOV.-ANGLIAE		•	●	•					
TETRAPHIS PELLUCIDA		•	●						
PLAGIOTHECIUM DENTIC.			●	●	●				
MNIUM CUSPIDATUM			●	●	•	•			•
ACER SACH. (seedling)			●	●					
CIRCAEA ALPINA			●						
IMPATIENS CAPENSIS			●						
TSUGA CANADENS. (seedling)		•	●						
OXALIS MONTANA		•	●						
BRACHYTHECIO - HETEROPHYLLIETUM									
BRACHYTHECIUM SALEBR.			•	●		•	•		•
ONCOPHORUS WAHLENBERGII		•		●					
BRACHYTHECIUM SPEC. I			•	●	●		•		
HETEROPHYLLIUM HALDAN.		•	•	●	●	•	•	•	
LOPHOCOLEA HETEROPH.		•	•	●	•		•		
HYPNUM PALLESCENS		•	•	●	●	●	•	●	●
DICRANUM SCOPARIUM		•	•	●					
PLAGIOMNIO - CAMPYLIETUM									
CEPHALOZIA MEDIA		•	•		●				
PLAGIOMNIUM CILIARE			•	•	●	•			●
CAMPYLIUM HISPIDULUM				•	●	•	•		•
FOMES IGNIARIUS					●				
CLADONIO - PTILIDIETUM									
CLADONIA SPEC. (squamules)	●	•	•	•		•	●	●	
CLADONIA BACILLARIS	•	•				•	●		●
PTILIDIUM PULCHERRIMUM		•	•	•	•		●	•	•
DICRANUM FLAGELLARE		•	•	•	•		●		•
BACIDEA SPEC. II		•	•			•	●		•
CLADONIA CONIOCRAEA							●		•

PRESENT IN • 1-20, ● 21-40, ● 41-60, ● 61-80, ● 81-100 % of sampled quadrat.

POSITION ON THE GRADIENT: 1 2 3 4 5 6 7 8 9

triquetrum are characteristic species for the *Leptodictyetum*. This association is found on logs which are most of the time in contact with open water; on the other hand *Chiloscyphus pallescens*, *Climacium dendroides* (pro parte *C. americanum*) and *Hypnum lindbergii* are bryophytes which are frequent on logs which become inundated during spring runoff. In these habitats they form a distinct association *Chiloscypho-Climacietum*. In the region with mudflats the *Bryhnietum* is well developed with *Bryhnia novae-angliae*, *Tetraphis pellucida*, *Plagiothecium denticulatum* and *Mnium cuspidatum* as the more important members of this association. *Myrica gale* and *Sium suave* become more important in the *Chiloscypho-Climacietum* whereas in the *Bryhnietum*, *Acer saccharum* and *Tsuga* seedlings together with *Circaea alpina*, *Impatiens capensis* and *Oxalis montana* are the more frequent phanerogams.

(ii) Mesic and dry habitat associations:

From mesic to dry forests three associations are found on logs which may be called *Brachythecio-Heterophullietum*, *Plagiomnio-Campylietum* and *Cladonio-Ptilietum*. The ecological amplitude of the most frequent members of these three associations is much wider than those amplitudes of plants in associations close to the lakeshore. Species with wide amplitudes along the gradient are in some cases (e.g. *Cladonia bacillaris*) difficult to place in any association. In the strict Zürich-Montpellier tradition they would be companion species for particular associations and would be used for the differentiation of higher ranks in that hierarchical system.

Since the author did not attempt to follow the tradition for higher ranks, he placed critical species in associations after consideration of the center of their most frequent abundance.

d) Floristic analysis of plants on decaying logs:

The overall picture of floristic variability in the previous paragraphs will be described more in detail when vegetational changes in relation to wood decay are presented in the form of complete floristic tables.

When the data for position 1 on the gradient (plot 1, Fig. 1) are summarized a clear zonation is observed (Table 12). In all the other plots a zonation is not observed and microquadrat data are summarized in constancy classes for each stage of decay.

For plot 1, which is located close to the shore in shallow water, the relevés are arranged according to the height above the mid-summer water level. The extreme hygrophytes *Fontinalis* and *Leptodictyum*, which seem to be in this habitat for the greater part of the year in contact with water, contrast against a group of lichens which colonize the upper parts of logs and twigs and are never inundated. All logs in this habitat apparently stay in decay stage 2 and may therefore represent a relatively stable habitat. An indication of this substrate stability is also suggested by the rare occurrence of the foliose rock lichen, *Parmelia plittii*, outside plot 1 on a log in a similar habitat.

In the subsequent plots a zonation was not observed. In

TABLE 12

Zonation of species close to the water level (plot 1) on logs in decay stage 2.
(1 to 4 = degree of cover, o = reduced vitality)

Number of relevé		1	2	3	4	5	6	7	8	9	10	Constancy Class
Number of species in each microquadrat		2	3	5	3	4	4	6	4	3	8	
Height above or below water level	upper limits	-0.05	-0.1	0	0	0.01	0	0.03	0.03	0.1	0.03	
	lower limits	-0.3	-0.5	-0.05	-0.05	-0.05	0.03	0.03	0.1	0.15	0.20	
Tree species		d	A	A	c	A	Po	Pi	A	c	A	
Stage of decay		2	2	2	2	2	2	2	2	2	2	
Fontinalis novae-angliae		1										I
Phycophyta (filamentous)		1	2	1	1	1	1°	1°				IV
Leptodictyum riparium			1		2	1	3	2				III
Bryum pseudotriquetrum				1		1	1	1				III
Leptodictyum cf. *trichopodium*			3			1						II
Leptodictyum sp.				2								I
Climacium americanum				1								I
Leskea polycarpa f. *paludosa*				1								I
Campylium polygamum					1		1	1	1	1	1	IV
Platygyrium repens								1°	1	3°		III
Cladonia sp. (squamules)								1°	1		1	IV
Phycophyta (coccal)									1	1		
Lecanora saligna											2	I
Bacidia cf. *chlorococca*											4	I
Cladonia cristatella											2	I
Cladonia coniocraea											1	I
Physcia millegrana											1	I

d = deciduous; c = coniferous; A = *Acer*; Po = *Populus*; Pi = *Pinus*.

plots 2 and 3 (Tables 13 and 14) logs in all stages of decay were present. In these plots most logs are inundated in spring. Mosses and lichens on logs in stage 1 are replaced by more hydrophytic mosses and hepatics. These evidently entrap more organic material (e.g. bud scales, needles, parts of leaves, etc.) every year and eventually a thin layer of soil develops which allows herbs and tree seedlings to become established on the logs at a relatively early stage of decay (e.g. 2).

The absence of the *Hypnum lindbergii* group in plot 2 and decay stages 4 and 5 should be noted. In plot 3, species such as *Brotherella recurvans* and *Bryhnia novae-angliae* either persisted on the log after establishment in stage 2 or species such as *Heterophyllium haldanianum*, *Rhizomnium appalachiensis* and *Thuidium delicatulum* had time to reestablish on the log. On hollow logs the presence of *Cladonia chlorophaea* s.l., *Cladonia coniocraea* and *Cladonia cristatella* was noted. When at certain locations on the log the outer sapwood (decay stage 4) is broken off, the following group is often found: *Lepidozia reptans*, *Tetraphis pellucida*, *Leucobryum glaucum*, *Bazzania trilobata*.

In plot 3 in decay stage 5 a group of small hepatics is noteworthy: *Blepharostoma trichophyllum*, *Cephalozia media*, *Harpanthus drummondii*, *Scapania apiculata*. In gaps on top of logs where larger mosses had been removed by mechanical breakdown of the wood, these hepatics are present only in low constancy classes. On the sides of the logs, however, they can form large homogeneous patches.

Table 13

Constancy classes (I-V) of plants on logs in certain decay stages (1-5) for plot 2.

Stage of decay	1	2	3	4	5
Number of species	9	26	49	22	16
Parmelia sulcata	IV				
Bacidia sp.	III				
Hypogymnia physodes	II				
Lecanora chlarona	II				
Parmelia subaurifera	II				
Platygyrium repens	II				
Brachythecium plumosum	IV	II	I		
Jamesoniella autumnalis	III		II		
Dicranum flagellare	II		II		
Hypnum lindbergii		II			
Leptodictyum sp.		II			
Riccia fluitans		II			
Hypnum lindbergii f. *demissum*		IV	II		
Heterophyllium haldanianum		III	II		
Ptilidium pulcherrimum		II	II		
Bryum pseudotriquetrum		II	II		
Conocephalum conicum		II	II		
Lophocolea heterophylla		II	II		
Rhizomnium appalachiensis (*Mnium punctatum* s.l.)		II	II		
Sphagnum squarrosum		II	I		
Amblystegium serpens		II	I		
Climacium dendroides		III	III	III	
Chiloscyphus pallescens		III	II		IV
Climacium americanum (p.m.p.)		II	II		V
Dicranum scoparium f. *paludosa* (p.p. *Dicranum bonjeanii*)		II	II	IV	V
Cladonia chlorophaea			III		
Cladonia coniocraea			III		
Cladonia cristatella			III		
Cephalozia media			III		
Nowellia curvifolia			II		
Oncophorus wahlenbergii			II		
Hypnum pallescens			II		
Dicranum montanum			II		
Pohlia nutans			II		
Hypnum imponens			II		
Cladonia sp. (squamules)			I		

Table 13 cont.

Stage of decay	1	2	3	4	5
Bryhnia novae-anglide			I		
Pellia epiphylla			I		
Calypogeia integristipula			I		
Plagiomium ciliare			I		
Brotherella recurvans			II	V	IV
Plagiochila asplenoides				III	
Lepidozia reptans				V	
Tetraphis pellucida				V	
Leucobryum glaucum				IV	
Bazzania trilobata				III	
Geocalyx graveolens				III	
Thuidium delicatulum var. *radicans*				III	
Galium obtusum		II			
Chrysosplenium americanum		II			
Lemna minor		III	II		IV
Cicuta bulbifera		II	II		I
Sium suave		II	II	III	IV
Lycopus uniflorus		II	II		
Onoclea sensibilis		I	III	III	
Lycopus americanus		I	II		
Viola pallens		I	II		
Lythrum salicaria			II		
Osmunda cinnamomea			II		III
Dryopteris spinulosa			II		III
Galium triflorum			III	III	IV
Athyrium filix femina var. *michauxii*				III	
Maianthenum canadense				II	
Trientalis borealis				II	
Clintonia borealis				II	
Carex sp.					III
Oxalis montana					III
Shrub seedlings					
Myrica gale		III	III	III	V
Cornus stolonifera			II		III
Ribes sp.				III	
Tree seedlings					
Alnus rugosa		II	II	III	
Tsuga canadensis			II	III	V
Betula sp.			II	IV	

cf. = confer; s.l. = sensu lato; p.m.p. = pro maxima parte

Table 14

Constancy classes (I-V) of plants on logs in decay stages 1 to 5 for plot 3

Stage of decay	1	2	3	4	5
Number of species	14	25	40	34	41
Parmelia sulcata	III				
Parmelia rudecta	III				
Bacidia sp. II	III				
Phycophyta (coccal)	III				
Bacidia cf. *chlorococca*	II				
Parmelia subaurifera	II				
Pertusaria velata	II				
Platygyrium repens	II				
Physcia millegrana	II				
Physcia orbicularis	II				
Graphis scripta	II				
Coriolus velutinus	II				
Irpiciporus tulipiferae	II				
Ischnoderma resinosus	II				
Hypnum pallescens f. *reptile*		III			
Ptilidium pulcherrimum		III			
Protonema (Musci)		III			
Lophocolea heterophylla		III	III		
Dicranum flagellare		IV		III	
Brachythecium plumosum		III	II	III	
Heterophyllium haldanianum		V	II		III
Rhizomnium punctatum s. str.		IV	II	II	
Thuidium delicatulum		III	III		II
Rhizomnium appalachiensis		IV	III		III
Cladonia spp. (squamules)		III		III	III
Brotherella recurvans		III	II	III	IV
Tetraphis pellucida		III	II	III	V
Bryhnia novae-angliae		III	IV	III	II
Conocephalum conicum		III	III	III	II
Plagiothecium denticulatum		III	III	IV	III
Plagiomnium cuspidatum		III	III	IV	II
Pellia epiphylla			II		
Chiloscyphus pallescens			II		
Leucobryum glaucum			II		
Lepidozia reptans			II		
Brachythecium sp.			III		V
Brachythecium reflexum			III	III	

Table 14 cont.

Stage of decay	1	2	3	4	5
Bazzania trilobata			II	III	III
Plagiochila asplenoides f. *integrifolia*			II	III	II
Chiloscyphus polyanthus				II	
Jamesoniella autumnalis				III	
Geocalyx graveolens				III	
Dicranum montanum				III	
Pohlia nutans				III	III
Dicranum scoparium				III	III
Sphagnum capillaceum					V
Calypogeia integristipula					V
Plagiomnium ciliare					V
Rhynchostegium serrulatum					III
Dicranum fuscescens					III
Brachythecium salebrosum					II
Thuidium recognitum					II
Blepharostoma trichophyllum					II
Cephalozia media					II
Harpanthus drummondii					II
Scapania apiculata					II
Laportea canadensis		II	II		
Athyrium filix-femina var. *michauxii*		II	II		
Tiarella cordifolia		II	II	II	
Impatiens capensis		II	III	IV	III
Circaea alpina		II	III	IV	V
Caltha palustris			II		
Onoclea sensibilis			II		
Carex sp.			II		
Viola pallens			II		
Clintonia borealis			I		
Filices (prothallia)			I		
Trientalis borealis			II		III
Lycopus uniflorus			II	II	V
Oxalis montana			II	IV	V
Maianthemum canadense			II	III	V
Osmunda cinnamomea				III	
Dryopteris spinulosa				II	V
Streptopus roseus				IV	III
Arisaema atrorubens					III
Lycopodium lucidulum					III

Table 14 cont.

Stage of decay	1	2	3	4	5
Tree seedlings					
Acer rubrum		III	II		
Acer saccharum		III	III	IV	III
Betula sp.		III	II	IV	IV
Tsuga canadensis			IV	III	V
Acer spicatum			I	III	
Abies balsamea				III	IV
Viburnum alnifolium				III	IV

In plot 4 (Table 15) the first seedling establishment (*Cornus alternifolia*) takes place on decay stage 3 in fissures of the outer wood cylinder. In decay stages 4 and 5 most seedlings are not growing in microhabitats (e.g. fissures) but are found all over the softened outer wood cylinder. Seedling establishment is, however, suppressed in those areas on birch logs where patches of the highly decay resistant bark remain. Eight out of 18 mosses and two out of four hepatics are restricted to one stage of decay. One moss *Leskella nervosa* is found only on logs in decay stage 1. No species are peculiar to logs in decay stage 2. On logs in decay stage 3, however, there is a group of two mosses, two hepatics, one fungus, and one shrub seedling which is restricted to these kinds of logs. In decay stage 4 no cryptogams with restricted occurrence are noted. There are, however, three herbs and one tree seedling which are restricted to logs in stage 4. The situation changes when logs in decay stage 5 are considered. Here five mosses, 11 herbs, one shrub species and two tree species are found.

In plot 5 (Table 16) no logs in decay stage 5 were encountered. *Cephalozia media* is the only species which is found continuously in all decay stages from 1 to 4. All other plants are either restricted to one stage of decay (e.g., decay stage 1: one fungus, one moss; decay stage 2: one lichen; decay stage 4: one hepatic, two mosses, three herbs, one tree species) or are found on two decay stages (decay stages 2 and 3: four mosses) or extend over three decay stages (one moss).

Table 15

Constancy classes (I-V) of plants on logs in decay stages 1 to 5 for plot 4

Stage of decay	1	2	3	4	5
Number of species	3	6	13	15	32
Leskeella nervosa f. nigrescens	V				
Hypnum pallescens f. reptile	V		III	III	IV
Brachythecium sp.	V	V		III	V
Heterophyllium haldanianum		V	V	V	V
Lophocolea heterophylla		V	III	III	
Campylium hispidulum		V		III	IV
Brachythecium salebrosum		V		III	III
Haplocladium microphyllum		II			III
Jamesoniella autumnalis			III		
Dicranum flagellare			III		
Ptilidium pulcherrimum			III		
Favolus alveolaris			III		
Entodon seductrix			III		
Oncophorus wahlenbergii			III	III	III
Dicranum scoparium			III	III	III
Plagiomnium cuspidatum			III	V	V
Geocalyx graveolens			III		III
Mnium spinulosum					IV
Bryhnia novae-angliae					IV
Plagiothecium laetum					III
Plagiomnium ciliare					III
Plagiothecium sp.					III
Mitchella repens				III	
Uvularia sessiliflora				III	
Circaea lutetiana				III	
Taraxacum officinale					IV
Aralia nudicaulis					III
Maianthemum canadense					III
Asarum canadense					III
Adianthum pedatum					III
Epipactis helleborine					III
Thalictrum dioicum					III
Viola septentrionalis					III
Caulophyllum thalictroides					III
Trillium grandiflorum					III
Geranium robertianum					III

Table 15 cont.

Stage of decay	1	2	3	4	5
Shrub seedlings					
Cornus alternifolia			III		III
Ribes sp.					III
Tree seedlings					
Acer saccharum				V	V
Acer spicatum				III	III
Tsuga canadensis				III	
Betula sp.					III
Ostrya virginiana					III

Table 16

Constancy classes (I-V) of plants on logs in decay stages 1 to 5 for plot 5.

Stage of decay	1	2	3	4	5
Number of species	3	9	7	9	0
Fomes fomentarius	IV				
Dicranum montanum	II				
Cephalozia media	II	III	V	V	
Ptilidium pulcherrimum		III			
Plagiothecium laetum		III			
Brachythecium sp.		IV			
Hypnum pallescens f. *reptile*		III	V		
Plagiomnium ciliare		IV	V		
Campylium hispidulum		IV	V		
Plagiothecium sp.		III	V		
Heterophyllium haldanianum		III	V	V	
Lepraria sp.			II		
Lophocolea heterophylla				V	
Plagiothecium denticulatum				II	
Plagiomnium cuspidatum				II	
Aralia nudicaulis				II	
Dryopteris spinulosa				II	
Filices (prothalli)				II	
Tree seedlings					
Acer spicatum				II	

In plot 6 (Table 17) logs in all decay stages are present. On logs in decay stage 1 two fungi, four lichens and one moss are found. This moss, the appressed growing *Hypnum pallescens*, occurs also on logs in decay stages 2 to 4. Two mosses are restricted to stage 2. One moss and one lichen are present on logs in decay stages 2 and 4 whereas the moss *Heterophyllium haldanianum* occurs continuously on logs in decay stages 2 to 4. Two mosses are found only on logs in decay stage 3 and one moss and one lichen are restricted to stage 4. On logs in decay stage 5 two mosses, two herbs and one tree species are present. Logs on steep slopes (20^{o} to 40^{o}) and especially those which are deposited along the contour lines are exposed to moving rubble and soil. It was observed that this material accumulated on one side of the log and became mixed with the broken decayed wood pieces. In these sites soil-inhabiting species such as *Plagiomnium cuspidatum* and *Eurhynchium pulchellum* established themselves on the log.

In plot 7 (Table 18) no distinct species group can be noted for logs in decay stage 1. On logs in decay stages 3, 4 and 5, however, mosses, hepatics and lichens are found which are specific for a particular decay stage (e.g. decay stage 3: three lichens, one moss; decay stage 4: one moss, one hepatic, one shrub species and one tree species; decay stage 5: three mosses, one hepatic, two herb species and one shrub species). The other species show either some continuous distribution over certain decay stages or are absent in a certain stage of decay (e.g. three lichens in decay stage 2). One

Table 17

Constancy classes (I-V) of plants on logs in decay stages 1 to 5 for plot 6.

