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THE ECOLOGY OF TERRICOLOUS LICHENS OF THE NORTHERN CONIFER-HARDWOOD FORESTS OF CENTRAL CANADA

by

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Master of Science.

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INTRODUCTION

The Northern Conifer-Hardwood Forests of Central Canada occupy a small but important portion of Canada's surface area. The relatively little quantitative information available concerning this forest community is surprising in view of its interesting vegetational characteristics. In addition the greater part of the Canadian population has been concentrated in the area for two centuries. Settlement of the eastern areas began in the 1600's and in the western parts of the study region in the late 1700's. The land and climate in the extreme southern region of Ontario favoured agricultural settlements at the expense of the original forest. Logging has also taken its toll of a large proportion of forest in central and northern parts of the region. Today with the continued push northward of the populated areas in the St. Lawrence and Ottawa River valleys, new areas are being developed and the forest communities are being heavily utilized. It is essential that an understanding of the ecological processes of this mixed conifer-hardwood community and its successional stages be gained before it becomes too decimated and modified.

In the past, the few ecological studies of this type were primarily qualitative. Where methods were used they were often applied subjectively and were then difficult to treat statistically. Investigations into the availability of lichens as winter food for caribou have been undertaken in the Labrador region of the boreal Forest - Tundra ecotone (Hustich, 1951). This region together with most northern areas has been thought of as optimum sites for lichen development in the northern temperate zone.

No previous quantitative study has been undertaken of the ecology of the terricolous lichens in the Northern Conifer-Hardwood Forests of North America. A lack of knowledge of many of the lichens found coupled with the meagre records available of species collected in the region, added to the difficulties in the initial phase of the study.

The principal objectives were to obtain an adequate sample of the stands of tree vegetation and of the tree species in the region. At the same time the terricolous lichen vegetation was sampled in the same stands. With this basic quantitative field data it is then possible to analyze objectively the responses of the different tree and lichen species of the forest community along major environmental gradients. The correlation of the lichen vegetation of the various stands with the changes in tree composition and microenvironment due to these tree changes gives an expression of the ecological tolerance of the lichens within the community and in relation to the different environmental factors.

This objective analysis of the quantitative data follows the present phytosociological trend whereby community structure is described with a maximum of quantitative information. The changes produced by succession can be more readily measured with these methods.

The lichen community within this forest community is generally unnoticed, but it is hoped that this study will be of value in emphasizing the continuous pattern of not only this, but all vegetational complexes.

The opportunity to undertake a quantitative ecological study with the above object in mind was presented when Dr. P.F. Maycock initiated the first quantitative study of the Northern Conifer-Hardwood Forests of central Canada in the summer of 1963. This afforded the writer the opportunity to investigate the ecology of the terricolous lichens within this forest complex; a vegetation type not generally thought of as supporting a luxuriant lichen component.

AREA DESCRIPTION

Topography

Topographic conditions within the area show a transition from the uniformity of the southwestern region to the rolling conditions of much of the Boreal Forest region to the north.

The southern section of the Northern Conifer-Hardwood Forest Region is somewhat irregular, but shows a general rise toward the Algonquin Highlands in the northeast. The central section which stretches from Georgian Bay in the west to Quebec City in the east is rough and irregular, and glacial deposits of varied character cover the greater part (Halliday, 1937). The Upper St. Lawrence Valley is a well marked lowland through which drain the waters of the Great Lakes. The Algoma section bordering the northern shores of Lake Huron, and the eastern shore of Lake Superior consists generally of valleys and rough, high ridges with a coastal lowland.

Topographically the area is surrounded by extensive lowlands, a large part of which are covered by lake water. Eastward there is the extensive plain of the Upper St. Lawrence Valley, along the northeast there is the Ottawa Valley, while in the north central region there is the Lake Nipissing lowland (Putman and Chapman, 1938).

There are three major highland regions with areas above 1300 ft. in elevation. The Western Ontario Uplands south of Georgian Bay, Algonquin Park and adjacent districts, and the range which lies north of Lake Superior, extending from

Kirkland Lake west to Lake of the Woods. These three areas have an appreciable affect on climate, because the isolines of many climatic features tend to parallel the lake shores and circle the higher ground (Putman and Chapman, 1938).

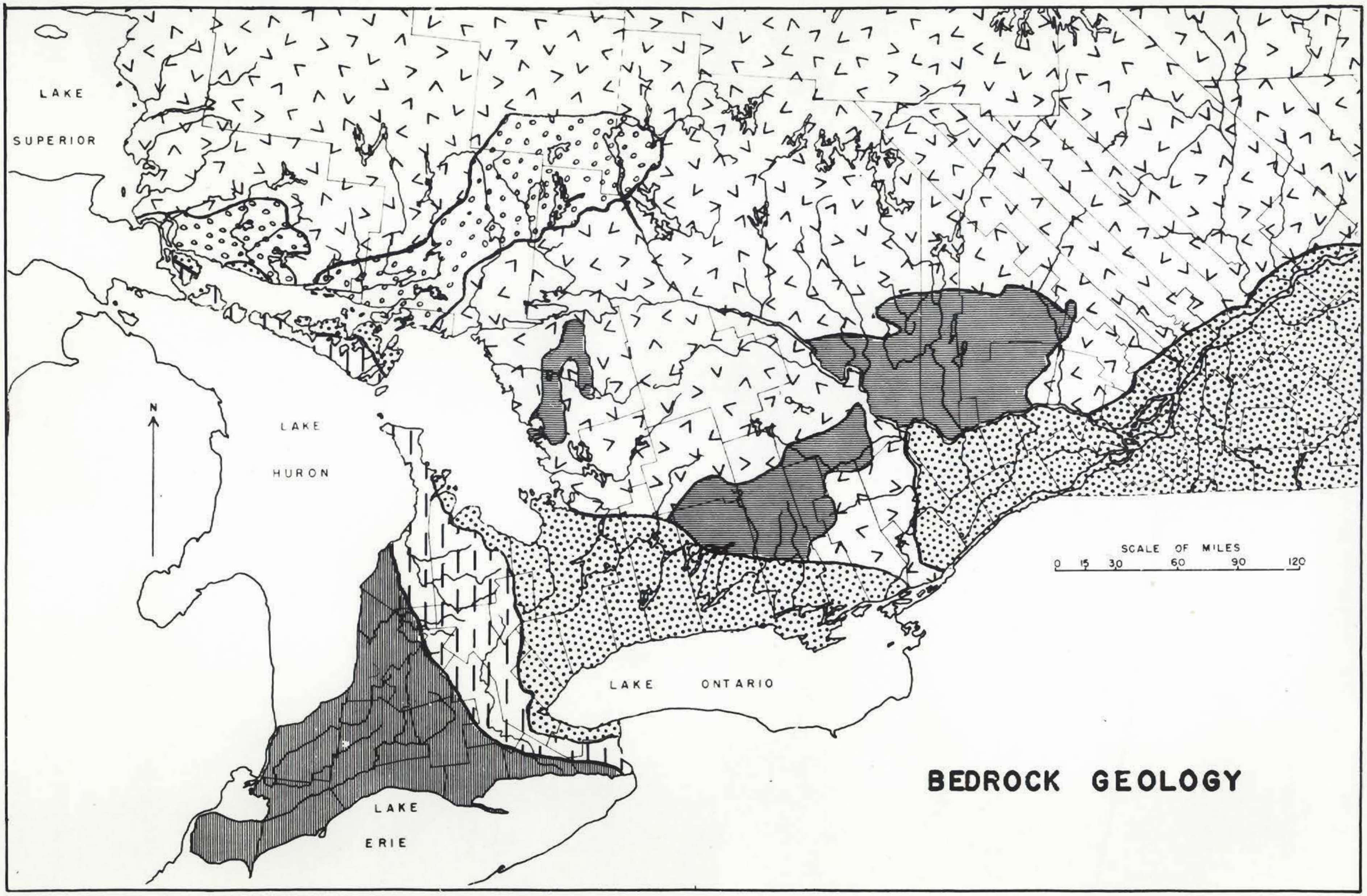
Geology

The Precambrian bedrock of the Canadian Shield, composed for the main part of granite with schists, crystalline limestones, and gneisses underlies more than 50.0 per cent of the Northern Conifer-Hardwood Forest Region included in this study. This glacier-scraped bedrock extends southward to a line from Kingston in the west to the southeast sector of Georgian Bay. North of Lake Huron, bedding consists of early Proterozoic sedimentary and volcanic rocks. Along the southeast shore of Lake Superior a series of late Proterozoic sedimentary and volcanic rocks form the bedrock.

The extension of the Precambrian bedrock to the St. Lawrence River in the Kingston area separates two main areas of Ordovician bedrock. The boundary between these two series is irregular and is for the most part composed of altered limestones and granite intrusives of the Grenville-Hastings series (Halliday, 1938). A western section of the Ordovician extends to Georgian Bay and south to Niagara Falls while to the east, Ordovician rocks underly the St. Lawrence and Ottawa Rivers, the two major basins of the area. This is a series of sedimentary rock composed mainly of limestones, dolomites, shales and sandstones.

FIGURE 1

The bedrock geology of eastern central Ontario and western Quebec. The serrated lines indicate the most southward extension of Precambrian outcrops. Horizontal lines indicate Proterozoic sedimentary and volvanic rocks. Open dots indicate late Proterozoic sedimentary and volcanic rocks. Stippled areas are Ordovician sedimentary rocks. The Silurian bedrock is indicated by broken vertical lines. Devonian bedrock is indicated by vertical lines.


LAKE
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ONTARIO
LAKE
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SCALE OF MILES
0 15 30 60 90 120
BEDROCK GEOLOGY

Between the flat Devonian limestones, shales and volcanic rocks of southwestern Ontario and the Ordovician bedrock to the northeast there lies a band of Silurian bedrock which is sedimentary in origin. (Figure 1.)

Effects of Glaciation

Substrata that were available for forest establishment developed from the parent materials that were considerably disturbed and reshaped by ice movements in the glacial periods. Ontario and Quebec were entirely glaciated and most of the mineral soils have developed on glacial tills and related water lain sediments.

A greater number of the soils in the southern section of the region of study are related to glacial drift derived from local underlying Paleozoic bedrock, that was transported only relatively short distances, but with a great many erratics evident. Much of the exposed rock in this southern region was above lake levels after the glacial retreat and the drift material was deposited as ground moraine, the depths of which varied from deep on the Lake Ontario edge to shallow on the Precambrian boundary in the north.

An interlobate area, situated between two glacier lobes, covers an area of 600 square miles in south central Ontario between Castleton in the east and Aurora in the west. This region is today the most elevated, hilly, and agriculturally poor land in south central Ontario (Putman and Chapman, 1936).

Sandy soils predominate, and were laid down in run off from the two glacial lobes. Glacial till predominates to the south, while drumlins and moraines in the north and northeast cover extensive areas.

The Grenville area of the St. Lawrence River Valley dominates the eastern sector of the study area. Here Wisconsin glaciation deposited shallow tills and later stream valleys occupied by gravel and sand formed. The Pembroke-Renfrew area was a delta of the Champlain Sea and consequently water laid materials, mainly sands, predominate. The higher outcrops of this area were exposed to the wave actions of the glacial Champlain Sea, and consequently the irregular Precambrian rocks today have only shallow till or in some cases completely lack a soil mantle.

The Lake Algonquin plain to the west of the Grenville area has deposits divided into two groups (Dell, 1962). The eastern section has sands laid down as off-shore deposits in glacial Lake Algonquin. These deposits were derived from the underlying granite and granitic-gneisses, and were mainly deltaic, others were kames and eskers. The sands of the western section were eroded from the granitic rocks together with volcanic and basic intrusions of the Pre-Huronian rocks on the north shore of Lake Huron.

North of the Algonquin sands and Grenville deposits of the south, an area of deposits of extremely variable nature exists.

They range from granitic tills, and sands to deposits of abundant greenstones, shale fragments and micas. Later, alluvial and lacustrine deposits were added from Lake Algonquin in the west.

Climate

Trewartha 1954, places this area of southeastern Canada in the Humid Microthermal Climatic zone and describes the general characteristics as follows:

"A climate where a general winter is emphasized by the usual snow mantle, is combined with a genuine, although many times short summer to produce the characteristic annual climatic cycle. Fall and Spring, the transition seasons, not only are brief, but are also chiefly a composite of winter and summer weather elements. Colder and snowier winters, shorter frost - free seasons, and the larger annual ranges of temperature distinguish the severe microthermal climates from the southern mesothermal types."

The snow cover of the Northern Conifer-Hardwood Forest region is of a sufficient duration to have a marked effect on the ground temperatures, because it keeps the surface warmer and prevents deep freezing.

Climatic data have been carefully compiled and summarized for southern Ontario by Putman and Chapman, 1938, and for

Table 1

Summary of averages for important climatic features in the southern and northern areas of Central Canada within the region studied

	Northern Extreme	Southern Extreme
Mean annual temperature	38°F	44°F
Winter temperature (Dec.,Jan.,Feb.)	5°F	23°F
Summer temperature (June,July,Aug.)	65°F	70°F
January isotherm	10°F	21°F
July isotherm	62°F	68°F
Daily range of temperature	23°F	19°F
Extreme low temperature	-55°F	-35°F
Extreme high temperature	95°F	100°F
Beginning of growing season	Apr.30th	Apr.15th
End of growing season	Oct. 14th	Nov. 1st
Length of growing season	160 days	200 days
Average length frost free period	100 days	150 days
Annual precipitation	30"	36"
Total snowfall	100"	60"
Days of snow cover	150	90
Frequency of drought	?	20 days
Potential evapotranspiration	20"	23"
Water surplus	12"	15"

Northern Ontario by Chapman 1952. This information together with data from Quebec have been presented by the Department of Mines and Technical Surveys in their Atlas of Canada. Those climatic factors that are considered important in relation to vegetation development are presented in Table 1.

The climatic values for the approximate northern limit of the Southern Deciduous Forests of Southwestern Ontario, as compiled by Maycock, 1963, from Putman and Chapman, 1938, agree closely to the values in Table 1 for the southern limits of the Northern Conifer-Hardwood Forests of this region. However, the climatic isolines for the northern areas do not follow the northern boundary of the Northern Conifer-Hardwood Forests, except in the western regions. Climatic conditions show a relatively wide range between east and west, the Great Lakes and Hudson Bay influencing the western section while the Coastal Atlantic modifies eastern climates.

Soil

Glacial and glacial lake deposits overlie all of the region studied and have exerted a considerable effect on the soil patterns, especially through their varied degrees of comminution, drainage and reaction. The southern area of Ontario was the first part of the region to be exposed during the recession of "Wisconsin Ice" and soils there show fewer characteristics of the parent material than do the soils of the central and northern areas. Soil development had started in the south at a time when the central part was inundated by the Champlain Sea and northern areas were under glacial ice.

South of the Precambrian boundary the young soils are mainly of the brown forest type with grey brown podzolic soils related to the invasion of more deciduous species. More mature types are the grey brown podzolic and dark grey gleisolic soils of southwest Ontario. The latter soils have developed on the better drained sites where the deciduous forests have been present for a considerable time.

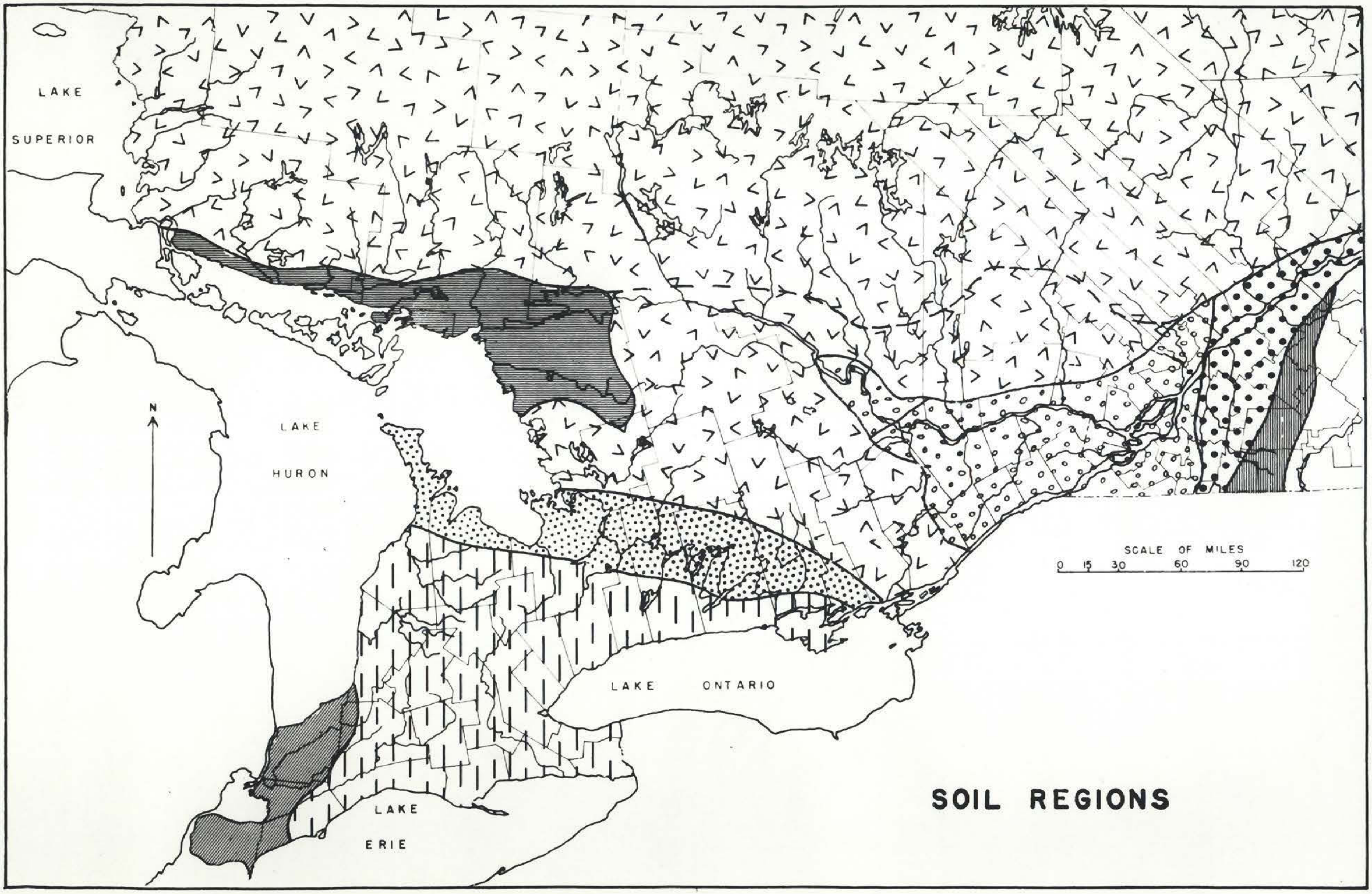
The Upper St. Lawrence Valley has relatively young soils due to inundation of the area by the Champlain Sea. These are predominantly dark grey gleisolic soils, brown forest soils and podzolic soils which generally develop in close relation to coniferous stands. Brown forest soils are generally absent from the Lower St. Lawrence Valley. The north shores of Lake Huron and the Georgian Bay area have podzols and grey wooded profiles on the well drained uplands with peats and mucks on the poorly drained lowlands. These more mature soils may have resulted from the extensive areas of deciduous species found in the sector.

Forests of much of the central portion of the region are distributed on podzolic soils while northward rock outcrops and peats in poorly drained lowlands increase in extent.

The generalized nature of these soil groups is emphasized and considerable local variation occurs in soil type. These variations are all related to the interacting factors of

FIGURE 2

The soil regions of eastern central Ontario and western Quebec. Podzol soils are serrated. Grey wood soils with podzol soils are indicated by horizontal lines. Brown forest soils with grey brown podzolic soils are stippled. Dark grey gleisolic soils with brown forest soils and podzol soils are indicated by open dots. Black dots indicate dark grey gleisolic soils with podzol soils. Vertical broken lines indicate grey brown podzolic soils with dark grey gleisolic soils. Dark grey gleisolic soils with grey brown podzol soils are indicated by diagonal lines.


LAKE
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LAKE ONTARIO
LAKE
ERIE
SCALE OF MILES
0 15 30 60 90 120
SOIL REGIONS

parent material, topography in relation to drainage conditions areal climate, vegetation composition and time as related to soil maturity. (Figure 2).

General Vegetation

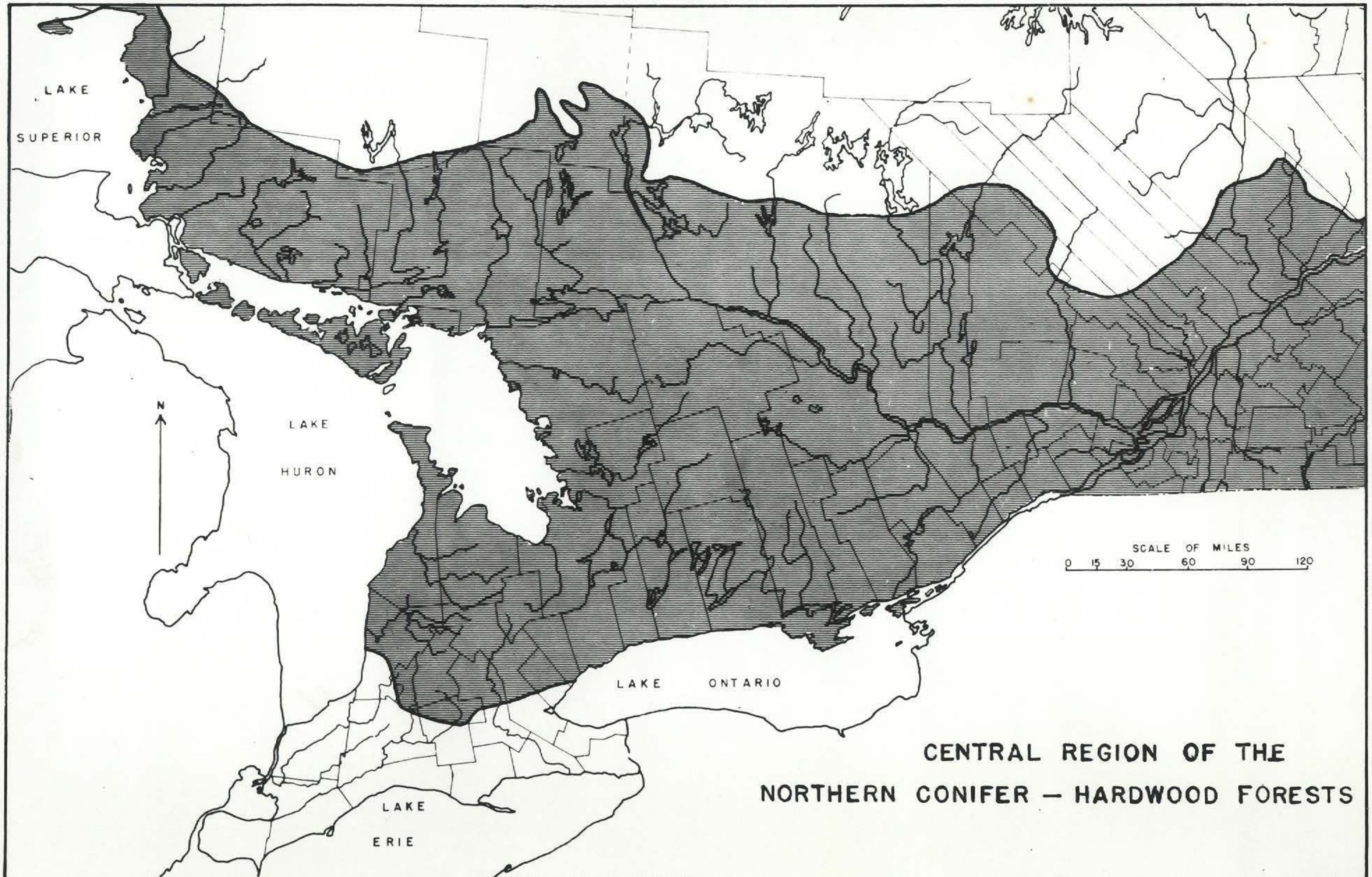
The climatic variation and irregular topography of the region have probably been two of the major reasons for the development of such a mixed forest type which have resulted in the designation of Northern Conifer-Hardwood Region. Northern elements and the Laurentian Shield itself have been a barrier against the intrusion of many southern deciduous forest species while the relatively hot summers enhance the competition from vigorous northern deciduous trees and preclude much boreal encroachment from the north. (Figure 3).

The southern portion of the Northern Conifer-Hardwoods which grades into the deciduous forest formation shows a mixed forest type in which a great number of deciduous and coniferous species are evident. In direct contrast, is the far northern portion where only isolated deciduous stands are encountered among many dominated by northern conifer and boreal conifer species.

Several workers (Halliday, 1937; Weaver and Clements, 1938) relate the area physiognomically to the Coast and Montane Forests of the western regions of North America, and question its ultimate survival. With indiscrimate logging and the technique of clear felling of all unsuitable trees, vast areas of Pinus strobus (White Pine) have been cut and burn in the past. This led to the invasion of broad leaf dominants from the

FIGURE 3

Map of eastern central Ontario and western Quebec showing approximate limits of the Northern Conifer-Hardwood Forests.


LAKE SUPERIOR
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SCALE OF MILES
0 15 30 60 90 120
CENTRAL REGION OF THE
NORTHERN CONIFER – HARDWOOD FORESTS

adjoining regions, at the same time the blocking by beaver dams and road construction has increased swampy lowland areas suitable for invasion by boreal species.

In southern sections Acer saccharum and Fagus grandifolia are most common and occupy a greater area of the forests than any other species. Associated with them are Tilia americana, Acer rubrum, Quercus alba, Quercus rubra and Ulmus americana. With these hardwoods Tsuga canadensis, Pinus strobus and Abies balsamea are frequently found together with a scattering of Populus grandidentata, Betula papyrifera, Juglans cinerea and Prunus serotina. On bottomland sites Ulmus americana and Acer saccharinum dominate associated with Fraxinus pennsylvanica, Fraxinus nigra and Populus tremuloides. Lowland sites with their poor drainage, and consequently poorly aerated water are dominated by Thuja occidentalis, Larix laricina, Ulmus americana and lesser amounts of Abies balsamea, Fraxinus pennsylvanica, Acer rubrum and Acer saccharinum. On upland dry rocky sandy soils the dominants are: Pinus strobus, Pinus resinosa, Quercus rubra and Quercus alba. The Precambrian bedrock strongly influences vegetation in the St. Lawrence Thousand Islands area, where it supports stands of Pinus rigida and Juniperus virginiana on the dry slopes and ridges. Elsewhere Pinus strobus and Pinus rigida are prominent on most of these islands and rocky shores. Pinus rigida in the Thousand Islands section occupies the most northerly limits of its geographical range.

Southern limits of the altered Precambrian limestones divide the region into two approximately equal subregions, a fact of great ecological significance. This boundary determines the northern limit of such deciduous species as Juglans cinerea and Carya cordiformis, while the southern limit of Pinus banksiana is determined by the change in substratum.

North of the Precambrian line, dominance by Acer saccharum is greatly reduced, and Fagus grandifolia drops out altogether just north of the Algonquin National Park. It is in this section that Pinus strobus, and Pinus resinosa probably reached their maximum development in Canada, but widespread lumbering and burning have removed most of the original extensive stands (Halliday). Forest cover begins to show a greater degree of boreal influence especially in the lowland areas. In addition to the dominant species varying amounts of Quercus rubra, Ulmus americana, Fraxinus americana, Tsuga canadensis, Tilia americana and Betula lutea are present. A tendency of the hardwoods to segregate out on the finer textured soils of warm slopes and hilltops is noticeable.

On the lighter, sandy soils scattered throughout the section Pinus banksiana usually forms pure stands, while where burning has occurred either naturally or after logging, Populus tremuloides and Populus grandidentata are usually present. In such situations Acer saccharum, Betula papyrifera, Pinus strobus, Abies balsamea and Quercus rubra often gain a foothold.

The extreme northwestern area along the east shore of Lake Superior on upland south facing slopes *Pinus strobus* and *Pinus resinosa* are dominant together with *Thuja occidentalis*. On ridge tops some pure stands of *Acer saccharum* are found together with a scattering of *Betula lutea*, *Abies balsamea* and *Tsuga canadensis*. The characteristic feature is the development of *Picea glauca* on beach terraces along the shore line with *Larix laricina* , *Thuja occidentalis*, *Picea mariana*, *Abies balsamea* and *Betula papyrifera* occupying wetter sites. Halliday, 1937, explains the well marked distribution of the northern hardwood species of the area and their absence to the northeast, by means of the Mackinac Peninsula land bridge at Sault Ste. Marie. It could possibly have been the point of early entry of deciduous species in post glacial times, allowing a general replacement of *Pinus* species. The extensive logging operations in the northern regions of Central Canada combined with a population advance from the south have no doubt greatly aided this deciduous invasion.

LITERATURE REVIEW

General Forest Ecology

In his report of 1884, on the forests of North America Sargent distinguishes the Northern Pine Belt as one of the six natural forest divisions in the eastern portion of the continent. He considered it to be characterized by *Pinus strobus*, which appeared to be the most dominant and widely distributed tree species. Weaver and Clements (1938) restricted this formation to the Great Lakes, bordered to the north by Boreal Forest and by Deciduous Forest in the south. According to Weaver and Clements, the Lake Forest Formation consisted of a single association in which *Pinus strobus*, *Pinus resinosa* and *Tsuga canadensis* were the climax dominants. Associated with these climax trees were *Pinus banksiana* and *Thuja occidentalis* in subclimax positions. Deciduous species, apart from *Populus tremuloides* and *Betula papyrifera* were not mentioned. An earlier study of Bergman and Stallard (1916) in northeastern Minnesota reported that the original forests were composed of *Pinus strobus* and *Pinus resinosa*, and *Pinus strobus* was considered to finally replace *Pinus resinosa*. An *Acer*-*Fagus* association was present but only in restricted sites and was therefore termed a subclimax. Nichols (1935) considered the Northern Conifer-Hardwood Forests of Central Canada within the Great Lakes and St. Lawrence River Basin as a distinct region. He further hypothesized that the region showed a climatic climax in which the forests show a mixture of evergreen coniferous and deciduous tree types. Weaver and Clements avoided discussing the ecological aspects of the deciduous species involved in the complex.