Stage of decay	1	2	3	4	5
Number of species	7	6	4	6	5
Fomes fomentarius	III				
Ganoderma applanatum	II				
Parmelia sulcata	II				
Parmelia physodes	II				
Pertusaria sp.	II				
Bacidia sp.	I				
Hypnum pallescens f. *reptile*	II	IV	V	V	
Dicranum viride		III			
Dicranum flagellare		III			
Cladonia squamosa		IV		V	
Dicranum montanum		III		V	
Heterophyllium haldanianum		III	V	V	
Campylium hispidulum			II		
Plagiomnium ciliare			II		
Brachythecium salebrosum				V	
Cladonia coniocraea				III	
Plagiomnium cuspidatum					V
Eurhynchium pulchellum					II
Epipactis helleborine					III
Solidago sp.					II
Tree seedlings					
Ostrya virginiana					V

Table 18

Constancy classes (I-V) of plants on logs in decay stages 1 to 5 for plot 7

Stage of decay	1	2	3	4	5
Number of species	4	4	13	9	10
Cladonia sp. (squamules)	V	V	V		V
Lecidea scalaris	V		III		
Bacidia sp. II	V		IV		
Cladonia bacillaris	V		IV		
Dicranum flagellare		IV	V	V	V
Cladonia coniocraea		III	III	V	
Hypnum pallescens f. *reptile*		II	II		
Ptilidium pulcherrimum			III	V	
Heterophyllium haldanianum			II	V	
Cladonia cristatella			II		
Lecidea sp.			II		
Cladonia floerkeana			II		
Dicranum montanum			II		
Dicranum viride				V	
Jamesoniella autumnalis				V	
Brachythecium sp.					V
Campylium hispidulum					V
Bryum caespiticium					V
Lophocolea minor					II
Aralia nudicaulis				V	V
Vaccinium myrtilloides (seedl.)				II	
Thalictrum dioicum					II
Saxifraga virginiensis					II
Viburnum alnifolium (seedl.)					II
Tree seedlings					
Betula sp.				V	

herb is found on logs in decay stages 4 and 5, whereas all other herbs are restricted to either stages 4 or 5.

In plot 8 (Table 19) one moss *Hypnum pallescens* is present on logs in all decay stages. Restrictive species/groups are encountered only on logs in decay stage 2 (one lichen, one hepatic and one fungus) and in stage 5, (three herbs). One moss is present from decay stages 2 to 5, whereas another one is found on logs in stages 3 to 5.

In plot 9 (Table 20) *Hypnum pallescens* shows an ecological behaviour similar to that in plot 8. This moss is present on logs in all decay stages. On logs in stage 2 a distinct group can be noted (three mosses, two (?) lichens and one fungus). A group peculiar to logs in decay stage 3 contains two mosses, and three lichens whereas one moss shows restrictive occurrence on logs in decay stage 5. A group of three mosses and one hepatic which is found on logs in decay stage 2 extends either to logs in decay stage 3 or reappears on logs in decay stages 4 or 5. Only one moss is restricted to decay stages 3 and 5. Two herbs are found only on logs in decay stage 4 and one herb only in stage 5. Four herbs and two tree species are found on logs in decay stages 4 and 5.

The vegetational change on logs at different stages of decay is apparent for all plots. The richer a particular habitat is in species the better logs of different stages of decay can be differentiated.

e) Growth-forms:

A detailed analysis of growth-forms is a starting point for differentiating the structure of a plant community. The

Table 19

Constancy classes (I-V) of plants on logs in decay stages 1 to 5 for plot 8

Stage of decay	1	2	3	4	5
Number of species	1	5	3	3	6
Hypnum pallescens f. *reptile*	V	V	III	V	V
Cladonia sp. (squamules)		IV			
Ptilidium pulcherrimum		III			
Fomes fomentarius		II			
Brachythecium sp.		II	III	V	V
Heterophyllium haldanianum			V	V	V
Aralia nudicaulis					V
Maianthemum canadense					II
Carex communis					I

Table 20

Constancy classes (I-V) of plants on logs in decay stages 1 to 5 for plot 9

Stage of decay	1	2	3	4	5
Number of species	1	11	8	10	12
Hypnum pallescens f.	V	III	IV	IV	IV
Platygyrium repens		IV			
Cladonia squamosa		III			
Dicranum scoparium		III			
Cladonia sp. (squamules)		III			
Ganoderma applanatum		III			
Amblystegium juratzkanum		III			
Brachythecium salebrosum		III	IV		
Ptilidium pulcherrimum		III		II	
Brachythecium sp.		III			V
Plagiomnium ciliare		III			IV
Campylium hispidulum			III		
Cladonia coniocraea			I		
Dicranum flagellare			I		
Leskeella nervosa f. *nigrescens*			I		
Cladonia bacillaris			I		
Micarea prasina var. *sordidescens*			I		
Plagiothecium laetum					IV
Aster acuminatus				IV	
Smilacina racemosa				I	
Maianthemum canadense				III	V
Aralia nudicaulis				I	V
Uvularia sessilifolia				I	IV
Trillium grandiflorum				I	IV
Thalictrum dioicum					IV
Tree seedlings					
Acer saccharum				IV	V
Quercus rubra				I	IV

sum of the average cover degree for each species of a particular growth-form is indicated in the following diagrams (Figs. 30 to 32) by circles of different sizes

(i) Bryophyte growth-forms:

It is evident from Fig. 30 that turfs are present on logs especially in the wetter sites, from stage 2 on. There is a somewhat opposite tendency for the cushions, which show a high degree of cover on the slopes and only rarely extend to the wetter sites. Mats of all size classes are especially important on the wet, mesic, and dry-mesic sites (positions 2 to 5). In the small size class in which most hepatics fall, there are only minor fluctuations of cover from positions 2 to 5. For the larger mats of size classes 2 and 3, coverage values vary for different stages of decay. The mesic and dry-mesic habitats show high values. Coverage values from slope quadrats, positions 5 to 8, show no clear trend. However, in some positions, especially 3, coverage values for plants in size classes 2 and 3 increase gradually from wet to mesic habitats.

(ii) Lichen growth-forms (Fig. 31):

Foliose lichens are characteristic for the predominently corticolous stage 1. These are accompanied by crustose lichens on the wetter sites and by small fruticose and squamulose lichens on the drier sites.

Logs on the open shore in position one for stage 2 show considerable variety in growth-forms. Especially on the drier sites (positions 5 to 9) in this stage of decay fruticose and

Figure 30. Growth-forms of bryophytes (turfs, mats and cushions) in relation to positions on the gradients (1 to 9) and stages of decay (1 to 5); position 1 is situated on the lakeshore and position 9 is placed close to the hilltop; the size classes are defined on p. 40).

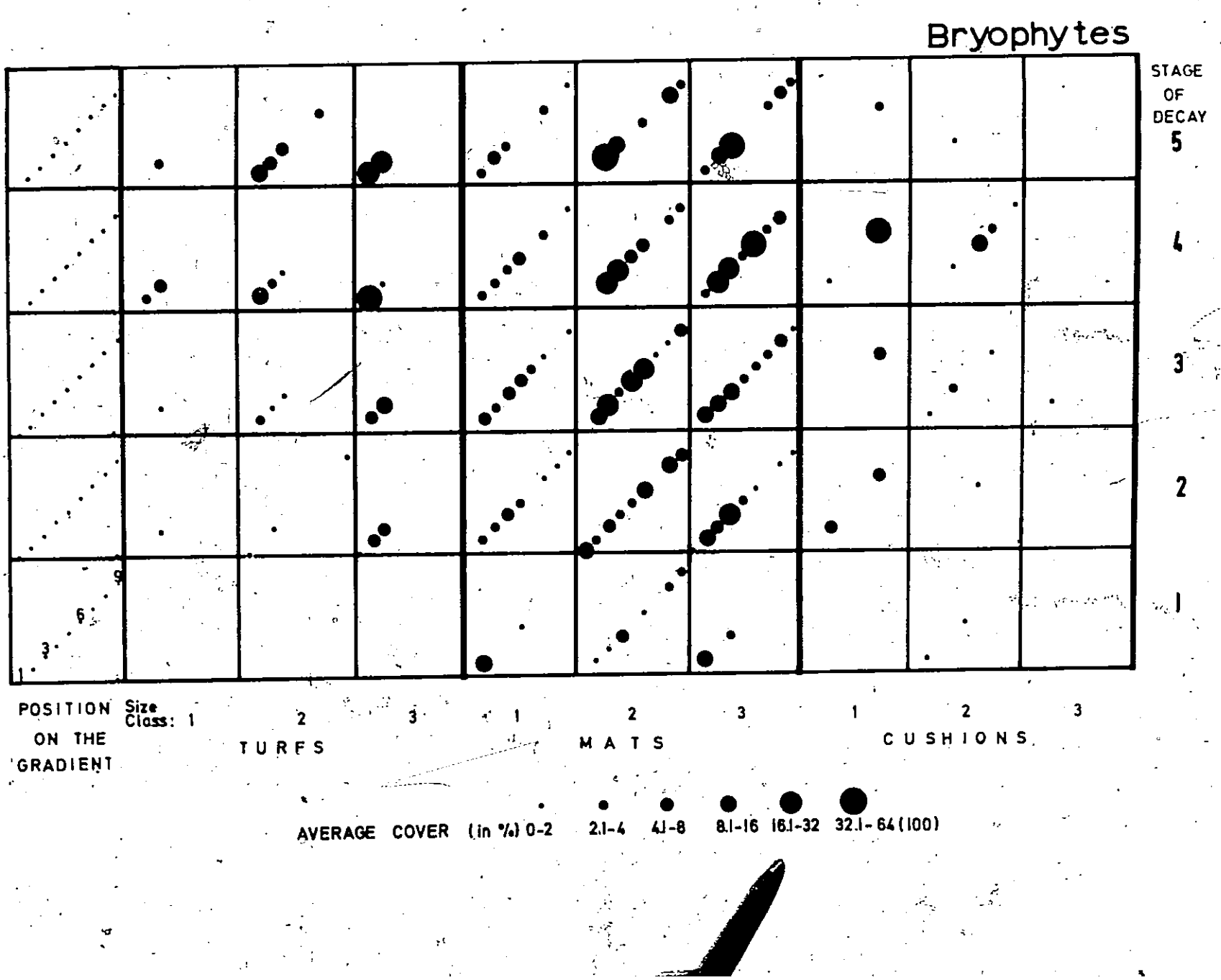
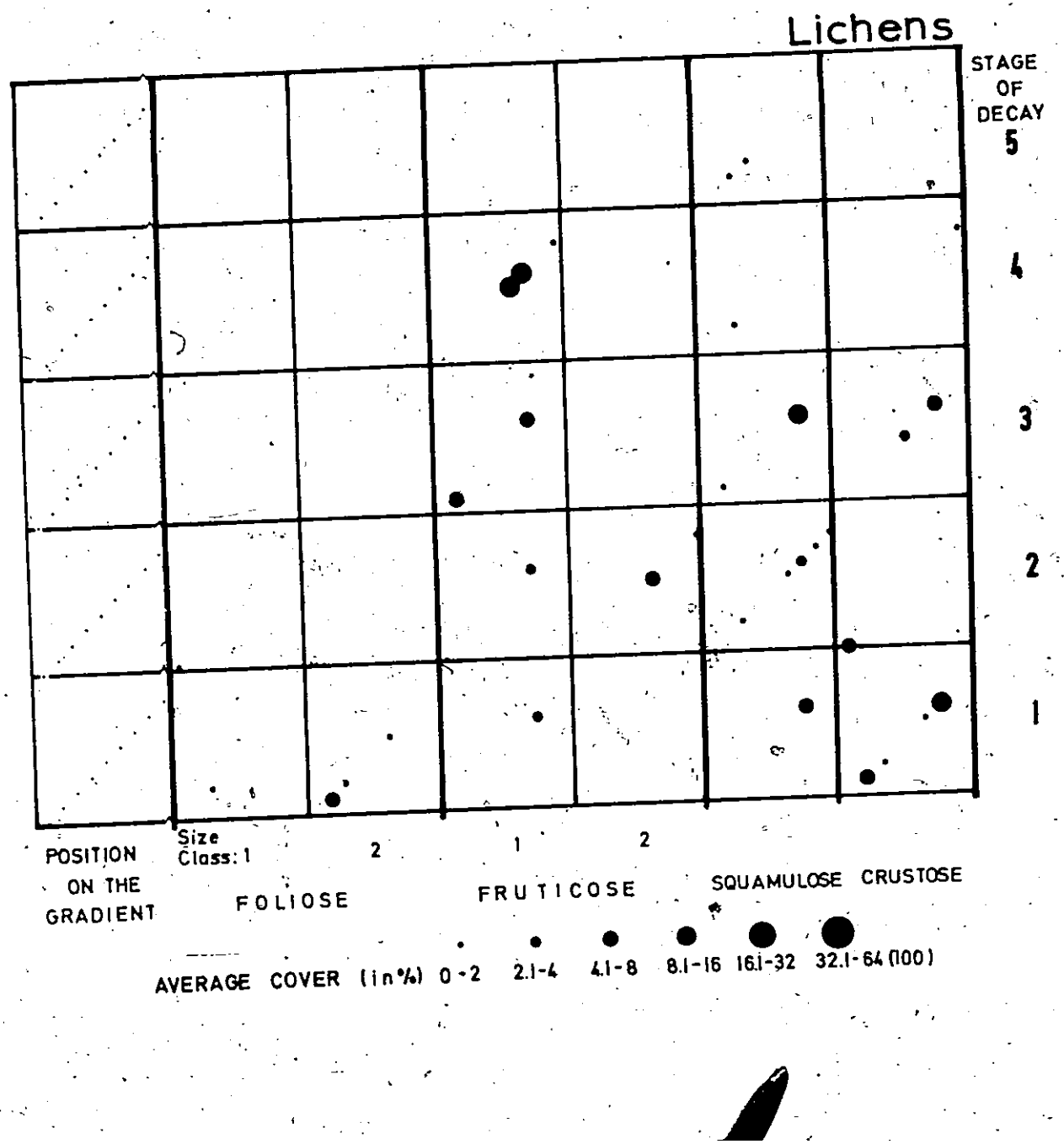

Bryophytes
STAGE OF DECAY
5
4
3
2
1
9
6
3
1
POSITION ON THE GRADIENT
Size Class: 1 2 3 1 2 3 1 2 3
TURFS
MATS
CUSHIONS
AVERAGE COVER (in %) 0-2 2.1-4 4.1-8 8.1-16 16.1-32 32.1-64 (100)

Figure 31. Growth-forms of lichens (foliose, fruticose, squamulose and crustose) in relation to positions on the gradient (1 to 9) and stages of decay (1 to 5).


Lichens
STAGE OF DECAY
5
4
3
2
1
POSITION ON THE GRADIENT
Size Class: 1
2
1
2
FOLIOSE
FRUTICOSE
SQUAMULOSE
CRUSTOSE
AVERAGE COVER (in %) 0-2
2.1-4
4.1-8
8.1-16
16.1-32
32.1-64 (100)

squamulose lichens have some importance. But as decay progresses all lichens are replaced by other plants and only a few squamules are present on the sites in stage 5. It should be noted that the squamulose growth-form has a certain morphological affinity with the fruticose growth-form. With the exception of squamules from *Psora scalaris* the squamulose growth-form is represented by young or suppressed forms of *Cladonia* species with a morphological potential of becoming a fruticose type.

(iii) Cormophyte growth-forms (Fig. 32):

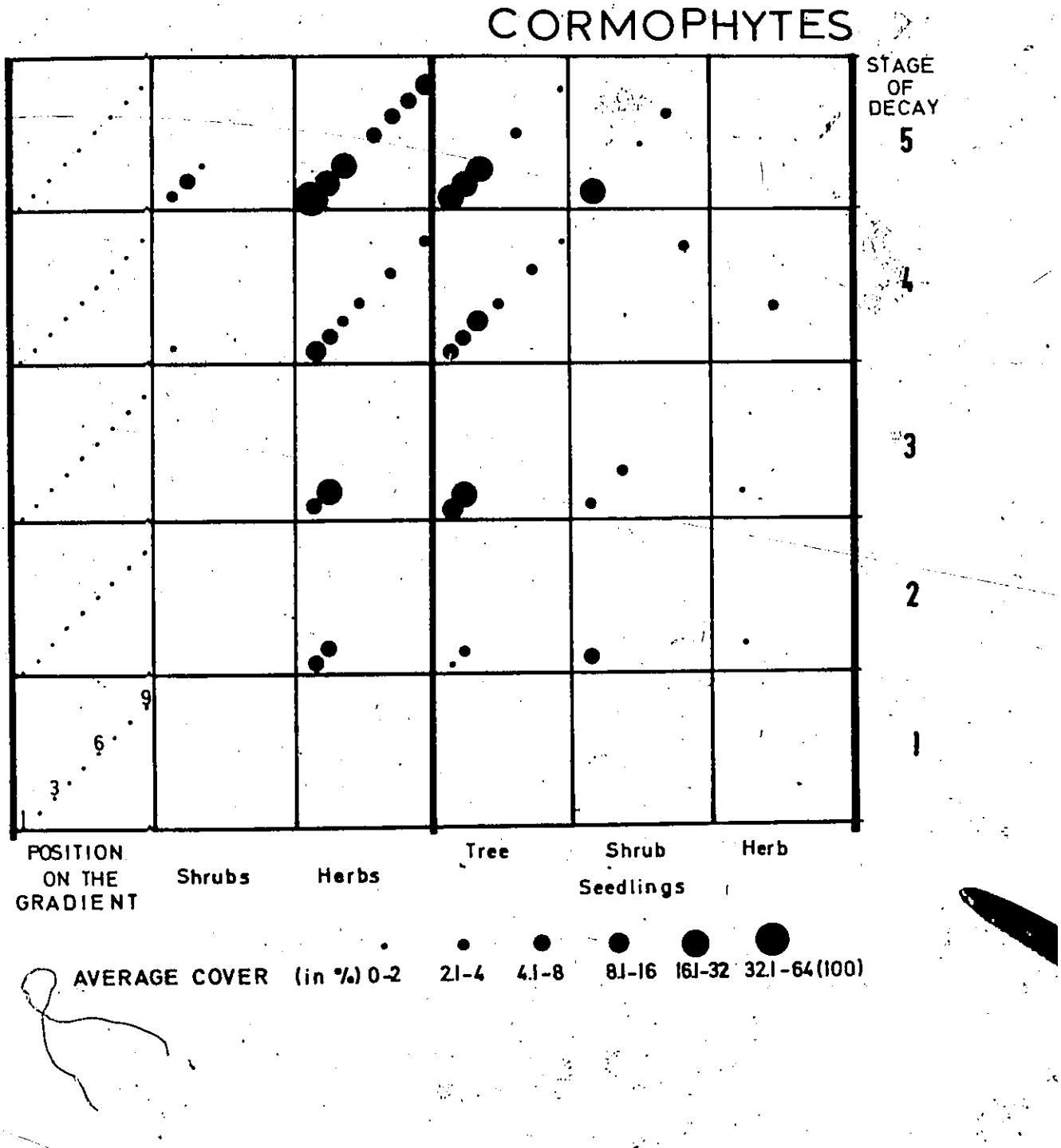
Whereas lichens decrease as decay progresses, vascular plants, especially herbs and tree seedlings increase in coverage. Both shrubs and trees (up to 0.2 m.d.b.h.) have been observed growing on logs in the wetter sites.

f) Discussion and conclusions

Species composition and growth-forms change along the investigated gradient. In a discussion of these changes as well as in the interpretation of succession of plant assemblages on decaying logs, some clarifications are necessary.

The first point that has to be made is that microquadrat data can best be integrated, for a particular stage of decay, when the chemical nature of the outer surface (bark, phloem, and xylem) is similar. One can expect the wood (xylem) of different logs to be comparable when it is in a particular stage of decay and has similar type of vegetation growing on it. Cryptogams were recorded on the bark proper mainly in decay stage 1 and less frequently in decay stage 2; on the

Figure 32. Growth-forms of cormophytes in relation to positions on the gradient (1 to 9) and stages of decay (1 to 5).