Nichols further stated that the conifer trees were of comparative minor importance in the climax stands.

Halliday in 1937, published the first notable description of Canadian forests in his "Forest Classification for Canada", in which he claimed to follow the basic system of climax classification as outlined by Weaver and Clements. In reality he segregated the forests into regions which, in turn were divided into sections, purely on the geographical importance of individual or groups of species. His Great Lakes-St.Lawrence Forest region follows a similar boundary in Canada to that shown by Nichols. However, whereas Clements concluded that Pinus strobus, Tsuga canadensis and possibly Pinus resinosa were the indicator species, Halliday rightly pointed out that the Deciduous Forest species or northern hardwoods had also to be considered. The hardwood species he referred to were Acer saccharum, Betula lutea, Tilia americana and Fagus grandifolia. It was considered that secondary roles were exerted by Thuja occidentalis and Pinus banksiana, the former an intrusive from the south, the latter from the north. Additional boreal species, Abies balsamea, Picea glauca and Picea mariana were present in lowland areas as "relic" stands. Halliday also suggested that the northeastward push of the major deciduous species reflected the influence of the land bridges across the Great Lakes system and positions of ice-sheets in the last glaciation. In this central region presently considered Halliday outlined six separate sections.

Lucy Braun (1950) in her discussion of the region follows Nichols hypothesis and considered it as part of the Eastern

Deciduous Forests. She further considered that it was made up of two main divisions, the Great Lakes-St.Lawrence division in the west, and the Northern Appalachian Highland division in the east. The former was essentially the same Lake Forest area designated by Weaver and Clements (1938). This division was segregated into sections, one including the Laurentian Uplands which was closely related to the area studied in the present investigation. The general mixed forest type was dominated by Acer saccharum, Tsuga canadensis, Betula lutea and Pinus strobus and included a variety of other species most of which were more common southward. Toward southern limits the proportion of pure deciduous forest was greater, while in the north boreal species increased in presence and frequency.

In 1959, Rowe published "Forest Regions of Canada" in which a revision of Halliday's earlier work was made. Rowe pointed out, that a classification like that of Halliday implied the provision of a system of purely vegetative categories based on consistently applied criteria. The change of title to Forest Regions removed this implication, while expressing more aptly this purpose. Halliday claimed to base his forest regions mainly on the presence of certain climax species that resulted in climatically controlled formations. Both of these papers provided a geographical description of the forests, and outlined their areal distribution and were not classifications in the accepted sense.

For the central region of the Northern Conifer-Hardwood Forests in Canada, Rowe has divided several of Halliday's sections into subsections due to the presence of certain associations which show in the main, a character difference from the other parts of the section. The lack of ecological knowledge on these sections was acknowledged, but was qualified by stating that until it was available the presented approach must be used.

In Canada, Halliday and Brown (1943) presented the distribution of some important forest trees in Canada and showed that the northern boundary of the Northern Conifer-Hardwood Forests was largely determined by the range limit of Betula lutea. Dansereau (1944) described the restricted stands of deciduous forest present on the shores of Lake St. John, Quebec. There, Pinus strobus and Pinus resinosa also reach their northern limits. North of Mont Laurier, Quebec, Quercus rubra and Betula lutea are found associated with Acer saccharum, but these again are in largely isolated areas.

The earlier workers, Sargent, Weaver and Clements and Bergman and Stallard were all proponents of the Pinus or Pinus-Tsuga climax forest and all relied on the descriptions made by early travellers through the region. In this early period no quantitative data was collected in relation to actual forest composition. The inaccessibility of the hinterland would no doubt have been a factor in causing workers to rely on second hand information.

Recent Ecological Studies

Few if any of the foregoing Canadian studies have included a sufficient number of stand descriptions to allow analysis of the actual composition and extent of distinct forest communities. Isolated areas have been studied in the Northern Conifer-Hardwood region, but little quantitative information is available. Maycock (1955) was the first to collect detailed quantitative information of a segment of the forest community on a large scale in the region, but the stands studied were upland boreal conifer stands. This forest type which is characteristic of more northerly sections within the region was not included in the present investigation.

A series of recent studies on the Northern Conifer-Hardwood Forests of Wisconsin have not confirmed the terminal nature of Pinus strobus or Pinus strobus-Tsuga canadensis forest. These studies were based upon detailed phytosociological investigations and reviewed by Curtis (1959) in his book "The Vegetation of Wisconsin". Two separate ordinations were constructed, one by Brown and Curtis (1952) for the Upland Conifer-Hardwood Forests, the other by Clausen (1957) for the Lowland Conifer Swamps. The forest continuum revealed that the stands of each study were all part of one great community grading from dry to mesic and from wet to mesic. To represent the full moisture range these ordinations were combined into one single vegetational complex. When the importance values for individual tree species were averaged and plotted for each of the five moisture segments, curves were obtained which represented the amplitudes of species on a quantitative basis. The peaks of these curves corresponded with habitats of optimum development for the particular tree species.

The present investigation is, therefore, the first to include compositional data for a large number of stands in the Northern

Conifer-Hardwood forests of Central Canada. The quantitative data collected in the field and the analysis of this data followed closely the lines of these earlier phytosociological investigations in the Lake States.

Ecology of Lichens

If quantitative data on the forests of Central Canada is not abundant, it is non-existant for the ecology of terricolous lichens. Almost all of the initial studies in lichenology were taxonomic in nature and apart from habitat records of actual collection sites very few ecological observations were made. Fink (1902) pointed out that lichens were extremely interesting ecologically and called on workers to stop neglecting this branch of the field.

An interesting series of ecological studies by Brinkman (1931) were possibly the first of their kind in North America in which he attempted to use lichens, mosses and liverworts as indicators of forest site values. His paper "Lichens in Relation to Forest Site Values" was published after conducting research in the Spruce-Fir Forests of Alberta. He was able to relate the presence of lichens to absolute tree dominance per acre and to the age of the stands. In young stands with a low total basal area he found Cladonia species dominant on the soil litter, while with increase in tree age and size lichens became more frequent on logs. With the continued development of the sites, Brinkman found that at a value of 7000 cubic feet per acre and an approximate age of 80 years, Cladonia species were absent on all sites. He further suggests that although Peltigera and Parmelia species were found throughout the range of forest types from the lowest to the highest density, the lichen species would probably have a tendency to occupy different site values. It was suggested that a closer study of several of the more commonly occurring species would have probably shown them to have had some forest site indicator value. His table followed very closely the table presented by Cajander (1926) on a study of Scots Pine in Europe, in which he related lichen presence to age of stands.

Berry (1937),published a preliminary list of lichens with ecological notes in the deciduous forests of Central Missouri. His study involved the establishment of associations within the different types of communities. While the lichen substrate was given, no quantitative data were collected and no comparisons even on a basis of presence were made between the association types.

Adding to the knowledge of lichens and bryophytes within the Spruce-Fir forests of the Colorado Rockies, McCullough (1948) described plant succession on fallen logs in forests at an elevation of 2500 feet. The period of log disintegration was divided into 8 stages from the initial fall until it had been incorporated into the humus layer. Epiphytic Usnea species were the only lichens present when trees fell. The first terricolous lichens to appear were Cladonia species in association with the tiny liverwort Lophozia. These two co-existed for several decay classes before the Cladonia species began to give way to a moss, Brachythecium. Terricolous lichens were present on logs of spruce and fir in all decay stages except the first of the three forest moisture conditions studied, namely mesic, bog and xeric.

Moss (1953), in a study of the forest communities of Alberta, listed the common lichen species recorded in types studied. He presented tables in which all plant species were recorded as dominant, abundant, frequent, scattered or rare. For the Black Spruce stands the frequencies of bryophytes were recorded as percentages in relation to coverage. No statement was made concerning the size or number of quadrats studied within each type . Stands of the major tree associations were investigated and included combinations of Picea glauca, Picea mariana, Larix laricina, Pinus banksiana and Populus tremuloides. An interesting observation was made in a Pinus banksiana stand that had been invaded by Populus tremuloides. The number of lichen species present was very high. A return visit to the same site twenty years later showed the number of lichen species had been greatly reduced. Moss considered this to be due to the gradual reduction of rotten wood on the forest floor. Where Pinus logs were still recognizable there were lichens present.

It appears that the studies by Hustich (1951) were the first completed in Canada where much attention was paid to lichen ecology. This work was in the Boreal Forest - Tundra ecotone in Labrador and has descriptions relating to abundance or sparsness.

The first quantitative study of terricolous lichens succession in North America was undertaken by Robinson (1959) on abandoned agricultural fields in North Carolina. Earlier old field studies included those of Bard (1952) and Evans and Dahl (1955) in which lichen presence was recorded. Johnson (1959) had carried out studies on the effects of raking and burning on the terrestrial lichen vegetation in 60 year old Pine stands in North Carolina. Robinson used 100 square feet quadrats in each of 12 fields studied. At each corner of the large quadrat a plot 6 feet by 2 feet was sampled in which frequency was recorded. The only lichens recorded were Cladonia species in seven out of nine periods of succession from the first year to climax Oak-Hickory Forests (121 years). During the first few years after abandonment lichens were absent, and again in the 120 year old stages no lichens were found. Three groups of lichens were distinguished by their occurrence in various successional stages. Pinus appeared at the third year and remained dominant until the seventy year old stage when deciduous trees started to take over. Robinson concluded that variation in the nature of organic debris during the succession process was a major factor controlling composition of the lichen vegetation.

Mozingo (1961) initiated a study of the genus Cladonia in Eastern Tennessee and the Great Smokey Mountains. Ecological investigations were performed but so far have not been published.

Two of the first two quantitative studies on corticolous lichens in North America were carried out by Culberson (1955) and Hale (1955) in Wisconsin. The forest section of their study dealt with a phytosociological analysis of the tree vegetation of the stands studied and was completed by the Quarter Method. Then a system of objectively sampling the lichen population of specific trees in stands was established. Individual trees were checked for lichen presence at the base and at breast height, and frequency of lichen species on these trees was recorded. A relationship was shown between lichen presence at base and breast height and host specificity of certain species. Additionally, Culberson was able to establish the presence of distinct northern and southern species with some lichens common to both regions.

LeBlanc (1963) has carried out studies of corticolous lichen species in relation to host tree specificity and exposure in woods of Southern Quebec.

While many plant ecological papers today list the lichen species recorded in the studies, it appears little more has been accomplished regarding an understanding of their position or role in the vegetation complex. It would appear from a study of the recent literature that earlier workers who had undertaken ecological studies have turned to the biochemical aspects of lichenology.

Weber (1962) in his paper "Modification of Crustose Lichens" stresses the lack of qualified lichenologists today, but points that great quantities of distributional records and ecological observations have been contributed by alert amateurs. This situation has lead to the publication of many new taxa by untrained biologists. The result is a mass of names of which only relatively few are useful. The distributional and ecological patterns of all lichens should be studied on a broader scale. Such an undertaking would help to reduce the naming of new species when in all probability they are depauperate or well-developed individuals of known taxa.

Recently, Smith (1962) from his physiological studies of Peltigera has called for the "elucidation of various problems in the autecology of lichens", by suggesting deliberate changes of habitat and environmental factors. Valuable as such investigations would be, their study is at present made extremely difficult by the relatively meagre information available concerning quantitative lichen distribution, growth, and environmental controls in natural vegetation.

METHODS

Limits of the Region

Halliday (1937), Braun (1950) and Rowe (1959) have defined areas for the Northern Conifer-Hardwood Forests in Canada, and except for the southern limits in southwestern Ontario their definitions are more or less in agreement. Soper (1955) using extensive floristic studies of the many species in southern Ontario, considers the northern limits of the Carolinian Zone as the approximate boundary between Deciduous and Northern Conifer-Hardwood Forests in the region. On the basis of extensive ecological studies in southern Ontario, Maycock (1963) felt that the transition zone between these two formations would be twenty five miles north of Soper's Carolinian Zone. All stands in the present study were north of the region included by Maycock within the southern deciduous forest region.

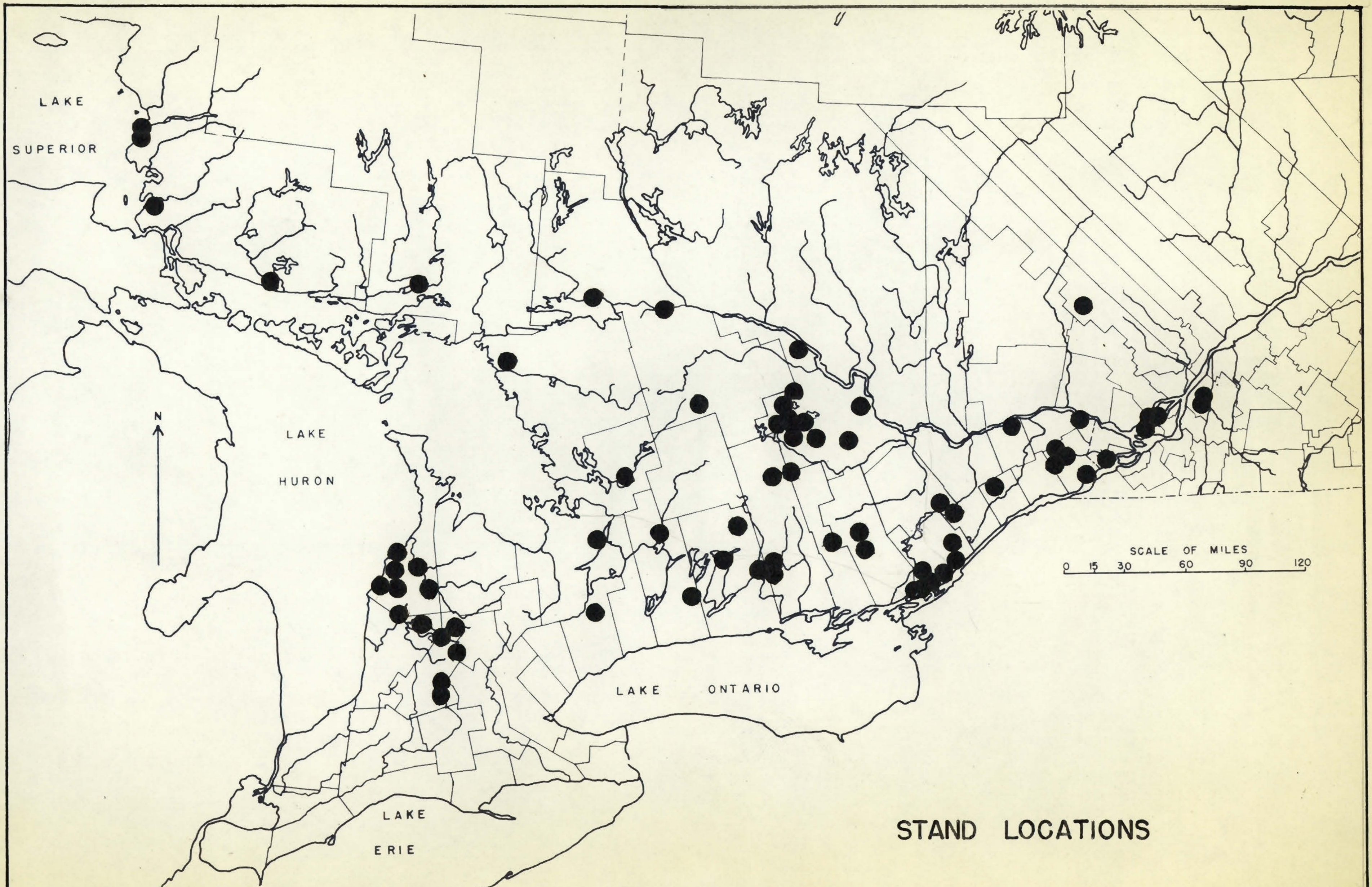
Selection of Stands

The initial criteria for selecting stands was strictly in relation to tree composition as the author had no knowledge of lichen composition within the Northern Conifer-Hardwood Forests. Stands were required to be undisturbed, homogeneous with respect to both topography and tree species composition and a minimum of approximately 10 acres in size. The size requirement was most important to insure that the edges of stands did not show external influences such as a greater light penetration. It is possible in the avoidance of edge sampling that insufficient area is left in small stands for adequate quantitative sampling. When occasionally open areas in stands, either man made or natural, were encountered they were bypassed if by their size they showed a different plant species composition from the stand. On the other hand if these areas were small and showed no change in species composition they were sampled. It should be stressed here that whereas these large open areas within stands might have increased the total lichen presence for the individual stands they could not have been sampled as they did not comply with the original requirements of homogeneity as listed above. In the rejection of apparently suitable stands grazing was the predominant factor of disturbance in the southern part of the area, while logging was more prominent in the northern areas.

Throughout, but increasing in occurrence northwards, relic boreal sites were frequently encountered in wet lowland areas. Where such boreal species as *Picea glauca* and *Picea mariana* were present as dominants, such stands were not studied in this investigation. Some difficulty was experienced in differentiating between wet Northern Conifer-Hardwood and wet Boreal sites, and it was decided that where deciduous species as *Ulmus americana*, *Fraxinus pennsylvanica*, *Fraxinus nigra*, *Acer rubrum* and *Acer saccharinum* were present in sufficient

FIGURE 4

Map of eastern central Ontario and western Quebec, showing the location and distribution of the 71 stands sampled.


LAKE
SUPERIOR
N
LAKE
HURON
LAKE ONTARIO
LAKE
ERIE
SCALE OF MILES
0 15 30 60 90 120
STAND LOCATIONS

numbers the site could be considered as Northern Conifer-Hardwood Forest. In addition Thuja occidentalis, though penetrating well into the Boreal regions is predominantly a Northern Conifer-Hardwood associate, being found well into the southern United States, and stands dominated by it were sampled whenever they satisfied the above requirements.

Throughout the region relatively pure stands of deciduous and coniferous species were found. The former tended to grow on the mesic sites with deeper more developed soils, the latter tended to occur on the dry, sandy, rocky upland soils or in wet lowland sites.

A total of 71 different forest stands were studied quantitatively in the region. Figure 4, gives the location of all the stands in relation to the counties of central Ontario and southwestern Quebec. The stands occur within an area of approximately 393,120 square miles. The most westerly stand is found near the Montreal River on the eastern shore of Lake Superior and is 728 miles from the most easterly site at Mont St. Hilaire, P.Q. The Montreal River stand is also the most northern site and is 540 miles north of the most southern stand near Stratford, Ontario.

Collection of Field Data

Throughout the study quantitative data for trees and shrubs were obtained using the 'Quarter' Method as described by Curtis (1959) and Maycock (1963). In following this method, an additional survey of each stand was made in which the presence of all terricolous lichens was recorded on prepared data sheets. In addition, the nature of lichen substrata was recorded, i.e. whether rock, log, soil and debris, or tree base to a height of 6" above ground level. Not having a thorough knowledge of all terracolous and corticolous lichens that might be encountered it was decided that only the first 6" of the tree base would be sampled. In this way the migration of terracolous lichens onto the tree base would be followed. At the same time the corticolous species that showed a preference for this medium or migrated from here onto the other substrata would be accounted for. Frequencies of terracolous lichens and their substrata were recorded in metre square quadrats at the same time as the herbs and tree seedlings.

In addition to the above quantitative information other environmental measurements were made. Canopy coverage over each point was recorded as a percentage from ocular estimates of amount of shade. Soil data included descriptions of the A_0, A_1, A_2 and B horizons and parent material with pH measurements taken of the A_1 layer. The topography of each stand was described in relation to surface conditions and classified as to moisture class. Three samples were pooled for analysis of the A_1 layer.

A representative sample of each species recorded in every stand was collected, Where positive identification in the field was not possible it was later determined in the laboratory. Over 1000 samples were collected in the field, determined in the laboratory and packaged according to stand.

A sample of each lichen species in each stand was sent to Dr. J. W. Thomson, University of Wisconsin, who very kindly checked all identifications and retained a representative collection for the Wisconsin Herbarium. The remaining samples have been deposited in the McGill College Herbarium.

LABORATORY PROCEDURES

Trees

In the laboratory all the tree data recorded in the field were reduced to averages that best described the stand composition. Separate summation sheets were prepared for the herb data. Frequency was obtained by dividing the number of points at which each tree was recorded by the total per cent of points sampled. Relative frequency was then calculated as a percentage of the sum of all these frequencies. Relative density was determined by calculating the total number of stems of each tree species as a percentage of the total number of stems of all species. Relative dominance was calculated by summing all basal area measurements of each individual tree species and calculating it as a percentage of the sum total basal area for all tree species. These three relative values were then summed for each tree species to provide an importance value. The importance values when summed gave a total of 300. The importance values for each of the different trees comprising a stand were found to provide a quantitative expression for the performance of that tree in the environmental and vegetational complex provided by the data.

After the importance values for each stand had been computed, the total was divided into per cent conifer and per cent deciduous. The ocular estimates of percentage canopy coverage at each point were totalled and averaged for all of the points of the stand. These figures were added to the other quantitative data of the stand.

The water retaining capacities of the soil samples from each site were determined following previously used procedures (Maycock, 1963). The soil samples taken in the field were prepared for analysis by passing through a 2 m.m. mesh and sent to the Provincial Laboratory at Ste. Anne de la Pocatiere for analysis of acidity (pH) and important minerals (calcium, potassium, phosphorus and magnesium).

Lichens

All lichen data recorded in the field were reduced to averages that best described the actual lichen composition of the individual stands of the Northern Conifer-Hardwood Forests.

The data recorded in quadrats were summarized to give frequency values which were calculated as the total quadrats of occurrence as a percentage of the total number of quadrats recorded in the stand for each species. This value provides an accurate measure of both the presence and absence of all species in the samples. The ecological importance of this value is further emphasized when related to the environmental conditions of the individual stands.

PRELIMINARY ANALYSIS AND RESULTS

As a prerequisite to the analysis of the terricolous lichens, an analysis of the tree composition had first to be completed. The initial step was to sort out certain statistics from the quantitative data. This was necessary because of the scarcity of previous quantitative data on the Northern Conifer-Hardwood Forests of this region. The following information is presented to assist in the understanding of the basic floristic components and ecological relationships of this forest region. The data on the forest stands used in the lichen study was the first collected of a more comprehensive vegetational study initiated in the summer of 1963. Additional stands may possibly change the forest patterns to a small degree especially with the addition of more northern communities.

There was a total of 50 tree species encountered in the 71 stands studied. Of these species twenty-two were dominants as indicated by the highest importance value in at least one stand.

Summarized in Table 2 are a group of phytosociological characteristics for each of the fifty tree species. The values presented in this table provide a good indication of the overall importance of each tree in the region. The number of stands of occurrence, or constancy, is indicative of the reliability of finding a particular tree in a randomly selected forest, on a percentage basis. The average importance value for a species was calculated by summing all importance values and averaging them

Table 2

List of all tree species in 71 stands
of the Northern Conifer-Hardwood Forests with data indicating
the relative importance of each

Species	Stands of Occurrence	Constancy	Average Import. Value	Max. Import. Value	Stands Lead. Domin.
Abies balsamea	31	43.7	6.1	140.5	1
Acer negundo	1	1.4	0.9	63.6	
Acer nigra	9	12.7	0.7	15.6	
Acer pensylvanicum	8	11.3	0.3	10.9	
Acer rubrum	38	53.5	6.8	55.9	
Acer saccharinum	13	18.3	15.8	209.1	6
Acer saccharum	50	70.4	67.9	288.8	23
Acer spicatum	3	4.2	0.1	7.2	
Alnus rugosa	1	1.4	0.03	1.0	
Amelanchier sp.	9	12.7	0.15	1.8	
Betula lutea	34	47.9	7.6	82.6	1
Betula papyrifera	38	53.5	8.1	90.4	1
Betula populifolia	3	4.2	1.6	109.8	1
Carpinus caroliniana	9	12.7	0.2	3.3	
Carya cordiformis	15	21.1	1.7	38.9	
Carya ovata	7	9.9	0.6	20.6	
Crataegus sp.	4	5.6	0.06	1.0	
Fagus grandifolia	29	40.8	15.5	185.0	3
Fraxinus americana	42	59.2	6.0	51.9	
Fraxinus nigra	21	29.6	8.4	159.1	1
Fraxinus pennsylvanica	17	23.9	8.5	120.9	1
Juglans cinerea	9	12.7	0.4	6.9	
Juniperus virginiana	4	5.6	4.5	227.0	1
Larix laricina	4	5.6	2.1	149.3	1
Ostrya virginiana	39	54.9	5.8	42.3	
Picea glauca	23	32.4	1.6	17.4	
Picea mariana	2	2.8	0.5	25.4	
Picea rubens	1	1.4	0.1	9.6	
Pinus banksiana	5	7.0	8.2	300.0	2
Pinus resinosa	13	18.3	10.6	229.4	4
Pinus rigida	3	4.2	2.3	92.9	1
Pinus strobus	28	39.4	19.3	228.0	6
Populus balsamifera	8	11.3	1.6	38.1	
Populus deltoides	1	1.4	0.01	1.0	
Populus grandidentata	19	26.8	8.3	225.4	2
Populus tremuloides	25	35.2	7.3	151.8	1

Table 2 (cont'd.)

Species	Stands of Occurrence	Constancy	Average Import. Value	Max. Import. Value	Stands Lead. Domin.
Prunus pensylvanica	7	9.9	0.3	4.6	
Prunus serotina	25	35.2	1.4	24.1	
Prunus virginiana	4	5.6	0.2	4.9	
Pyrus americana	3	4.2	0.2	6.1	
Quercus alba	10	14.1	4.6	97.1	2
Quercus marcocarpa	10	14.1	0.4	10.0	
Quercus rubra	29	40.8	11.3	280.5	2
Salix nigra	6	8.4	0.1	2.8	
Thuja occidentalis	26	36.6	12.2	279.0	2
Tilia americana	41	57.7	8.9	55.1	
Tsuga canadensis	31	43.6	7.0	108.5	2
Ulmus americana	47	66.2	27.7	237.8	7
Ulmus rubra	10	14.1	0.6	9.6	
Ulmus thomasii	6	8.4	1.2	54.9	

for the total number of stands studied. This provides a knowledge of the relative influence of that species in forest stands. Throughout the region it can be seen that this value would have only limited use if considered alone. As an example, Fraxinus americana has a high constancy of 59.2 per cent, and an average importance value of only 6.0. Tilia americana has a constancy value of 57.7 per cent and an average importance of 8.9. Ostrya virginiana has similar values with a constancy of 54.9 per cent and an average importance value of 5.8. The high constancy values of these species indicate that they are widespread, but because their maximum importance values do not exceed 56.0 they make only a minor contribution to the character of the forest community. Pinus resinosa, a species restricted to drier sites, has a constancy of only 18.3 per cent, but an average importance value of 10.6. Acer saccharinum occurring only in wet sites has values of 18.3 per cent and 15.8. Both species thereby show a restricted distribution, but exert a greater relative influence and show the ability to dominate in their specific sites.

The high constancy and average importance values for Acer saccharum of 70.4 per cent and 67.0 respectively indicate that it is the most widespread species, and it is the leading dominant in 23 stands within the limits of the region studied. Only five other trees are dominant in more than two stands: Ulmus americana in 7, Acer saccharinum in 6, Pinus strobus in 6, *Pinus resinosa* in 4 and *Fagus grandifolia* in 3. These six species dominated 69.0 per cent of all stands sampled, with the remaining 31.0 per cent being divided between sixteen other species. Of these sixteen species only six were broad ranging and had high constancy values, these included, *Abies balsamea*, *Betula lutea*, *Betula papyrifera*, *Populus tremuloides*, *Thuja occidentalis* and *Tsuga canadensis*. The remaining ten species were restricted to their own very specialized habitats.

Tree Ordination Procedures and Results

The Northern Conifer-Hardwood Forests of Central Canada occur over a wide range of moisture conditions from excessively wet to dry sites. This has resulted in a variety of environmental features which are in a large part related to the moisture conditions.

Recent phytosociological studies undertaken in the forests of North America have shown that ground moisture has a strong influence in determining forest composition in any site (Curtis, 1959, Maycock and Curtis, 1960 and Maycock, 1963). At the time field data was collected, special attention was taken of the moisture conditions prevalent in each stand. Following methods used by the above mentioned writers the stands were divided into five moisture classes of Dry, Dry-mesic, Mesic, Wet-mesic and Wet. By using this system of determination a total of 13 stands were designated on the moisture gradient as dry, with 22 as dry-mesic, 14 as mesic, 10 as wet-mesic and 12 as wet. The values for these trees and other environmental characteristics could then be averaged to determine whether trends existed in the patterns of the forest structure.

Moisture Gradient Ordination

Following the grouping of all stands in the above manner, the percentage presence and average importance value of each tree species was calculated for each moisture segment. These figures were then critically examined for relationships between the species and their occurrence along the moisture gradient. Data for presence and importance values were used for the 71 stands studied, and along with the other environmental characteristics, patterns were produced showing ecological relationships.

Presented in Table 3 are the average per cent presence and average importance values in the moisture segments for the 50 tree species recorded. The values of each species show a tendency to attain importance in a particular category. Consequently all the tree species have been arranged according to their optimum segment. For example, *Pinus rigida* has an average per cent presence of 15.6 in the dry and 4.8 in the dry-mesic stands. From the average importance values it has a value of 12.3 in the dry and only 0.1 in the dry-mesic. Clearly, *Pinus rigida* is a species restricted to the dry end of the moisture segment.