CORMOPHYTES
STAGE OF DECAY
5
4
3
2
1
9
6
3
1
POSITION ON THE GRADIENT
Shrubs
Herbs
Tree
Shrub
Herb
Seedlings
AVERAGE COVER (in %) 0-2
2.1-4
4.1-8
8.1-16
16.1-32
32.1-64 (100)

phloem, however, they were present only rarely in decay stage 2. Although the substrate for logs in decay stage 2 is somewhat heterogeneous, it seems that substrates for the other decay stages are uniform enough to justify the integration of microquadrat data.

The second point to be clarified is to know whether species assemblages growing on decaying wood interact or respond to a gradient of overriding importance in a linear fashion. The joint absence of species within plots for most stages of decay suggests that a curvilinear plant response (Groenewoud, 1965) cannot be expected for wood decay and associated substrate changes.

The physical and chemical interactions of the substrate on which cryptogams grow are still poorly understood. Little is known of the effects of wood breakdown substances on the physiological processes in lichens and mosses and of the effects of lichen substances on organisms which decompose wood. The astonishing patchiness of colonization phases on recently fallen logs, also observed by Philippi (1965), suggests that breakdown products may control processes of bryophyte establishment on some logs. It could, however, very well be that these open pioneer stages of succession reflect only the incomplete invasion phases of species due to other environmental factors (e.g. entrapping diaspores on rough substrate surface, etc.). When the outer wood cylinder is exposed over longer time spans, these possible effects seem to be masked by humus accumulated on the surface of the log. Another possibility

is that these substances have been chemically altered in such a way that they no longer exhibit allelopathic effects (Kleinert, 1970).

Fungistatic effects of lichen substances have been well documented (Rypacek, 1956, 1966) and antibiotic effects of lichens on bryophytes have been suggested (Sharp, 1963) though the ecological importance of these findings is not known. It seems possible that lichens could affect wood decaying organisms in the dry part of the gradient where acid-producing lichens (Culberson, 1969; Iskander et al., 1971) have some importance.

Wood decaying organisms may not only be affected by autotrophic plants on logs, as suggested above, but may indirectly have an effect on the green plants themselves on the logs. The action of decaying organisms can be expected to be in a two directions: (1) with moisture increase from decomposition products by wood-rotting fungi, the moisture available to green-cryptogams can be affected; (2) with increase of activity of wood decaying organisms, the CO_2-concentration will increase in the outer wood cylinder (Seifert, 1962) and, therefore, probably also in the ambient air. The first point may be responsible for the moist condition in which most spongy wood was generally found in mesic and wet sites. The second point is thought to be especially important for those cryptogams which are photosynthetically active in niches with very low light intensity.

The process of substance accumulation on logs has a cha-

racteristic impact on periodically inundated logs close to the lakeshore. Therefore, this part of the gradient with dominance of allochthonous nutrient supply will be discussed first while mesic and dry habitats will be discussed second.

Most logs in the wetter sites close to the lakeshore are inundated every year. As a result a thin subsoil develops on the logs and substrate factors from the outer wood cylinder no longer have an immediate effect on the species composition of cryptogams. It is only in the later stages of decay that wood may be exposed. Recolonization of these patches produces a mosaic which can be objectively analysed with pattern analysis techniques (Kershaw, 1964). Visually evident floristic pattern controlled by the dynamics of wood breakdown of the outer cylinder of the log can be directly recognized (e.g. Bongard, 1970).

In the mesic and dry habitats accumulation of humus was observed only in the later stages of decay suggesting that some steady state condition was reached. This steady state condition was found mainly in decay stage 3 and is reflected in a comparatively high number of species of mosses and lichens. Up to this stage, mechanical breakdown with gap formation and recolonization is not an important factor. The change in species composition along this part of the gradient is, therefore, attributed to the overriding importance of evaporation on the water balance, photosynthesis and respiration of cryptogams.

The mechanical breakdown of the outer wood cylinder from

stage 3 on was not comparable over the whole elevational gradient. It was observed that the logs in the wet forests changed in the later stages from round (crossectional view) to a more ellipsoid shape exposing the inner sapwood or heartwood only rarely in the segment investigated whereas in the dry and mesic sites, mechanical breakdown of sapwood frequently exposed the heartwood.

Results of this study indicate that trends in species composition and growth-forms exist on logs at different decay stages along an evaporational gradient of overriding importance from lakeshore to hilltop.

Succession takes place on decaying logs in each of the quadrats. With increasing porosity and breakdown of the log from decay stages 1 to 5 most sporophore forming polypores and lichens are replaced by mosses, herbs and tree seedlings.

3. Heney Lake

The aim of this section is to analyse ecological groups and species richness based on growth-forms as they occur along an elevational gradient at Heney Lake. The abundance of conifers observed along this elevational gradient contrasts to their relative scarcity as described in the Mont Saint-Hilaire section.

a) Plant communities present along the transect:

Trees and shrubs of the plant communities are presented here in the form of a differentiated table. In Table 21 eight plots (quadrats) and three subplots are listed. Degree of cover and approximate height classes are given.

(i) Lakeshore and wet forests:

The first plot is located in the lake and has scattered habitats suitable for tree and shrub growth (e.g. on old decayed stumps). In this plot there is evidence of beaver activity shown by a consistent deposition of logs across small creeks. The same phenomenon was also common in the second plot (2a, 2b). In these two habitats with extensive mudflats, trees such as *Fraxinus nigra*, *Ulmus rubra*, *Thuja occidentalis* and *Alnus rugosa* form an open woodland of communities which may best be placed in the *Thujetum occidentale* (Dansereau, 1959).

(ii) Wet-mesic forests:

In subplot 2c the forests consists of *Fraxinus nigra*, *Abies balsamea* and *Thuja occidentalis*. The frequent windthrow in this area results in differentiation of microtopographic

Table 21

Coverage of trees and shrubs along the Heney Lake transect.

Number of quadrat (plot)	1	2			3	4	5	6	7	8
Number of subplot		2a	2b	2c						
Tree layer I 15-20 m										
Tilia americana					3	2				
Betula papyrifera					2	2				
Betula alleghaniensis					2					
Fraxinus americana					2					
Acer saccharum						3				
Populus grandidentata						3				
Pinus strobus								2		
Tree layer II 10-15 m										
Fraxinus nigra				4						
Abies balsamea				2	2		3	2		
Acer saccharum					3	2	2			
Fagus grandifolia						2				
Tsuga canadensis							2	1		
Pinus strobus							2	3		2
Betula papyrifera							2			
Populus balsamifera							1			
Quercus rubra var. *borealis*							1	2	2	
Pinus resinosa								2	3	4
Picea glauca								2		
Populus grandidentata									2	
Tree layer III 5-10 m										
Thuja occidentalis	1									
Fraxinus nigra		3	4	1						
Salix sp.		1								
Abies balsamea				2	1	1	2	2	2	
Acer saccharum					2		2		2	
Acer spicatum					1	1				
Fraxinus americana					1					
Ostrya virginiana						2			2	
Acer pensylvanicum						2				
Tsuga canadensis							3		2	
Quercus rubra var. *borealis*							1		3	2
Betula papyrifera									2	
Picea glauca									2	
Pinus resinosa										3

Table 21 cont.

Number of quadrat (plot)	1		2		3	4	5	6	7	8
Number of subplot		2a	2b	2c						
Shrub layer I 1-5 m (or tree layer IV)										
Ulmus rubra	1	1	2							
Nemopanthus mucronatus		1								
Thuja occidentalis		2	2	2						
Alnus rugosa		2	2	2						
Picea mariana		1		1						
Betula papyrifera		1							2	1
Fraxinus nigra			2							
Abies balsamea			2	3	1	2	3	3	2	
Acer spicatum				1	2	2				
Corylus cornuta				1						
Ostrya virginiana				1			2	2	1	
Fagus grandifolia					2					
Acer pensylvanicum					2	2	2	1	2	
Acer saccharum					3	3				
Tsuga canadensis						3	3			
Pinus strobus							2		2	
Amelanchier canadense							2			
Picea glauca							2			
Amelanchier laevis							1	2	2	
Cornus rugosa								3	2	
Quercus rubra var. *borealis*								2	2	
Pinus resinosa								1		
Acer rubrum									2	
Shrub layer II 0.3-1 m										
Spiraea alba	3									
Myrica gale	3	3	2							
Alnus rugosa	1		2							
Ulmus rubra			1							
Abies balsamea				2	1	2	2	2	2	2
Acer spicatum				1	2	2	2			
Corylus cornuta				1	1	3	1	1	2	
Tilia americana				1	1				1	
Amelanchier sp.				1			1			
Betula papyrifera					1		2			
Viburnum alnifolium					1	1				
Acer pensylvanicum					1	2	2	1	1	
Cornus stolonifera						1				
Acer saccharum						2	2			
Tsuga canadensis						1		1	2	
Diervilla lonicera							1	1	1	
Amelanchier canadense								2		
Cornus rugosa								1	3	
Ostrya virginiana								1	2	
Shepherdia canadense								1	2	2

Table 21 cont.

Number of quadrat (plot)	1				3	4	5	6	7	8
Number of subplot		2a	2b	2c						
Shrub layer II cont.										
Amelanchier laevis								1	2	2
Pinus strobus								1		2
Picea glauca								1		
Juniperus communis								1	2	
Acer rubrum									2	
Salix discolor									1	
Quercus rubra var. *borealis*									2	1
Amelanchier stolonifera										1
Tree seedlings										
Fraxinus nigra				3						
Thuja occidentalis				2						
Fraxinus americana					3					
Betula papyrifera					2	1	1			
Picea sp. *glauca*					1		1	1	1	
Acer saccharum						2	2		1	
Quercus rubra var. *borealis*						1		1	2	1
Tilia americana						1				
Populus sp.						1				
Pinus strobus						1	1	1	2	1
Acer spicatum							1			
Acer pensylvanicum							2	1	1	1
Abies balsamea								1	2	
Acer rubrum								1		

features. Parts on this nutrient-rich soil harbor a number of floristic elements which characterize the *Caryeto-Aceretum* (Grandtner, 1966).

(iii) Mesic forests:

These forests (quadrats 3, 4 and 5) apparently produce the tallest trees in the area, such as *Tilia americana*, *Acer saccharum*, *Betula alleghaniensis*, *Betula papyrifera* and *Populus grandidentata* and forests are best placed in the *Acereto-Betuletum* (Grandtner, 1966).

(iv) Xeric forests:

On the slope (quadrats 6, 7 and 8) *Abies balsamea*, *Tsuga canadensis*, *Pinus resinosa*, *P. strobus* and *Quercus borealis* may dominate locally. Most of these forests belong to the *Quercion boreale* (Grandtner, 1966) and apparently have been influenced in their species composition by past fires (dominance of pines) and/or by acidic litter produced by such plants as *Tsuga*, *Abies* and *Picea*.

b) Plants growing on decayed wood along the transect:

The species composition on logs along the gradient is evident from Table 22. Species with similar frequency curves are grouped together. These groups are called ecological groups (Ellenberg, 1956) when they contain plants with similar habitat preferences. A number of ecological groups in similar habitats are called an ecological sequence (Ellenberg, 1956). Twelve ecological sequences of cryptogams are distinguished and are presented in more detail in connection with Fig. 33. Parts of the ecological sequences are in a wide sense equiva-

Table 22

Percent frequency of plants on logs for all decay stages in relation to position on the gradient (plots 1 to 8).

No. of Ecol. Group	Number of quadrat (plot)	1	2	3	4	5	6	7	8
1.1	*Calliergonella cuspidata*	33							
	Hypnum lindbergii f. *demissum*	19							
	Campylium polygamum	13							
	Fissidens osmundioides	2							
1.2	*Aulacomnium palustre* f. *polycephala*	19	2						
	Climacium dendroides	8	46						
1.3	*Bryum pseudotriquetrum*	20	4	2					
	Chiloscyphus pallescens	6	14	1					
1.4	*Hypnum lindbergii*	44	30	17	0.4				
1.5	*Brachythecium plumosum*		6						
	Rhizomnium appalachiensis		6						
	Fissidens cristatus		4						
	Mnium marginatum		2						
	Hypnum pratense		2						
	Plagiomnium rugicum		0.3						
	Leptodictyum riparium		0.3						
	Atrichum altecristatum		0.3						
	Trichocolea tomentella		0.3						
1.6	*Conocephalum conicum*		5	5					
	Bryhnia novae-angliae		3	4					
2.1	*Cephaloziella rubella* var. *sullivantii*		1						
	Cephalozia catenulata		2						
2.2	*Sphagnum nemoreum*		11						
	Leucobryum glaucum		1						
2.3	*Plagiochila asplenoides*		16	0.3					
	Rhytidiadelphus triquetrus		14	1					
	Riccardia palmata		4	1					
2.4	*Lepidozia reptans*		3	1		2			
2.5	*Thuidium delicatulum* var. *radicans*			5					

Table 22 cont.

No. of Ecol. Group	Number of quadrat (plot)	1	2	3	4	5	6	7	8
3.1	*Oncorphorus wahlenbergii*		7	3	3				
	Jungermannia lanceolata		4	3	2				
	Herzogiella turfacea		4	3	2				
	Riccardia latifrons		3	4	2				
	Blepharostoma trichophyllum		3	3	4				
	Harpanthus drummondii		2	5	8				
	Hypnum fertile		2	2	3				
	Geocalyx graveolens		2	1	1				
3.2	*Peltigera horizontalis*			1					
3.3	*Scapania glaucocephala*				2	1			
4.1	*Dicranum flagellare*	22	13	10	12	30	28	20	15
4.2	*Hypnum pallescens*	6	2	14	26	36	30	33	9
4.3	*Heterophyllium haldanianum*	2	18	34	45	11	4	12	8
5.1	*Haplocladium microphyllum*		15	7	25	1			
	Rhizomnium punctatum s. str.		5	25	3	1			
	Plagiomnium cuspidatum		3	21	16	2			
	Peltigera canina		2	7	5	0.2			
5.2	*Brachythecium oxycladum*			5	3				
	Brachythecium reflexum			4	1				
	Peltigera evansiana			3	0.2				
	Leptogium cyanescens			1	1				
	Entodon cladorrhizans			1	0.4				
5.3	*Plagiomnium ciliare*			22	9	3			
5.4	*Rhodobryum ontariense*				1				
	Brachythecium populeum				0.4				
	Peltigera praetextata				0.2				
	Eurhynchium pulchellum				0.2				
6.1	*Nowellia curvifolia*		7	6	7	0.4			
	Cephalozia media		7	6	1		0.3		
6.2	*Amblystegium serpens*		1					5	
6.3	*Amblystegium juratzkanum*			6	10				
	Campylium hispidulum			2	1				
	Mnium orthorrhynchum			2	1				
	Calypogeia suecica			1	0.2				
6.4	*Brachythecium rutabulum*			1			1		2

Table 22 cont.

No. of Ecol. Group	Number of quadrat (plot)	1	2	3	4	5	6	7	8
7.1	*Ptilium crista-castrensis*		6		1	1	3		
7.2	*Odontoschisma denudatum*		1			1	1		
7.3	*Pohlia nutans*		1				2	3	4
7.4	*Pleurozium schreberi*		5	2		11	13	8	11
7.5	*Jamesoniella autumnalis*		8	14	16	15	10	2	
	Tetraphis pellucida		4	6	4		4	2	
	Brachythecium salebrosum		2	33	21	4	0.3	9	
7.6	*Hypnum imponens*		17	19	4	10	3	1	1
	Dicranum scoparium f. *fragilifolium*		10	3/2	3	7	3	2	3
	Ptilidium pulcherrimum		5	5	11	65	76	46	70
	Lophocolea heterophylla		2	15	14	17	3	18	11
7.7	*Dicranum fuscescens*			1					
7.8	*Brotherella recurvans*			6	1				
7.9	*Plagiothecium laetum*			0.3		1	0.3		
7.10	*Drepanocladus uncinatus*			1		2		2	
7.11	*Dicranum longifolium*					0.2			
8.1	*Leucodon brachypus* var. *andrewsianus*		2						
	Neckera pennata		2						
	Parmelia saxatilis s.l.		1						
	Anaptychia palmatula		1						
	Rinodina sp.		0.3						
	Pyxine sorediata		0.3						
	Lepraria incana		1						
8.2	*Frullania eboracensis*		2	1	1				
8.3	*Crustose lichen* (sterile)		1	1			5		
8.4	*Platygyrium repens*		0.3	14	24	4			
8.5	*Physcia orbicularis*			1	1				
	Physcia millegrana			0.3	1				
	Heterodermia sp.			1	0.2				
8.6	*Pylaisiella polyantha*				1				
	Anomodon attenuatus				0.4				
	Porella platyphylloides				0.4				
	Orthotrichum obtusifolium				0.4				

Table 22 cont.

No. of Ecol. Group	Number of quadrat (plot)	1	2	3	4	5	6	7	8
8.6 (cont.)	*Physcia grisea*				0.2				
	Arthonia sp.				0.2				
	Radula complanata				0.2				
	Ulota coarctata				0.2				
9.1	*Graphis scripta*			1					
9.2	*Dicranum viride*				2	1			
	Bacidea sabuletorum				0.4	1			
9.3	*Ramalina* sp.						0.3		
9.4	*Physcia stellaris*						1	1	
10.1	*Mnium spinulosum*					4	1		
10.2	*Dicranum drummondii*					0.2	2	2	
10.3	*Bazzania trilobata*						3	1	
11.1	*Cladonia bacillaris*	6							
	Cladonia macilenta	2							
	Parmelia conspersa	2							
11.2	*Lecidea scalaris*	5				1			
11.3	*Cladonia cristatella*	11				3	1		7
	Cladonia gracilis	2				1	4	1	10
	Cladonia parasitica	2				1	1	2	2
11.4	*Cladonia chlorophaea*	14	1			3	13	5	7
	Hypogymnia physodes	2	2			1	11	4	
11.5	*Cladonia* sp. (squamules)	48	9	1	4	27	34	20	45
	Bacidia chlorococca	26	2	1		1	5	1	9
	Cladonia coniocraea	25	4	5	1	14	7	1	18
	Cladonia squamosa	5	5		9	7	10	10	9
	Parmelia sulcata	3	9	2	2	3	13	4	5
	Lecanora conizaea (*L. strobilina*)	3	1	2	2	2	2	12	7
11.6	*Usnea hirta*		0.3						
11.7	cf. *Calicium* sp.		3						
11.8	*Cetraria pinastri*		1				1		
11.9	*Parmeliopsis ambigua*		2			1	2		4
11.10	*Parmelia subaurifera*		2	0.3		1	5	1	9
11.11	*Parmelia rudecta*		3	1	3	1	1		

Table 22 cont.

No. of Ecol. Group	Number of quadrat (plot)	1	2	3	4	5	6	7	8
11.12	*Cetraria oakesiana*			1	3				
11.13	*Platismatia tuckermanii*			0.3			0.3		
11.14	*Dicranum montanum*			0.3	1		0.3		
11.15	*Lecanora chlarona* f. *pinastri*			6		1/3	5	11	9
11.16	*Micaraea prasina*					1			
	Lepraria sp.					1			
11.17	*Stenocybe* sp.					1	1		
11.18	*Mycocalicium parietinum*					1			4
11.19	*Ochrolechia androgyna*					1	2	7	
11.20	*Cladonia rangiferina*					0.4	12	2	8
11.21	*Usnea comosa*						1		
11.22	*Cladonia botrytes*						1	1	
	Cetraria halei						1	1	
11.23	*Cladonia cenotea*						2		2
11.24	*Bacidia* sp. II						3	2	7
11.25	*Cladonia floerkeana*							4	
11.26	*Lecidea granulosa* (ster.)								2
12.1	*Schizophyllum commune*			1					
	Fomes fomentarius			1					
12.2	*Phellinus igniarius*					1			
	Polyporus sp.					1			
12.3	*Polyporus tomentosus* s.l.							1	13	10
Herb and Shrub layer									
13.1	*Bidens frondosa*	54							
	Calamagrostis canadensis	30							
	Agrostis scabra	13							
	Spiraea alba	11							
	Carex leptalea	8							
	Ericaulon septangulare	5							
	Nemopanthus mucronatus	5							
	Lycopus americanus	5							

Table 22 cont.

No. of Ecol. Group	Number of quadrat (plot)	1	2	3	4	5	6	7	8
13.1 (cont.)	*Iris versicolor*	3							
	Sium suave	3							
	Sagittaria cuneata	2							
	Juncus brevicaudatus	2							
13.2	*Myrica gale* (0.01-0.2 m)	44	17						
	Hypericum ellipticum	34	11						
	Eleocharis acicularis	31	3						
	Lycopus uniflorus	30	18						
	Mimulus ringens	5	1						
	Cicuta bulbifera	5	0.3						
	Potentilla palustris	2	5						
	Carex pseudocyperus	2	3						
	Campanula uliginosa	2	0.3						
13.3	*Myrica gale* (0.2-2 m)		20						
	Carex disperma		13						
	Bidens connata		8						
	Carex blanda		1						
	Mentha canadensis		1						
	Thalictrum pubescens		1						
	Carex tribuloides		1						
	Aster cordifolius		1						
	Glyceria borealis		0.3						
	Onoclea cinnamomea		0.3						
	Muhlenbergia mexicana		0.3						
	Galium labradoricum		0.3						
	Chrysoplenium americanum		0.2						
13.4	*Galium obtusum*		5	0.3					
	Viola sp.		4	6					
	Rubus sp.		3	1					
	Dryopteris spinulosa		1	2					
	Circaea alpina		1	1					
	Viola pallens		1	1					
	Onoclea sensibilis		1	1					
	Arisaema atrorubens		1	1					
	Laportea canadensis		1	1					
13.5	*Trientalis borealis*		2		1				
13.6	*Maianthemum canadense*		1	0.3	5		2	2	5
13.7	*Brachyelytrum erectum*			2					
	Parthenocissus quinquefolia			1					
	Mitella nuda			1					
	Athyrium thelypteroides			1					
	Carex sp.			0.3					
	Ribes americanus			0.3					
	Dryopteris phegopteris			0.3					
	Dryopteris disjuncta			0.3					
	Athyrium filix-femina var. *michauxii*			0.3					

Table 22 cont.

No. of Ecol. Group	Number of quadrat (plot)	1	2	3	4	5	6	7	8
13.8	*Tiarella cordifolia*			16	1				
	Streptopus roseus			1	0.4				
	Lycopodium obscurum			0.3	2				
13.9	*Aralia nudicaulis*			2	2	1	1	5	1
13.10	*Pyrola secunda*				0.4				
	Medeola virginiana				0.2				
	Lonicera canadensis				0.2				
	Viburnum alnifolium				0.2				
13.11	*Cornus rugosa*				1			2	
	Gaultheria procumbens				0.4		1	3	
	Aster macrophyllus				0.2	1	0.3	4	
13.12	*Aster ptarmicus*				0.2				2
13.13	*Dryopteris marginalis*					0.2			
13.14	*Vaccinium myrtilloides*					0.4		7	
13.15	*Amelanchier* sp.						0.3		
	Cypripedium acaule						0.3		
Tree layer I 0.01-0.1 m									
14.1	*Ulmus* cf. *rubra*	2							
14.2	*Alnus rugosa*	5	2						
14.3	*Thuja occidentalis*	13	4	3					
14.4	*Betula* sp.		15	24					
	Fraxinus nigra		6	7					
	Picea glauca		5	2					
14.5	*Acer spicatum*		1	0.3		0.2			
14.6	*Acer rubrum*		1	1			1		
14.7	*Tsuga canadensis*			1	0.2	0.2			
14.8	*Acer pensylvanicum*			0.3	0.4	1	2		
14.9	*Acer saccharum*				4				
	Betula papyrifera				3				
	Ostrya virginiana				1				
14.10	*Quercus borealis*				1		2	2	1
14.10	*Pinus strobus*						0.3	1	3

Table 22 cont.

No. of Ecol. Group	Number of quadrat (plot)	1	2	3	4	5	6	7	8
Tree layer II 0.5-5 m									
15.1	*Thuja occidentalis*		8						
	Ulmus rubra		2						
	Alnus rugosa		2						
	Picea mariana		2						
15.2	*Betula papyrifera*		4	1					
15.3	*Abies balsamea*		10					3	
15.4	*Fraxinus nigra*			1					
	Acer pensylvanicum			1					
15.5	*Tsuga canadensis*			1	1				
	Acer spicatum			1	0.4				
Tree layer III 5-10 m									
16.1	*Acer saccharum*				3				
	Fagus americana				1				
	Abies balsamea				1				
	Ostrya virginiana				0.4				

lent to the associations described on page 121. Such a system of data organization permits also the groupings of the rarer species.

From Table 22 it is evident that the ecological groups of wet and mesic stands (quadrats 1 to 4) are very rich in species. The ecological amplitude of the species increases from positions one to eight (e.g. species in 1.1, 1.5 vs. 11.6 to 11.26; see Table 22). With greater environmental stresses as one moves up the gradient plants with high frequencies become less and less important. The "closed" ecological groups (i.e., with cover in most microquadrats close to 100 percent) whose members have high frequencies in the wet and mesic sites are gradually replaced by "open" groups (i.e., with coverage in a given quadrat never complete) when the hilltop is approached. Overlapping between groups along the gradient is found and this is evidently the result of the distribution of logs. The vertical component of this distribution is examined in terms of species richness. The horizontal component is examined in terms of sum of microquadrats of given types for particular log species and per position on the gradient. The results are presented in Fig. 32.

c) Space available to plant growth:

It is evident from Fig. 32 that some stands produce a large number of thin logs (e.g. positions 5,2; conifer logs, probably mostly *Abies*. See Fig. 33). In other stands large logs of certain species dominate (e.g. *Tilia*, position 4; *Pinus*, position 6). The rest of the stands either show similar

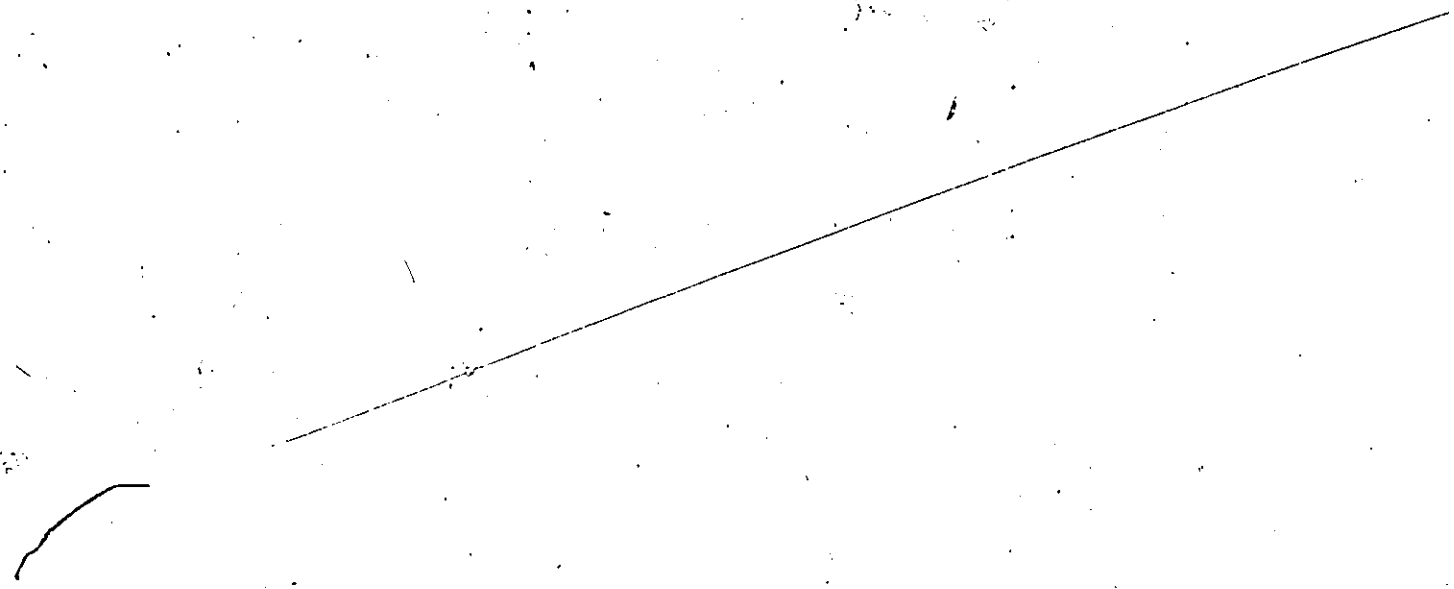
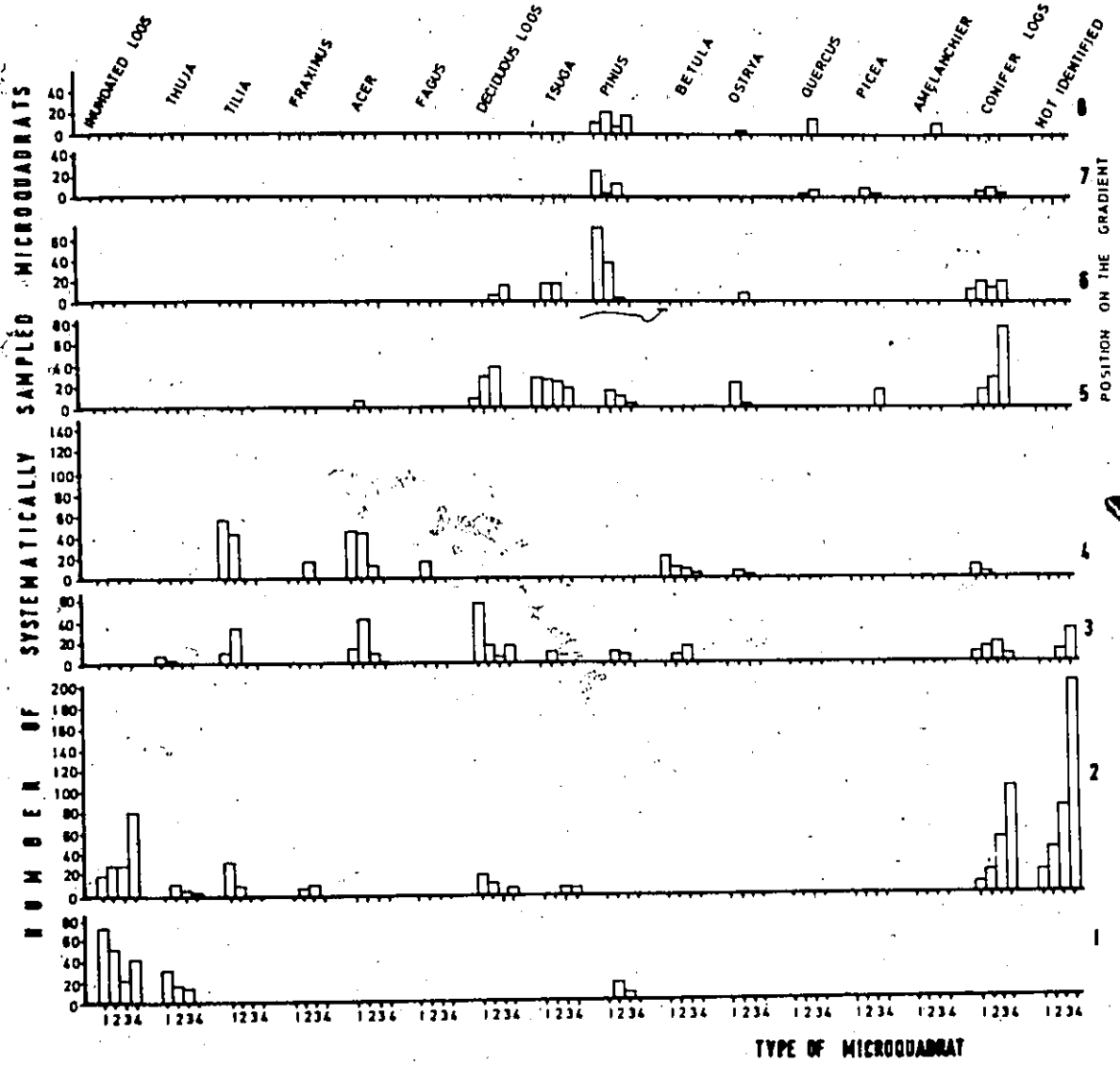


Figure 33. Total number of systematically sampled micro-quadrats per log-species as a function of position on the gradient.


UNRELATED LOGS
THUJA
TILIA
FRAXINUS
ACER
FAGUS
DECIDUOUS LOGS
TSUGA
PINUS
BETULA
OSTRYA
QUERCUS
PICEA
AMELANCHIER
CONIFER LOGS
NOT IDENTIFIED
NUMBER OF SYSTEMATICALLY SAMPLED MICROQUADRATS
POSITION ON THE GRADIENT
TYPE OF MICROQUADRAT
SIZE OF MICROQUADRATS 1 = 20 x 20 cm 2 = 14 x 29 cm 3 = 7 x 57 cm 4 = 3 x 133 cm

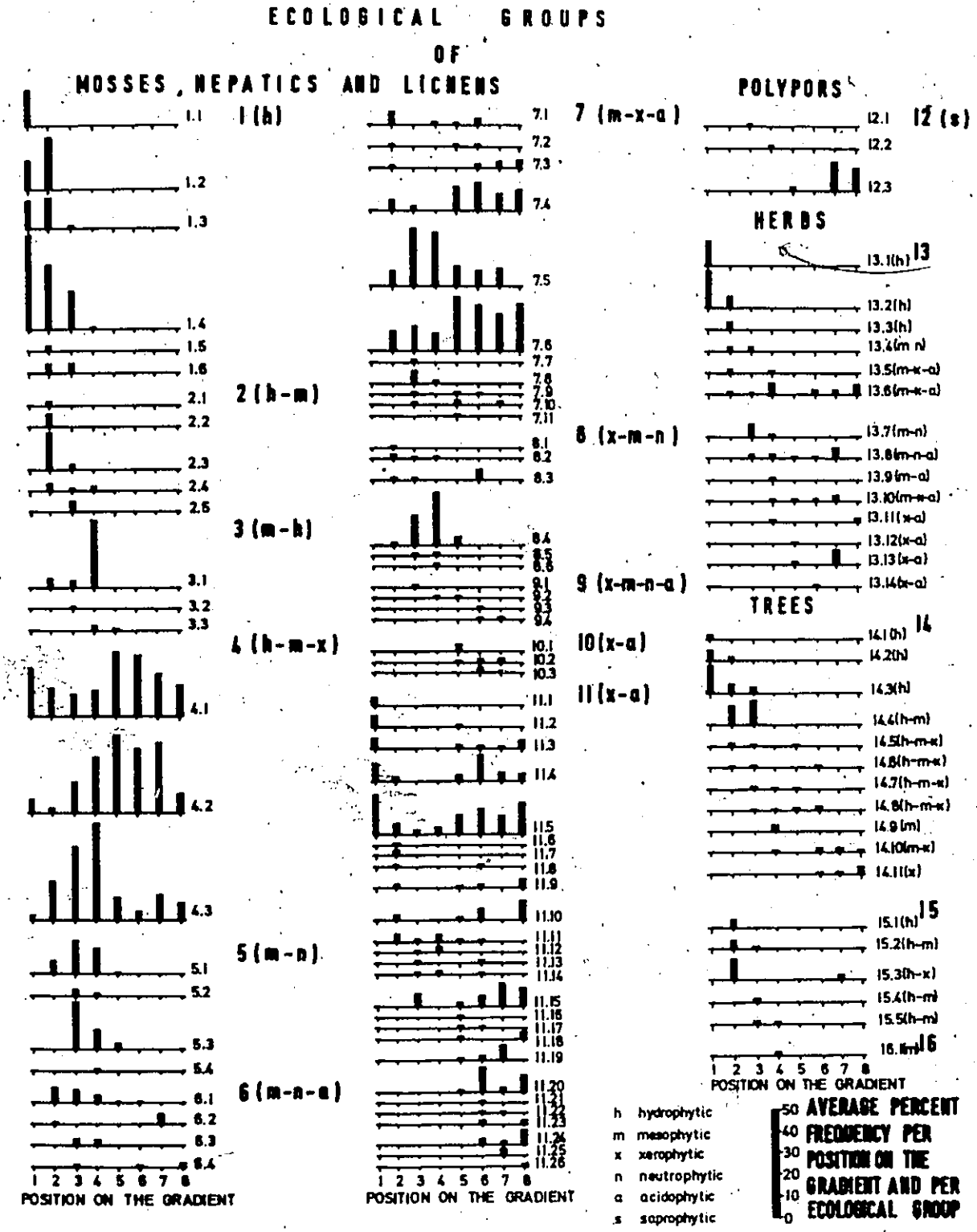
tendencies or have logs present in all diameter classes. The nearly even-aged structure of the dominant tree layer mentioned elsewhere (p. 87) does not seem to be present in larger areas along the investigated transect. Individual life spans of the different tree species along the gradient are evidently not synchronous. This means that the basic factor - log space - is not strictly comparable over the gradient. Allowance for this intrinsic error has to be made in subsequent discussions.

d) Ecological groups:

The data for the ecological groups are summarized in Fig. 34. The frequencies for each position and for all group members were averaged. This simplification allows us to compare the plant response of certain groupings with a few factor complexes of overriding importance (hydrophytic, mesophytic, xerophytic, etc., see Fig. 34). This reduction of a complex mass of microquadrat data to a simpler form facilitates its examinations. Since logs in all quadrats were systematically sampled and since log density is highest in forests close to the lakeshore but lowest on dry hilltop, data originating from the wetter sites seem less distorted by averaging frequencies than those of the drier sites. This procedure was preferred since it represents computations rather easy to understand and has been advocated for hypothesis generation (Goodall, 1970).

If one takes into consideration Gauch and Whittaker's (1972) coenocline data, it is evident from Fig. 34 that simple

Figure 34. Average percent frequency per position on the gradient and per ecological group.


ECOLOGICAL GROUPS
OF
MOSSES, HEPATICS AND LICHENS
1 (h)
2 (h-m)
3 (m-h)
4 (h-m-x)
5 (m-n)
6 (m-n-a)
7 (m-x-a)
8 (x-m-n)
9 (x-m-n-a)
10 (x-a)
11 (x-a)
POLYPORS
12 (s)
HERBS
13
TREES
14
15
16
POSITION ON THE GRADIENT
h hydrophytic
m mesophytic
x xerophytic
n neutrophytic
a acidophytic
s saprophytic
AVERAGE PERCENT FREQUENCY PER POSITION ON THE GRADIENT AND PER ECOLOGICAL GROUP

bell-shaped frequency curves rarely occur. They are either highly skewed towards the wet part of the gradient (e.g. 1.4) or towards the dry part (7.3, 11.24). Bimodal and irregular curves can also be extrapolated from Fig. 34. It is especially noteworthy that some more frequent species show a tendency towards a bimodal frequency curve (e.g. 4.1, 11.5, Fig. 34).

e) Species richness and stage of decay:

The vertical component within each quadrat is presented in relation to species richness per unit area (Fig. 35 and 36). The quadrats on the lakeshore and in the wet stands (Fig. 35) with extensive mudflats show logs lying at different levels above the ground or the water. The mesic and dry stands (positions 4 to 8) do not show zonal differentiation (Fig. 36).

In this study, decay stage of the wood and bark was not found to be synchronous. In Fig. 35 a capital A after the decay stage indicates that wood in microquadrats was found with bark while a B represents wood without macroscopically recognizable bark. The capital A and B are used only when, within a certain decay stage, both substrate types are present. No capital letter was used when only one substrate type was present. Bark is present in general in an early stage of decay whereas at later stages wood is mainly found.