From Table 3 it may be seen that *Acer saccharum* was the most widespread of all the tree species. Although a mesic species it was present in every mesic stand and also dominant in

TABLE 3

Percent Presence and Average Importance Values for

trees by moisture segments (71 stands)

Species	Percent Presence					Av. Importance Value				
	D	DM	M	WM	W	D	DM	M	WM	W
Juniperus virginiana	31.2					24.4				
Pinus rigida	15.6	4.8				12.3	0.05			
Pinus banksiana	31.2	4.8				44.6	0.1			
Quercus alba	39.0	23.8				15.1	6.0			
Pinus resinosa	62.4	24.0	7.1			45.5	7.7	0.1		
Populus grandidentata	62.4	47.6	7.1			26.3	10.8	1.6		
Quercus rubra	77.8	71.4	28.6			30.1	17.7	2.7		
Carya ovata	31.2	9.5	7.1			1.8	0.7	0.2		
Amelanchier sp.	23.4	19.0		18.2		0.3	0.2		0.2	
Pyrus americana	7.8	4.8		9.1		0.08	0.3		0.5	
Acer pensylvanicum		19.0	21.4				0.3	0.9		
Juglans cinerea		23.8	21.4				0.6	0.9		
Acer nigrum		9.5	50.0				0.5	2.8		
Acer spicatum	9.5			9.1		0.4			0.09	
Fagus grandifolia	7.8	66.7	85.7	18.2		0.3	32.7	27.2	2.5	
Pinus strobus	77.8	43.2	28.6	9.1	16.7	59.6	27.3	1.6	0.1	0.2
Prunus pensylvanica	15.6	9.5	7.1	9.1	8.3	0.2	0.3	0.1	0.7	0.2
Ostrya virginiana	62.4	80.9	78.6	18.2	8.3	5.0	11.4	7.2	0.8	0.2
Carya cordiformis	7.8	23.8	35.7	27.3	8.3	0.5	2.6	2.2	2.2	0.1
Betula papyrifera	70.2	76.2	28.6	45.4	33.3	7.1	16.3	1.6	7.3	2.5
Tsuga canadensis	46.8	42.4	64.3	54.5	8.3	2.8	10.3	4.5	16.8	0.1
Acer saccharum	54.6	90.5	100.0	72.7	16.7	6.3	92.4	183.4	19.9	1.0
Tilia americana	15.6	80.9	78.6	81.8	16.7	0.3	12.0	17.3	11.4	0.6
Acer rubrum	77.8	52.4	21.4	54.5	66.7	4.6	4.5	4.5	12.3	14.3
Fraxinus americana	31.2	76.2	71.4	45.4	50.0	2.2	10.0	5.9	6.2	2.0
Prunus serotina	23.4	38.1	57.1	36.4	16.7	0.9	2.1	1.7	1.0	0.7

TABLE 3 (cont'd.)

Species	Percent Presence D	DM	M	WM	W	Av. Importance Value D	DM	M	WM	W
Abies balsamea	39.0	47.6	28.6	36.4	66.7	3.6	10.5	0.9	7.2	3.0
Populus tremuloides	31.2	33.3	7.1	45.4	66.7	2.5	8.1	0.07	22.8	5.4
Carpinus caroliniana	7.8	9.5	x10.2	18.2	16.7	0.25	0.1	0.1	0.2	0.3
Picea glauca	31.2	38.1	28.6	18.2	41.2	1.5	2.1	0.9	0.7	1.5
Betula lutea	7.8	33.3	71.4	81.8	50.0	0.6	5.1	11.9	18.0	4.7
Populus balsamifera	7.8		42.9	45.4	16.7	0.7		5.7	3.2	5.5
Picea mariana	7.8				16.7	1.7				9.2
Betula populifolia	7.8				16.7	0.08				9.2
Ulmus americana	15.6	52.4	42.9	90.9	100.0	0.4	3.2	12.1	62.0	80.4
Thuja occidentalis	7.8	33.3	21.4	63.6	66.7	0.1	4.6	0.3	42.1	25.1
Ulmus rubra		19.0	21.4	9.1	8.3		0.8	1.1	0.1	0.5
Ulmus thomasii		14.3	15.2		8.3		2.9	0.9		0.7
Quercus marcocarpa		4.8	7.1	36.4	33.3		0.05	0.1	1.4	0.8
Crataegus sp.		4.8			25.0		0.05			0.3
Fraxinus pennsylvanica			7.1	72.7	66.7			0.1	21.0	24.3
Fraxinus nigra			7.1	72.7	100.0			0.1	10.7	33.8
Picea rubens				9.1					0.9	
Prunus virginiana				27.3	8.3				1.0	0.1
Acer saccharinum				45.4	66.7				29.8	66.0
Salix nigra				9.1	41.2				0.1	0.6
Larix laricina				9.1	25.0				0.1	12.7
Acer negundo					16.7					5.3
Alnus rugosa					8.3					0.2
Populus deltoides					8.3					0.1

	Dry	Dry-Mesic	Mesic	Wet-Mesic	Wet
Total conifer importance value per segment	2551.5	1337.5	115.9	727.8	561.6
Percentage conifer per segment	65.5	20.3	2.8	23.5	14.5

every one with an average per cent presence of 100.0 per cent and an average importance value of 183.4. The species was of considerable influence in adjacent segments, particularly the dry-mesic segment where it attained the highest average importance value (92.4) of any of the tree species in that segment. These figures indicate that *Acer saccharum* has a broad range of tolerance in relation to moisture and that mesic sites are ecologically optimum. *Acer saccharinum* is presented as an example of a species of the wet segment in a similar manner. It has a percentage presence in the wet of 66.7, and of 45.4 in the wet-mesic, and an average importance value of 66.0, and 29.8 respectively in the same two moisture classes. Both sets of values are high and it is interesting to note that there is a gradual decline in values to an absence in the mesic segment. Wet conditions, therefore, appear to exert a strong environmental influence for this species. The highest values for *Fagus grandifolia* were recorded in the dry-mesic with an average per cent presence of 66.7 and an average importance value of 32.7, while highest values for *Thuja occidentalis* were recorded in the wet-mesic with an average per cent presence of 63.6 and an average importance value of 42.1.

From these examples it can be seen that each tree attains an ecological optimum and exerts a considerable influence in only one of the five moisture segments. This is true even though the species have a broad amplitude of tolerance or are restricted to one end of the moisture gradient. Only five species were restricted to one particular segment; Populus deltoides, Alnus rugosa, Acer negundo in the wet segment, Picea rubens in the wet-mesic and Juniperus virginiana in the dry moisture segment.

Interpretation of the data in Table 3 shows that certain groups of trees are usually associated in the moisture segments. In the dry segment the following species usually attain their greatest ecological influence: Pinus rigida, Juniperus virginiana, Pinus strobus, Pinus resinosa, Quercus alba and Quercus rubra although only Juniperus virginiana was found restricted to this segment. Acer saccharum, Fagus grandifolia, Tilia americana and Betula lutea are the trees with the greatest influence in the mesic sites. Ulmus americana, Acer saccharinum, Fraxinus nigra, Thuja occidentalis and Larix laricina are important trees in the wet areas studied.

From Table 3 it can be seen that the number of conifer species is greatest in the dry segment where 10 of a total of 33 tree species are conifer and they represent 65.5 per cent of the total importance value for that segment. In the dry-mesic segment 8 of 35 tree species were conifer, here the deciduous species were dominant with the conifers having only 20.3 per cent of the total importance value. While 6 of 32 tree species in the mesic were conifers they were of such low values for per cent presence and importance value that their latter values only amounted to 2.8 per cent of the total importance value. A similar number of conifer species were present in the wet-mesic, 6 of 32 tree species but their importance value was 23.5 per cent of the total for that segment. Finally, while the number of conifers in the wet increased to 7 of 34 tree species present the importance value dropped to 15.6 per cent of the total. From these figures it is demonstrated that the conifer species are the dominant life form in only the dry segment of the moisture gradient.

In the mesic segment of the moisture gradient only Acer saccharum and Tilia americana were important, with the former the dominant in every case. This great dominance by Sugar Maple indicates how successful this species is in establishing and maintaining itself in mesic conditions, and in addition, the effective way in which it restricts all tree species reproduction especially by its very dense canopy.

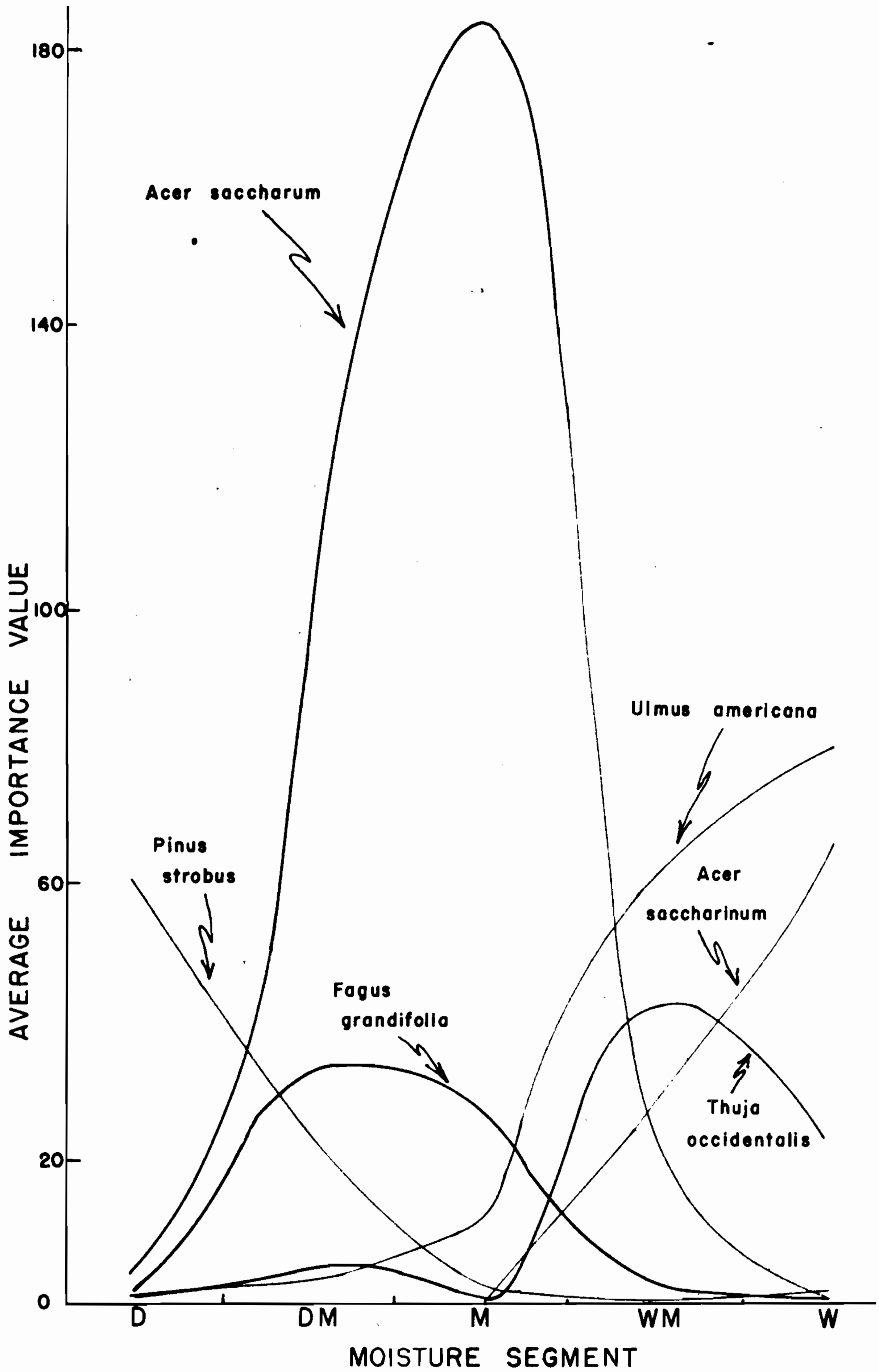
A series of graphs were prepared to aid in interpreting patterns of some of the important canopy trees, and are shown in Figures 5 to 9. In each case the vertical axis represents the average importance values and the horizontal axis the five segments of the moisture gradient from dry to wet.

In Figure 5, average importance values of the six trees of greatest influence in the forests of the region are plotted for the five moisture segments. The fact that several species tend to develop optimally in the same moisture segment is noted in the following graphs, Figures 6 to 9.

It is evident in the individual segments at extreme ends of the moisture gradient that a mingling of coniferous and deciduous trees occurs at high levels of importance and an exception to this

FIGURE 5

The patterns of six major tree species in relation to the moisture gradient, based on average importance value.



AVERAGE IMPORTANCE VALUE
180
140
100
60
20
0
Acer saccharum
Ulmus americana
Pinus strobus
Acer saccharinum
Fagus grandifolia
Thuja occidentalis
D
DM
M
WM
W
MOISTURE SEGMENT

FIGURE 6

The patterns of seven tree species restricted to the dry end of the moisture gradient, based on average importance value.

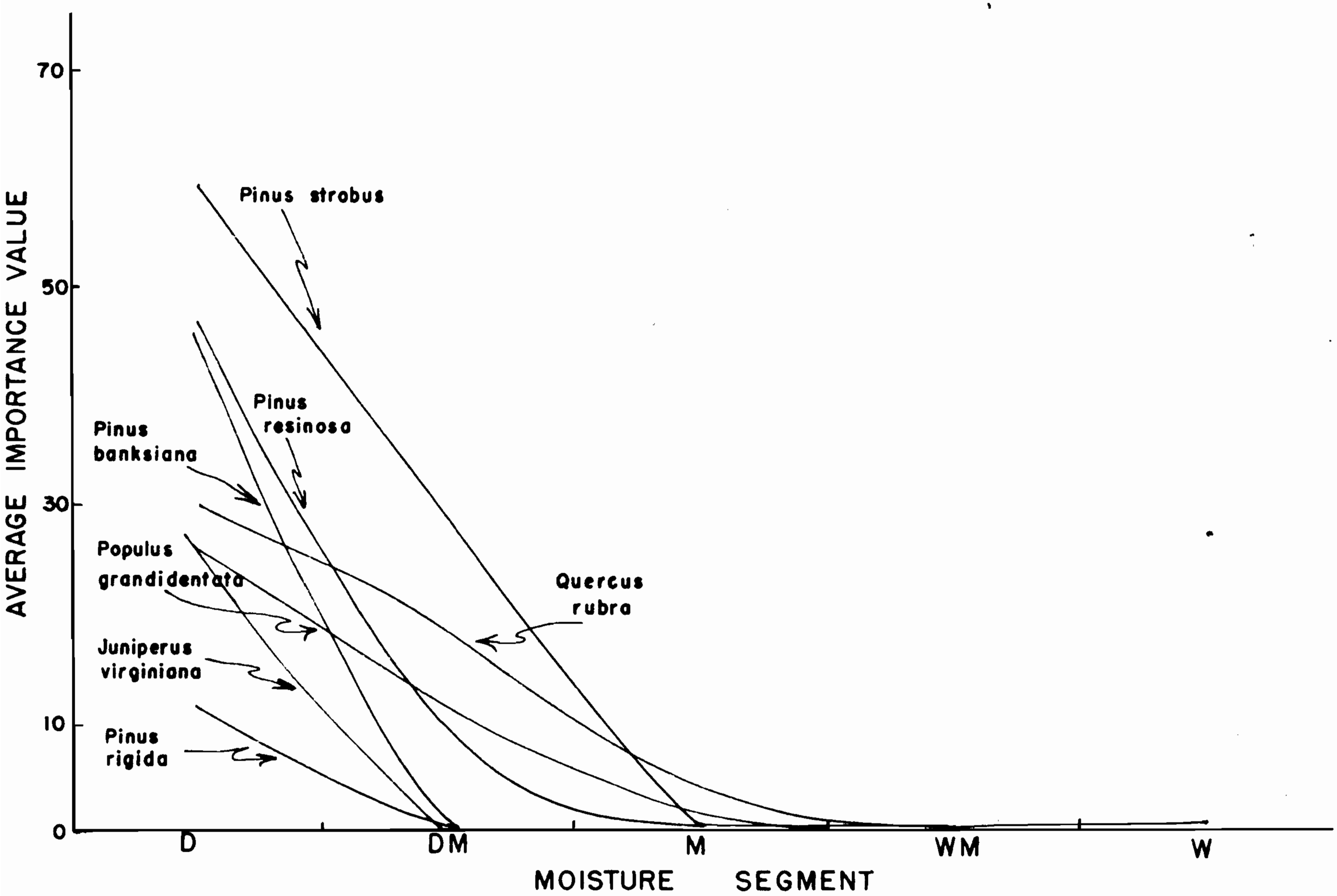
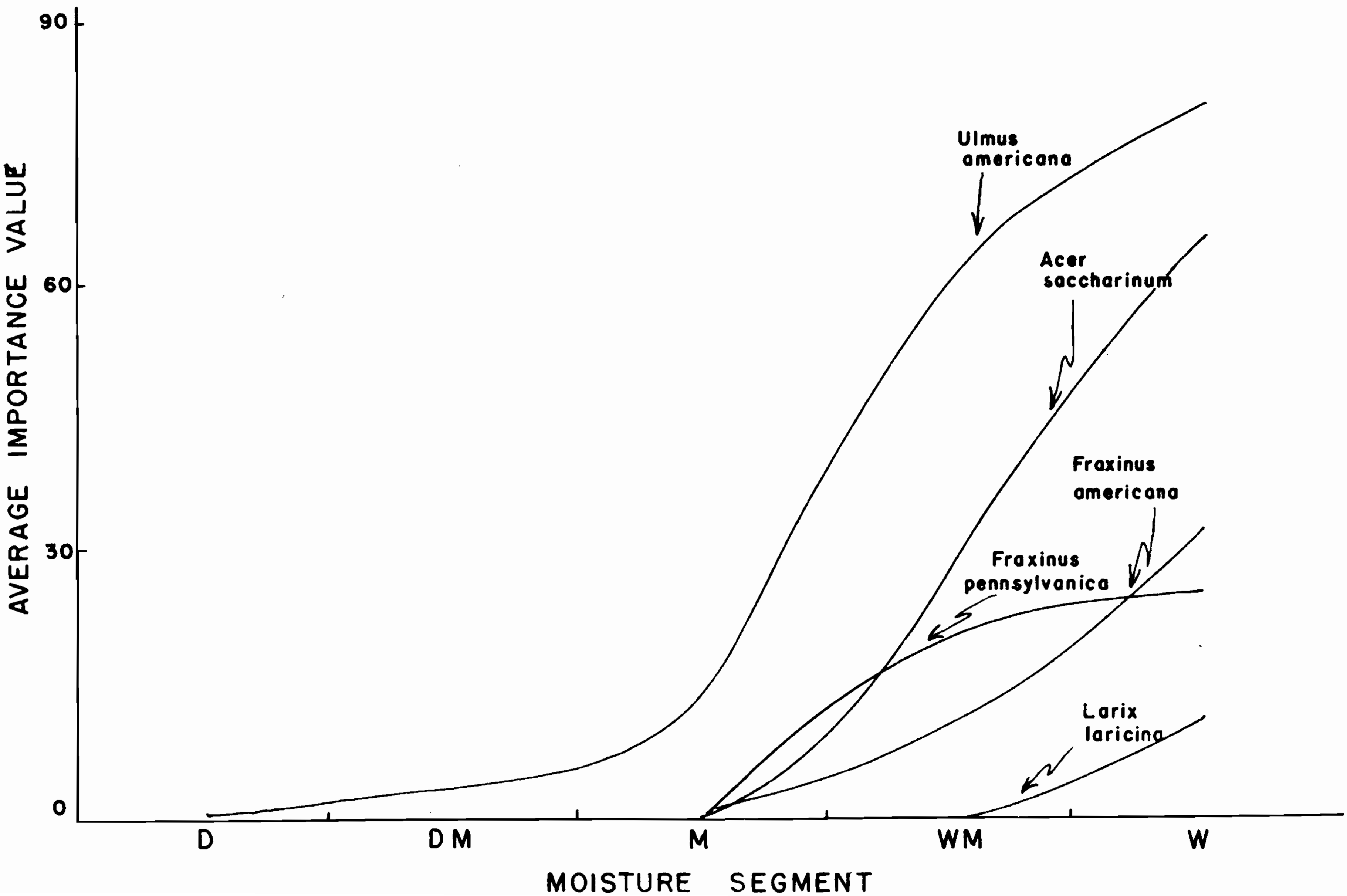

AVERAGE IMPORTANCE VALUE
70
50
30
10
0
Pinus strobus
Pinus resinosa
Pinus banksiana
Populus grandidentata
Quercus rubra
Juniperus virginiana
Pinus rigida
D
DM
M
WM
W
MOISTURE SEGMENT

FIGURE 7

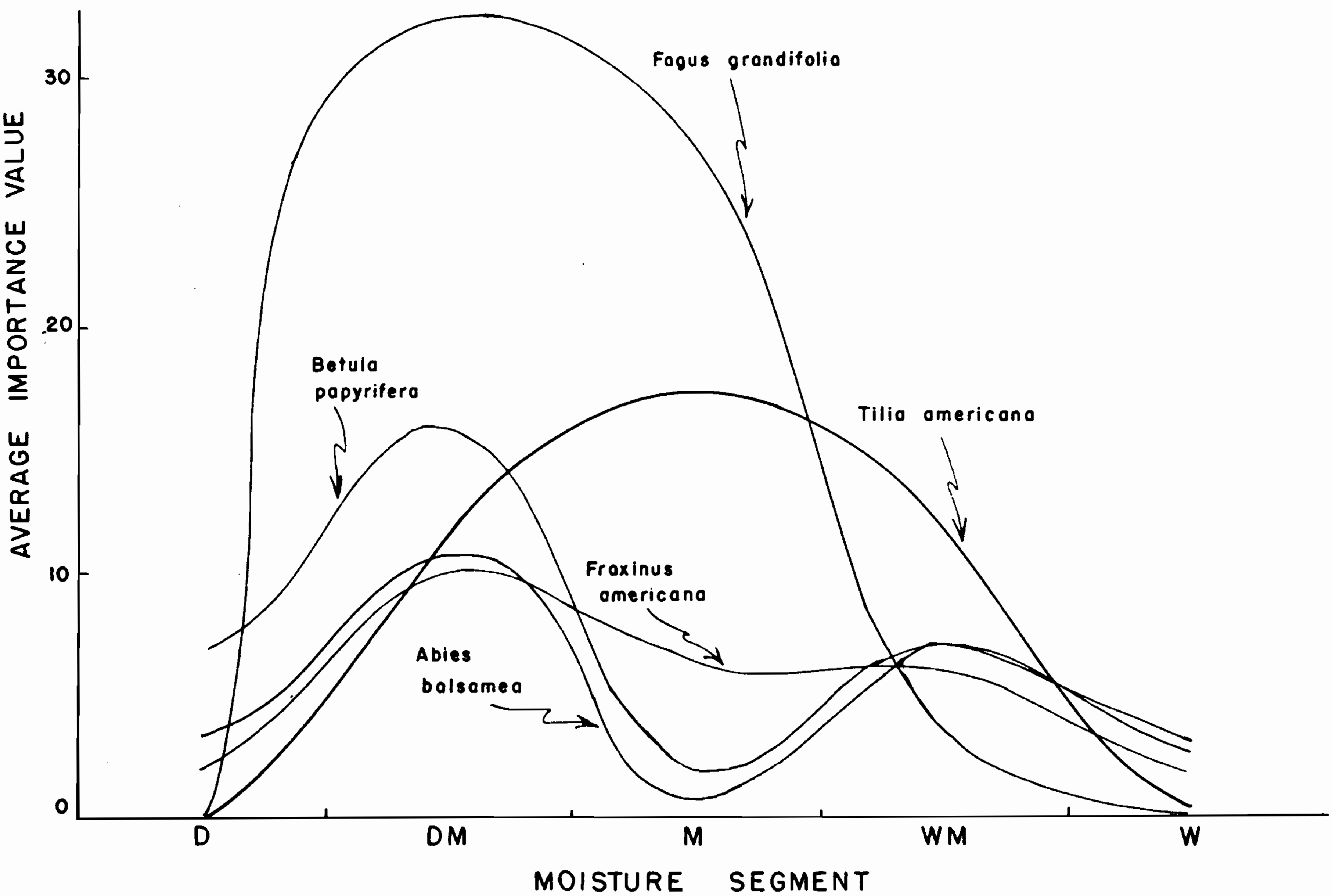
The patterns of five tree species restricted to the wet end of the moisture gradient, based on average importance value.



AVERAGE IMPORTANCE VALUE
90
60
30
0
D
DM
M
WM
W
MOISTURE SEGMENT
Ulmus americana
Acer saccharinum
Fraxinus americana
Fraxinus pennsylvanica
Larix laricina

FIGURE 8

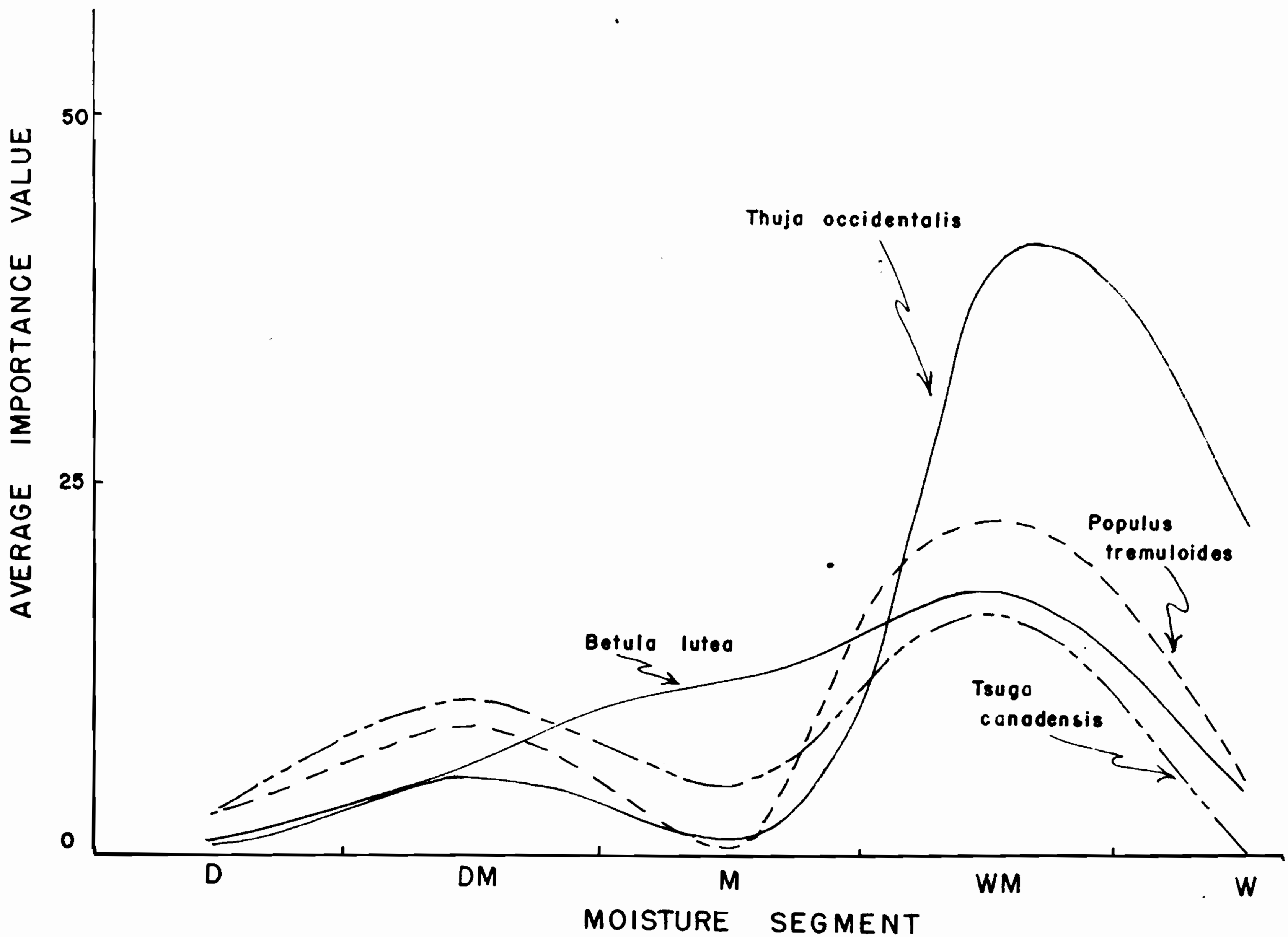
The patterns of five tree species showing moderate importance levels with their optimum in the dry-mesic and mesic segment of the moisture gradient. Average importance is plotted.



AVERAGE IMPORTANCE VALUE
30
20
10
0
Fagus grandifolia
Betula papyrifera
Tilia americana
Fraxinus americana
Abies balsamea
D
DM
M
WM
W
MOISTURE SEGMENT

FIGURE 9

The patterns of four tree species showing moderate importance levels with their optimum in the wet-mesic segment of the moisture gradient. Average importance plotted.



AVERAGE IMPORTANCE VALUE
50
25
0
Thuja occidentalis
Populus tremuloides
Betula lutea
Tsuga canadensis
D
DM
M
WM
W
MOISTURE SEGMENT

situation is found in the mesic sites. This feature emphasizes the mixed nature of the Northern Conifer-Hardwood Forests.

In Figure 6 and Figure 7 the major species of both dry and wet segments respectively are presented. These tree species were all dominants in these segments and showed preference for these moisture sites. In many cases the species at the dry end of the continuum had individual importance values in excess of 200, and in this segment a maximum value of 300 was recorded for Pinus banksiana. Pinus strobus is the major dominant of the dry segment and is present across the moisture gradient with very low values in the mesic, wet-mesic and wet segments. In the wet segment there are six dominant species, all but two are deciduous; Larix laricina and Thuja occidentalis are coniferous. Ulmus americana shows a reverse pattern to that of Pinus strobus, and is the only wet species present in all moisture segments having very low values in the mesic, dry-mesic and dry segments. With the exception of Pinus strobus and Ulmus americana all other species attain an optimum importance in either the dry or wet conditions and are either absent or of sporadic occurrence in the mesic sites.