On the open lakeshore (Fig. 35, position 1) all logs stay in decay stage 2. They may gradually lose their bark, break into pieces and fall over the years closer to the water (decay stage 2A with bark and 2B without bark). In the partially open wet forest (position 2) logs in decay stages 1 to 3 are found at the highest level above ground. When they slowly

Figure 35. Species richness per growth-form in relation to stage of decay and height above ground or water level for open lakeshore and wet forests.

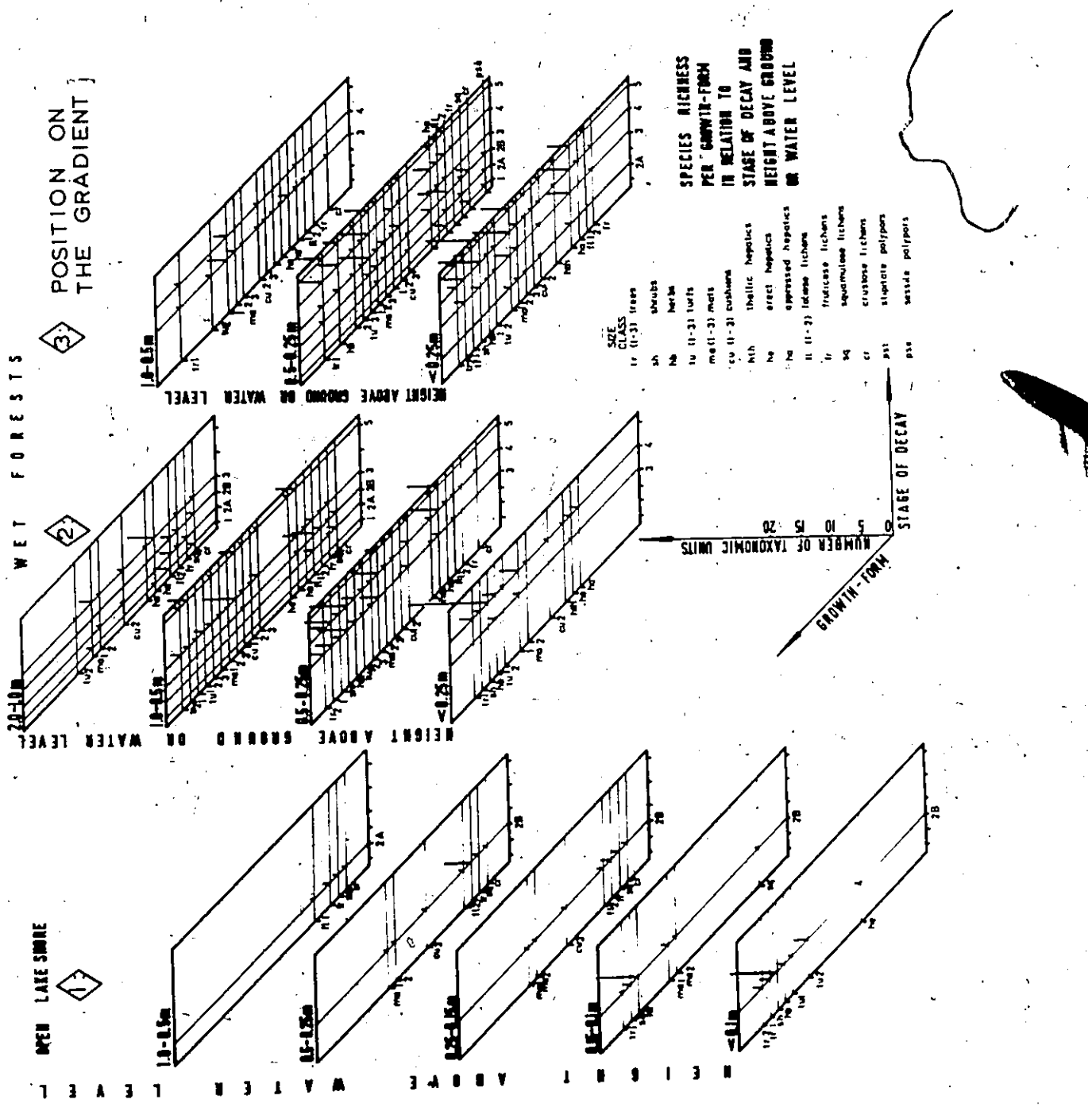
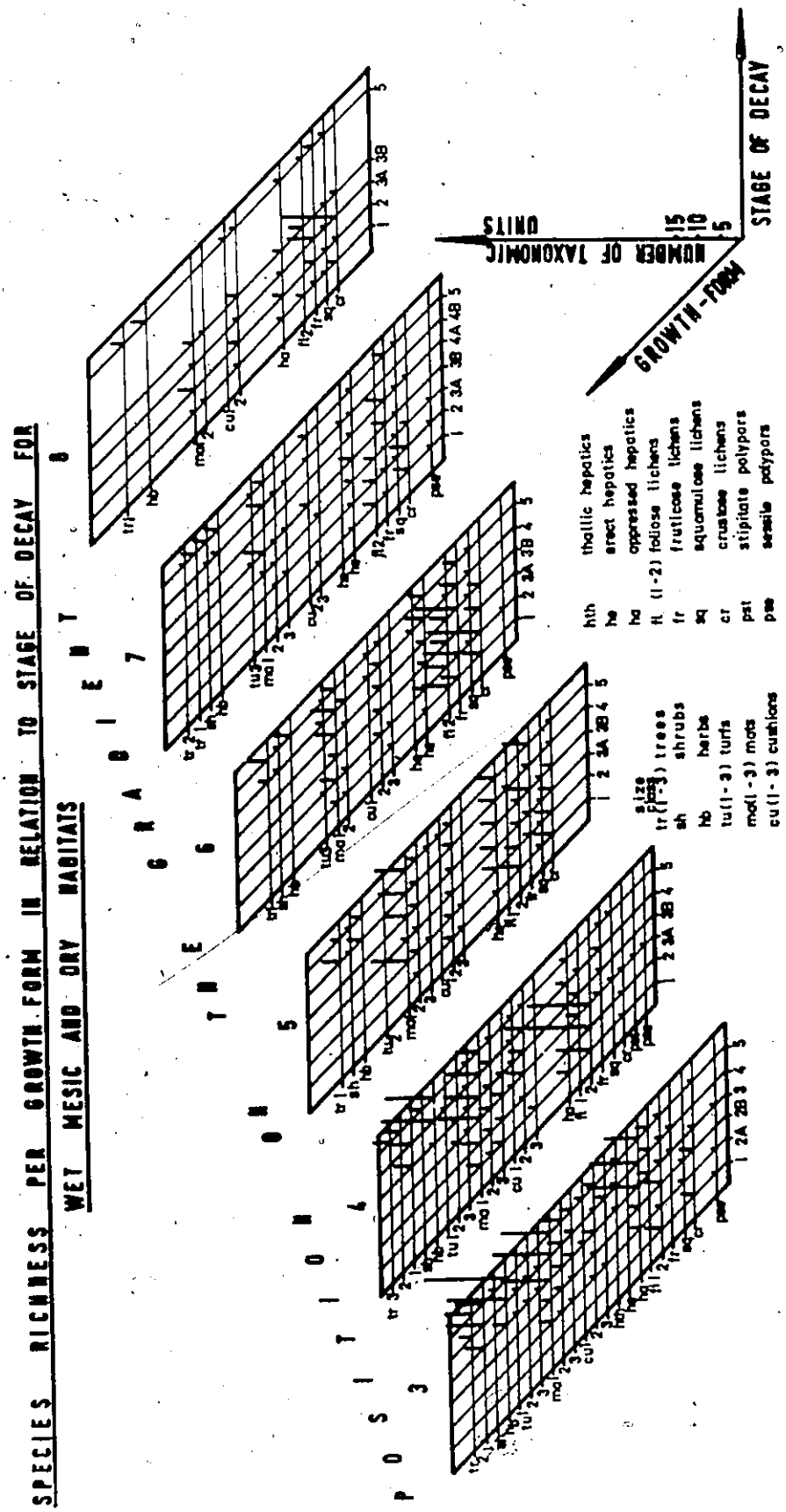

OPEN LAKE SHORE
WET FORESTS
POSITION ON THE GRADIENT
WATER LEVEL
HEIGHT ABOVE GROUND OR WATER LEVEL
SPECIES RICHNESS PER GROWTH-FORM IN RELATION TO STAGE OF DECAY AND HEIGHT ABOVE GROUND OR WATER LEVEL
SIZE CLASS
GROWTH-FORM
NUMBER OF TAXONOMIC UNITS
STAGE OF DECAY

Figure 36. Species richness per growth-form in relation to stage of decay for wet and dry habitats.


SPECIES RICHNESS PER GROWTH-FORM IN RELATION TO STAGE OF DECAY FOR
WET MESIC AND DRY HABITATS
POSITION 3 4 5 6 7 8
GRADIENT
NUMBER OF TAXONOMIC UNITS
5 10 15
GROWTH-FORM
STAGE OF DECAY
1 2A 2B 3A 3B 4A 4B 5
tr trees
sh shrubs
hb herbs
tu(1-3) turfs
mo(1-3) mats
cu(1-3) cushions
hth thallic hepatics
he erect hepatics
hd depressed hepatics
fl (1-2) foliose lichens
fr fruticose lichens
sq squamulose lichens
cr crustose lichens
pst stipitate polypore
pse sessile polypore

break down they finally may end up close to the ground or water in decay stages 3 to 5. When the forest becomes denser and multilayered (position 3) one can also find logs at a higher level above ground in a more advanced stage of decay. From Fig. 36 it is evident that the breakdown of bark does not seem to occur at the same rate as wood decay. When the dry hilltop is approached, logs with bark are found not only in decay stage 3 (as 3A), but also in decay stage 4 (as 4A).

On the open lakeshore, shrub and turf growth-forms have importance on logs close to the water level whereas lichens, especially fruticose forms, become more important at heights of 1 to 0.5 m above the water level. This tendency persists in position 2 where the number of growth-forms increases considerably. In these forests cushions, mats and hepatic growth-forms are well developed. In the closed wet forest (position 3) the species richness of the mat growth-form is noteworthy. When the species richness in wet-mesic stands (position 3, Fig. 36) is compared with that of mesic stands (positions 4 to 5) it is important to notice the sudden decrease in the number of appressed hepatics and herbs. The logs in position 3 show an increase in species richness with the advance of the decay. In positions 4, 5, and 6, however, an overall decrease in species richness with the progress in decay can be noticed. Only the lichen growth-forms show a somewhat reverse trend.

f) Discussion and conclusions:

The floristic gradient on logs for the Heney Lake tran-

sect is somewhat similar to the one described for Mont Saint-Hilaire. The assumptions mentioned and discussed in the Mont Saint-Hilaire section (p. 144) are also valid for this study. One difference between the two transects, however, is outstanding. The abundance of conifers on the upper slopes of the Heney Lake transect results in a higher species richness in lichen growth-forms especially fruticose *Cladonia* species. The floristic sequence is, therefore, influenced by the "resource availability" (Whittaker, 1972) along the gradient as well as by biogeographic factors. Generally speaking, abundance of resources means that a habitat is favourable for plant growth. This favorableness (Monk, 1967) with respect to cryptogams is discussed in more detail in the next paragraph.

To understand quadrat to quadrat variation in species richness or to interpret frequency curves of ecological groups one has to rely usually upon notions which express some intrinsic quality of habitat differences. When the only parameter for favorableness is species richness, then there is danger of circular arguments. In this study, however, some knowledge about variation in the log-space resource was obtained (Fig. 33, p. 164). In addition to this resource the general microclimatic variation along the transect (MacHattie and McCormack, 1961) is evident (p. 17). The favorableness for cryptogams seems directly influenced by atmospheric resource factors (e.g. light intensity, radiation, precipitation, etc.). In some cases these factors seem to operate

additively (open lakeshore) creating an overabundance of resource for certain species, for example lichens which are not able to establish themselves on constantly wet surfaces. From space and microclimatic factors one may, therefore, conclude that favorableness for bryophytes is highest in wet-mesic and mesic stands, whereas lichens require drier habitats.

From the frequency curves of the ecological groups certain hypotheses can be formulated. It is evident from Table 22 that certain ecological groups in the wet and mesic stands contain a large number of species. Positive association within one group resulting from similar habitat requirements seems to be the dominant operative mechanism of species distribution. When one considers only groups with similar operational habitats (Vandermeer, 1972) it looks as if positive association of plants within one group could be masked by negative association resulting from spatial exclusion. Both types of association between species cannot be differentiated from field data by direct means.

In the wet-mesic stands competitive spatial exclusion (Gause, 1934) may still be operative. Here a number of species with similar growth-forms and similar ecological amplitudes (4.1 and 4.2 versus 4.3) are found for which this competitive mechanism is still thought to be of prime importance.

Habitats with certain resource shortages (e.g. dry, excessively wet, highly unstable habitats, etc.) are either colonized by highly specialized species or by unspecialized adaptive species. For both opportunistic species groups,

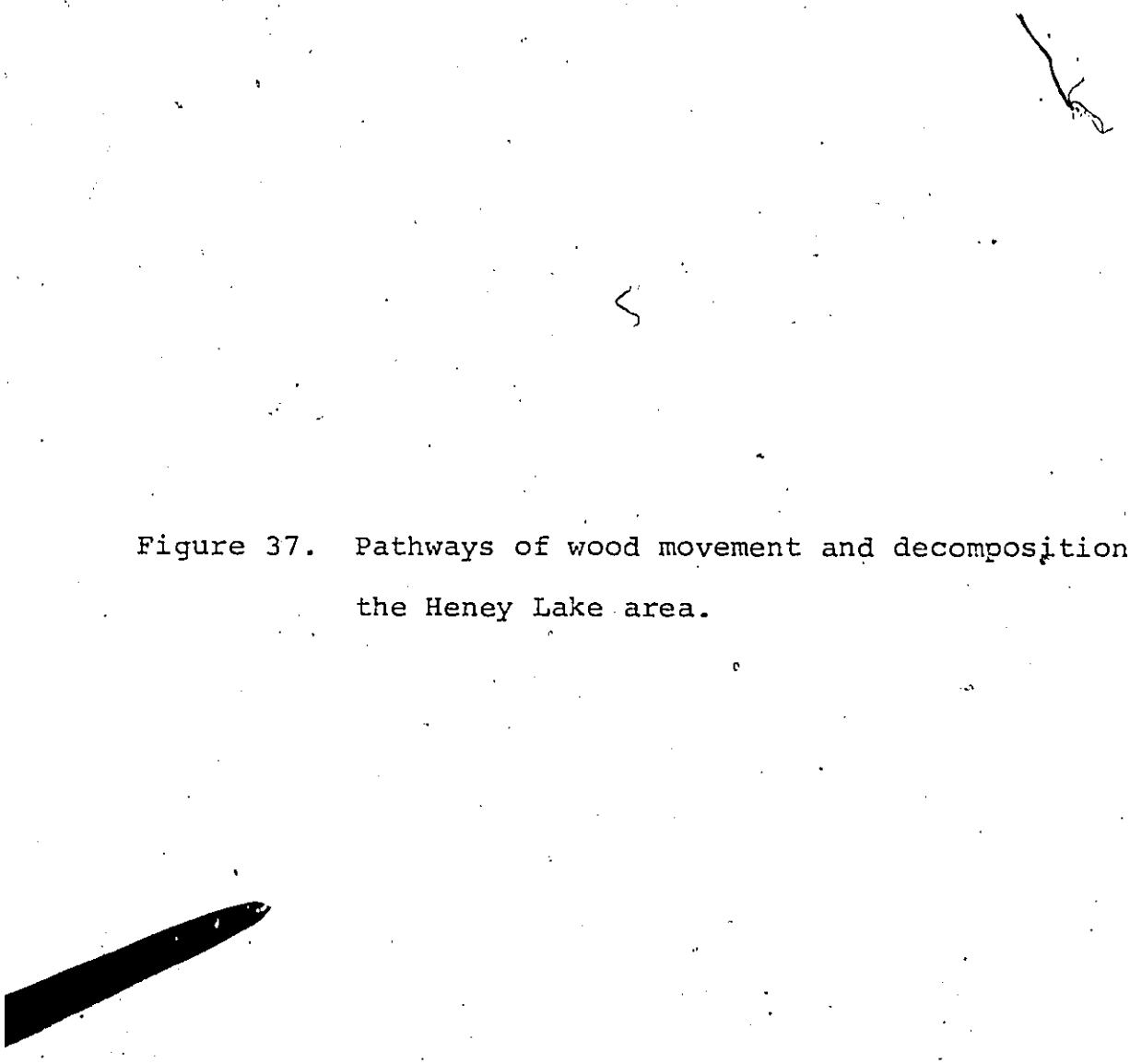
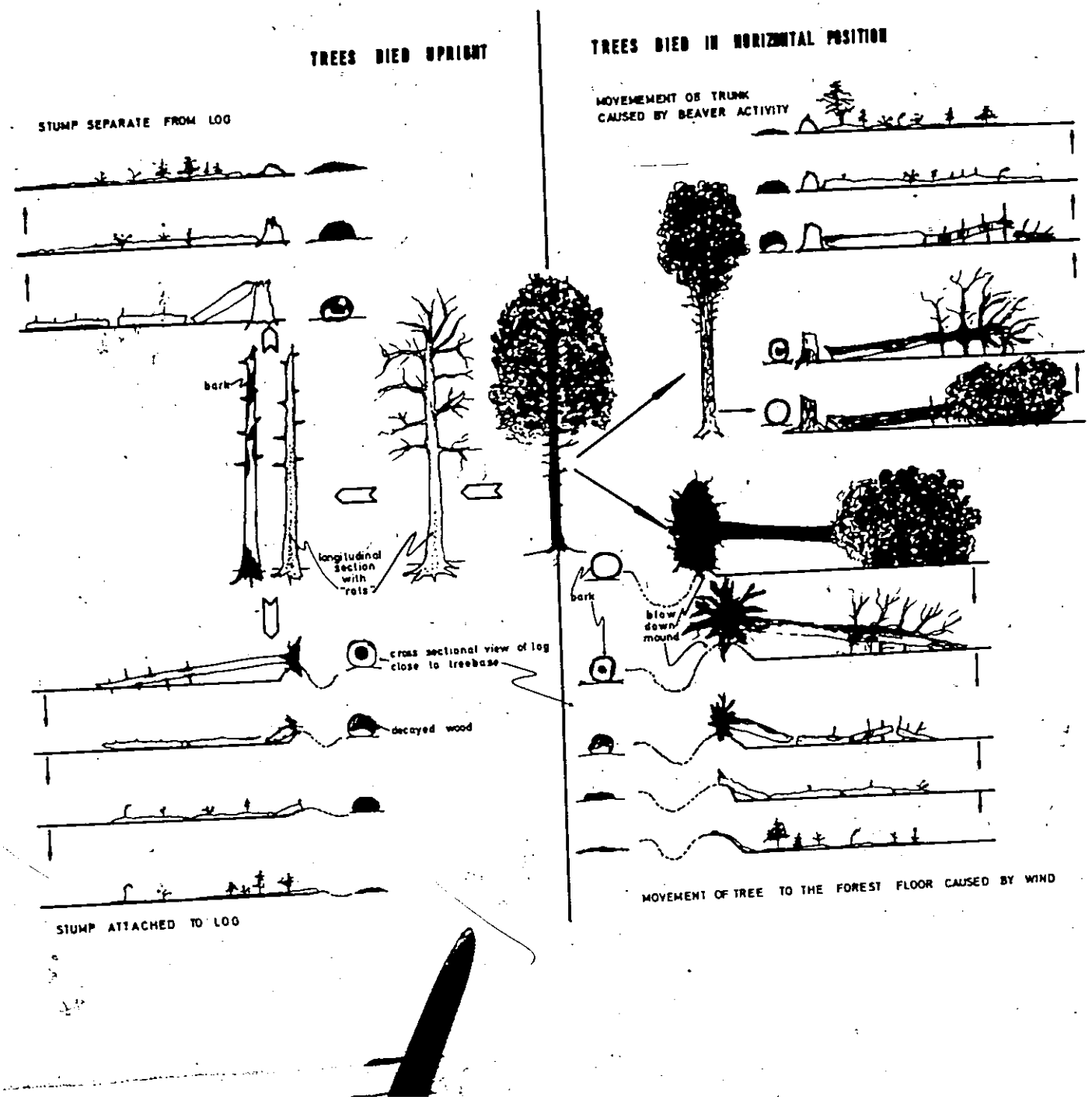


Figure 37. Pathways of wood movement and decomposition in the Heney Lake area.


TREES DIED UPRIGHT
STUMP SEPARATE FROM LOG
bark
longitudinal section with roots
cross sectional view of log close to treebase
decayed wood
STUMP ATTACHED TO LOG
TREES DIED IN HORIZONTAL POSITION
MOVEMEMENT OF TRUNK CAUSED BY BEAVER ACTIVITY
bark
blow down mound
MOVEMENT OF TREE TO THE FOREST FLOOR CAUSED BY WIND

other insects not only mine in the wood or in the area just below the bark, but often introduce secondary wood decaying organisms which all together are responsible, for loosening the bark. The beetle invasions take place in dead vertical trees as well as in those in a horizontal position. In these dead trees with rotten central portions ants and other insects establish their nests (Sanders, 1970). They often attract woodpeckers or even larger mammals such as Black Bears (*Ursus americanus*) which evidently are responsible for breaking out pieces of large logs to find the nests of bees or other insects.

The habitat diversity for insects must be quite enormous when logs in all decay stages are present (Blackman and Stage, 1924). As more logs in a certain area are found in advanced stages of decay, animals of the heterotrophic litter food chains are active until all wood material is recycled in the litter horizons of the soil.

4. Mont Albert

The objective of this section is to investigate the floristic pattern occurring on dead bark and wood at different stages of decay along a gradient from shrub communities of alpine tundra through the various krummholz forests to subalpine forests. Logistic problems made it necessary to arrange the plots in an irregular fashion but these plots include the main forest types which are present on the northern exposures of Mont Albert.

a) Plant communities of the elevational gradient:

The change in species composition along the elevational gradient is evident from Table 23. Certain plant assemblages show floristic similarities to some plant associations described by Dansereau (1959), Grandtner (1966) and Jurdant (1970).

Quadrat 1 (Table 23) probably represents a *Betuletum grandulosi* (Dansereau, 1959) with patches of the chionophilic *Juncetum trifidi* (Dansereau, 1959) in more elevated areas. Quadrat 2 at the treeline is, in major part a typical krummholz association which Grandtner (1966) named *Abietum-hudsoniae*. On top of the peaty mounds a *Vaccinietum vitis-idaeae* is developed while in the depressions a *Deschampsietum atropupureae* may be distinguished. Close to the top of the Amphibolite ridge one finds a subalpine krummholz association which could be named *Abietum hudsoniae empetretosum* if its recurrent presence could be demonstrated from other subalpine habitats of the Shickshocks. On the north side of the ridge,

Table 23

Coverage of plants in an altitudinal sequence of quadrats.

Quadrat (plot)	1	2	3	4	5	6	7	8	9
Tree layer I 10-25m									
Abies balsamea						4	1	4	2
Picea glauca							2		
Tree layer II 5-10m									
Picea glauca					3		2		2
Abies balsamea					2			3	4
Betula papyrifera var. *cordifolia*					2	2		2	2
Tree layer III 1-5m									
Abies balsamea f. *hudsonia*			4	4	3	3	1	2	3
Picea glauca f. *parva*			3	2	2		1		
Betula papyrifera s.l.					2	1	2	1	2
Amelanchier bartramiana						2			
Shrub layer I 0.3-1m									
Abies balsamea f. *hudsonia*	3	2	2			2	3	3	3
Picea glauca f. *parva*	2		2				3		
Betula glandulosa		2			1				
Sorbus americana		1						1	
Viburnum edule		1	1				1	1	
Amelanchier bartramiana		2	2				2	1	
Betula papyrifera var. *elobata*		2				1	2	2	
Vaccinium ovalifolium								1	
Shrub layer II 0.03-0.3m									
Betula glandulosa	3	2							
Rhododendron lapponicum	2								
Salix reticulata	2								
Salix cf. *brachycarpa*	1								
Arctostaphylos alpina	1								
Vaccinium uliginosum var. *alpinum*	2	2							
Ledum groenlandicum	2	2							
Empetrum nigrum s.l.		1	1						
Kalmia angustifolia		1							
Kalmia polifolia			2						

Table 23 cont.

Quadrat (plot)	1	2	3	4	5	6	7	8	9
Shrub layer II cont.									
Betula papyrifera s.l.			1						
Rubus sp.			1						
Cornus canadensis			1	3	2	2	2	2	
Vaccinium uliginosum			2						
Phyllodoce coerulea				1					
Ribes lacustre				1					
Ribes glandulosa					2				
Rubus ideaus var. *strigosus*					2			1	
Vaccinium ovalifolium							1		
On exposed mounds									
Vaccinium vitis-idaea var. *minus*		2							
Vaccinium caespitosum		1							
In wet depressions									
Andromeda glaucophylla									2
Sorbus americana									2
Rubus idaeus									1
Rubus sp.									1
Cornus stolonifera									2
Acer spicatum									
On rocks									
Taxus canadensis									2
Tree seedlings									
Abies balsamea							1	2	
Betula papyrifera								2	
Herb layer I 0.3-2m									
Heracleum lanatum						2			
Actaea rubra						1			
Calamagrostis canadensis s.l.						2			
Solidago macrophylla						3			
Geum macrophyllum						1			
Athyrium filix-femina						1			
Herb layer II 0.01-0.3m									
Carex scirpoidea		2	1						
Juncus trifidus		2							
Deschampsia caespitosa var. *littorale*		2							

Table 23 cont.

Quadrat (plot)	1	2	3	4	5	6	7	8	9
Herb layer II cont.									
Scirpus caespitosa var. callosus	2	3							
Arenaria marcescens	1								
Solidago chlorolepis	1								
Streptopus roseus var. perspectus				1		1		2	
Solidago macrophylla var. tyrsoidea			2 1	1	1	1		2	
Clintonia borealis									
Linnaea borealis var. longiflora			2 1	2	1	1	1	2 1	
Trientalis borealis									
Lycopodium annotinun var. acrifolium				1	1				
Coptis groenlandica			1	2				1	
Dryopteris phegopteris			1	1	1			2	1
Maianthemum canadense			2	1					
Deschampsia flexuosa			1	2					
Athyrium cf. thelypteroides			1						
Smilacina trifolia			1						
Castilleja septentrionalis			1						
Scirpus sp.									
Lycopodium clavatum var. monostachyon			1						
Aster foliaceus s.l.				1					
Drypteris spinulosa s.l.					2	4		3	1
Oxalis montana					1	2	2	3	1
Mitella nuda					1			1	
Equisetum pratense					1				
Epilobium hornemanni					1				
Lycopodium lucidulum						1		2	
Aralia nudicaulis							1	2	
Dryopteris disjuncta								2	1
In wet depressions									
Deschampsia atropupurea			2						
Carex vaginata			1						
Carex paupercula			1						
Galium triflorum									2
Viola incognita									1
Calamagrostis canadensis s.l.									1

the typical krummholz association, the *Abietum hudsoniae* (Grandtner, 1966) is present.

The *Abies balsamea* forests at higher elevations are floristically similar to what Jurdant (1970) describes as *Betulo-Abietum athyrietosum*. However, nearby tall herb communities dominated by *Heracleum lanatum* are sufficiently distinct that they would be placed as a separate entity by researchers of the Zürich-Montpellier tradition (Braun-Blanquet, 1948). Quadrats 6 to 9 are composed of boreal forests of different age structures and are closely related to the *Betulo-Abietum dryopteritosum* (Jurdant, 1970). The assignment of this vegetation to this subassociation is uncertain. The presence of *Vaccinium ovalifolium* and a great number of cryptogams, especially hepatics, suggest that there is a difference between the vegetation of the Lac St-Jean area (Jurdant, 1970) and that of central Gaspé. Although the boreal forest in this area is much more uniform in floristic composition than are the forests of Mont Saint-Hilaire and Heney Lake, the local situation close to the treeline is an intricate mosaic of vegetation in which homogeneous patches are restricted to small areas only. The local richness of cryptogams is especially astonishing in niches which are relatively free of direct competition from higher plants.

b) Vegetational change on logs along the gradient:

In Table 29 the percent frequency for cryptogams on logs for each quadrat of the altitudinal sequence is given. The small twigs of the *Betula glandulosa* community harbour a

Table 24

Percent frequency in quadrat (plot) 1-9 calculated from presence absence data of all microquadrats sampled.

Number of plot	1	2	3	4	5	6	7	8	9
Number of microquadrats sampled in a plot	14	19	47	16	98	110	132	141	145
Lecidea symmicta	86								
Lecanora coilocarpa	7								
Cetraria nivalis	36	32							
Cetraria saepincola	36	10							
Ochrolechia frigida	14	16							
Cetraria islandica	7	4	2	6					
Cetraria halei	7			6					
Parmeliopsis hyperopta	14		38	38	22	24	31	6	1
Alectoria nigricans		16							
Ochrolechia frigida f. *gonatodes*		16							
Ochrolechia sp. I		16							
Parmelia septentrionalis		10							
Xylographa abietina		68			1				
Alectoria bicolor		16		13					
Cladonia mitis		5	4						
Cladonia bacillaris		5	11						
Cladonia sp. I (squamules)		16		13	21				
Mycoblastus sanguinarius		42		38			43		
Parmelia saxatilis		21		38	4		14		
Platismatia glauca		21		19			21	4	
Cladonia coccifera s.l.		10	55	44	8		2		
Cetraria pinastri		37	23	25	11	1	16	3	
Parmeliopsis ambigua		10	32	19	13	12	35	6	4
Cladonia cyanipes			15						
Lophozia hatcheri			6						
Crustose lichen (sterile)			6						
Bacidia sp.			4						
Stenocybe major			2						

Table 24 cont.

Number of plot	1	2	3	4	5	6	7	8	9
Lecidea granulosa (sterile)			21	19					
Cladonia carneola			11	6				3	
Cephalozia catenulata			4					6	
Plagiothecium sp.			2					3	
Cladonia bacilliformis			2	6					
Cladonia sylvatica			6		3				
Cladonia botrytes			26			3			
Cladonia alpestris			2				2		
Nephroma bellum			2	19	3				
Dicranum montanum			2		3	3			
Cladonia digitata			6		11	2			
Cephalozia media			4					11	5
Cladonia deformis			34	56	15		8		
Cladonia chlorophaea			1	19	4	1		1	
Cladonia rangiferina			6	6			2	9	
Ochrolechia androgyna			4			4	52	8	
Lophozia ventricosa s.l.			4				5	5	3
Cladonia cenotea			11		17	5	9	13	
Lophozia porphyroleuca			17	31	36		3	9	6
Cladonia squamosa			34	19	21	8	4	24	3
Lophozia longidens			13	50	13	9	12	11	
Dicranum fuscescens			17	38	10	34	21	45	37
Ptilidium pulcherrimum			15	50	23	39	31	23	20
Pleurozium schreberi			4	25	24	66	14	40	19
Cladonia amaurocraea				19					
Alectoria nadvornikiana				25					
Hypogymnia vittata				19					
Peltigera aphthosa				19					
Lecidea granulosa (fertile)				19					
Lophozia ventricosa var. *silvicola*				19	24				
Lophozia lycopodioides				6	2				
Hypogymnia physodes				13			14		
Icmadophila ericetorum				38				6	
Hylocomium umbratum				6	7	5			
Brachythecium starkei				19	26			2	
Ochrolechia sp. II				38	4	1			
Alectoria sarmentosa				19		4			
Cladonia cf. *coniocraea*				6			11	10	
Hylocomium splendens				19		21		5	49
Hypnum pallescens f. *pallescens*				19	15	6	5	4	11

Table 24 cont.

Number of plot	1	2	3	4	5	6	7	8	9
Cladonia cornuta					8				
Cladonia crispata					5				
Riccardia latifrons					5				
Micarea sp.					5				
Lecidea cf. *helvola*					4				
Brachythecium cf. *acutum*					3				
Bacidia arceutina					2				
Rhizomnium pseudopunctatum					1				
Cladonia uncialis					1				
Drepanocladus uncinatus					1				
Pohlia nutans					10	7			
Polytrichastrum alpinum					3		3		
Rhytidiadelphus subpinnatus					4		2		
Cladonia pleurota					14		1		
Cladonia gonecha					1			19	
Anastrophyllum hellerianum					8			18	
Calypogeia suecica					9			4	
Blepharostoma trichophyllum					10	3		14	
Cephalozia sp.					4		3		2
Lecanora chlarona f. *pinastri*					4	3	10	1	
Plagiothecium laetum					5	27		6	8
Plagiothecium roeseanum						2			
Lecidea cf. *cinnabarina*						3	4		
Mylia taylori						4		36	
Jamesoniella autumnalis						15		6	
Cephalozia leucantha						13		4	
Lophocolea heterophylla						6		4	
Cladonia cf. *cristatella*						3		2	
Brachythecium rutabulum						20			4
Brachythecium salebrosum						5			1
Anastrophyllum michauxii						5	4	3	
Cladonia gracilis var. *dilatata*						15	2	2	
Cladonia sp. II (squamules)						2	11	7	
Alectoria capillaris							8		
Ischnoderma resinosus							3		
Hypogymnia cf. *enteromorpha*							3		
Polyporus tomentosus s.l.							2		
Usnea dasypoga							2		
Calypogeia sp.							3	1	
Lophozia incisa								11	
Rhizomnium punctatum s.l.								7	
Lepidozia reptans								5	
Dicranum flagellare								5	

Table 24 cont.

Number of plot	1	2	3	4	5	6	7	8	9
Nowellia curvifolia								3	
Geocalyx graveolens								2	
Tetraphis pellucida								2	
Calypogeia cf. *neesiana*								1	
Scapania apiculata								1	
Lophozia ascendens								10	1
Herb and Shrub layer									
Lycopodium clavatum			6						
Chiogenes hispidula			6						
Rubus sp.			4						
Vaccinium uliginosum			2						
Linnaea borealis var. *longiflora*			4	19			1		
Coptis groenlandica			4				2	2	
Clintonia borealis			6		1	3		3	
Trientalis borealis			9	6	2		4	18	
Cornus canadensis			11	6	5	6	5	2	
Maianthemum canadense				6		2			
Streptopus roseus				13			1		
Oxalis montana				19	7	33	8	36	8
Galium triflorum					1				
Dryopteris phegopteris					1				22
Solidago macrophylla					7	26	2		
Mitella nuda					2	3		1	
Dryopteris spinulosa						3			
Lycopodium lucidulum						4		8	
Ribes lacustre								1	
Vaccinium sp.								1	
Aralia nudicaulis								1	
Tree seedlings									
Abies balsamea					8	28	8	22	4
Betula papyrifera						18	1	9	
Picea glauca						3	3	1	
Taxus canadensis								1	

special *Parmeliopsis* community. The presence of *Lecidea symmicta*, *Lecanora coilocarpa* and the usually soil-inhabiting *Cetraria* spp. show the floristic distinctness of this community. In quadrat 2 the *Cetraria* spp. persist and are accompanied by *Alectoria nigricans* and *Ochrolechia* spp. both of which are characteristic of alpine and arctic heather communities subjected to considerable mechanical or other environmental stresses during the winter (Friedel, 1961). Communities of old grey weathered wood are intricately mixed in quadrat 2. When these communities are situated above the mean snow level they often show *Xylographa abietina;* when they are close to the ground one finds a *Parmeliopsis* community with a number of *Cladonia* spp. When the continuous cover of the interwoven crown layer of the dwarf krummholz is present in quadrats 4 and 5 the epigaeic *Cetraria* spp. vanish and species of the *Parmeliopsis* community increase in frequency. *Cladonia cyanipes*, *C. carneola*, and *C. bacilliformis* are characteristic for these krummholz logs in open areas, where they occur rarely. Hepatics, mosses and lichens, especially *Peltigera aphthosa* and *Icmadophila ericetorum*, are more important under the densely interwomen krummholz layer.

The cryptogam component on logs in the boreal forest close to the krummholz (quadrat 5) reflects both openess as indicated by *Cladonia cornuta* and *C. crispata*, and the moist habitat with springs as indicated by the presence of *Rhizomnium pseudopunctatum* and *Riccardia latifrons* of this subalpine area. A distinct group of hepatics make it possible to dis-

tinguish the communities of quadrats 6 and 8 from those of quadrats 7 and 9. Logs in quadrat 7 are particularly rich in epiphytes, whereas the hepatics common to plots 6 and 8 are missing in quadrat 9.

c) Percent frequency of species within quadrats 1 to 4 in relation to stage of decay:

The data for this elevational sequence is presented in two parts. The first deals with the logs in the tundra and the krummholz communities whereas the second part describes the plant assemblages on rotten logs within the boreal forest.

In quadrat 1 and 2, wood in decay stages 1 and 4 was observed macroscopically. No fungal hyphae could be detected microscopically in wood at a "decay stage" 4 and it seems that the breakdown of grey weathered wood is mainly mechanical. The assignment of this wood to decay stage 4 is, therefore, tentative.

In quadrat 1 on thin decorticated twigs of *Betula glandulosa* only *Lecidea symmicta* is able to recolonize these unstable twigs (Table 25). Close to treeline, however, these grey weathered wood surfaces are more extensive and probably more stable as indicated by species richness (Table 26, see also Fig. 38). Only in protected fissures do *Ptilidium pulcherrimum* and *Dicranum* sp. appear (Table 26).

In quadrats 3 and 4 (Table 27 and 28) wood in decay stages 2 and 5 is not present. The logs remain in decay stage 1 in quadrat 3 for such a long time that even herbs can find a suitable habitat there. Floristic similarities exist for

Table 25

Percent frequency of species in relation to stage of decay in quadrat 1.

Stage of decay	1	2	3	4	5
Number of species	8	0	0	1	0
Lecidea symmicta	88			100	
Cetraria nivalis	63				
Cetraria saepincola	63				
Ochrolechia frigida	25				
Parmeliopsis hyperopta	25				
Lecanora coilocarpa	13				
Cetraria islandica	13				
Cetraria halei	13				

Table 25

Percent frequency of species in relation to stage of decay in quadrat 2

Stage of decay	1	2	3	4	5
Number of species	9	0	0	12	0
Platismatia glauca	80				
Parmelia saxatilis	80				
Alectoria bicolor	60				
Cladonia sp. (squamules)	60				
Ochrolechia sp.	60				
Parmelia septentrionalis	40				
Cetraria halei	40				
Cetraria pinastri	100			14	
Mycoblastus sanguinarius	20			50	
Xylographa abietina				93	
Parmeliopsis hyperopta				43	
Alectoria nigricans				21	
Ochrolechia frigida f. *gonatodes*				21	
Cladonia mitis				7	
Cladonia coccifera				7	
Cladonia bacillaris				7	
Cetraria islandica				7	
In fissures					
Dicranum fuscescens				7	
Ptilidium pulcherrimum				7	

Table 27

Percent frequency of species in relation to stage of decay in quadrat 3

Stage of decay	1	2	3	4	5
Number of species	30	0	17	20	0
Cladonia sylvatica	10				
Crustose lichen	10				
Cladonia mitis	6				
Ochrolechia androgyna	6				
Stenocybe major	3				
Dicranum montanum	3				
Cetraria islandica	3				
Peltigera canina	3				
Nephroma bellum	3				
Cladonia botrytes	32		11		
Parmeliopsis hyperopta	29		47		
Parmeliopsis ambigua	26		37		
Lecidea granulosa (sterile)	26		11		
Cetraria pinastri	13		37		
Cladonia cyanipes	13		16		
Ptilidium pulcherrimum	10		21		
Lophozia longidens	6		21		
Cladonia cenotea	6		16		
Cladonia carneola	3		21		
Pleurozium schreberi	3			14	
Cladonia coccifera s.l.	45		58	14	
Cladonia deformis	19		37	29	
Cladonia squamosa	13		47	43	
Dicranum fuscescens	13		5	43	
Lophozia porphyroleuca	6		11	57	
Cladonia chlorophaea			5		
Cladonia bacilliformis			5		
Lophozia ventricosa s.l.				57	
Cladonia digitata				43	
Cladonia rangiferina				43	
Cephalozia catenulata				29	
Cephalozia media				29	
Lophozia hatcheri				29	
Plagiothecium sp.				14	

Table 27 cont.