Finally in Figure 8 and Figure 9 the major species of the dry-mesic and wet-mesic segments are graphed. In all cases the species are found along the moisture gradient, although only Fagus grandifolia and Thuja occidentalis can be said to have moderate importance values. Although the other species are of minor importance they are capable of attaining dominance on their optimum sites. These graphs clearly show that the trees are not confined to one moisture segment. Whereas the major trees have binomial curves, the species mentioned above seem to be affected by factors in addition to moisture.

Each of these species shows two peaks of importance, one of greater magnitude than the other. In the wet-mesic segment Thuja occidentalis is the major species, with Populus tremuloides, Betula lutea and Tsuga canadensis, all attaining greatest importance in this segment. Tsuga canadensis was present in a larger percentage of stands in the mesic than all other segments with a constancy value of 64.3 per cent and an average importance value of 4.5. In the wet-mesic segment a constancy value of 54.5 per cent and an average importance value of 16.8 was recorded. It would appear that the deciduous species in the mesic sites restrict Tsuga to a position of minor importance.

Populus tremuloides shows an average per cent presence value of 66.7 per cent in the wet and 36.4 in the wet-mesic, and average importance values of 5.4 and 22.8 respectively in the same segments. The wet sites while showing a high presence for Populus tremuloides do not appear optimum as the average importance value is low. On the other hand, the wet-mesic sites appear more restricted, but with the likelihood of more heavily populated stands of Populus tremuloides being present.

Under dry-mesic conditions similar patterns are evident for four species, Fagus grandifolia, Betula papyrifera, Fraxinus americana and Abies balsamea which attain their highest levels of importance in this moisture segment. At the same time they occur with minor importance in other segments.

Of the twenty-one trees considered of major influence across the moisture gradient, thirteen species are deciduous and nine are coniferous. Species of conifers were present as dominants in all moisture segments except the mesic. The dry and wet-mesic segments included the largest number of dominant coniferous species, 5 and 3 respectively. When relating those two sites it is found that the dry coniferous stands are for the most part on Precambrian bedrock while the wet-mesic sites are on Paleozoic bedrock. There were three dry stands not on the Precambrian bedrock; these were dominated by mature Pinus strobus.

By combining data of all major species it can be seen that certain groupings are evident along the moisture gradient. All species differ in respect to optimum development and ecological amplitude (relationship) and the data presented in the tables does point to the complexity of the vegetation in the region investigated. The remaining trees of minor importance are not graphed, but it can be seen from Table 3 that they follow similar patterns to those of the major species and in many cases are associated in specific moisture segments with the major dominants.

Discussion

The quantitative data collected in the field and sorted out in the laboratory have been presented to indicate the relation between forest composition and major environmental factors.

A preliminary analysis of the tree composition shows that the vegetation of Central Ontario and Western Quebec is complex in nature, with 38 deciduous (13 dominant species), and 12 coniferous (9 dominant species)present. A reduction in the number of species is to be expected as one enters the microthermal climatic zone from the southerly mesothermal climatic zone. Twelve species recorded in the deciduous forests of the extreme southwestern area of Ontario were not recorded in this region. The great variety of dominant trees in the area of study emphasizes the diversity of such characteristics as soil type, topography, drainage and areal climate. The communities cannot be considered in traditional classification categories due to the great variability in the groupings of the dominant species.

The almost negligible number of coniferous species in the mesic sites emphasizes the dominance by deciduous species on generally well developed soils. A high degree of compositional stability is exhibited with the ability of Acer saccharum to replace all other species, including other shade-tolerant species, and maintain itself on mesic sites. In this study, Acer saccharum is the most important tree in the terminal mesic areas, where it attains the highest percentage presence and average importance value of all trees and attains its ecological optimum. The coniferous species largely intolerant of shade are unable to compete nor tolerate these mesic conditions unless there is disturbance, such as fire or logging.

In the wet bottomland sites along rivers, coniferous species were not usually found, possibly because of seasonal flooding. The alluvial soils have no permanent humus layer and the alkaline pH conditions may not be conducive to conifer establishment. On the other hand in the lowland sites *Larix laricina* and *Thuja occidentalis* dominate under favourable conditions of low pH, peat, muck or soils of low oxygen levels, impeded drainage, slow turn over of organic matter and the high water retaining capacity of organic layers. With the invasion of such deciduous species as *Fraxinus pennsylvanica*, *Ulmus americana* and *Acer saccharinum* the soils become heavier and are less acidic; they have moderate levels of oxygen and a moderate turn over of organic matter. The resulting water retaining capacities are usually lower in the soil types of the wet-mesic forests due to the reduced amount of organic matter that is being incorporated into the soil at a faster rate.

Throughout the region the dry upland sites support two general types of forest, coniferous, with *Pinus strobus* and *Pinus resinosa* as dominants, and deciduous dominated by species of Oak forming open canopied forests. While these two life forms are found in relatively pure stands there is considerable intermingling of both the coniferous and deciduous trees referred to above. In southern regions on Precambrian outcrops in the vicinity of the Thousand Islands, *Pinus rigida* and *Juniperus virginiana* are present as dominants, while in other parts of the region, except in the east, *Pinus banksiana* forms almost pure stands on sandy soils after fire. These two types of site usually occur on different soils of rock and sand, but surface layers have some common features, acidic, mor humus types resulting from the accumulation of needles, leaves and branches. The *Pinus banksiana* stands usually lack thick soil organic matter accumulations as a result of repeated fires. However, the other dry sites have a true A_1 layer and a leached, well developed A_2 layer and are classified as podzol or podzolic soil types.

Forest succession in the dry segments results in a replacement of the pioneer species by others more tolerant of increased shade, such as *Acer saccharum*, *Fagus grandifolia*, *Quercus alba*, *Abies balsamea* and *Tsuga canadensis*. This initial stage of dry land succession usually begins after fire. When deciduous species are present the soil becomes less acidic and has a moderate turn over of organic matter. There is a reduction of light penetration through the canopy. In mesic conditions tree crown canopy is very dense, there is little accumulated debris on the forest floor, and the organic matter is well incorporated into the mineral soil surface horizon; soils are usually grey brown forest and related types.

These forests, therefore, occur on a very wide range of topographical sites, from dry to wet in the moisture classification; they are characterized by the presence of coniferous genera including, Pinus, Juniperus, Abies, Tsuga, Thuja and Larix growing within a larger element of deciduous species. These are best understood when studied along the moisture gradient, in relation to which each tree species has an optimum situation. This is a situation where the magnitude and interaction of critical ecological factors satisfies physiological and reproductive requirements resulting in greatest development of that species. Thus, dry stands with light and rocky soils were dominated by Pinus strobus, Pinus resinosa and Pinus banksiana. The heavier soils supported the true mixed conifer-hardwood forests of Pinus, Tsuga and Abies as conifers, and Acer saccharum, Betula papyrifera, Betula lutea, Tilia americana, Fagus grandifolia, Fraxinus americana and Quercus alba as hardwoods. The wet habitats contained either lowland conifer swamps of Larix, Thuja and hardwoods, or bottomland and lowland sites dominated by Ulmus americana, Acer saccharinum, Fraxinus nigra Fraxinus pennsylvanica and Acer rubrum. This quantitative ecological investigation into the tree composition of the forests has helped to emphasize the many different tree species which are found as dominants under a variety of environmental conditions.

LICHEN ANALYSIS

General Quantitative Characteristics

Analysis of the terricolous lichen vegetation was carried out from three separate points of view. In the first approach a statistical analysis of the lichens was undertaken to show their general relationship to the forests of the region. The purpose of the second analysis was to emphasize the patterning of these lichens as a component of the forest community and their relationship to the major tree species. Finally an analysis was made in relation to the environmental features produced by this forest complex and how changing conditions affected the general distribution of all terricolous lichens.

As an initial step, a complete presence list of lichen species was determined, including all species on rocks, logs, all ground habitats and on the first six inches of the tree bases. A total of 87 lichen species were collected and identified from the 71 stands and of this total 38 were fruticose, 39 were foliose and 10 were crustose. Listed in the appendix are 126 lichen taxa including 87 species, plus varieties and forms. A large number of these varieties and forms were not discernable in the field and were only identified later in the laboratory before samples of all taxa were sent to Dr. J. W. Thomson, University of Wisconsin, for determination.

The 87 lichen species which occurred in the stands, all show different ecological characteristics. Only six species can be classified as having a broad range of ecological tolerance because they were recorded in a wide range of habitats. The remaining 81 species are all influenced in their occurrence by dominant vegetation, topography and other ecological factors. Among the six species mentioned above are included the majority of those for which highest frequencies were recorded in the forests sampled.

An approach similar to that followed for trees allows the presentation of quantitative information regarding lichen distribution and frequency within the forest communities of variable composition. The wide selection of stands throughout the region was sufficiently varied to be statistically representative of the individual species and their ecological performance.

Listed in Table 4 are statistics for each of the 87 species recorded. They provide a good indication of the ability of any species to tolerate conditions within the forests of the region. Stands of occurrence give the number of stands within which each species was recorded. Constancy places this record on a percentage basis and indicates the probability of finding the particular species in a randomly selected stand within the region. Average frequency was determined from the quadrat counts by totalling the frequencies of each species and dividing that total by the total number of stands studied. The number of stands in which a particular species was the dominant has also been included.

In view of the large numbers of species with a constancy below 25.0 per cent, Table 5 is presented to show the number of lichen species, and the morphological forms, present in the five constancy groups. Only seven species have a constancy value greater than

Table 4

List of all lichen species in 71 stands of the Northern Conifer-Hardwood Forests with data indicating the relative importance of each

Species	Stands of Occurrence	Constancy	Av. Freq.	Stands Dominant
Actinogyna muhlenbergii	5	7.0	0.1	
Alectoria nidulifera	2	2.8		
Bacidia chlorococca	3	4.2		
Bacidia fusca	1	1.4		
Bacidia incompta	1	1.4		
Candelaria concolor	3	4.1		
Cetraria ciliaris	1	1.4		
Cetraria oakesiana	12	16.9	0.6	
Cetraria pinastri	5	7.0	0.6	
Cetraria tuckermanii	2	2.8		
Cladonia alpestris	4	5.6		
Cladonia bacillaris	10	14.1	0.6	
Cladonia botrytes	6	8.5	0.4	
Cladonia cenotea	3	4.2		
Cladonia chlorophaea	36	50.8	6.5	4
Cladonia coccifera	1	1.4		
Cladonia coniocraea	56	79.0	16.1	28
Cladonia crispata	11	15.5	0.8	
Cladonia cristatella	19	26.8	1.2	
Cladonia cylindrica	1	1.4		
Cladonia deformis	10	14.1	0.5	
Cladonia delicata	1	1.4		
Cladonia digitata	3	4.2		
Cladonia farinacea	2	2.8		
Cladonia fimbriata	28	39.5	3.9	
Cladonia furcata	7	9.9	0.6	
Cladonia gracilis	15	21.2	1.3	
Cladonia macilenta	9	12.7	0.7	
Cladonia mitis	3	4.2	0.1	
Cladonia multiformis	5	7.0	0.5	
Cladonia nemoxyna	2	2.8		
Cladonia ochrochlora	2	2.8		
Cladonia pleurota	1	1.4		
Cladonia pyxidata	2	2.8	0.6	
Cladonia rangiferina	14	19.7	2.9	1
Cladonia scabriuscula	1	1.4		
Cladonia squamosa	11	15.5	0.3	

Figures not checked

Species	Stands of Occurrence	Constancy	Av. Freq.	Stands Dominant
Cladonia subtenuis	4	5.6		
Cladonia subulata	1	1.4		
Cladonia sylvatica	4	5.6	0.4	
Cladonia turgida	4	5.6	0.4	
Cladonia uncialis	4	5.6	0.2	
Cladonia verticillata	5	7.0	0.3	
Crocynia neglecta	6	8.5	0.4	
Crocynia membranacea	31	43.7	2.9	2
Evernia mesomorpha	5	7.0		
Lasallia papulosa	1	1.4		
Lecanora pallescens	1	1.4		
Lecanora subfuscata	1	1.4		
Leptogium cyanescens	6	8.5	0.5	
Lobaria pulmonaria	3	4.2		
Microphiale diluta	1	1.4		
Nephroma bellum	3	4.2		
Parmelia aurulenta	1	1.4		
Parmelia caperata	5	7.0	0.1	
Parmelia conspersa	3	4.2	0.2	
Parmelia frondifera	2	2.8		
Parmelia lusitana	1	1.4		
Parmelia physodes	9	12.7	0.1	
Parmelia plitti	2	2.4		
Parmelia rudecta	3	4.2		
Parmelia stenophylla	20	28.2	3.1	2
Parmelia subaurifera	1	1.4		
Parmelia subtilis	1	1.4		
Parmelia sulcata	7	9.9	0.1	
Parmeliopsis ambigua	4	5.6	0.5	
Parmeliopsis hyperopta	4	5.6	0.5	
Peltigera canina	33	46.5	2.9	2
Peltigera canina var spuria	2	2.8	0.3	
Peltigera evansiana	6	8.5		
Peltigera horizontalis-polydactyla	5	7.0	0.1	
Peltigera polydactyla	2	2.8	0.1	
Pertusaria sp.	1	1.4		
Physcia adscendens	1	1.4		
Physcia aipolia	3	4.2		
Physcia ciliata	2	2.8		
Physcia millegrana	2	2.8		
Physcia orbicularis	2	2.8		
Physcia phaea	2	2.8	0.1	
Pyxine sorediata	1	1.4		
Ramalina intermedia	1	1.4		
Ramalina obtusata	1	1.4		
Rhizocarpon geographicum	1	1.4		
Stereocaulon evolutoides	5	7.0	0.1	
Umbilicaria deusta	2	2.8		
Umbilicaria mammulata	1	1.4		
Xanthoris polycarp`a	2	2.8		

Table 5

Constancy Class in per cent	No. of Species	Forms
50 - 100	2	2 Fruticose
25 - 49	5	2 Fruticose 2 Foliose 1 Crustose
15 - 24	5	4 Fruticose 1 Crustose
5 - 14	25	13 Fruticose 10 Foliose 2 Crustose
1 - 4	50	17 Fruticose 26 Foliose 7 Crustose

25.0 per cent which is a good indication that the Northern Conifer-Hardwood Forests are not optimum sites for most of these terricolous lichens.

Only two species, both fruticose forms, have a constancy greater than 50.0 per cent. Cladonia coniocraea, recorded in 56 stands, with a constancy of 79.0 per cent, and having an average frequency of 16.1, was by far the most common lichen species, and was the dominant lichen in twenty-eight stands. Cladonia chlorophaea was present in 36 stands and had a constancy of 50.8 per cent, an average frequency of 6.5 and was dominant in 4 stands. With constancies of from 25 to 49.0 per cent, five species were recorded: two fruticose, two foliose and one crustose. Cladonia fimbriata was recorded in 28 stands with a constancy of 39.5 per cent, and with an average frequency of 3.9. Cladonia cristatella was present in 19 stands with a constancy of 26.8 per cent and an average frequency of 1.2 and was not dominant in any stand. Peltigera canina was present in 33 stands with a constancy of 46.2 per cent and an average frequency of 2.9 and was dominant in two stands. Parmelia stenophylla was present in 20 stands with a constancy of 28.2 per cent and an average frequency of 3.1 and was dominant in two stands. The crustose species Crocynia membranacea was recorded in 31 stands with a constancy of 43.7 per cent and an average frequency of 2.9 and was dominant in two stands.

The seven most commonly recorded species referred to above usually occurred together in the same stands although the latter three species tended to dominate in sites that were not optimum for the former four species. In all cases, except for Cladonia cristatella absent in mesic stands, the species were shown to have a broad range of tolerance in all five segments of the moisture gradient.

In the 15-25.0 per cent constancy group there were only five species, four were fruticose and one was crustose. In the 5-14.0 per cent constancy class twenty-five species were recorded. There were thirteen fruticose, ten foliose and two crustose. The remaining and largest group was that in which the species had a constancy of between 1.0 and 4.0 per cent. Fifty species were recorded in this group: seventeen fruticose, twenty-six foliose and seven crustose.

A study of Table 4 shows that 39 species of the total 87 recorded were present in only one stand in this investigation. This points to the extremely narrow ecological range of these lichens in these forests. Of another 39 species with frequency values only six attained a level of frequency that placed them as a frequency dominant in a stand. Cladonia rangiferina was the only species with a constancy value less than 25.0 per cent which was recorded as a frequency dominant. Cladonia pyxidata was recorded in only two stands, but in one it showed a high frequency. Consequently, in averages for the 71 stands it attained a higher average frequency than many species recorded in a greater number of stands.

Although these figures are not of the same magnitude as those for the trees they still present an accurate statistical account of the lichens in randomly selected stands in the region. These statistics for lichens indicate that frequencies would be extremely low and emphasize that lichens are minor components of the community complex as a whole. Only 7.0 per cent of all the lichens recorded were able to be dominant and show high frequencies. These outstanding species were Cladonia coniocraea, Cladonia chlorophaea, Cladonia fimbriata, Cladonia rangiferina, Peltigera canina, Parmelia stenophylla and Crocynia membranacea.

The constancy values indicate the capability of lichen species to become established and to survive in this forest complex. The low constancies recorded for 44.9 per cent of all terracolous lichens suggests that many of these plants possess narrow amplitudes of tolerance and are probably restricted to particular habitats. The purpose of the investigations which follow were to investigate these habitat relationships.

Moisture Gradient Analysis

It was evident from the tree analysis that the forest composition changed across the moisture gradient and it is reasonable to infer that lichens would follow a similar pattern. The lichen data were analysed according to the moisture gradient to find out whether they were influenced directly by moisture or by the effect of moisture on the tree composition. The lichen species were at first listed alphabetically in a table. They were then checked for presence in the stands which were arranged according to their moisture classification, Dry, Dry-mesic, Mesic, Wet-mesic and Wet. On the basis of these figures, constancy values for lichens in each moisture segment were obtained. At the same time the average frequency value for each species was calculated for each moisture segment. These average values were then critically examined to determine whether or not significant patterns of occurrence were apparent. From this examination it was seen that there is a tendency for individual species to attain optimum ecological importance in one of the five moisture segments. A moderate number of lichen species appear to show a broad range of tolerance, while for the majority a narrow range is clearly discernable along the moisture gradient.

The average per cent presence or constancy value of each lichen species in relation to moisture segments is presented in Table 6. In the same table the average frequency values for all lichens are provided. The order of presentation in this table is based on the magnitude of these values in relation to specific moisture segments. As an example, Cladonia pleurota was present in only 7.7 per cent of the dry stands, and was completely absent from all other segments and no frequency values were recorded. Umbilicaria deusta was present in 15.4 per cent of the dry stands and similarly had no frequency values. Cladonia turgida had a per cent presence value of 30.8 per cent and an average frequency of 1.9. These three species are restricted to the dry segment of the moisture gradient and only Cladonia turgida had sufficient density to be recorded in the quadrats. In all,23 species of lichen were restricted to the dry segment and had per cent presence values that ranged from 7.7 per cent to 38.5 per cent. Of these

Table 6

Percent Presence and Average Frequency for

terracolous lichens in moisture segments (71 stands)

Species	Percent Presence D	DM	M	WM	W	Average Frequency D	DM	M	WM	W
Rhizocarpon geographicum	7.7									
Cladonia pleurota	7.7									
Alectoria nidulifera	7.7									
Lasallia papulosa	7.7									
Lecanora pallescens	7.7									
Umbilicaria mammulata	7.7									
Ramalina intermedia	7.7									
Physia adscendens	7.7									
Parmelia subtilis	7.7									
Cetraria ciliaris	7.7									
Parmelia lusitana	7.7									
Cladonia coccifera	7.7									
Cladonia nemoxyna	15.4									
Umbilicaria deusta	15.4									
Parmelia plitti	15.4									
Cladonia pyxidata	15.4					3.5				
Cladonia mitis	15.4					0.8				
Cladonia alpestris	30.8									
Cladonia uncialis	30.8					1.1				
Cladonia turgida	30.8					1.9				
Parmeliopsis hyperopta	30.8					2.3				
Actinogyra muhlenbergii	38.5					0.4				
Stereocaulon evolutoides	38.5					0.8				
Cetraria tuckermanii	7.7	4.5								
Xanthoria polycarpa	7.7	4.5								
Physcia aipola	15.4	4.5								

Species	Percent Presence D	DM	M	WM	W	Average Frequency D	DM	M	WM	W
Parmelia conspersa	15.4	4.5				0.9				
Cladonia sylvatica	23.1	4.5				2.3				
Cladonia botrytes	38.5	4.5				2.3				
Peltigera horizontalis-polydactyla	7.7	13.6				0.6	0.5			
Cladonia furcata	30.8	13.6				3.1	0.2			
Physcia milligrana	7.7		7.1							
Crocynia neglecta	15.4	13.6	7.1			1.5	0.2	0.4		
Evernia mesomorpha	7.7	4.5		10.0						
Physcia ciliata	7.7			10.0						
Cladonia digitata	15.4			10.0						
Cladonia cenotea	7.7	4.5		10.0						
Cladonia verticillata	30.8			10.0		1.7				
Parmelia caperata	15.4		7.1	10.0	8.3	0.4				
Microphiale diluta		4.5								
Nephroma bellum		13.6								
Cladonia rangiferina	84.6	13.6			8.3	15.4	0.5			
Candelaria concolor	7.7		7.1		8.3					
Parmelia stenophylla	46.1	31.8	21.4	10.0	25.0	11.8	3.2			
Crocynia membranacea	38.5	50.0	42.8	50.0	33.3	4.2	4.1	1.1	2.5	1.7
Cladonia chlorophaea	92.3	59.1	21.4	30.0	41.7	25.4	5.4	0.4		0.8
Cladonia fimbriata	76.9	40.9	7.1	40.0	33.3	16.3	1.4		1.5	2.1
Peltigera canina	53.8	50.0	49.9	40.0	41.7	3.2	4.5	0.8	2.0	2.5
Cladonia coniocraea	100.0	86.3	64.3	70.0	66.7	42.8	18.0	3.2	7.5	6.2
Cladonia gracilis	76.9	13.6		10.0	8.3	6.5	0.2			
Cladonia crispata	53.8	4.5		20.0	8.3	3.1	0.5		0.5	
Cladonia deformis	46.1	4.5		20.0	8.3	1.9			0.5	0.4
Cladonia squamosa	46.1	9.1		10.0	16.7	1.5	0.2			
Parmelia sulcata	15.4	4.5		20.0	16.7	0.4				

Species	Percent Presence D	DM	M	WM	W	Average Frequency D	DM	M	WM	W
Cladonia bacillaris	38.5	4.5		20.0	16.7	3.1			0.5	
Cladonia cristatella	76.9	22.7			33.3	7.7	0.5			
Cetraria oakesiana	23.1	36.3			8.3	1.5	1.4			
Parmelia physodes	46.1	4.5			16.7	0.8				
Cladonia macilenta	38.5	9.1			16.7	1.5	0.9			
Cetraria pinastri	30.8				8.3	3.5				
Cladonia multiformis	30.8				8.3	2.7				
Cladonia subtenuis	23.1				8.3					
Parmeliopsis ambigua	15.4				16.7	2.3				0.4
Leptogium cyanescens		18.2	7.1		8.3		1.6			
Bacidia chlorococca		9.1	7.1							
Physcia phaea		4.5	7.1				0.2			
Peltigera canina var. spuria		4.5	7.1				0.9	0.4		
Peltigera evansiana		9.1	7.1	20.0	8.3					
Parmelia rudecta		4.5		10.0						
Cladonia ochrochlora		4.5		10.0						
Cladonia farinacea		4.5			8.3					
Pyxine sorediata			7.1							
Bacidia fusca			7.1							
Physcia orbicularis			14.2							
Parmelia aurulenta			7.1							
Parmelia subaurifera			7.1							
Parmelia frondifera			7.1	10.0						
Lobaria pulmonaria			7.1	10.0	8.3					
Pertusaria sp.				10.0						
Cladonia cylindrica				10.0						

Species	Percent Presence D	DM	M	WM	W	Average Frequency D	DM	M	WM	W
Bacidia incompta				10.0						
Cladonia delicata				10.0						
Ramalina obtusata					8.3					
Cladonia subulata					8.3					
Lecanora subfuscata					8.3					
Cladonia scabriuscula					8.3					
Peltigera polydactyla					25.0					0.4

23 lichens, two were crustose, nine were foliose and twelve were fruticose. In this total only seven species were sufficiently abundant to have a frequency value in any of the stands.

At the opposite end of the moisture gradient only five species were restricted to wet forests. The major species was Peltigera polydactyla, with a percent presence of 25.0 per cent and an average frequency of 0.4. It should be emphasized here that positive identification of Peltigera polydactyla is only possible when fruiting bodies are present, and when they are absent it is impossible to distinguish it from Peltigera horizontalis. When fruiting bodies were absent the thalli were recorded as Peltigera horizontalis/polydactyla and appeared only at the dry end of the moisture segment. There is a possibility that Peltigera polydactyla only fruits in the wet segment, but as no positive specimens of Peltigera horizontalis were recorded in the study the ecological significance of fruiting stages cannot be substantiated.

The one crustose species, Lecanora subfuscata in the wet segment was recorded in the deciduous stands, as was the fruticose Ramalina obtusata and the foliose Peltigera polydactyla. The Peltigera species was also recorded in the lowland coniferous swamps with the two fruticose species, Cladonia subulata and Cladonia scabriuscala.

The twenty-two lichen species recorded in the mesic woods were the least in all the moisture segments. Of this total only three were fruticose, fifteen were foliose and four were crustose. The fruticose species were represented by the three Cladonia species recorded in all five moisture segments. Although some species showed an affinity to either the wet or the dry end of the moisture gradient there were three species that were recorded only in the mesic; *Pyxine sorediata*, *Physcia orbicularis* and *Bacidia fusca*.

Only six lichen species showed a broad amplitude of tolerance, these include one crustose, two foliose and three fruticose species. Of these six species, *Cladonia coniocraea*, *Cladonia chlorophaea*, *Cladonia fimbriata*, *Parmelia stenophylla*, *Peltigera canina* have their optimum in the dry, while dry-mesic conditions appear optimum for *Crocynia membranacea*. Not one of the major lichens referred to above would appear to be of value as indicator species. The possible exception could be *Cladonia fimbriata*, a species that was present in only one mesic stand. Of all the remaining species only those that were restricted to the dry or wet segments would be of indicator value, as the moisture segments opposite to their optimum segment would appear to be ecologically intolerant to their survival. *Cladonia coniocraea* was the only lichen species which was recorded with 100.0 per cent presence in any segment of the moisture gradient, and this was in the dry. *Cladonia chlorophaea* had a value of 92.3 per cent presence and was missing in only one stand of the same segment. *Cladonia fimbriata* did not have a frequency value in the mesic, nor did *Cladonia chlorophaea* in the wet-mesic segment.

Between the extremes of the moisture gradient a sharp decrease in average per cent presence of lichens occurred, and in many cases, frequency recorded in the mesic stands also decreased abruptly. Table 7 shows that the fruticose species, excluding the most widespread types, Cladonia coniocraea, Cladonia chlorophaea, Cladonia fimbriata have dropped out completely in the mesic stands.

The total number of lichens recorded in each segment, with the average number per stand in the segment, is indicated in the graph in Figure 10.

The trends in lichen presence values appear to follow those of the conifers, as seen in Table 3, and from this it would seem that lichens are ecologically related to conifers in the forest vegetation. Pinus species are present with high importance values in the dry, Pinus and Abies are present in the dry-mesic, Abies, Thuja and Tsuga present in the wet-mesic and Larix and Thuja are present in the wet. The abundant number of deciduous species in the majority of the wet stands precluded the chance of an increase in lichen density. The relatively low importance value of conifer, and limited presence of lichens in the wet segment is undoubtedly due to insufficient sampling as shown by the lack of Thuja occidentalis stands.

To illustrate the relationships of these species to the forest moisture gradient, selected groups of species have been graphed (Figures 11 to 16). In Figure 11, the six major species of lichens are presented to show their position in relation to each other across the moisture gradient. The species shown in Figure 12 include all those that were recorded in four segments, being absent in all mesic woods. The reason for the absence in the mesic sites of these species and those in the following graphs

FIGURE 10

Distribution of total number of lichen species per segment with average number of lichen species per stand.