Stage of decay	1	2	3	4	5
Herb layer:					
Vaccinium uliginosum	3				
Trientalis borealis	6			29	
Clintonia borealis	3			29	
Lycopodium clavatum	3			29	
Coptis groenlandica	3			14	
Cornus canadensis				71	
Chiogenes hispidula				43	
Linnaea borealis var. *longiflora*				29	
Rubus sp.				29	

Table 28

Percent frequency of species in relation to stage of decay in quadrat 4

Stage of decay	1	2	3	4	5
Number of species	15	0	17	21	0
Parmelia saxatilis	75				
Alectoria nadvornikiana	50				
Alectoria sarmentosa	38				
Hypogymnia vittata	38				
Cladonia squamosa	38				
Nephroma bellum	38				
Platismatia glauca	38				
Alectoria bicolor	25				
Cladonia chlorophaea	25				
Cladonia sp. (squamules)	25				
Hypogymnia physodes	25				
Cladonia coniocraea	13				
Cladonia bacilliformis	13				
Cladonia carneola	13				
Cetraria halei	13				
Mycoblastus sanguinarius	50		40		
Ptilidium pulcherrimum	38		100		
Parmeliopsis hyperopta	38		60		
Cladonia coccifera s.l.	25		100		
Cetraria pinastri	25		40		
Lecidea granulosa (sterile)	25		20		
Cladonia amaurocraea	13		40		
Cladonia deformis	38		100	33	
Lophozia longidens	25		80	67	
Parmeliopsis ambigua			60		
Hypnum pallescens f. *pallescens*			60		
Cladonia rangiferina			20		
Cetraria islandica			20		
Icmadophila ericetorum			80	67	
Lophozia porphyroleuca			80	33	
Dicranum fuscescens			60	100	
Pleurozium schreberi			40	67	
Lophozia ventricosa var. *silvicola*				100	
Lophozia attenuata				100	
Lecidea granulosa				100	
Hylocomium splendens				100	
Hylocomium umbratum				100	
Peltigera aphthosa				100	
Brachythecium starkei				100	
Lophozia lycopodioides				67	
Dicranum scoparium s.l.				33	

plant assemblages on logs in decay stages 1 and 5. The lichens *Stenocybe major* and *Nephroma bellum*, however, with low frequencies on bark, do not colonize wood in decay stage 3 and *Cladonia bacilliformis* is not found in combination with epiphytes. With increasing porosity of the wood, hepatics increase in frequency but are not accompanied by tree seedlings. Creeping herbs, such as *Chiogenes hispidula*, *Cornus canadensis*, *Lycopodium* ssp. and *Linnaea borealis*, may have invaded this habitat by vegetative means.

When the gaps within the krummholz are closed as compared to the open treeline habitats on that side where massive influx of snow is believed to occur, the species richness increases especially on the bark in decay stage 1. The vigorous hepatic and lichen species such as *Ptilidium pulcherrimum*, *Cladonia coccifera*, *Cladonia deformis* attain high frequencies and leave little space for competitors. When the logs in decay stage 4 are positioned under the dense cover of the krummholz, however, mats of *Hylocomium* and *Brachythecium*, and cushions of *Dicranum fuscescens* can successfully compete with most fruticose lichens. Especially competitive are the epibryic *Icmadophila ericetorum*, *Lecidea granulosa* or the large *Peltigera aphthosa*.

d) Percent frequency of species within quadrats 5 to 9 in relation to stage of decay:

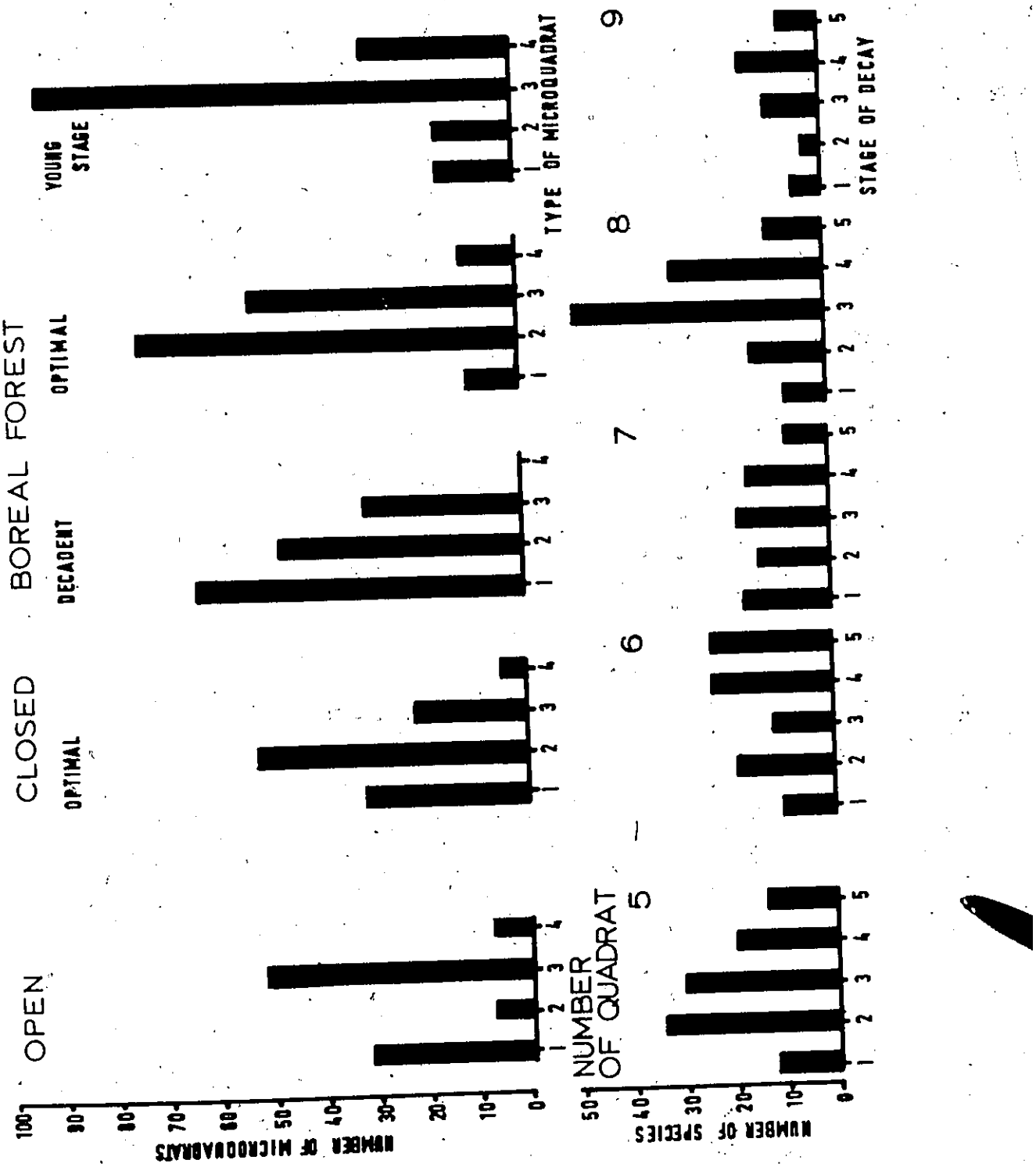
The typical cyclic pattern of northern forest types is here briefly described as an introduction to this section (Leibundgut, 1962; Plochmann, 1956). The cycle of the boreal

forest may be divided into three stages: young, optimal, and decadent or overmature stands. In young stands with high number of individuals per area competition results in a death rate of trees in small d.b.h. classes. In the optimal stands forests are characterized by a many-storied structure in which shade tolerant species occupy the space below the crown layer of the dominant trees. Most trees are in the middle age classes and since most logs belonging to the young stages have disappeared, the above-ground dead material is composed of medium-sized logs. The larger trees break down in the over-mature stands and the resulting gaps are filled in by younger trees. Therefore, one can expect the largest decaying logs in the decadent stages of the cycle. From the sequence of stages one can predict that a young stand should have a high number of elongated microquadrats (types 3 and 4, see p. 60). The optimal stand should yield a high number of rectangular microquadrats (type 2) whereas the decadent stage should produce big enough logs for square microquadrats (type 1).

In the upper part of Fig. 38 the actual sampled numbers of microquadrats are given. In the lower part of Fig. 37 species richness for a particular quadrat is indicated for stages of decay and will be discussed further below. It is evident from this figure that quadrats 6 and 8 fall within the predicted pattern for the optimal phase while quadrats 5 and 7 follow the expectations for the decadent phase, and quadrat 9 is typical for the young phase.

Most subalpine forests close to the krummholz, quadrat 5

Figure 38. Total number of systematically sampled microquadrats of certain types (see Fig. 9, p. 60) and number of species per stage of decay.


BOREAL FOREST
OPEN
CLOSED
OPTIMAL
DECADENT
OPTIMAL
YOUNG STAGE
NUMBER OF MICROQUADRATS
TYPE OF MICROQUADRAT
NUMBER OF SPECIES
STAGE OF DECAY
NUMBER OF QUADRAT
5
6
7
8
9

is an example, are usually quite open and have patchy vegetation patterns with large decorticated dead standing trees. These trunks fall as single trees to the forest floor and not in groups as most trees in the boreal forest do. Here dead trees or those weakened by heart rots fall to the forest floor usually with some bark left on the trunk. Therefore, the kinetics (Byallovich, 1969) of organic fractions from trees in the subalpine forests are different from those of the closed boreal forests.

Species richness, also included in Fig. 38, shows more or less low levels in the closed boreal forests of young and decadent stages (7, 9). The optimal stages (6, 8) of this forest on the other hand has high species numbers, especially on logs in the later stages of decay. The species numbers in quadrat 8 for stages 3 and 4 are larger than those in quadrat 6; however, they are small when compared with quadrats 7 and 9. This fact is thought to indicate that species richness is mainly controlled by factors associated with forest structure and less by factors which change with altitude.

Quadrat 5 (Table 29) as mentioned above has kinetics of wood fractions different from all other plots. The large standing grey weathered trees apparently decay in an upright position. The outer wood cylinder stays solid longer than any other log surface in the closed boreal forest. Decay seems to progress from the inside of the tree leaving the outer wood cylinder intact for considerable time spans. When

Table 29

Percent frequency of species in relation to stage of decay in quadrat 5

Stage of decay	1	2	3	4	5
Number of species	12	34	30	20	12
Parmelia saxatilis	24				
Lecanora chlarona	24				
Cetraria halei	18				
Lecidea cf. *helvola*	12	8			
Ochrolechia sp. II	12	5			
Parmeliopsis ambigua	35		20		
Cetraria pinastri	24		23		
Parmeliopsis hyperopta	47	27	13		
Ptilidium pulcherrimum	24	19	20		
Cladonia sp. (squamules)	18	41	10		
Hypnum pallescens f. *pallescens*	6	30	10		
Dicranum fuscescens	12		17	30	33
Cladonia cenotea		46			
Pohlia nutans		27			
Cladonia cornuta		22			
Cladonia crispata		14			
Cladonia chlorophaea		11			
Polytrichastrum alpinum		8			
Nephroma bellum		8			
Lophozia lycopodioides		5			
Cladonia uncialis		3			
Cladonia gonecha		3			
Brachythecium cf. *acutum*		3			
Lophozia longidens		32	3		
Cladonia pleurota		27	13		
Cladonia digitata		22	10		
Plagiothecium laetum		8	7		
Micarea sp.		8	7		
Dicranum montanum		5	3		
Cladonia sylvatica		5	3		
Lophozia attenuata		11		30	
Cladonia squamosa		19	43	10	
Pleurozium schreberi		19	3	100	
Cladonia coccifera s.l.		8	13	10	

Table 29 cont.

Stage of decay	1	2	3	4	5
Cladonia deformis		19	23		33
Dicranum scoparium s.l.		57	10	80	67
Lophozia porphyroleuca		54	37	30	33
Lophozia ventricosa var. *silvicola*		30	30	30	33
Brachythecium starkei		22	20	10	33
Calypogeia suecica		5	20	10	33
Cephalozia sp.			13		
Bacidia arceutina			7		
Drepanocladus uncinatus			3		
Rhizomnium pseudopunctatum			3		
Riccardia latifrons			10	20	
Blepharostoma trichophyllum			17	30	33
Rhytidiadelphus subpinnatus (=*R. squarrosus* var. *calvescens*)				30	33
Herb layer					
Mitella nuda			7		
Oxalis montana				70	
Cornus canadensis				50	
Trietalis borealis				20	
Galium triflorum				10	
Clintonia borealis				10	
Solidago macrophylla				50	67
Dryopteris phegopteris					33
Tree seedlings					
Abies balsamea				70	33

the wood in connection with the soil is rotten these prominent trunks finally fall to the forest floor. Here they stay in decay stage 2 and provide a suitable habitat for a distinct species group as shown in Table 29. When the typical brown rot reaches the outer wood cylinder to such an extent that the logs break mechanically into pieces, no distinct species group is noticed.

Since the structure of the forests in quadrats 6 and 8 is similar, data for those plots will be dealt with together and are presented in Tables 30 and 32 respectively. In quadrats 5 and 6 for decay stage 2 a floristically similar group is present. In this group (5, 6) *Hypnum pallescens* and *Lophozia longidens* are associated. In quadrat 8 (decay stage 4) and 6 the association of *Dicranum fuscescens* and *Mylia taylori* should be mentioned. Outstanding is the species richness of small hepatics in quadrat 8 and decay stage 4. These hepatics grow intricately mingled in small scale mosaics and are not found in quadrats 6, 7 or 9 although certain species of this floristically distinct group may be present locally.

The pattern outlined for quadrats 6 and 8 contrasts markedly to that of quadrat 7 (Table 31) which represents a decadent phase and quadrat 9 (Table 33) which is a young phase. Logs of the overmature forests show, as expected, high species richness for the epiphytic stage and a low species richness for the other decay stages. In quadrat 7 only five species out of 24 achieve frequency values of 50 or above whereas in quadrat 9 nine species out of 45 exceed frequencies of 50.

Table 30

Percent frequency of species in relation to stage of decay in quadrat 6

Stage of decay	1	2	3	4	5
Number of species	10	19	12	24	24
Ptilidium pulcherrimum	47				
Alectoria sarmentosa	27				
Lecanora chlarona	20				
Ochrolechia androgyna	7				
Lecidea cinnabarina	7				
Parmeliopsis hyperopta	80	37			
Parmeliopsis ambigua	47	16			
Hypnum pallescens f. *pallescens*	13	11			
Cladonia squamosa	7	21			
Dicranum fuscescens	7		8	38	5
Cladonia gracilis var. *dilatata*		45			
Lophozia longidens		26			
Cladonia botrytes		8			
Cladonia cristatella		8			
Cladonia digitata		5			
Cetraria pinastri		3			
Ochrolechia sp. II		3			
Cladonia cenotea		11		4	
Ptilium crista-castrensis		39		13	32
Plagiothecium laetum		5		75	45
Pleurozium schreberi		55	80	83	86
Plagiothecium roeseanum			16		
Cladonia sp. II (squamules)			16		
Brachythecium rutabulum			58		23
Dicranum scoparium			50	21	32
Lophozia attenuata			8	83	23
Lophocolea heterophylla				29	
Mylia taylori				17	
Blepharostoma trichophyllum				13	

Table 30 cont.

Stage of decay	1	2	3	4	5
Cephalozia leucantha				42	18
Jamesoniella autumnalis				38	36
Brachythecium salebrosum				17	4
Pohlia nutans				17	18
Anastrophyllum michauxii				13	9
Hylocomium splendens					41
Hylocomium umbratum					23
Herb layer					
Maianthemum canadense			16	8	
Clintonia borealis			16		4
Oxalis montana			92	41	64
Solidago macrophylla			33	46	59
Cornus canadense				13	18
Mitella nuda				13	4
Lycopodium lucidulum				4	14
Dryopteris spinulosa					18
Tree seedlings					
Abies balsamea		1f	50	46	59
Betula papyrifera		1f		67	14
Picea glauca				4	14

f: in fissures of outer wood cylinder

°: reduced vitality

Table 31

Percent frequency of species in relation to stage of decay in quadrat 7

Stage of decay	1	2	3	4	5
Number of species	17	14	18	16	8
Platismatia glauca	48				
Parmelia saxatilis	31				
Hypogymnia physodes	23				
Alectoria sarmentosa	19				
Lecanora chlarona	16				
Ischnoderma resinosus	6				
Hypogymnia cf. *enteromorpha*	6				
Lecidea cf. *cinnabarina*	6				
Usnea dasypoga	5				
Polyporus tomentosus	3				
Mycoblastus sanguinarius	79	26			
Ochrolechia androgyna	50	60			
Cetraria pinastri	16	31			
Parmeliopsis ambigua	45	43	17		
Parmeliopsis hyperopta	39	40	11		
Ptilidium pulcherrimum	5	83	50		
Hypnum pallescens f. *pallescens*		14			
Cladonia coccifera s.l.		6			
Cladonia coniocraea		37	11		
Cladonia sp. II (squamules)		14	50		
Dicranum fuscescens		17	78	57	
Lophozia longidens		9	44	29	
Cladonia cenotea		6	28	14	
Pleurozium schreberi		14	6	43	100
Dicranum scoparium			17		
Cladonia gracilis var. *dilatata*			17		
Ptilium crista-castrensis			17		
Calypogeia sp.			17		
Cladonia alpestre			11		
Cladonia pleurota			6		
Cladonia squamosa			11	21	
Lophozia ventricosa			28		13

Table 31 cont.

Stage of decay	1	2	3	4	5
Lophozia attenuata				43	
Polytrichastrum alpinum				29	
Hylia taylori				29	
Rhytidiadelphus subpinnatus					25
Herb layer					
Solidago macrophylla				14	
Coptis groenlandica				14	
Streptopus roseus				7	
Oxalis montana				29	78
Cornus canadensis				29	25
Trientalis borealis				14	25
Tree seedlings					
Betula papyrifera			6		
Abies balsamea				21	88
Picea glauca				7	38

Table 32

Percent frequency of species in relation to stage of decay in quadrat 8

Stage of decay	1	2	3	4	5
Number of species	8	15	49	30	11
Cetraria pinastri	50				
Hypogymnia physodes	20				
Lecanora chlarona	20				
Ochrolechia androgyna	70	13			
Parmeliopsis ambigua	70		3		
Parmeliopsis hyperopta	60		3		
Platismatia glauca	40		3		
Ptilidium pulcherrimum	20	67	21	28	
Cladonia sp. II (squamules)		53	3		
Cephalozia media		20	16		
Jamesoniella autumnalis		13	9		
Lophozia ventricosa s.l.		13	7		
Blepharostoma trichophyllum		13		1	
Cladonia coniocraea		47	3	12	
Anastrophyllum hellerianum		47		16	
Lophozia attenuata		33	33	36	
Cladonia rangiferina		27	17	12	
Lophozia incisa		13	12	8	
Icmadophila ericetorum		13	7	8	
Dicranum fuscescens		33	49	72	50
Mylia taylori		20	26	52	10
Lophozia ascendens			18		
Lophozia porphyroleuca			17		
Lepidozia reptans			9		
Calypogeia suecica			8		
Lophocolea heterophylla			8		
Cephalozia leucantha			7		
Nowellia curvifolia			5		
Geocalyx graveolens			4		
Cladonia cristatella			3		
Calypogeia sp.			3		
Anastrophyllum michauxii			3		
Scapania apiculata			1		
Calypogeia cf. *neesiana*			1		
Drepanocladus uncinatus			1		

Table 32 cont.

Stage of decay	1	2	3	4	5
Cladonia squamosa			24	24	
Dicranum scoparium			22	12	
Lophozia longidens			16	12	
Ptilium crista-castrensis			14	16	
Cladonia cenotea			12	12	
Lophozia ventricosa var. *silvicola*			11	16	
Rhizomnium punctatum			9	12	
Cladonia digitata			8	12	
Hylocomium splendens			3	20	
Plagiothecium sp.			3	8	
Tetraphis pellucida			3	4	
Plagiothecium laetum			8		20
Pleurozium schreberi			51	16	60
Herb and Shrub layer					
Clintonia borealis			5		
Linnaea borealis var. *longiflora*			1		
Lycopodium lucidulum			1		
Oxalis montana			29	92	80
Coptis groenlandica				12	
Mitella nuda				8	
Ribes lacustre				4	
Vaccinium sp.				4	10
Aralia nudicaulis				4	10
Cornus canadensis					30
Taxus canadensis					10
Tree seedlings					
Abies balsamea			24	32	60
Betula payrifera			4	28	20

Table 33

Percent frequency of species in relation to stage of decay in quadrat 9

Stage of decay	1	2	3	4	5
Number of species	6	4	11	16	8
Ochrolechia androgyna	30				
Cladonia sp. II (squamules)	20				
Parmeliopsis hyperopta	10				
Parmeliopsis ambigua	50			2	
Ptilidium pulcherrimum	90		5	28	
Dicranum fuscescens	10	9	29	37	6
Ptilium crista-castrensis		90	33		
Pleurozium schreberi		27	33	15	6
Hylocomium splendens		18	60	53	44
Brachythecium salebrosum			2		
Dicranum scoparium			7	7	
Peltigera canina			5	3	
Plagiothecium laetum			7	7	25
Brachythecium rutabulum			5	2	19
Lophozia porphyroleuca				15	
Cephalozia media				12	
Lophozia ventricosa s.l.				7	
Cladonia deformis				7	
Lophozia attenuata				3	
Cephalozia sp.				3	
Tetraphis pellucida				2	
Herb layer					
Oxalis montana			2		63
Dryopteris phegopteris					13
Tree seedlings					
Abies balsamea					31

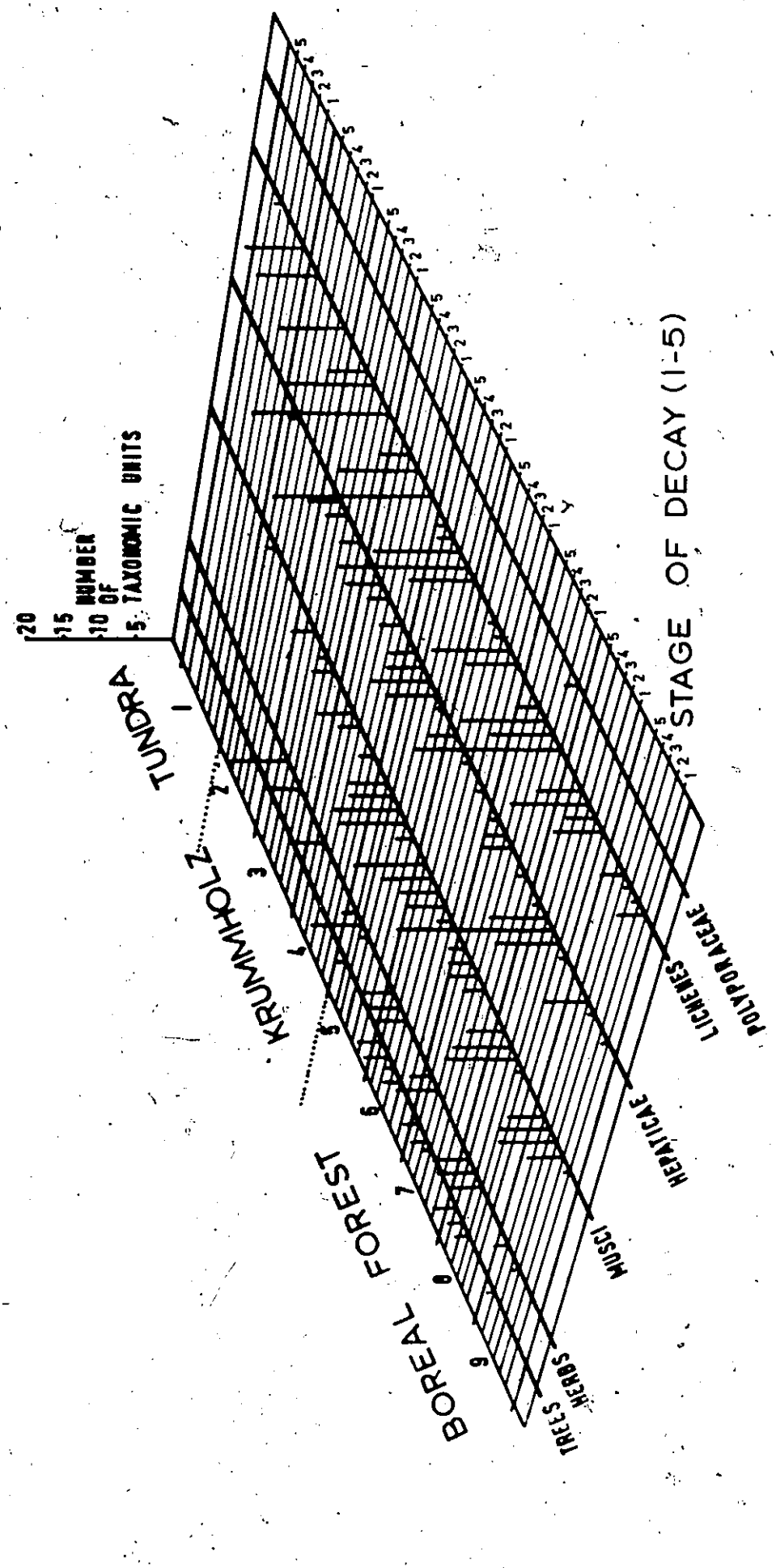
What is especially noteworthy is the dominance of *Entodon* in the rather open decadent phase and the high frequency values of *Hylocomium splendens* present in the relatively deep-shaded young phase (decay stages 3-5).

e) Discussion and conclusions:

The vegetational change along the elevational gradient will be discussed below in connection with species richness. The summary may be presented together with the following stereogramm (Fig. 39).

The tundra and the krummholz show the highest species richness with respect to lichens. Mosses and hepatics occur only sparsely in the krummholz zone. When one leaves this zone and proceeds downwards to the boreal forest, the substrate dynamics of the decay of the outer wood cylinder changes as well as the cyclic pattern of the forest regeneration. Niches especially suitable for hepatics and mosses are frequently encountered in these closed forests. When wet rocks with rich diaspore "pools" are present and the surrounding forest is in the optimal stage (quadrat 8), species richness on the logs is particularly high. On the other hand, the decadent phase in which bracket fungi on logs are frequently found is rich in epiphytic lichens but the overall species richness is poor. When the wood becomes gradually spongy, the number of herb species increases. The open boreal forest however and the krummholz plots do not show this directional change. Tree seedlings were not recorded in the krummholz zone. They were, however, found in the boreal forest. Here

Figure 39. Species richness for major taxonomic units per stage of decay along nine positions of an elevational gradient.


20
15
10
5
NUMBER OF TAXONOMIC UNITS
TUNDRA
1
KRUMMHOLZ
2
3
4
BOREAL FOREST
5
6
7
8
9
TREES
HERBS
MOSSI
HEPATICAE
LICHENES
POLYPODIACEAE
1 2 3 4 5
STAGE OF DECAY (1-5)

they show a pattern similar to the one presented by the herbs and increase in numbers with the progress of the decay. The changes in species richness mentioned above are in general controlled by microclimatic factors (see page 17f). Favorableness (Monk, 1967) for cryptogamic vegetation on logs in subalpine forests is especially high in this cool humid environment. Relatively slow decay rates (Henningson, 1968) and, therefore, comparatively high substrate stability seem to create conditions especially favorable for hepatics. Perturbations of the forest system have been described and seem to occur in the eastern areas of the continent over larger areas (Dawson, 1847; Stearns, 1949; Lyford and MacDean, 1966) synchronizing the life-spans of individual trees. Under the cover of those even-aged forests, vegetational changes of cryptogams on logs represent a forest structure-dependent plant succession.

CHAPTER IV

GENERAL DISCUSSION AND CONCLUSIONS

The log substrate is not only a favourable habitat for bryophytes and lichens but also, in a more advanced stage of decay, a suitable habitat for tree and herb seedlings. Tree seedlings are found on logs in all segments of the moisture gradient. Sometimes there was greater variety of seedling sizes found on logs than on soil (e.g. position 7, Fig. 36). It seems that the survival rate of tree seedlings growing on logs can be greater than the rate occurring on soil. Therefore, logs in an advanced stage of decay can become an important substrate in the processes related to forest regeneration.

From the results presented in connection with the permanent sampling plot at Petawawa, it is evident that a time-dependent directional vegetational change occurs on logs. This general trend is common also to all plots at the other three sites investigated. Because a detailed interpretation of the causes of vegetation differences on logs rests partly on assumptions, it is wise to make allowance for some inherent sources of error.

To be able to interpret species composition on logs at different stages of decay as degrees in succession, one must assume that the rate of decomposition of wood tissues is similar for most types of logs. Judging from mycological data (Wagener et al., 1954) it seems that this assumption

is not always justified. Bark, sapwood and heartwood cannot be expected to have similar decomposition rates under field conditions. In the Heney lake study, evidence was provided showing that bark at least has a different decay rate from that of the inner wood over part of the transect investigated. Another possibility is that logs in similar stages of decay may not have been decomposing for similar time spans. This seems to be especially true for logs of different diameter classes and different tree species in the later decay stages and must be considered when comparing logs from different sites. Logs in moist and mesic stands are still considered to break down faster than those which are more or less inundated or exposed to full sunlight. However, this rate may not be directly reflected in the substrate dynamics of the outer wood cylinder since most decay processes do not necessarily start and progress in this part of the log. At least for one plot, of an even-aged coniferous forest (Petawawa), data indicate that succeeding decay stages are reached in fairly similar time intervals.

In the case of an uneven-aged mixed forest, however, the situation is more complex. One has to be aware of the susceptibility of certain age classes of trees to mortality (Leak, 1970) and must also keep in mind the effects of wind in uprooting trees, both living and dead. In

even-aged phases of a forest, trunks seem to fall to the forest floor over longer periods of time at a more regular rate rather than by sudden and irregular catastrophic episodes due to wind and other factors. The uneven distribution of logs of a certain decay stage in some of the quadrats may have been caused by a combination of catastrophic episodes as well as by general density-dependent mortality due to spatial competition. Judging from the surficial topography (Denny and Goodlett, 1956) catastrophic episodes caused by winds were important for all areas where transects were studied. A number of standing dead birches with *Piptoporus betulinus* and *Fomes fomentarius*, of hemlocks with *Ganoderma tsugae* and of maples with *Ganoderma applanatum* indicate that mortality of trees is also a factor to be considered.

It is assumed that the distribution of diaspore sources along the gradient is not strictly comparable since the spatial distribution of logs and of observed niches (e.g. rocks, tree-bases, old moss-covered logs, etc.) are not the same over most parts of the transects. In a quadrat the availability of propagules does not seem to be uniformly distributed. Recently fallen trunks close to moss and lichen covered rocks or groups of old logs have a high probability of being reached by short distance dispersal of moss and lichen diaspores. Subsequent esta-

blishment and growth of these plants may still be controlled by certain factors, e.g. the log-plant interphase. Therefore, an element of uncertainty is introduced by the spatial distribution of logs and the processes related to diaspore availability and establishment of plants. Vegetation in the wet and moist sites with rich epigaeic bryophyte communities and considerable microrelief variation affects diaspore availability in particular. In dry habitats niches rich in prapagules from which short distance dispersal and subsequent colonization of logs can operate are scarce or unevenly distributed in some quadrats.

All the above-mentioned possibilities point to the fact that chance factors play an important role in cryptogam communities. The kind of processes outlined in the Petawawa study, for example, suggests that a decaying log system has associated processes which are, to a high degree, stochastic (Bartlett, 1966; Slack, 1971; Orloci, 1972). The "white-noise" problem (Pielou, 1972) makes interpretation and prediction from the results presented difficult to assess and limits comparability between samples.

In the discussion of stochastic relationships one has to consider the animal component of this decaying log system as well as the presence of decomposers. Although the bracket fungi, a group of prime importance for wood decomposition, were partly investigated, the interactions within the hetero-

trophic part of the decaying log system remain largely uninvestigated (Etheridge, 1969; Etheridge et al., 1967; Shigo, 1965). Therefore, conclusions drawn from the autotrophic part only should be treated cauticusly.

The general distribution of cryptogams on logs is clearly influenced by latitude and elevation. Lichen and mosses of boreal distribution (Ahti, 1969) are frequent on Mont Albert whereas on Mont Saint-Hilaire and to a lesser degree in the Heney Lake area, lichens with an affinity for the Great Lakes floristic elements (Hale, 1967) are found. Since there are biogeographic differences one has to keep in mind that comparisons based only on species richness are a somewhat incomplete statement of "diversity". The species richness of the first decay stage (mainly epiphytic stage) of the Mont Saint-Hilaire plots is rather small and reaches more than 10 species in one plot whereas in the Heney Lake area the species richness is several times above that value. It is the opinion of the author that this difference is not caused by chance factors resulting from different forest structures. It seems more probable that pollution effects had an impact on Mont Saint-Hilaire epiphytes (LeBlanc and De Sloover, 1972) resulting in their stunted growth or in the disappearance of certain species.

Distribution of cryptogams on logs is influenced by the structure of forests as shown by the results from boreal forests at Mont Albert. In the mixed forest region of Heney

Lake the impact of forest structure on decaying logs, as well as on plant assemblages on those logs, seem to be more complex. Even-aged phases seem to be much smaller than in the Mont Albert area and thus provide the investigator with a larger variety of logs having high values in species richness.

In all plots logs provide for some time a special niche of an exposed surface. Litter is usually not deposited in those habitats. On this elevated microhabitat, opportunistic cryptogams (Slack, 1971) find suitable space to grow, whereas cormophytes are excluded, since their roots cannot yet penetrate wood substrate. Therefore, ecological diversity and species richness of cryptogams increase until the conditions of these microhabitats change. These changes are caused by the decomposition and breakdown of the log as well as by deposition of litter, accumulated in part by the cryptogams themselves. Litter deposition seems to be for most mosses and lichens an unfavourable change in niche conditions. It is evident that there are more mosses in the coniferous and mixed forests that can adapt to litter fall than is the case in the decidous forests where mosses have to survive under the cover of leaf litter. These differences in adaptability to litter fall have never been investigated to the knowledge of the author.

For discussions of ecological diversity one must remember that the index used has an evenness or equitability component (Hill, 1973). This means that the dominance relations within an assemblage of plants can be shown. However, there

has been ample controversy about the heuristic value of a formula derived from information theory (see p. 55) applied to complex ecological data. When one considers this measure of diversity in the sense of Pielou (1969), that is the greater the diversity of a plant assemblage the greater the uncertainty of the identity of any individual plant sampled at random, the above-mentioned formula and its implied analogy may have its merits.

The result of the Petawawa study which shows that peak ecological diversity does not coincide with the highest stage of decay is especially noteworthy. Species richness in the other study areas often shows similar tendencies. The results have the same trend as those recorded by Loucks (1970) and Auclair et al. (1971) establishing that ecological diversity can decrease towards the end of a successional sequence. It must be pointed out that the similar tendencies in ecological diversity mentioned above are caused by different processes: on one hand litter-fall and breakdown of decayed wood makes the habitat gradually unfavorable for cryptogams, while, on the other hand, the closing of the canopy of the strong climax trees suppresses all potential invaders as well as the subordinate species which could persist in the more open seral forests but not in the late successional forests.

The author favors equating "diversity" with species richness (e.g. Whittaker, 1972) and treating equitability or evenness separate from the general diversity concept. The easy calculation of this value was found practical in simpli-

fying large species-microquadrat matrices. However, this calculation somewhat obscures dominance relationships. An attempt was made to resolve this dilemma by calculating species richness per growth-form (Heney Lake and Mont Albert), by calculating the sum of average cover per growth-form (Mont Saint-Hilaire), or by calculating the sum of average cover per Raunkiaerian life-form (Petawawa). This simplification of dominance relationships can still be considered as an expression of "dominance concentration" (Whittaker, 1965).

The study of the Petawawa permanent sampling plot can be considered in its basic approach as being an indirect gradient analysis (Whittaker, 1967). Microquadrat data were arranged in species-relevé groups. These overlapping, non exclusive groups could then be related to the time factor and the floristic gradient, therefore, represents a successional sequence.

In all other study areas the basic approach can be considered as being a direct gradient analysis. The resources (e.g. factors, microclimatic space-related factors) for which cryptogams compete have already been outlined.

Species richness within a plot for certain stages of decay was calculated and can be regarded as a measure of alpha-diversity in the sense of Whittaker (1970). The change in species richness within quadrats was discussed in detail for Mont Saint-Hilaire and some factors important for this change have been discussed on page 171. When one compares

positions 1 and 2 of the Heney Lake transect with the corresponding positions of the Mont Saint-Hilaire transect, it is evident that species turnover on logs in comparable stages of decay is quite similar. There are, however, small differences in the Heney Lake area. Microhabitat differentiation (see Fig. 35, p. 168) resulting from the deposition of logs at different heights above the water level, may account for this. The drier parts of the gradient are similar for both regions in respect to their alpha-diversities in individual quadrats. Only positions 8 and 9 from the Mont Saint-Hilaire transect differ from corresponding positions in quadrats 7 and 8 from the Heney Lake transect. Lichens, especially crustose, squamulose and fruticose growth-forms, attain more importance in the conifer-dominated hilltops at Heney Lake.

For changes in species composition along the three coenoclines studied, Whittaker (1970) suggests the term beta-diversity. The change in species richness from lakeshore to the dry hill top is evident for Mont Saint-Hilaire and Heney Lake. Both transects are rich in species in the wet-mesic and mesic forests but poorer on the open lakeshore and in the xeric parts of the transects. Their beta-diversity is therefore similar. The similarity is also evident when their total floristic inventory is considered. Different from these two regions with respect to beta-diversity is the Mont Albert area. The species richness is low at the top of the mountain as well as in some forests at lower elevations (Fig. 38,

plots 7 and 9). The comparatively high species richness in plots 6 and 8 (Fig. 38) is caused by the structure of these forests and the associated niche differences outlined on page 195.

For the regional differences which are expressed in these three coenoclines, Whittaker (1970) uses the term gamma-diversity. Although the information presented in these three transects is too scare and too restricted for such large regions for comparison of gamma-diversities, a final conclusion has to be pointed out. Most species present in the mesic parts of the decidous forests (see Table 22 and Table 24, p. 155, p. 181) are not found in the alpine tundra-boreal forest coenocline and vice-versa. Certain plants of the boreal forest may appear in the northern hardwood forests in places dominated by conifers and where sufficient supply in certain resource factors (substrate moisture, humidity, etc.) is present.

The author is aware that more relevant information could have been extracted in the field from the rotten log habitat. Especially the sides of the log, the rotten stumps or the inclined trunks of dead trees could have provided additional information. However, in an analysis like the one presented here one cannot be expected to extract all information present in a particular habitat. The additional information would generate a picture which would be far too complex for interpretation and for discussion within the present context of cryptogam ecology of plants on horizontally decaying logs.

The factors which control succession on decaying logs

are still poorly understood and some aspects of the decaying log system will be dealt with in future studies. At this time it cannot be the intention of the author to propose a general model of the decaying log system. Resampling of the same logs after a few years will provide useful data for this as well as details of a rarely investigated part of the carbon-cycle of forest ecosystems (Olson, 1970).

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