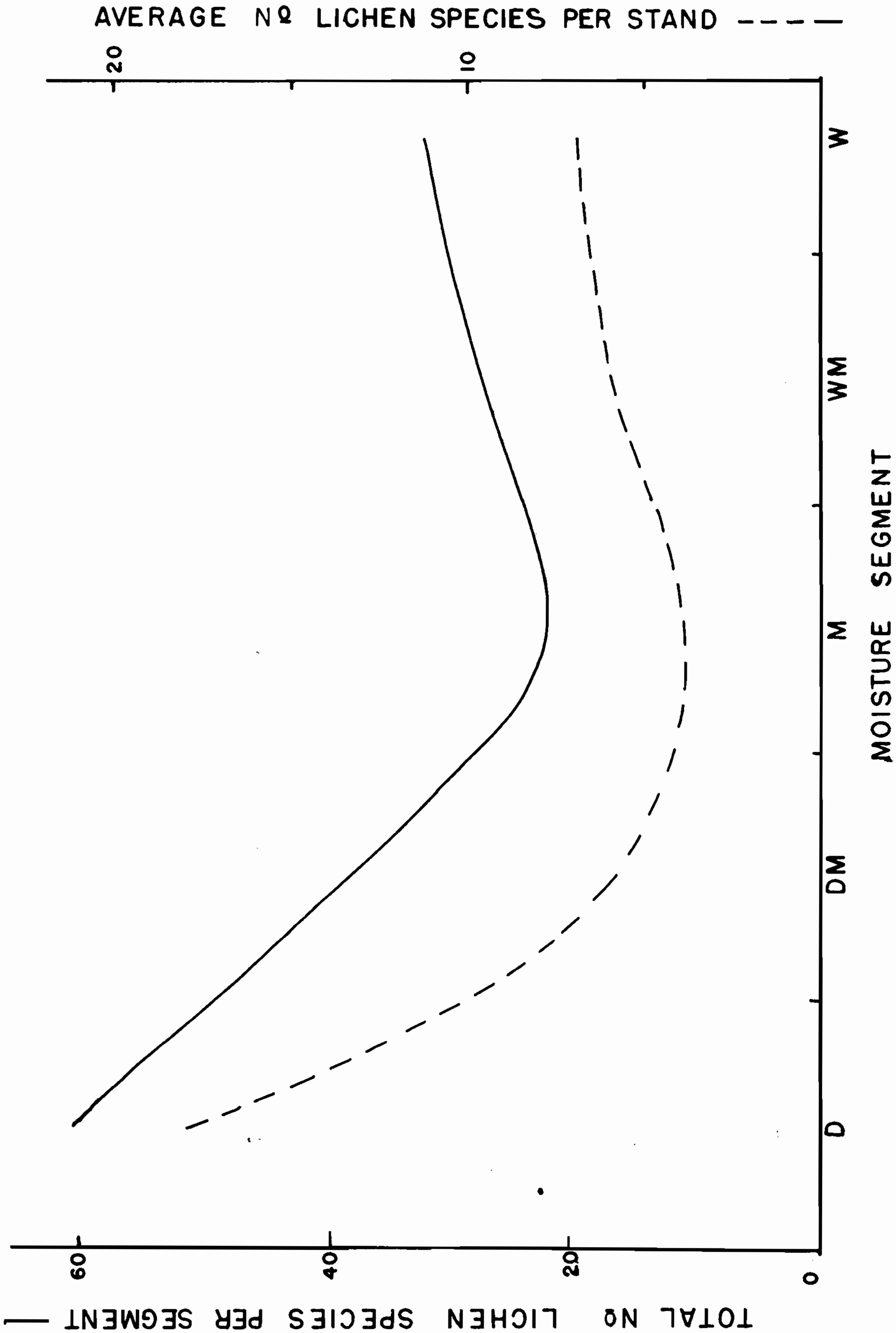
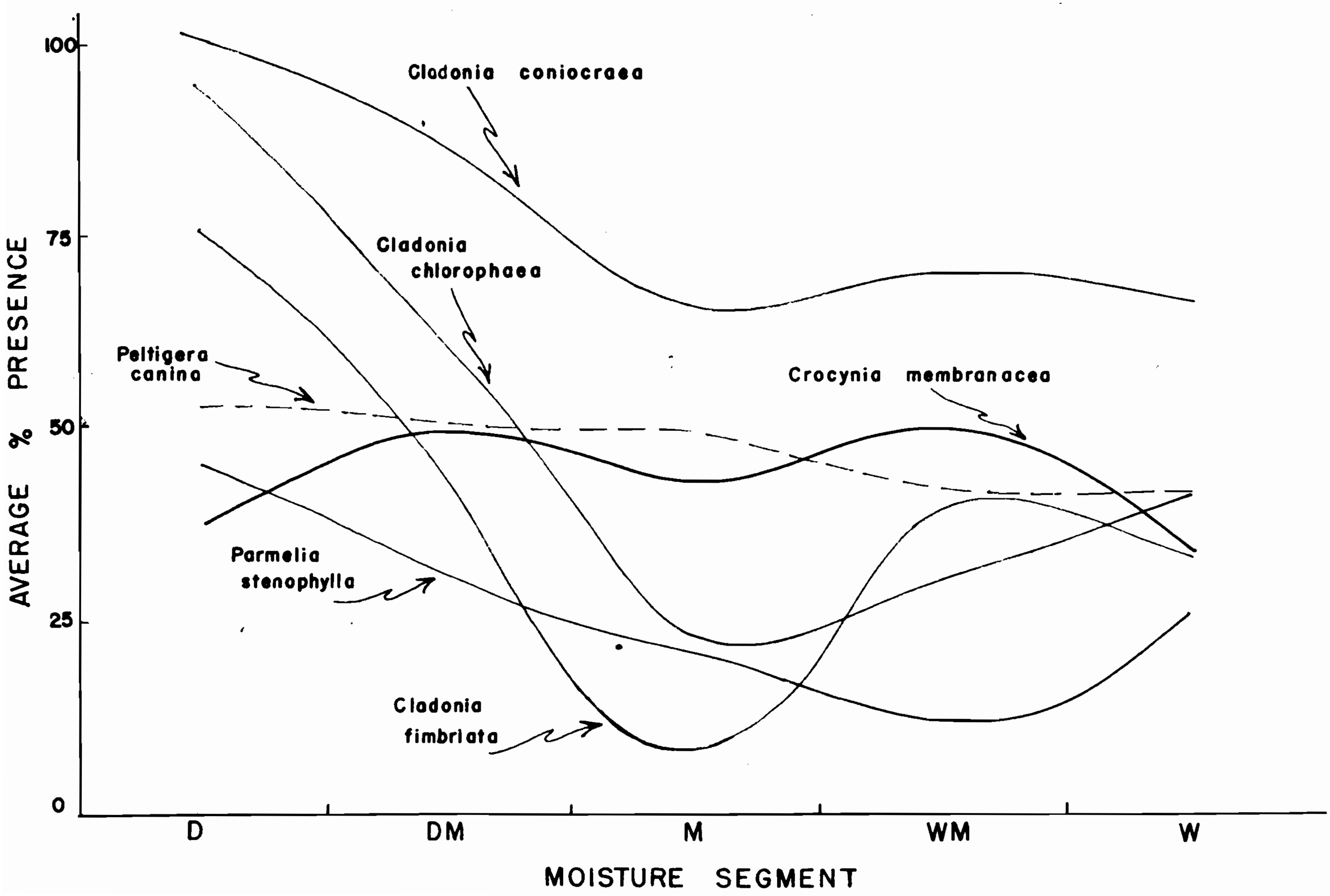

AVERAGE Nº LICHEN SPECIES PER STAND ----
20
10
W
WM
M
DM
D
MOISTURE SEGMENT
60
40
20
0
TOTAL Nº LICHEN SPECIES PER SEGMENT —

FIGURE 11

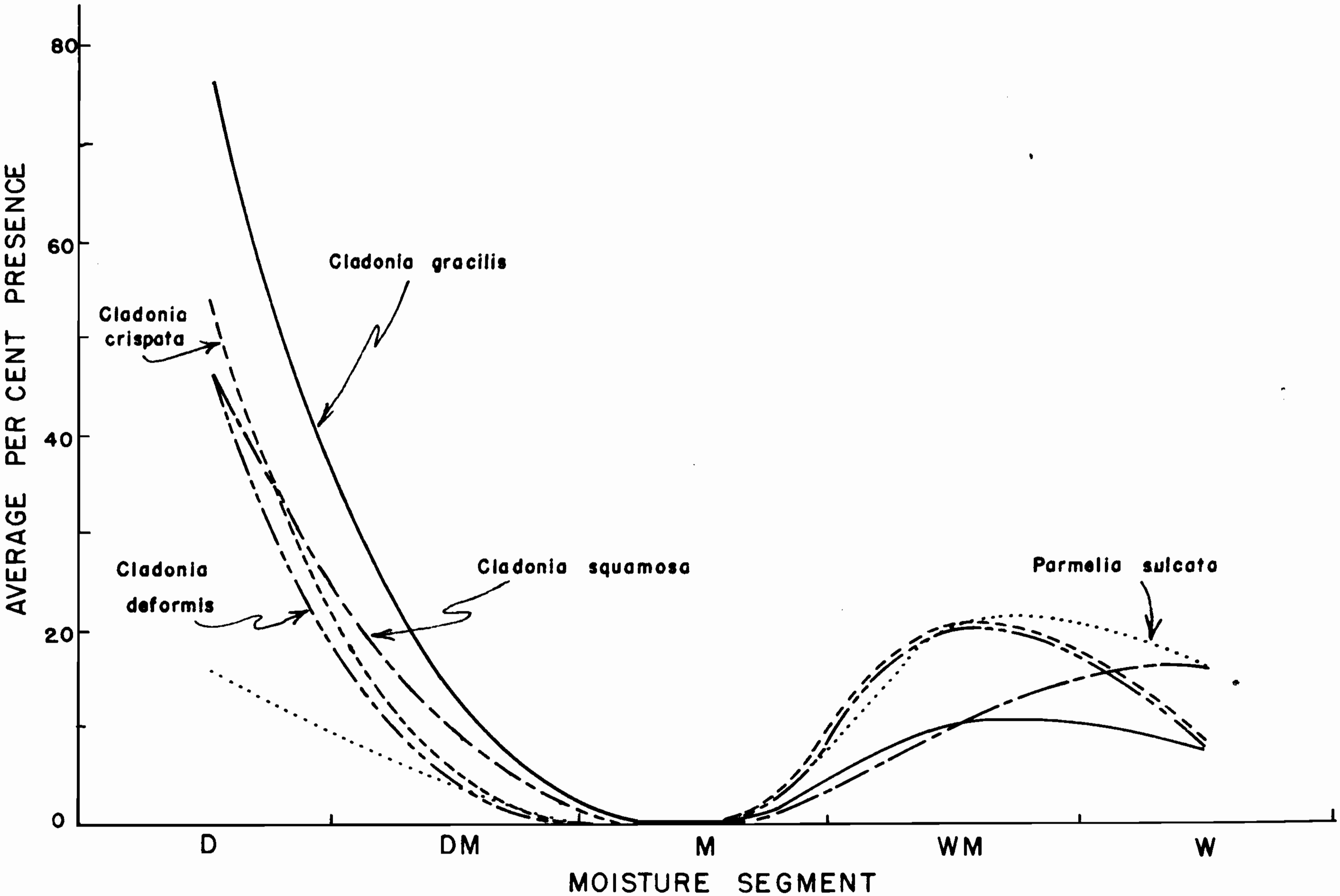
The patterns of six major lichen species in relation to the moisture gradient, based on average per cent presence.



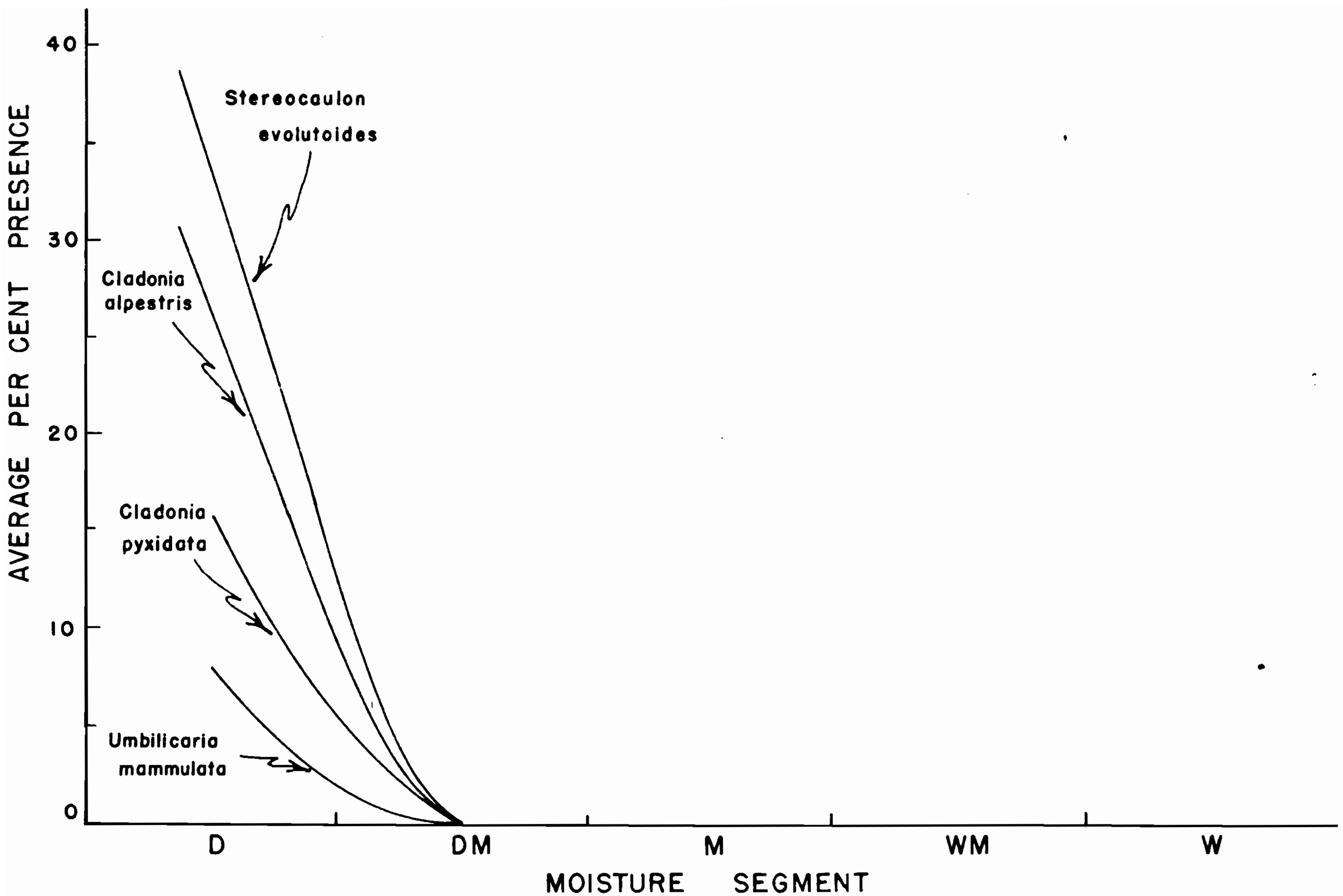
AVERAGE % PRESENCE
100
75
50
25
0
Cladonia coniocraea
Cladonia chlorophaea
Peltigera canina
Crocynia membranacea
Parmelia stenophylla
Cladonia fimbriata
D
DM
M
WM
W
MOISTURE SEGMENT

FIGURE 12

The patterns of five lichen species present in four segments of the moisture gradient, based on average per cent presence.



AVERAGE PER CENT PRESENCE
80
60
40
20
0
Cladonia gracilis
Cladonia crispata
Cladonia deformis
Cladonia squamosa
Parmelia sulcata
D
DM
M
WM
W
MOISTURE SEGMENT



40
30
20
10
0
AVERAGE PER CENT PRESENCE
Stereocaulon evolutoides
Cladonia alpestris
Cladonia pyxidata
Umbilicaria mammulata
D
DM
M
WM
W
MOISTURE SEGMENT

is probably due to the extreme conditions and the scarcity of habitats. These always appear occupied by the tree major Cladonia species in Figure 11. The Cladonia species of Figure 12 all show per cent presence values only slightly below those of the major species for the dry segment, but decrease rapidly in the dry-mesic. They are all present in the wet-mesic but show a decline in per cent presence values in the wet. Their frequency values for the four segments are all very low.

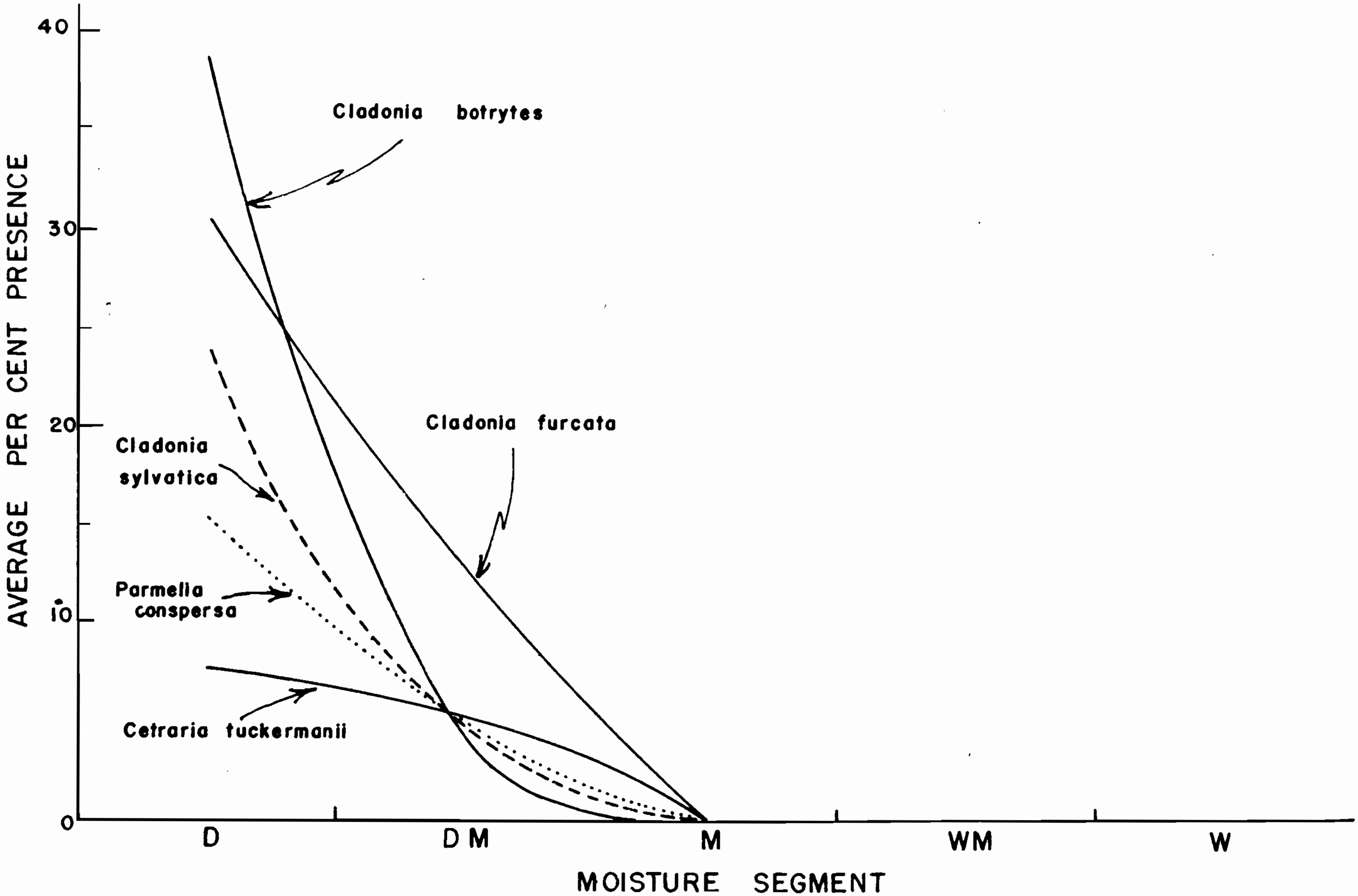
The lichens in Figure 13 are representative of those found only in the dry segment. This segment supported the greatest number (23) of restricted species. Of this total, twelve species were found in only one stand, five were found in two stands, five were found in only four stands, and two in only five stands. The seven abundant species with frequency values were Cladonia pyxidata, Cladonia mitis, Cladonia uncialis, Cladonia turgida, Stereocaulon evolutoides, Actinogyra muhlenbergii and Parmeliopsis hyperopta.

In the wet and wet-mesic segments there are only two species which appear to be of major importance: Peltigera polydactyla in the wet, and Peltigera evansiana in wet-mesic woods. The remaining species have low per cent presence values and no frequency values. These species are considered of minor importance in stands, but their restriction to the wetter forests may be of great ecological value.

In Figure 14, six species that were present in the dry and dry-mesic segments are graphed. Their average per cent presence values were all below 40.0 per cent. They were recorded in less

FIGURE 14

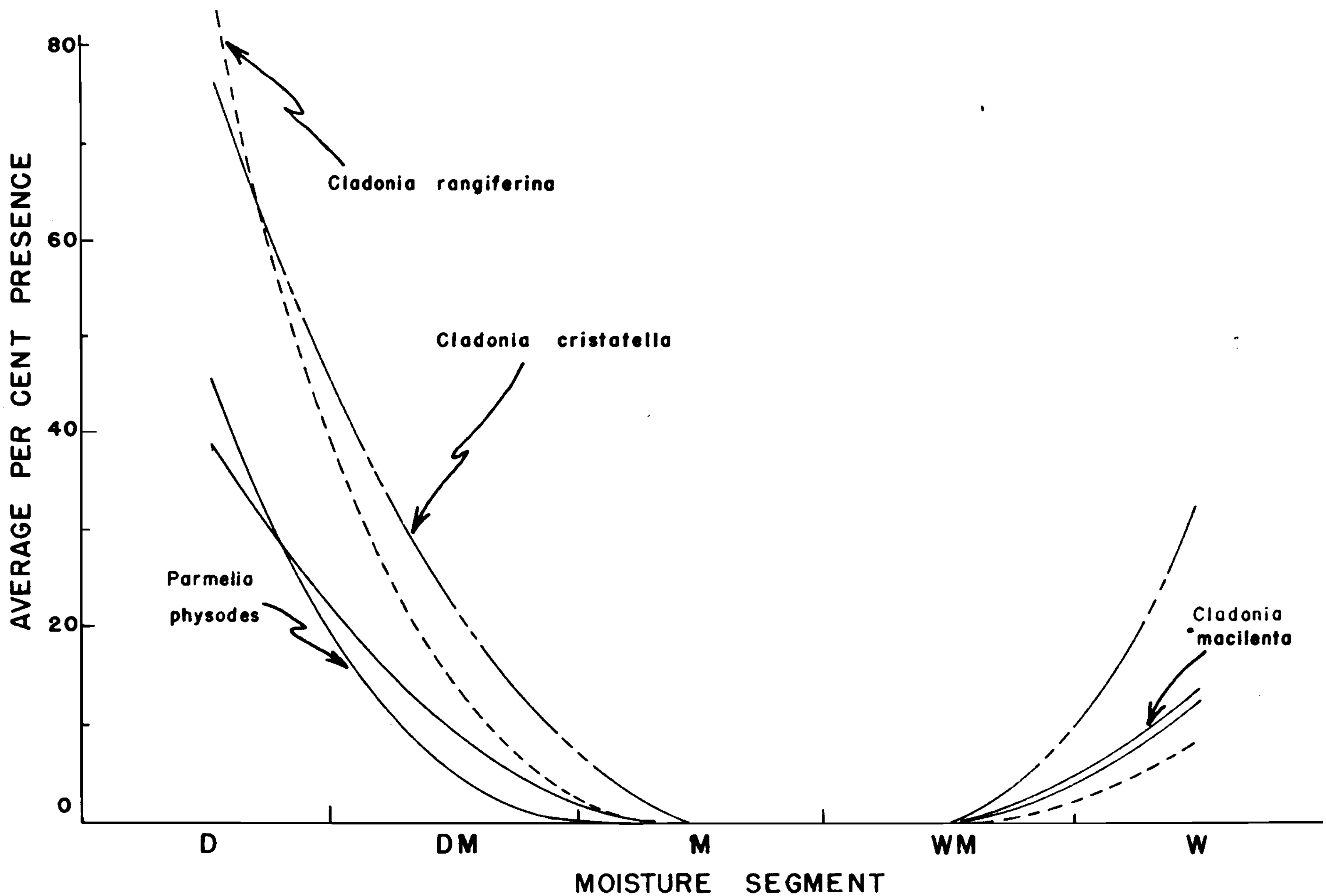
The patterns of five lichen species showing moderate presence levels but restricted to the dry and dry-mesic segments of the moisture gradient. Average per cent presence is plotted.



AVERAGE PER CENT PRESENCE
40
30
20
10
0
Cladonia botrytes
Cladonia furcata
Cladonia sylvatica
Parmelia conspersa
Cetraria tuckermanii
D
DM
M
WM
W
MOISTURE SEGMENT

FIGURE 15

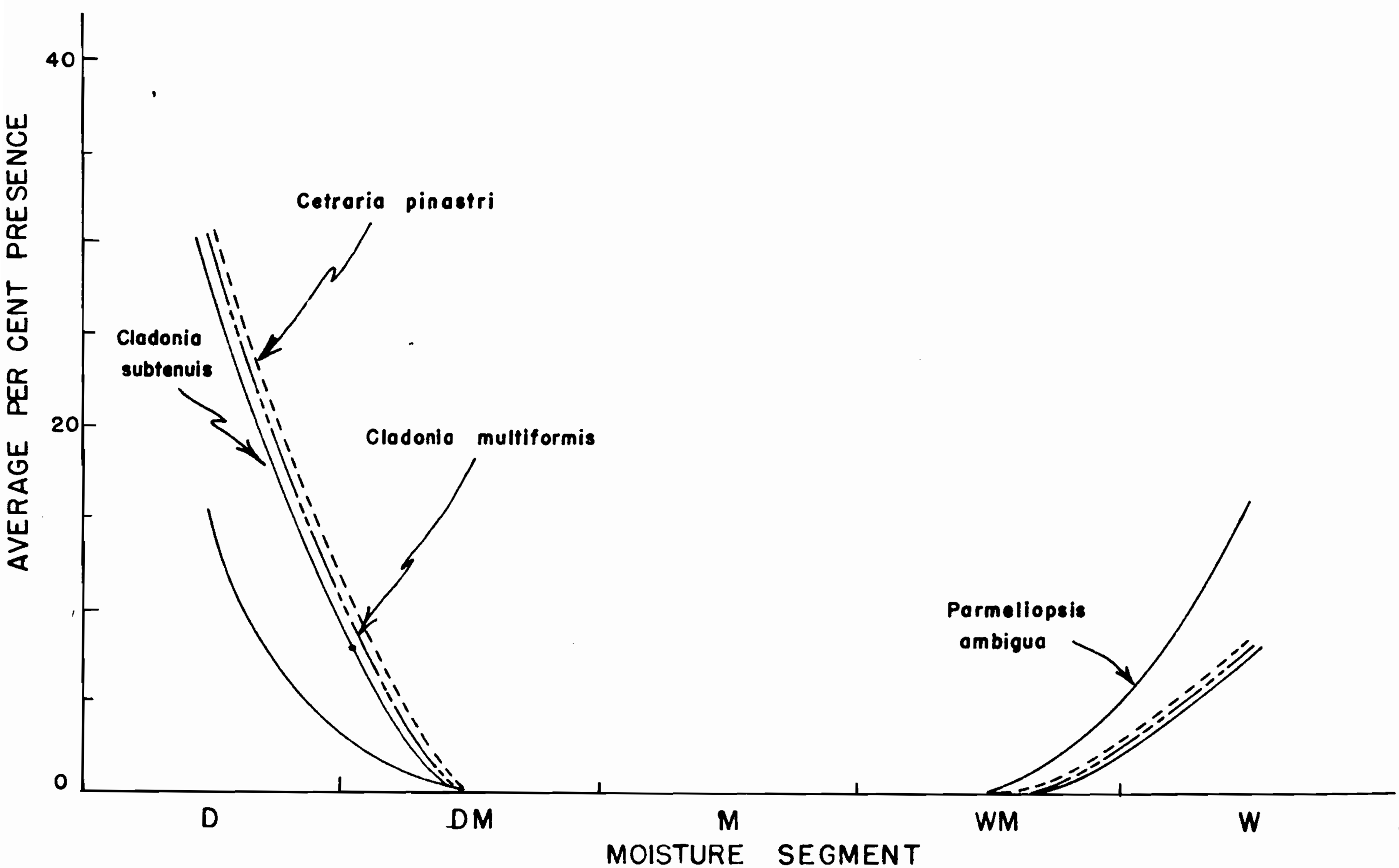
The patterns of four lichen species with high presence values in the dry-mesic and dry segments that are absent in the mesic and wet-mesic segments but reappear in the wet with reduced values. Average per cent presence is plotted.



AVERAGE PER CENT PRESENCE
80
60
40
20
0
Cladonia rangiferina
Cladonia cristatella
Parmelia physodes
Cladonia macilenta
D
DM
M
WM
W
MOISTURE SEGMENT

FIGURE 16

The patterns of four lichen species restricted to the dry and wet segments. Average per cent presence is plotted.


40
20
0
AVERAGE PER CENT PRESENCE
Cetraria pinastri
Cladonia subtenuis
Cladonia multiformis
Parmeliopsis ambigua
D
DM
M
WM
W
MOISTURE SEGMENT

than six stands in the dry, their segment of optimum occurrence on the moisture gradient. These species show a broader range of amplitude than those restricted to the dry, but indicate that the mesic sites produce intolerant environmental conditions for their development. They did not reappear in the wet-mesic or wet segment. Their average frequency values, where recorded, were all in the dry moisture segment except for two species, Cladonia furcata and Peltigera horizontalis/polydactyla which were recorded in dry-mesic woods.

In Figure 15, curves for a group of prominent species are shown. For all these species optimum development was in the dry stands, with reduced presence values in the dry-mesic, absent completely in the mesic and wet-mesic, but reappearing in the wet segment. These species appeared more tolerant than those restricted to either end of the moisture gradient. This was shown by their ability to develop under a forest canopy (markedly different with respect to tree species and ground moisture) from their optimum. For example, Cladonia rangiferina which showed a high average per cent presence value in the dry of 84.6 per cent, and an average frequency of 15.4, shows a rapid decline in the dry-mesic, but reappears in the wet with a presence value of 7.7. per cent, and no frequency.

Figure 16 presents extreme responses by lichen species to the moisture gradient. These species show low per cent presence and low average frequency values even in the dry segment which is their optimum. They are absent from all other segments, but reappear in in just one or two stands in the wet woods where conditions are apparently suitable for their survival.

It appears that lichen species presented in Figures 11, 12,15 and 16, display patterns that are not primarily influenced by ground moisture. On the other hand they would appear to follow a similar pattern to that produced by the coniferous species across the moisture gradient. A review of Table 6 will show that other minor lichen species, i.e. those having two or more low per cent presence values are species which do not seem to be influenced by the moisture conditions. An example, Candelaria concolor which was present in one stand only in the dry, mesic and wet segments.

The lichen data has been presented in similar fashion to that of the tree species data to enable comparisons to be made. Of the six major lichen species that were present across the moisture gradient, four decreased markedly in mesic woods. The presence of conifers is also low in the mesic segments indicating a possible relationship between coniferous tree species and these lichens. For Peltigera canina and Crocynia membranacea levels of presence across the moisture gradient show no appreciable change. The presence or absence of conifer species is possibly not related to their ability to show such even values throughout the forest continuum.

At the ends of the moisture gradient in the dry and wet lowland sites coniferous species are the dominant trees. Field data shows that the majority of lichen species in the wet forests were recorded in lowland conifer stands. Though the type of conifer species vary between the wet and dry segments, conditions created by their presence must be suitable for lichens. With the vegetational development toward mesophytic deciduous sites the conditions are changed, and the terricolous lichens tend to decrease gradually. While this was a study primarily of terricolous lichens, and not of corticolous lichens observations and collections did indicate that these latter species in the mesic woods migrate upwards to the crown of the trees, possibly in response to decreasing light energy in the lower strata of the increasingly dominated Sugar Maple stands.

In both wet lowland and dry forests where coniferous species are abundant, poorly developed soils, low pH, high light energy, and slow rate of accumulation of raw and organic matter are well known factors. This latter feature appears to be one of the main reasons for the high presence of terricolous lichens on these sites. These conditions change with the increase of deciduous species. The organic material is turned over faster, the soil is more developed, the pH rises, and the light intensity is moderated (Wilde, 1958). A very slow rate of growth does not allow the lichens to gain a foothold where the substrate, in this case the litter, is continually changing. The death of conifer species is due to their intolerance to shade as a result of an increase in deciduous species and their natural regeneration is restricted to isolated areas. Their death produces sites for lichen development until their logs and stumps have been incorporated into the A_0 layer. Although light may not appear to be the major factor for lichen presence, when other environmental factors are operating, it can be a critical factor. Thus it appears that although the tree species are distributed in direct relationship to the moisture gradient the terricolous lichens are more related to the conifer species and the conditions they produce.

With these features of lichen distribution in mind it was considered possible that the forest stands could be ordinated on an objective basis using quantitative data for lichen species and dominant tree species. It was hoped that such ordination treatment would elucidate some of the problems raised concerning the ecology of the terricolous lichens in the Northern Conifer-Hardwood Forests of Central Canada.

Ordination of Lichens and Forest Influences

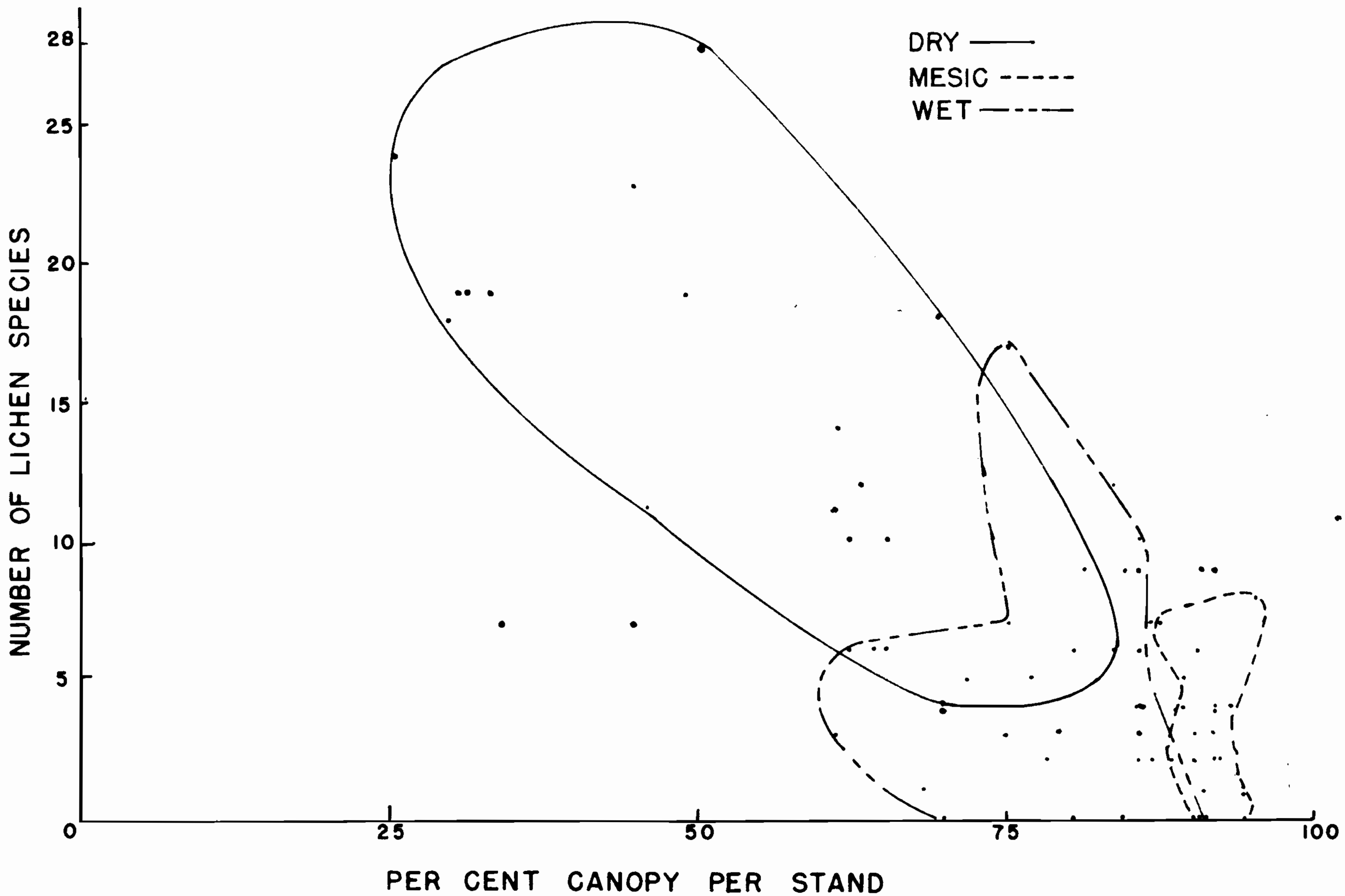
The method of stand ordination on the basis of moisture conditions provides a reliable insight into the relation of lichens in the communities. The resulting curves for the major species were smooth, but for a larger number curves represented a decrease in lichen presence from dry to mesic segments of the moisture gradient. Most of the lichens disappear in the mesic stands and then reappear in the wet segment, but usually with reduced values. For most of the lichen species the average per cent presence figures show a rapid decline and no subsequent rise in the wet sites. Several species of low per cent presence were shown to occur across several moisture segments. All these patterns indicated the necessity of ascertaining whether or not other specific compositional or environmental factors exert an influence on lichen relationships in the forest continuum.

During the collection of the quantitative field data the canopy coverage over each point was estimated as a percentage and the average for each stand was calculated from the forty estimates per stand. Average per cent canopy for individual stands ranged from a low of 25 to a high of 95. For each stand of the 71 stands studied, the total number of lichen species present was summed. The amount of light energy reaching the forest floor in the stands of dense canopy would be much less than that reaching the floor in the open forests. The ability of plants to survive this light energy reduction would have a significant affect on their density.

In plotting these points the X axis represented canopy, from 0 to 100.0 per cent, and the Y axis represented number of lichen species present per stand ranging from 0 to 28. In figure 17 distribution points of the 71 stands are plotted. When this was accomplished the moisture classification of each stand was added. The three lines represent the distribution of the three major moisture segments, dry, mesic and wet. It can be seen that there is a relationship between number of lichen species and the low per cent canopy and moisture. Over 70.0 per cent of the dry stands had an average per cent canopy of less than 55.0 per cent, and at the same time the highest number of lichen species. In the four dry stands that showed a high canopy per cent, three were dominated by Pinus strobus, a species which towards the terminal stage may produce a dense canopy allowing little light

FIGURE 17

The distribution of 71 stands in relation to numbers of lichen species and per cent canopy per stand. Limits of the dry, mesic and wet stands are indicated.


DRY
MESIC
WET
NUMBER OF LICHEN SPECIES
28
25
20
15
10
5
0
25
50
75
100
PER CENT CANOPY PER STAND

penetration. The fourth stand was dominated by relatively young *Populus grandidentata* trees which had come in after fire on a site previously dominated by *Pinus banksiana*, and was at that time showing advance growth of *Pinus strobus* and *Pinus resinosa*. The remaining dry deciduous stand, No. 50, dominated by *Quercus rubra*, had one of the lowest canopy percentages and in it 18 lichen species were recorded.

Mesic stands show a dense canopy coverage with a range of from 88-95.0 per cent, causing extremely low light penetration during the growing season. At the same time the greatest number of lichen species recorded in any mesic stand was only eight.

In the wet segment a wide range of canopy coverage appears, from 60-90 per cent, and the number of lichen species ranges from 0 to 17 per stand. A relatively high number of species were found in lowland conifer swamps dominated by *Larix laricina* and *Thuja occidentalis.* The rather high per cent canopy for these stands did not appear to have an adverse affect on lichen development, except where *Thuja occidentalis* was recorded in almost pure stands. Then the extremely dense canopy greatly reduced all lower plant life except mosses. That appreciable number of lichen species were found in wet stands may have been due to the other beneficial factors caused by accumulated organic matter, the presence of conifer logs and low pH. In the bottomland sites, a fluctuating water table with seasonal flooding produces unsuitable conditions for the establishment and survival of lichens. Lichen species when recorded under these conditions tended to be on logs or rocks because the soil and tree bases were subject to inundation.

Of the remaining two moisture segments the dry-mesic appears to be as variable in canopy as the dry segment, and this shows that denser canopies are to be expected with deciduous tree invasion which results in fewer lichen species. The wet-mesic sites show a relatively high per cent canopy. The largest number of lichen species were recorded in stands with high conifer importance values.

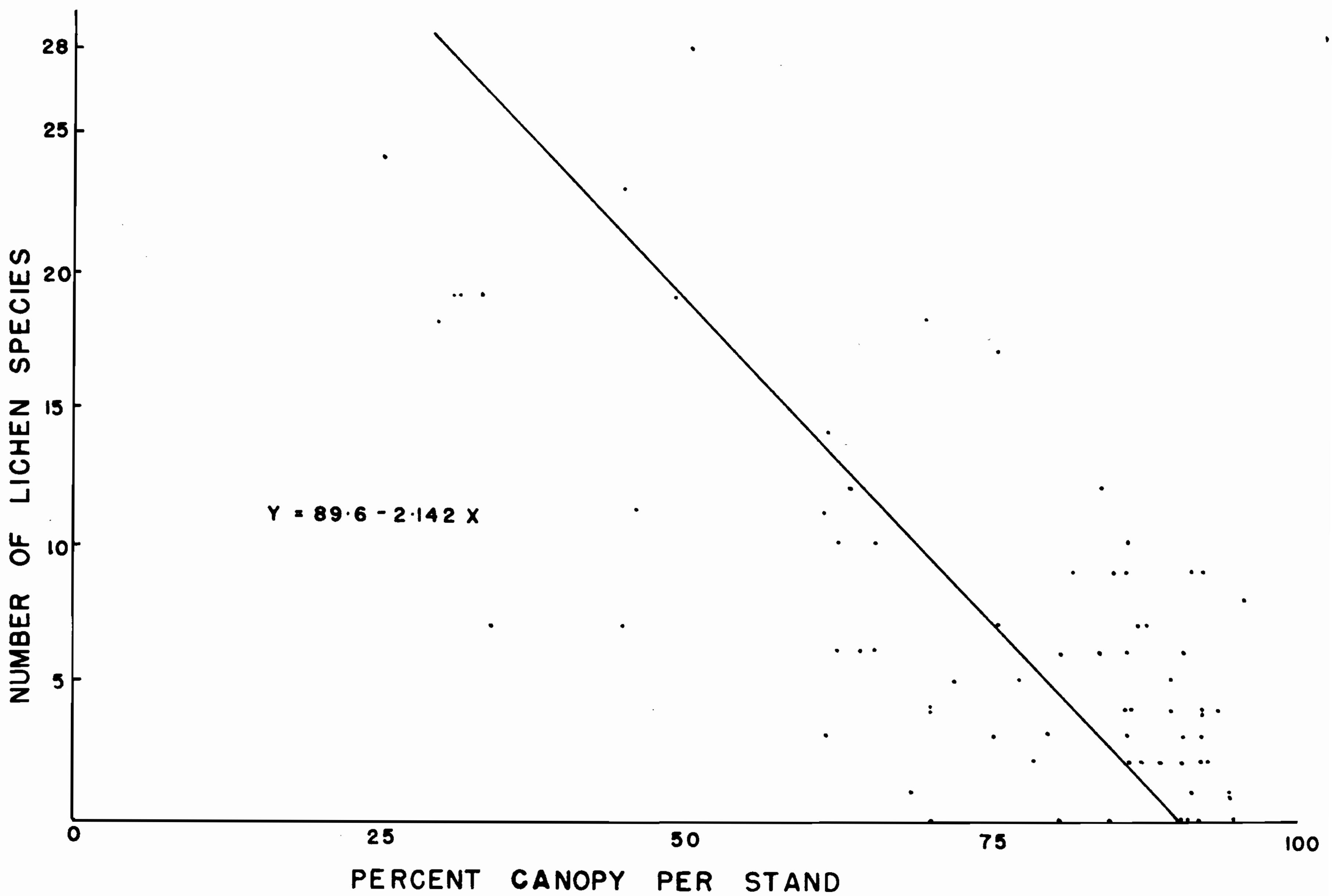
The inverse relationship between density of forest canopy and the number of lichen species is more readily apparent from Figure 18 where the "line of best fit" has been drawn for the plotted data. The regression equation for this line is $X = 89.6 - 2.142Y$, while the correlation coefficient for number of lichen species in relation to per cent canopy is -0.71, significant to the 0.01 per cent level. The amount of light reaching the forest floor appears to have considerable influence over lichen species.

The association of light and lichen distribution was further emphasized when the total lichen frequency per stand was plotted against per cent canopy per stand, as seen in Figure 19. The four dry stands with a greater canopy density had lower lichen frequency readings than did the other dry stands. This result compares favourably with all other stands where a percentage canopy of greater than 55.0 per cent usually resulted in a reduction of lichen density.

For the plotted data the "the line of best fit" has been drawn to emphasize the relationship between total frequency per stand and density of canopy. The regression equation for this

FIGURE 18

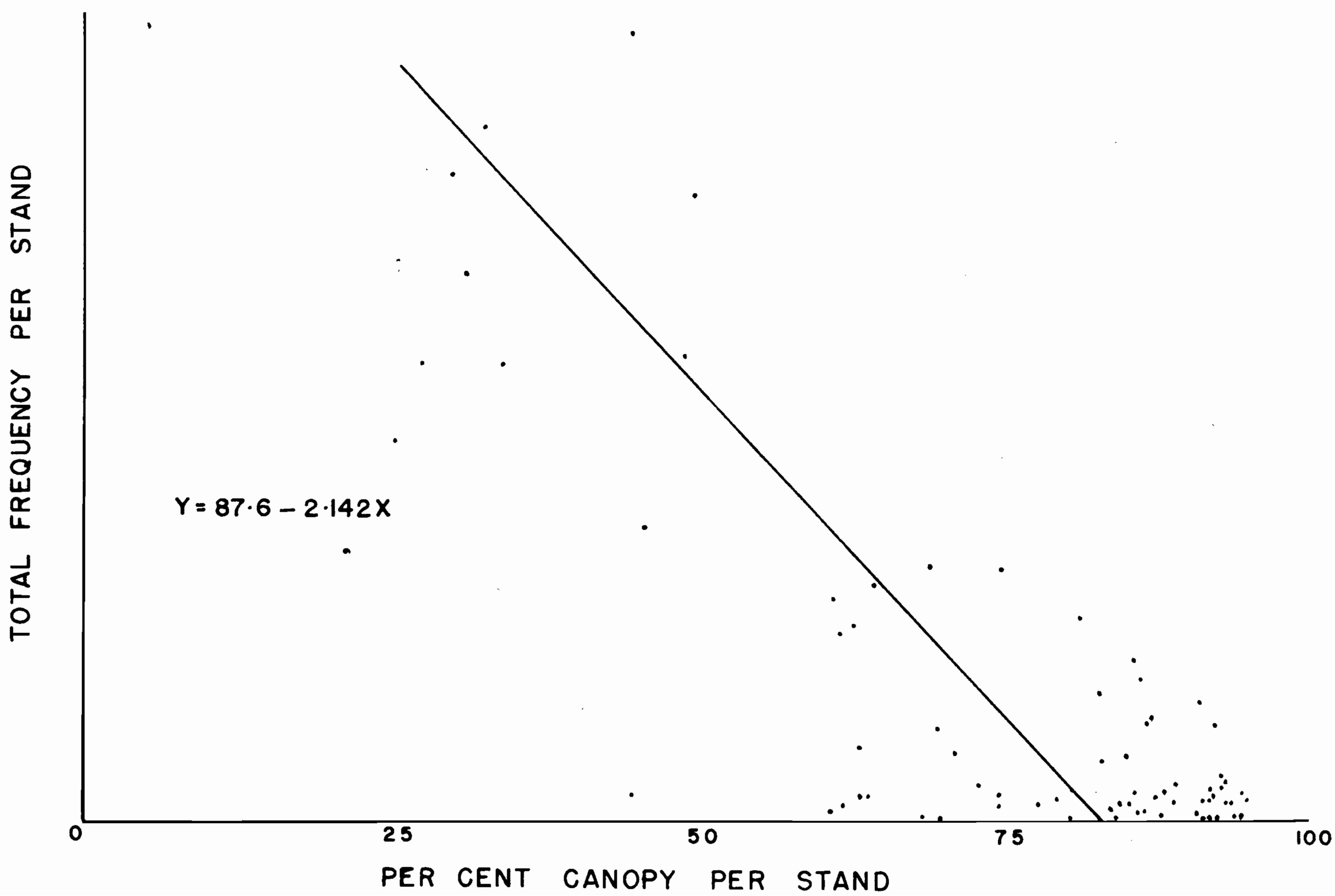
The distribution of 71 stands in relation to numbers of lichen species and per cent canopy per stand. Line of best fit is plotted.



NUMBER OF LICHEN SPECIES
28
25
20
15
10
5
0
25
50
75
100
PERCENT CANOPY PER STAND
Y = 89·6 − 2·142 X

FIGURE 19

The distribution of 71 stands in relation to total frequency of lichens and per cent canopy per stand. Line of best fit is plotted.



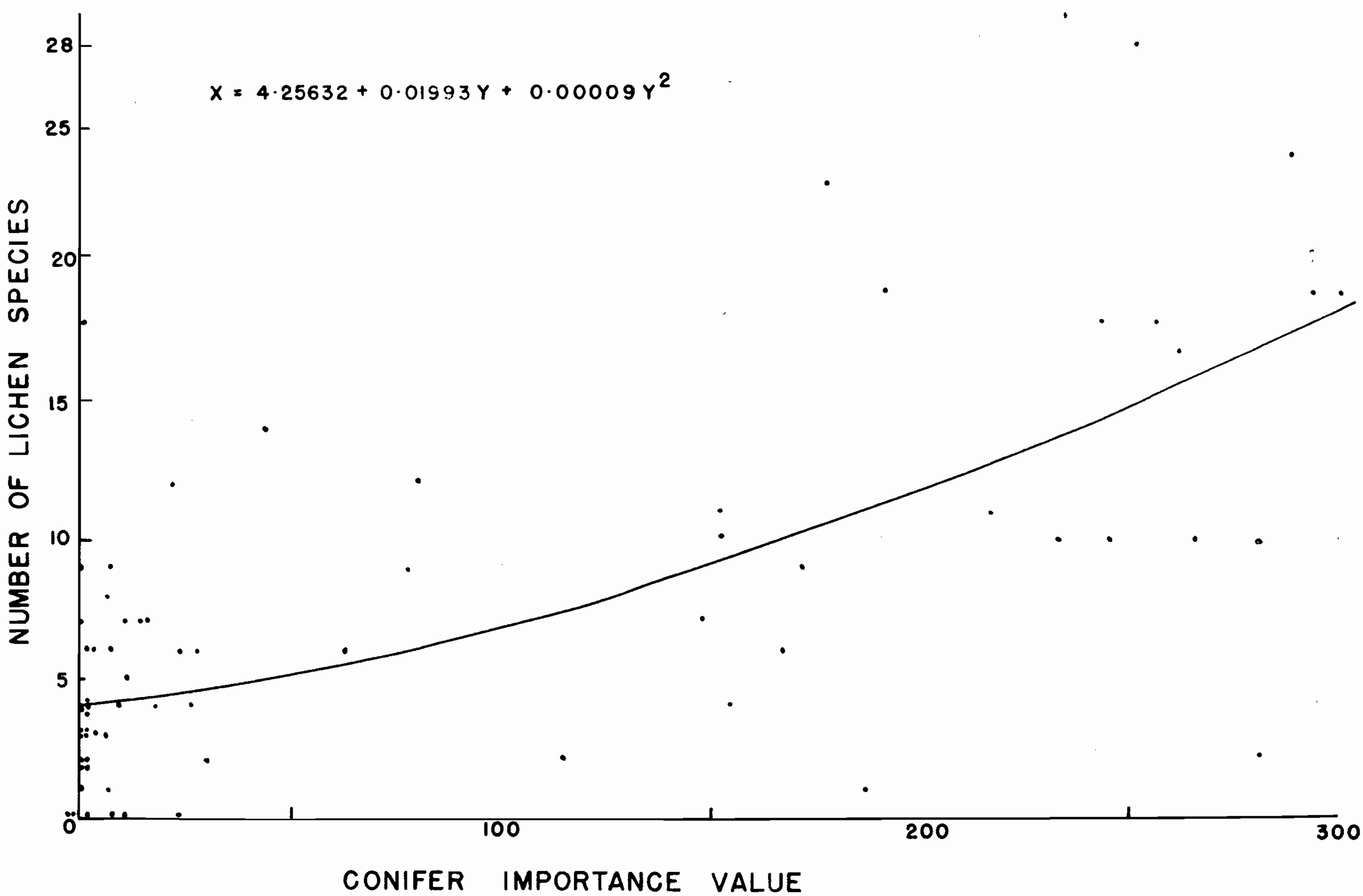
TOTAL FREQUENCY PER STAND
Y = 87·6 – 2·142X
0
25
50
75
100
PER CENT CANOPY PER STAND

line is $X = 84.2 - 0.176Y$, while the correlation coefficient for the total frequency of all species per stand in relation to per cent canopy is -0.81., significant to the 0.01 per cent level. The amount of light reaching the forest floor thus appears to have a great effect not only on the numbers but also on the quantities of lichen species, and follows a similar pattern to species density. Furthermore, by extrapolation from the graph, it is evident that the optimum habitats for abundant lichen growth are attained on dry, more open rocky forest sites, where within these stands, competition from higher plants would be slight. In these stands fairly extensive lichen colonies are evident when compared with the more closed conifer forests. In these latter sites the reduced light energy and the increase in density of herbaceous species aids materially in reducing the size of these lichen colonies.

The second step in analysing the position of the terricolous lichens within the forest communities was to relate the number of lichen species to the influence of coniferous species that on the basis of observation and experience seemed to exert considerable influence. After calculation of the importance value for each tree species within each stand, individual values for the conifer species were extracted and summed to give a total expression for the influence of conifers. For the graphic presentation, the Y axis again represented the number of lichen species, while the X axis represented conifer importance values which ranged from 0 to 300 per stand. In Figure 20 the distribution of all 71 stands

FIGURE 20

The distribution of 71 stands in relation to numbers of lichen species and importance value of conifer per stand. Line of best fit is plotted.



X = 4·25632 + 0·01993 Y + 0·00009 Y^2
NUMBER OF LICHEN SPECIES
28
25
20
15
10
5
0
100
200
300
CONIFER IMPORTANCE VALUE

has been plotted, each position carrying a reference to the moisture classification for that stand. The interpretation of this graph was not as straightforward as was the correlation of number of species with per cent canopy. The widespread nature of all points resulted in two groupings. The first with stands of high conifer importance value of 150 plus and the number of lichen species ranging from 1 to 28; the second with stands of importance values clustered between zero and 30, and the numbers of lichen species ranging from zero to 18. Between the conifer importance values of 30 and 150 only four stands were recorded and of these, three were wet-mesic and one dry-mesic with numbers of lichen species from 2 to 12.

This scattering of points was indicative of a possible curvilinear relationship between number of lichen species and conifer importance value per stand. With the aid of the Statistics Section of the Mathematics Department, McGill University, a three factor multiregression equation was calculated and a curve fitted to the plotted data. From this curve there appears a tendency toward increase in lichen species with increase in conifer importance value. However, there were some notable exceptions to this relationship at both high and low values of coniferous importance per stand. Firstly, there were the stands of low lichen species number dominated by Pinus strobus and Thuja occidentalis referred to earlier.

Secondly, at very low or zero conifer importance, high lichen species numbers were present, but only in three dry stands dominated by deciduous species, although a large number of stands have few or no lichen species present. Thus it appeared from the distribution of points that two types of communities were optimum for lichen presence within the forests of the region, those dominated by conifers and also a limited number of communities dominated by deciduous species.

These deciduous sites were shown to be dominated by *Quercus rubra* and *Populus grandidentata* and were dry stands. The stands of high conifer values and related high numbers of lichen species were all in the dry segment, and were dominated by such tree species as *Pinus resinosa*, *Pinus strobus*, *Pinus banksiana*, *Pinus rigida* and *Juniperous virginiana*. Stands with high conifer and low presence of lichen species were mainly in the dry-mesic and wet-mesic stands which were dominated by *Tsuga canadensis*, *Abies balsamea*, *Thuja occidentalis*, *Pinus resinosa* and *Pinus strobus*. Stands with only moderate amounts of conifer were represented by *Tsuga canadensis*, *Thuja occidentalis* and *Abies balsamea* and appeared numerically intermediate in terms of lichen species. In the majority of stands clustered toward the origin, that is where numbers of lichen species and conifer importance values were low, coniferous elements were represented by such species as *Tsuga canadensis, Abies balsamea, Pinus strobus* and lesser amounts of *Thuja occidentalis*. There were a total of three stands in which terricolous lichens and conifer species were completely absent. Ten stands had terricolous lichens and lacked coniferous species and four stands had coniferous species but no terricolous lichens.

The ocular estimate of per cent canopy coverage over each sample point in the field is possibly open to criticism as it is solely an estimate by the field worker. On the other hand, if the observer estimates the coverage regularly, his observations tend to be constant and any error is at least consistent by making forty estimates per stand. While the high correlation between numbers of lichen species present and per cent canopy does show a definite relationship it was felt that the introduction of additional quantitatively measured field data would confirm and amplify such relationships.

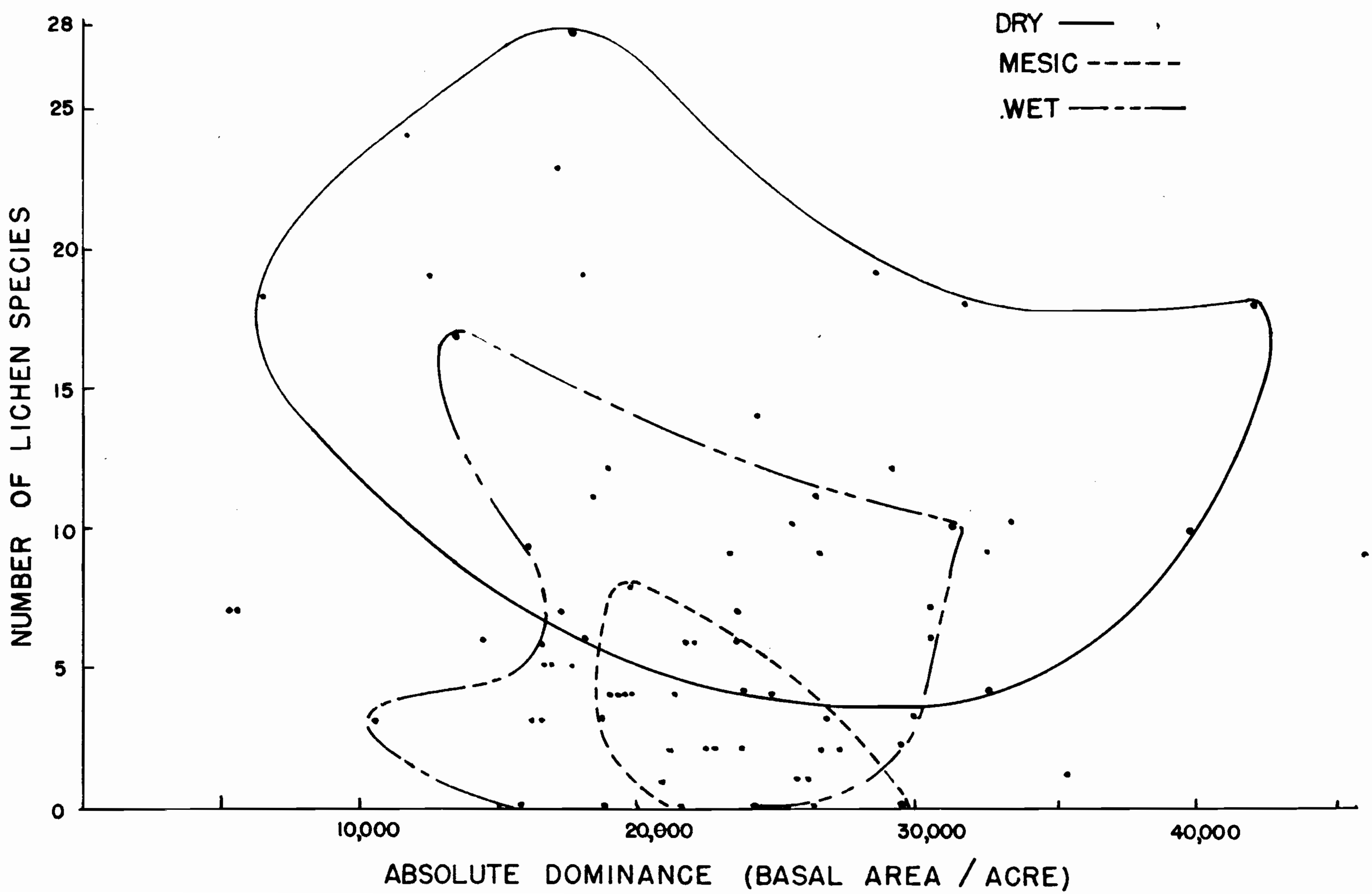
The total dominance of tree species in a stand is related to the average area occupied by any one tree, thus theoretically the terminal mesic forests should support large individual trees at relatively few per acre. In the wet and dry segments variations may occur in which sites have many trees per acre, low total absolute dominance values and usually a low per cent canopy value, as for example stands of *Thuja occidentalis* in the wet, and *Pinus banksiana* in the dry. At the same time there are other stands in these sites with relatively few trees per acre, a large total absolute dominance value and usually a high per cent canopy value. These latter stands are dominated by such tree species as *Ulmus americana* in the wet and *Pinus strobus* in the dry.

The tree data were obtained by totalling the distance to the tree species that were collected at each sampling point and averaged. This figure was squared and divided into 43560, the number of square feet per acre, to give the number of trees per acre. The basal areas of all sampled trees in a stand were totalled and averaged. Finally, the number of trees per acre was multiplied by the average basal area to give the basal area or the dominance per acre within each stand.

In Figure 21 the number of lichen species present per stand has been plotted against absolute dominance or total basal area of trees per acre. The pattern produced showed that for the dry stands there was the greatest range in basal area per acre, 6183 to 42120 square inches per acre, and that there were from 4 to 28 lichen species per stand. The range for dry-mesic stands was only

FIGURE 21

The distribution of 71 stands in relation to the absolute dominance and numbers of lichen species present. Limits of the dry, mesic and wet stands are indicated.


DRY
MESIC
WET
NUMBER OF LICHEN SPECIES
28
25
20
15
10
5
0
10,000
20,000
30,000
40,000
ABSOLUTE DOMINANCE (BASAL AREA / ACRE)

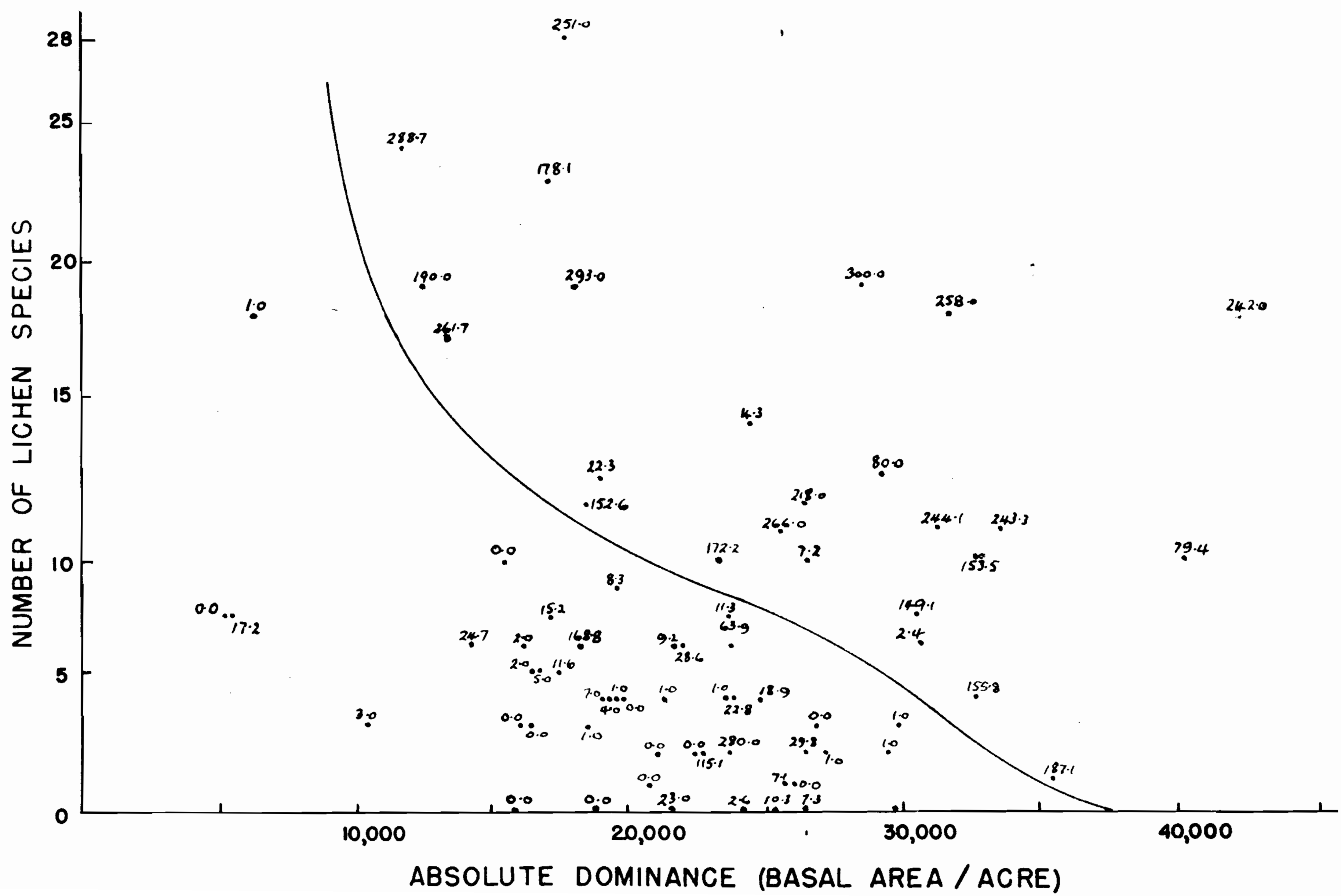
slightly less than that of the dry, 5334 to 40320 square inches per acre, with from 1 to 11 lichen species recorded per stand. Variation in wet stands was from 10642 to 31104 square inches per acre, and from zero to 17 lichen species per stand. The wet-mesic stands were more restricted in range than the wet stands with the basal areas ranging from 16515 to 30558 square inches per acre with from zero to 12 lichen species. The mesic stands had the narrowest range in basal area, 18770 to 29750 square inches per acre and the lowest number of lichen species per stand from zero to 8. At the same time the dense canopy produced would restrict the high frequency of herbs and establishment of shade intolerant tree species.

The percent canopy coverage by conifer species with their needle foliage is much less than that of deciduous trees. The high basal area per acre figures for some dry and dry-mesic stands and their high presence of lichen species, can be explained in most cases by their lower per cent canopy coverage.

Figure 21 appears, therefore, to indicate the interaction of several factors in determining the diversity of lichen species. In Figures 18 and 20, canopy and conifer importance value were plotted separately against numbers of lichen species present. Absolute dominance, as mentioned above, may be a more accurate assessment of tree influence than the canopy estimate. In Figure 22 the importance values of conifer are added to the points plotted in Figure 21. By this method a composite graph combining all three groups of data has been obtained. It is readily seen that a

FIGURE 22

The distribution of 71 stands indicating numbers of lichen species and absolute dominance per stand. Importance value of conifer is added. Line separates coniferous and deciduous dominated stands.


NUMBER OF LICHEN SPECIES
28
25
20
15
10
5
0
10,000
20,000
30,000
40,000
ABSOLUTE DOMINANCE (BASAL AREA / ACRE)

relationship exists between numbers of lichen species present and the relative dominance by conifer species.

To assist in the interpretation, a line has been drawn separating the major conifer-dominated stands from the deciduous stands, the former above the line, the latter below. A few stands are exceptions to this general situation. Several conifer stands dominated by Thuja occidentalis and one stand dominated by Pinus strobus, the basal areas per acre of which were quantitatively similar to the mesic stands, occur below the line. Thuja occidentalis appears mainly in wet-mesic and wet sites and can produce an extremely dense canopy under which plant life is sparse. The deciduous stands above the line are dominated by such species as Ulmus americana, Acer saccharinum, Populus grandidentata and Fagus grandifolia.

In general the conifer-dominated stands show a decrease in numbers of lichen species present as the absolute dominance per acre increases. Similarly, the importance values for conifer decrease with this increase of basal area. The conifer species usually associated with high absolute dominance values are Pinus strobus and Tsuga canadensis. In most cases, stands with high conifer importance values will show a low absolute dominance per acre value and have a high number of lichen species.

The stands above the line in Figure 22 where deciduous species have relatively high importance values, result in an adverse affect on ground conditions reducing the number of lichens, probably due to the reduced amount of light energy reaching the forest floor in the summer. Each Autumn the deciduous leaves cover suitable substrate, such as the extremely acidic needle litter and may smother those lichens established on the ground. All these factors are beneficial to an increase in density of herbaceous species and a reduction in numbers of lichen species.

The distribution of the terricolous lichens in the Northern Conifer-Hardwood Forests of the area studied appears related to several factors all of which must operate for abundant lichen growth. In Figures 18 and 20 it is seen that the more open dry conifer and deciduous-dominated forests produce more ecologically optimum sites for lichens than do the other stands throughout the moisture gradient. The mesic stands with their dense canopies and deciduous litter result in poor ground conditions for lichen growth. Although ground conditions in the wet conifer stands may be suitable for certain lichens, these forests, and the dry-mesic and wet-mesic stands tend to be intermediate between dry and mesic extremes with respect to lichen species and density.

Discussion

From the correlation between conifer importance value and number of lichen species per stand it is seen that the lichens were more related to coniferous than deciduous tree species. There were two exceptions: one stand of *Quercus rubra* and one of *Populus grandidentata* that were designated as dry types. All other deciduous stands produce conditions that were generally far from optimum for terricolous lichens. It is possible that there is a similarity in conditions for lichen growth between dry open stands of pure deciduous species and dry coniferous forests, however, additional stands of pure deciduous forest would be needed to test such a possibility. By combining these factors as absolute dominance and showing the amount of total conifer present as an importance value, a line with only a few exceptions could be drawn separating most of the conifer-dominated stands from the deciduous-dominated stands. Those stands with low conifer values above the line may have been burned, and the past dominants may have been conifers. The stands with high conifer values in the deciduous group were usually dominated by *Thuja occidentalis*, a species that produces an extremely dense canopy condition in the wet lowland and wet-mesic sites in which it may be dominant.

The young conifer species generally show a low basal area per acre with a high lichen species density, while the mature stands dominated by *Pinus strobus* and *Tsuga canadensis* produced a dense canopy and environmental conditions less suitable for lichens. It may therefore be concluded that the dry young conifer stands of low absolute dominance and fairly open canopy produce conditions more suitable for lichen growth than any other forest type along the moisture gradient.

Lichen Substrate Analysis

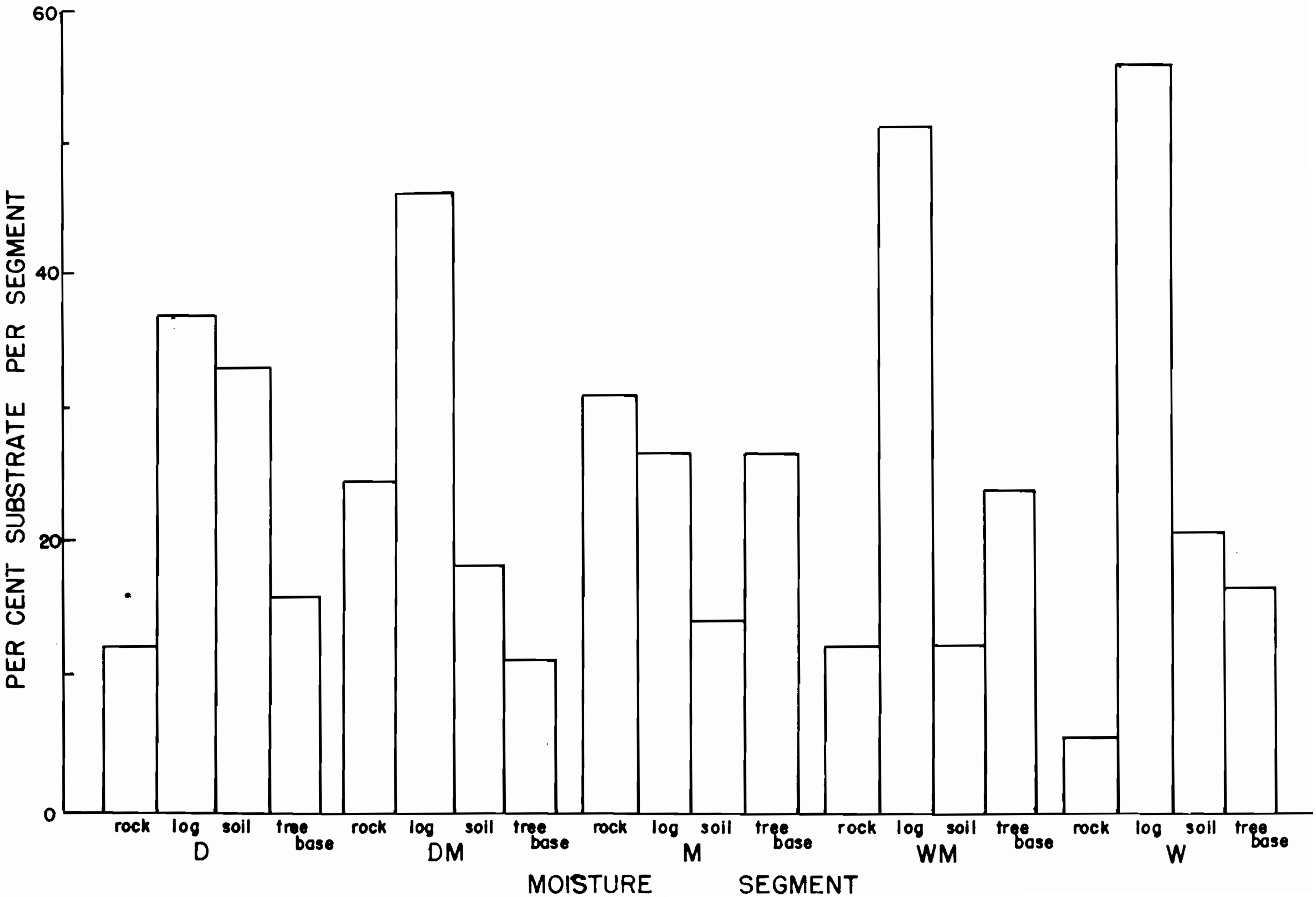
The preceeding analyses have been restricted to the influences of ground moisture and the standing tree vegetation on lichen behavior in the individual stands studied. It was shown that the lichen vegetation is controlled by a number of interacting factors. Quantitative aspects of the substrate specificity of terricolous lichens have not apparently been studied in any detail by earlier workers in North America. Therefore it is expected that the following analysis will allow a greater understanding of the ecological requirements of terricolous lichens.

During the collection of data, special attention was given to substrates upon which all lichen species were found, in recording both presence and frequency. The four major substrates discerned after the initial stands had been studied were rocks, logs, soil and tree bases. Rocks were usually in the form of outcrops and boulders within the stand, but did not include cliff faces or excessively large bedrock outcrops because these deviated markedly from the general topographical conditions. Logs and stumps were initially considered to be separate substrates but were later grouped together as one during the laboratory treatment because they appeared to be identical. The term "soil" is used in the widest sense for it may be covered by organic litter or debris including leaves, needles, twigs or colonies of mosses. In other situations it may be exposed soil.

The presence of all lichens were recorded on tree bases up

FIGURE 23

Histogram indicating the percentage relationship of substrate for each segment of the moisture gradient.


PER CENT SUBSTRATE PER SEGMENT
60
40
20
0
rock
log
soil
tree base
D
DM
M
WM
W
MOISTURE SEGMENT

to a height of 6" inches from the ground. In addition corticolous lichens were collected and included in the study when they were recorded on logs unless the tree had been recently windblown.

One of the most important features of this analysis was the manner in which lichen substrates changed in relative importance across the forest moisture gradient. In Figure 23 a histogram presents this variation. In the preparation of this histogram the occurrence of each substrate was calculated as a percentage of the total occurrence for all substrates within each moisture segment. Consequently the highest percentage value for a substrate does not necessarily occur in the optimum segment for lichen growth. Optimum sites for lichens in this region are the dry conifer-dominated stands and in these, logs and soil were by far the most dominant substrates.

The logs were in most cases from trees suppressed as a result of earlier competition between the young trees in such sites. Due to the slow breakdown of organic matter in the conifer sites these fallen trees often remain as recognizable stems for a considerable time. Similarly the soil in these stands was covered with a thick carpet of slowly decomposing needles and other debris resulting in very acidic substrate suitable for lichen growth and reproduction. Tree bases appear suitable as sites for lichens but little migration had occurred onto them. The one exception was in <u>Pinus banksiana</u> stands, where young stem bases showed a tendency to be populated by lichens. Raup (1928) has suggested that the fragmented bark of conifer species increases the chances of terricolous lichen migration onto their bases. The rock habitats were restricted mainly to the Pinus rigida and Juniperus virginiana stands of the Precambrian boundary in the Kingston area and appeared to be the least important lichen substrate throughout dry stands of the region studied.

In dry-mesic sites the dominance by conifers was far from complete as deciduous species were able to compete and in many stands produce adverse conditions for conifers. The forest floor conditions, therefore, showed a tendency to change in several ways. Deciduous tree leaves are more readily broken down thus allowing a more rapid return of organic material to the soil and the production of a definite A_1 layer. In such conditions of rapid litter turnover, the slow growing lichens appear unable to gain a permanent foothold. Hence the ability of soil to act as substrate for lichens becomes reduced. However, dead and fallen conifer trees are still slow to breakdown and at this time constitute the largest source of substrate available for lichens. In dry-mesic stands, rocks tended to represent a greater proportion of the substrates and in the less shaded areas usually supported lichen species. Both logs and rocks when supporting lichens were above the ground level and are not affected by the smothering effect or the rapid incorporation of the leaf litter into the soil. With the gradual disintegration of these conifer logs, annual litter begins to cover them and they finally are no longer suitable habitats for lichen species. The major conifer species in this segment providing suitable conditions for lichen growth were *Tsuga canadensis* and *Pinus resinosa*, and to a lesser degree *Pinus strobus*. Reduction in coniferous tree species proportionally reduced the number of tree base sites suitable for lichens. There appears to be no satisfactory explanation for the lack of migration of terricolous lichens onto deciduous tree bases. A number of factors have been suggested in the past such as increased hardness of bark chemical constituents and little breaking up of bark compared to that of conifer tree species. A satisfactory explanation of this phenomena would aid greatly in understanding host specificity.

The mesic sites which were completly dominated by deciduous species appear to produce conditions most unsuitable for lichen survival and in fact supported the least number of lichens of any moisture segment. In mesic woods, rocks formed the major proportion of substrate for all lichen species. Thus, though *Cladonia* species were dominant in the dry and dry-mesic stands, foliose forms such as *Peltigera* and *Parmelia* species assumed dominance in the mesic with only three fruticose forms finding conditions suitable for growth. These latter species, *Cladonia coniocraea*, *Cladonia chlorophaea* and *Cladonia fimbriata* were recorded mainly on logs or soil, and again the logs were *Tsuga canadensis* and the soil sites were usually around these logs. Soil was the least important substrate due probably to a rapid turnover of the litter and perhaps a lack of opportunity for saprophytic carbon nutrition, coupled with light energy levels below the compensation points for these species normally growing on this substrate. Tree bases appeared more important in mesic forests due perhaps to the increase in foliose species that found deciduous tree bark a suitable nutritive and mechanical medium.

At the wet end of the moisture gradient similar preferences for substrates to those in the dry were found. The majority of wet stands in this study were bottomland sites dominated by deciduous species, whereas the lowland sites were dominated by conifer species. The usually low lichen presence in the wet sites can be attributed to seasonal inundation especially of bottomland stands. Here again the major substrates were conifer logs with soil of secondary importance. Tree base records decline in the wet segment particularly in the bottomland sites where the seasonal flooding reduced their suitability. There were few rocks in the wet sites.

In wet-mesic stands the conifer-hardwood tree population was considerably easier to recognize. The major substrate type of this segment consisted of logs and stumps of *Thuja occidentalis* together with scattered *Tsuga canadensis*. Tree bases of these two species were the second most important substrate. Rocks were seldom sites for lichens possibly due to the absence of or inundation below spring water level, while soil had the same value as a substrate, supporting lichens only around the bases of the coniferous trees.

This histogram, therefore, indicates the most common substrate preferred by the majority of lichens present in each moisture segment on a proportional basis. Conifer logs which were the dominant substrate in all but the mesic sites appear extremely important in providing mechanical and nutritive media for forest lichens. This is to be expected because in these sites the conifer species tend to be relatively weak competitors and generally decrease in dominance as the deciduous species increase. Consequently coniferous stumps and rotting logs are readily found in most maturing Northern Conifer-Hardwood Forest stands. Soil, as a lichen substrate, shows an optimum level in thedry and in the wet stands where the organic material accumulates in almost raw condition. Lichens on rocks show their optimum to be in the mesic sites decreasing to both wet and dry segments. Though rock outcrops were dominant in the dry the lichens present on them almost always appeared in cracks and crevices where debris had accumulated. The Umbilicaria species and Parmelia stenophylla were the only lichen species recorded on the bare rock. Tree bases were of greatest influence in the mesic segment where the foliose forms were more common.

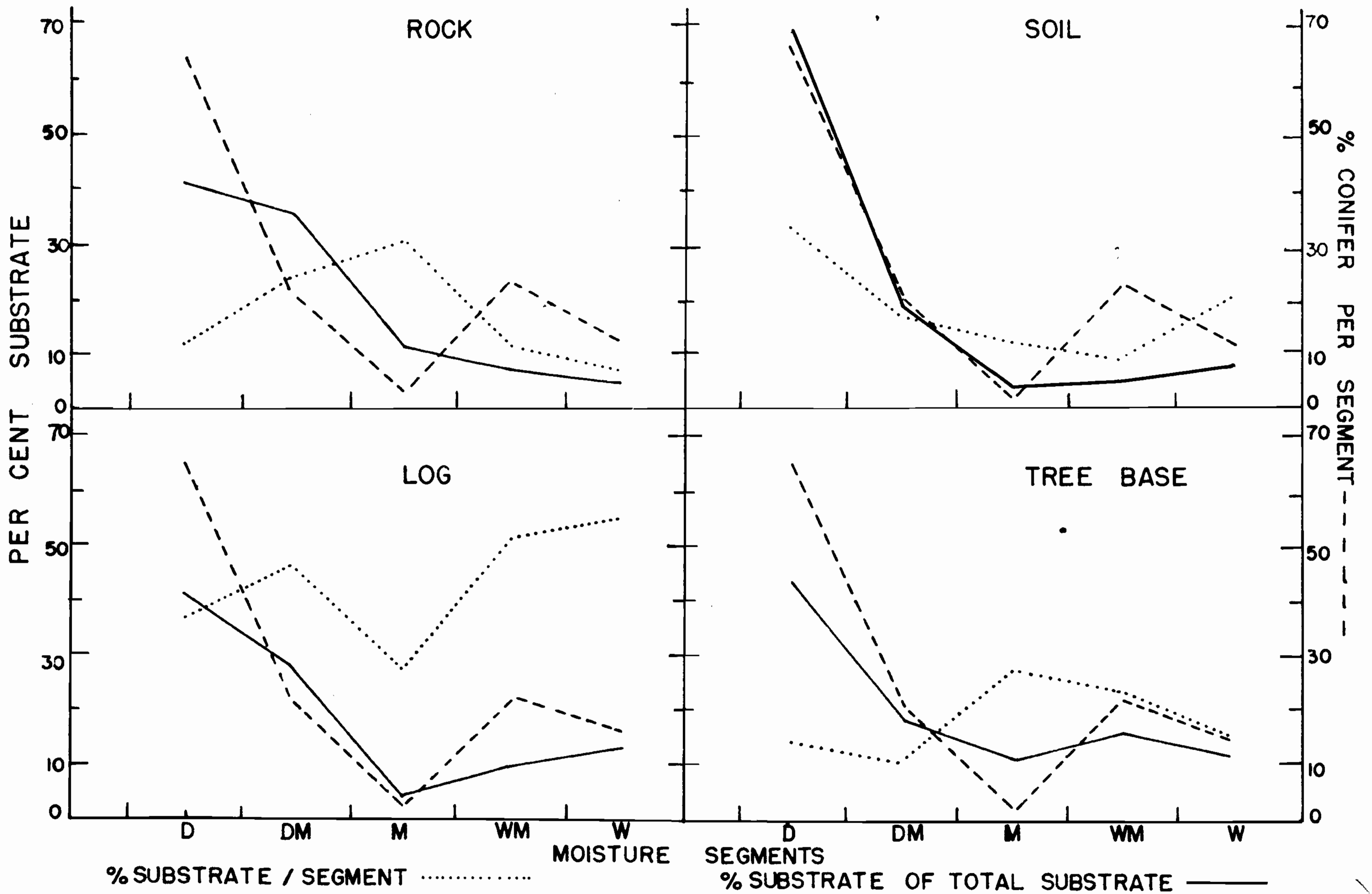
Relationship between Lichen substrates and conifer importance

Each of the four graphs represents one of the major substrates and shows the relative proportion of each substrate type in each segment across the moisture gradient. In addition, the amount of each lichen substrate type per moisture segment as a percentage of the total of the substrate for all segments has been included.

Relationships between substrates and the importance of coniferous species is presented in Figure 24. Average conifer importance value per moisture segment has been plotted on the same graphs in

FIGURE 24

Patterns showing the relationship of substrate to conifer importance.


ROCK
SOIL
LOG
TREE BASE
PER CENT SUBSTRATE
% CONIFER PER SEGMENT - - - -
70
50
30
10
0
D
DM
M
WM
W
MOISTURE SEGMENTS
% SUBSTRATE / SEGMENT ....
% SUBSTRATE OF TOTAL SUBSTRATE ———

which substrate is plotted in relation to the forest on an exact proportional basis in relation to the moisture gradient.

The average per cent of rock habitats shows it to be the least favourable base for growth in relation to the other sites available in the dry stands, but optimum in the mesic under deciduous tree species, and decreasing in the wet. The per cent rock of all rock habitats in all moisture segments shows that as a substrate in the dry it has more lichen species present on it than in any other segment. Log substrate had the highest number of lichens in the dry than any of the other substrates, showed a minimum value in mesic, and increased to a maximum in the wet-mesic and wet sites. The high values in the wet are influenced by the 17 species recorded in a single lowland Larix laricina - Thuja occidentalis stand. Values for soil habitats are at a maximum in the dry and tend to follow the conifer importance value pattern except in the wet-mesic segment. The record of lichen species on tree bases similarly showed their highest values in the dry and minimum in the mesic stands.

When comparing the two patterns for lichen substrate values in Figure 24, the relative rock and tree base values per segment appear to have little relationship with the conifer importance values and distribution of individual substrates along the moisture gradient. The relative substrate values per total substrate do on the other hand, follow similar patterns in the dry segment to that of the conifer species. Patterns in the wet segments vary only with the tree base values similar to the conifer importance values. The prominance of rocks and tree bases as lichen media in mesic forests is readily apparent. The ability of logs and soil to function as lichen substrates therefore appears related to the presence of conifers. The presence of rocks and tree bases for supporting lichen, while appearing to only show a similar pattern under dry conditions differs markedly in the wet-mesic and wet segments. Although this might be construed to be related to deciduous species it is probably related more to conditions that may be produced by the conifers in the dry segment, i.e. high light intensity at ground level. If this is so this supports the previously stated contention that canopy quality produced by *Thuja occidentalis* and *Tsuga canadensis* at the wet end of the moisture gradient is much different from that produced by *Pinus* species at the dry end.

Individual lichen species substrate - Presence Data

Having shown that the substrate preference changes for all lichens across the moisture gradient, a study of the relationships of individual lichen species and substrates was logically the next step. Figures 25, 26 and 27 illustrate substrates upon which each major species was recorded. The X axis again represents the five segments of the moisture gradient and the Y axis the per cent presence of each substrate for that species per segment. Values were determined by totalling the substrates of each species in all five moisture segments, then each individual species value in each segment was calculated as a percentage of the total substrate for that species. For example, *Cladonia coniocraea* was recorded

FIGURE 25

Presence of each lichen substrate as a percentage of total substrate is plotted for four lichen species on the moisture gradient.

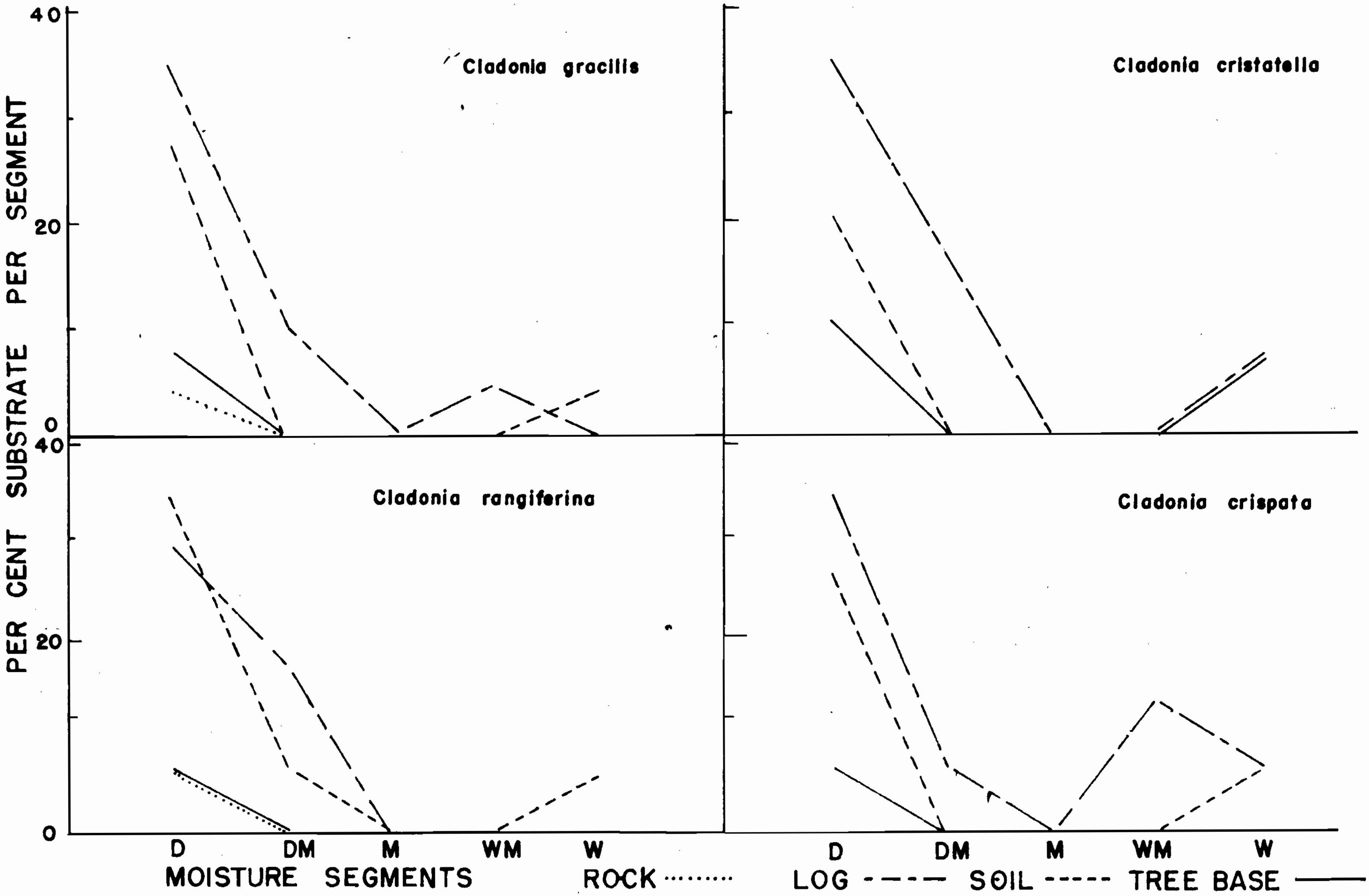
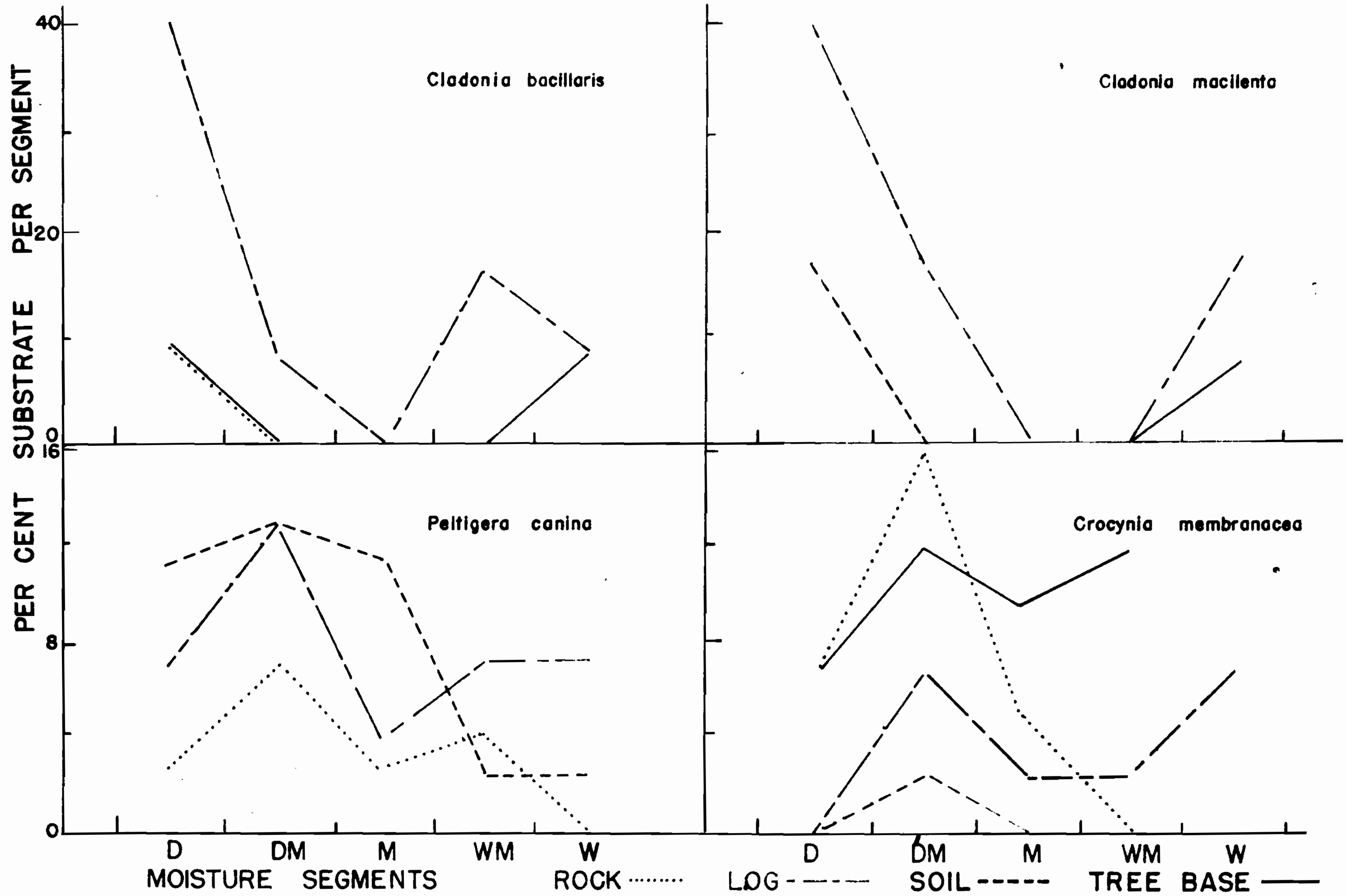

Cladonia gracilis
Cladonia cristatella
Cladonia rangiferina
Cladonia crispata
PER CENT SUBSTRATE PER SEGMENT
40
20
0
D
DM
M
WM
W
MOISTURE SEGMENTS
ROCK
LOG
SOIL
TREE BASE

FIGURE 26

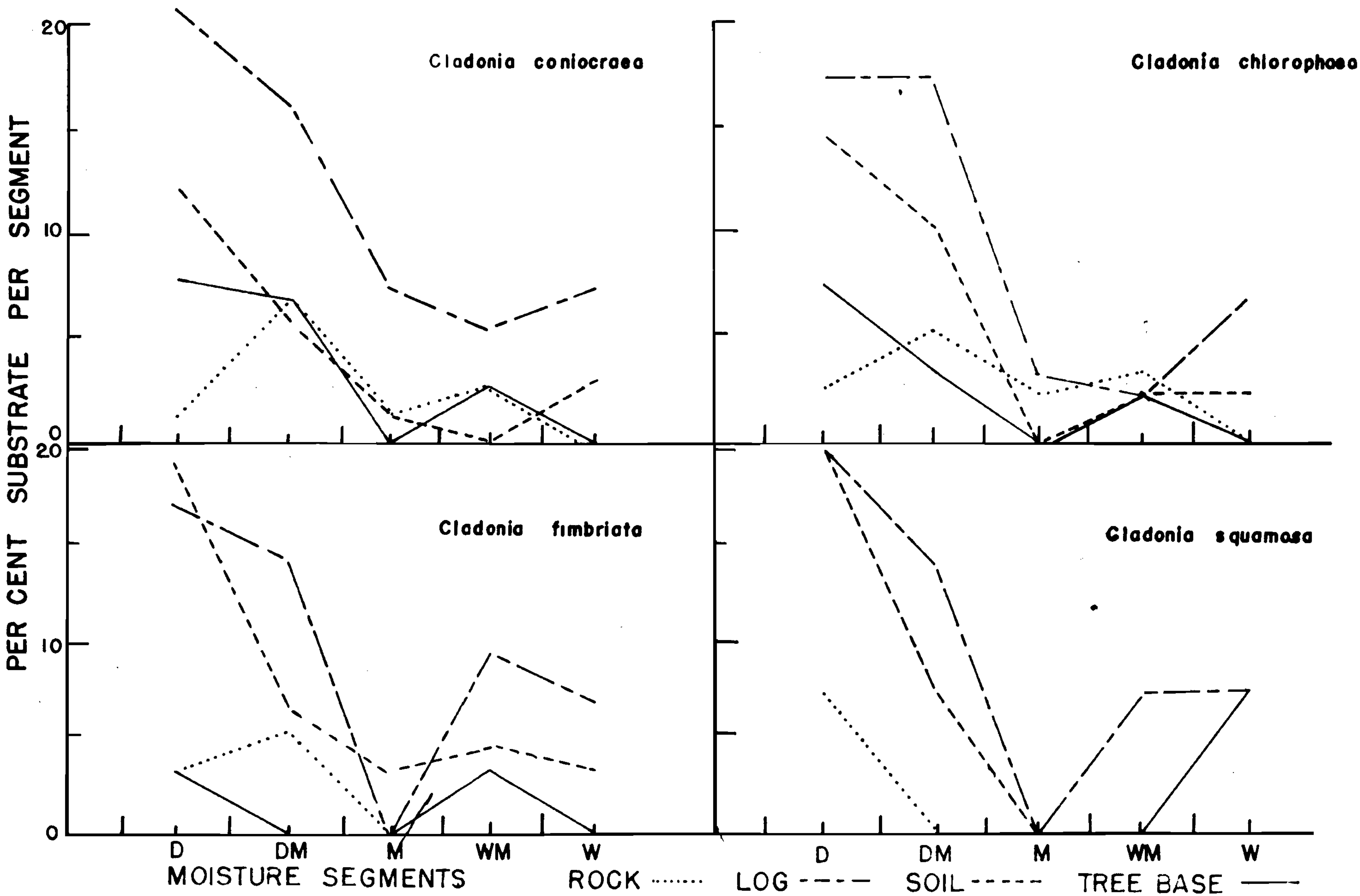
Presence of each lichen substrate as a percentage of total substrate is plotted for four lichen species on the moisture gradient.



Cladonia bacillaris
Cladonia macilenta
Peltigera canina
Crocynia membranacea
PER CENT SUBSTRATE PER SEGMENT
40
20
0
16
8
0
D
DM
M
WM
W
MOISTURE SEGMENTS
ROCK
LOG
SOIL
TREE BASE

FIGURE 27

Presence of each lichen substrate as a percentage of total substrate is plotted for four major lichen species on the moisture gradient.


Cladonia coniocraea
Cladonia chlorophaea
Cladonia fimbriata
Cladonia squamosa
PER CENT SUBSTRATE PER SEGMENT
20
10
0
D
DM
M
WM
W
MOISTURE SEGMENTS
ROCK
LOG
SOIL
TREE BASE

93 times on the four substrate types throughout the 71 stands studied. It was recorded in 12 dry stands on logs, giving this *Cladonia* species a value of 13.2 per cent. In Figure 24, the six major lichen species recorded in all five segments of the moisture gradient show that environmental factors governing lichen species presence are related to a suitable substrate that best satisfies growth requirements. These graphs clearly show that for the majority of lichens there is a marked change in the manner in which different lichens, and even the same lichen species responds in a physiological way to the four major substrates across the gradient. The one exception was that of *Parmelia stenophylla* which was recorded only on rock wherever present.

The species of greatest frequency in the study, *Cladonia coniocraea* showed a preference for log substrate in all five moisture segments. This was followed by a preference for soil substrate in the extreme dry and wet segments, whereas a tree base substrate was relatively important in the dry and dry-mesic sites, unimportant in the mesic, but again influential toward the wet end of the forest moisture gradient. *Cladonia coniocraea* was also recorded on rocks in all segments except the wet. *Cladonia chlorophaea* produced similar patterns except that it was not found on soil on the mesic stands. For *Cladonia fimbriata* soil was the only substrate upon which it was recorded for all five segments, while it was present on logs in all sites except those of the mesic segment. This species occurred on rock substrate only at the dry end of the gradient with a high value in the dry-mesic segment. Tree bases were sites for *Cladonia fimbriata* only in the dry and wet-mesic stands. Similar examples could be cited for a majority of the lichen species.

The presence of all these *Cladonia* species appears to be related to the presence of coniferous species within the stands. As far as can be ascertained the logs were coniferous with *Pinus* species most prominent in the dry, *Tsuga canadensis* in the mesic, *Thuja occidentalis* and *Larix laricina* in the wet. Where the above lichens were recorded on tree bases these conifer species were in the majority of cases the substrate. Presence of these lichen species on rocks is related to the earlier dominance by coniferous trees which would have allowed increased light and a greater number and quantity of lichen species. The present species recorded on rocks are the only types able to withstand the adverse conditions, usually low light intensity produced by invasion of deciduous tree species and these remaining lichens are usually far from vigorous. Also the changing litter conditions and the effects of smothering results in the inability of most of the lichens to survive. *Peltigera canina* was the only lichen species that showed a high presence value for soil substrate in the majority of mesic woods where it was present, although in the wet and wet-mesic segments situations on logs had slightly higher values. Rock was found to be suitable in the dry-mesic, mesic and wet-mesic, while tree bases were also media for *Peltigera canina* in the dry-mesic and wet forests. The ability of this species to survive on soil in the mesic sites is probably due to the thallus being able to absorb available water and to carry on photosynthesis at low light intensities.

Crocynia membranacea was the only crustose species attaining a high degree of constancy in the study. Tree bases were the major substrate upon which high presence values were recorded in the dry-mesic, wet-mesic and wet segments. Whereas the *Cladonia* species occurred on conifer species, *Crocynia membranacea* was in the majority of cases recorded on deciduous tree bases. This species also occurs on logs in all but the dry sites. It was only recorded on soil on a single occasion in a dry-mesic forest.

The remaining species included among the graphs are all *Cladonia* species and not one was recorded in all five moisture segments. These species have substrate preferences similar to those of the three broad ranging *Cladonia* species in that growth on logs and soil was by far the most common in the dry. Both rocks and tree bases appear to be suitable, but only in the wet and dry segments. The reduction in preferred substrates in the dry-mesic, mesic and wet-mesic segments is at the same time very closely related to the reduction in light intensity at the forest floor level. It is likely that the compensation points of these species are much higher than the three major *Cladonia* species so that regardless of availability of substrate they would be unable to survive. The per cent presence values for the remaining lichens were considered not sufficiently complete to give clear distribution patterns and further field work may be required before more may be said concerning them.

Average Frequency of Substrates for Moisture Gradient

Only eight species had frequency values high enough to show a relationship with substrate. Species frequency was computed by averaging the values for each species in the stands of each moisture segment. The results are presented in Figures 28 and 29. In *Cladonia coniocraea* it is apparent that logs were the dominant substrate closely followed by soil. Tree bases supported appreciable quantities of *Cladonia coniocraea* at the dry end and some towards the wet segment, while on rocks in drier sites it had low frequency values. *Cladonia chlorophaea* frequency values show that soil was the major substrate with a value considerably greater than that for rotting logs. The species had frequency values on tree bases in the dry segment, and on rock in all but the wet-mesic sites. *Cladonia fimbriata* has similar frequency and presence patterns with the exception of frequency on tree bases and rocks recorded only in the dry segment. *Cladonia gracilis*, *Cladonia cristatella* and *Cladonia rangiferina* have shown frequency values only in the dry end of the moisture gradient. The major factor borne out by these frequency patterns is that the optimum sites for these species is definitely in the dry segment indicating that their ecological requirements are more readily met here than in the other segments.

Peltigera canina was more frequent in the dry segment predominantly on soil, but relatively abundant also on logs and rocks. In the dry-mesic this lichen is found less on soil with

FIGURE 28

Patterns of four major lichen species with average frequency of substrate per segment plotted on the moisture gradient.

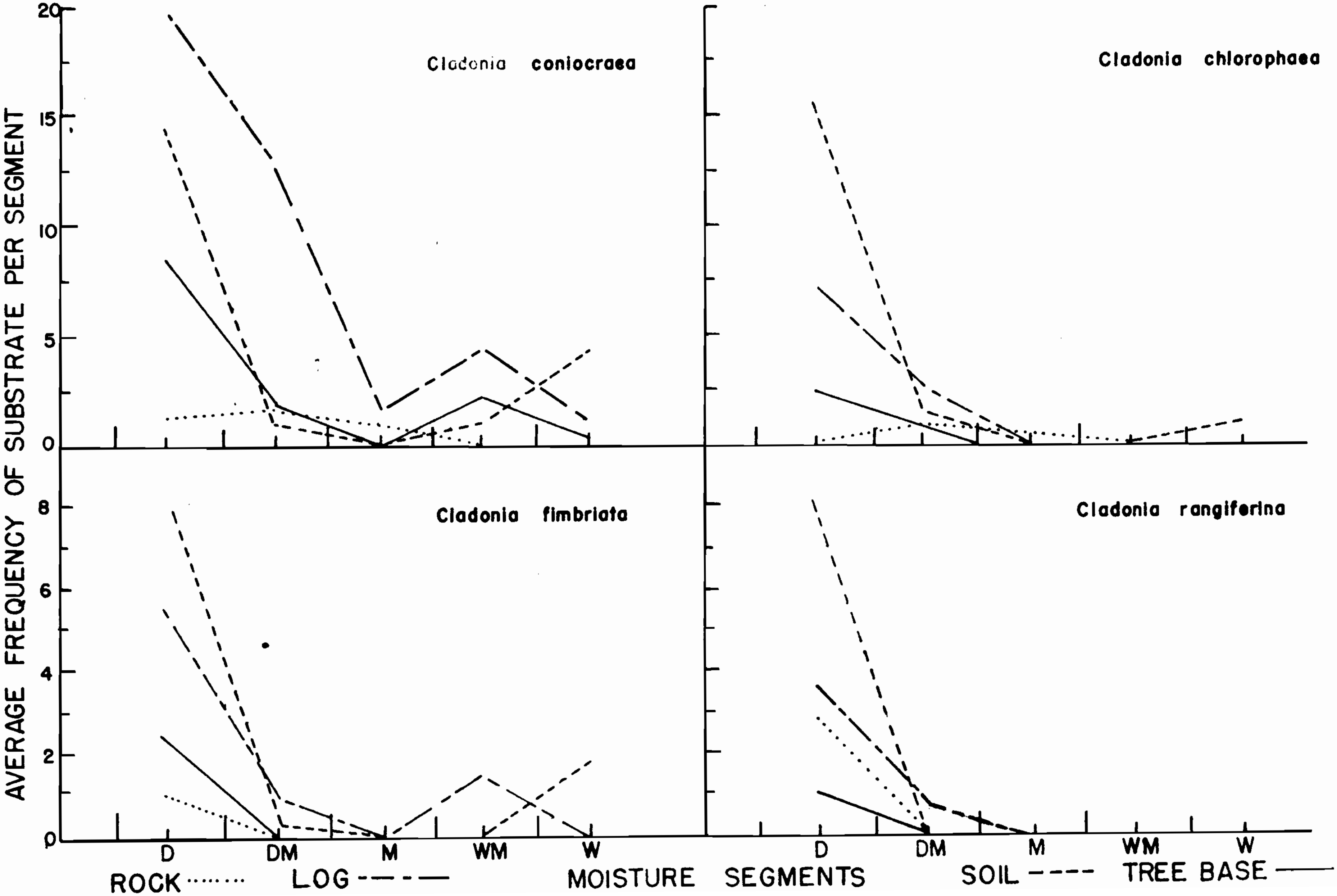
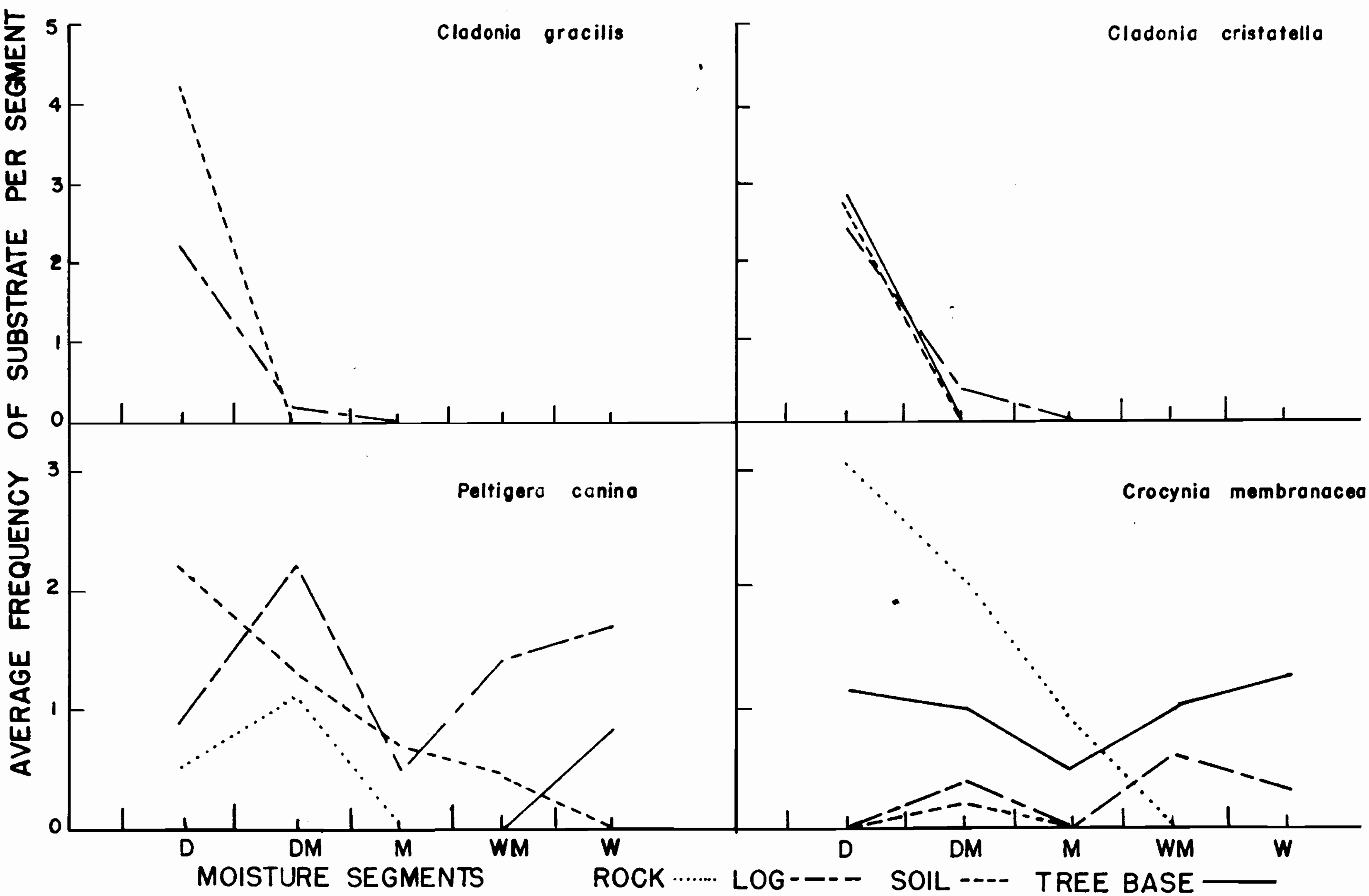

Cladonia coniocraea
Cladonia chlorophaea
Cladonia fimbriata
Cladonia rangiferina
AVERAGE FREQUENCY OF SUBSTRATE PER SEGMENT
20
15
10
5
0
8
6
4
2
0
D
DM
M
WM
W
ROCK
LOG
MOISTURE SEGMENTS
SOIL
TREE BASE

FIGURE 29

Patterns of four lichen species with average frequency of substrate per segment plotted on the moisture gradient.



AVERAGE FREQUENCY OF SUBSTRATE PER SEGMENT
Cladonia gracilis
Cladonia cristatella
Peltigera canina
Crocynia membranacea
5
4
3
2
1
0
D
DM
M
WM
W
MOISTURE SEGMENTS
ROCK
LOG
SOIL
TREE BASE

logs becoming the preferred substrate, similarly rock substrate values show an increase. In mesic sites frequency even on logs decreases markedly, but returns to a high value in wet-mesic and wet woods. The frequency values for soil were highest in the mesic but decrease and become absent in the wet.

While rock and tree base were equal regarding presence for Crocynia membranacea, frequency on rock is considerably greater than that on tree bases. Frequency values on rocks, however, show a total decline to zero in wet-mesic sites. Tree base frequency of Crocynia membranacea, while decreasing in value in the mesic remains fairly constant for the other four moisture segments. A similar pattern is shown by the species on logs though the frequency values are low.

Discussion

From the relationships of terricolous lichens to various substrates an understanding of their ecological requirements within the Northern Conifer-Hardwood Forests becomes apparent. The fruticose forms represented mainly by Cladonia species are definitely associated with coniferous substrates. They are found on conifer logs, conifer tree bases and the soil and debris of stands where conifers are the major constituents. In the tree analysis conifer species occupied ecologically optimum positions in the dry and wet lowland segments of the moisture gradient. The Cladonia species were able to flourish on these conifer substrates apparently showing no marked preference for particular species even though Thuja occidentalis and Larix laricina were optimum in the wet and Pinus species in dry sites.

Where total suitable substrates showed a marked decrease in dry and wet-mesic sites, optimum substrates were still logs and soil for the Cladonia species. Rock and tree bases that were not usually occupied in optimum sites for lichens were utilized even less in stands of intermediate position on the moisture gradient. In mesic sites the extremely low presence of conifer species reduced the amount of suitable log substrate available. The logs available in the dry-mesic would be broken down and incorporated into the A_o layer of the soil profile at a greater rate as the sites showed greater domination by deciduous species. Tsuga canadensis, a conifer that is able to occur with Acer saccharum appears to be the only log substrate in the mesic sites. While favourable conditions prevail in the wet lowland stands they do not in the bottomland forests. Here deciduous trees dominate and seasonal flooding of the forest floor is a normal occurrence rendering most sites below the high water mark unsuitable for the growth of lichens.

Data for certain foliose species such as Parmelia physodes, Parmeliopsis hyperopta, Parmeliopsis ambigua, Cetraria tuckermanii and Cetraria pinastri which were not presented on graphs indicated that these species showed a preference for conifer substrates on either log or tree base. However, data for these species was insufficient to exhibit interpretable trends. Their optimum sites were the dry stands as seen in Table 6 , and they appear to find their highest frequency in the Pinus banksiana stands. Cetraria oakesiana was an exception, however, having the dry-mesic as an optimum site and appearing to be indifferent in respect to substrate. It was present on oonifer logs but was recorded on both conifer and deciduous tree bases. All Umbilicaria species were recorded only at the dry end of the gradient and then only in stands on Precambrian bedrock. These sites were usually open and the ground was exposed to sunlight. While a few of the Cladonia species were able to survive in non-optimum sites on suitable substrates, the majority of types showing similar ecological optima were unable to survive the restricted light and other unfavourable conditions even when substrata were available.

Two species, Peltigera canina and Crocynia membranacea showed only slight variation in their constancy values across the moisture gradient. However, their values in conifer and dry stands dominated by deciduous species were low. Peltigera canina was recorded predominantly on logs and soil in all segments with their occurrence being recorded on tree bases in wet forests. Under wet conditions they grew in bottomland forests on tree bases and lowland forests, on tree bases and soil. These two species would have to be considered as showing a preference for deciduous ground conditions, but are also likely to be present on coniferous species.

The majority of foliose species with low constancy values were recorded in the dry-mesic, mesic and wet-mesic segments. Their substrates were mainly rock in the mesic and log or tree base in the two intermediate segments. Whereas conifer logs during decomposition appeared to be favourable sites for almost all species, no lichens were found on decomposing deciduous logs. Though these foliose species were more frequent in the mesic woods their growth appeared as depauperate as that of _Cladonia_ species surviving in the same stand. _Peltigera canina_ was the only species of those collected in the mesic segment that appeared healthy and vigorous.

The results indicate that optimum environmental conditions required by all lichen species are not present for terricolous lichens in terminal Maple-Beech woods of this region. The dense canopy, a forest floor usually without debris and the smothering effect of seasonal litter that is quickly incorporated into humus, combine to produce conditions unfavourable for lichen survival.

DISCUSSION

In the results of the tree analysis the continuous aspects of the conifer-hardwood vegetation in the region investigated is clearly indicated. The majority of species examined tended to occupy a definite portion of the moisture gradient. The quantitative analysis showed that not all the trees were equal in importance in the forests. Of the fifty trees recorded only 22 were able to attain the position of leading dominant in a stand. When the tree responses were considered as a whole, it was evident that the tree communities of this region of eastern central Canada constituted a forest continuum. All these species form a community complex and appear to be arranged in an independent manner along environmental gradients. A gradual transition takes place in most cases from the optimum site of development to the point at which each individual species becomes only a minor component or is absent. In all cases in the present analysis individual trees were shown to attain optimum importance in only one particular moisture segment.

The continuum represents all species and emphasizes how individuals position themselves in environmental situations most suited for their optimum development. Effects resulting from the interactions of species is perhaps one reason for the wide or narrow ranges of tolerance shown by individual species.

Discussion

In the Northern Conifer-Hardwood Forests region high abundance and numbers of terricolous lichen species are most commonly found in stands of the dry segment. Their relationship to this segment appears to be partly controlled by the conifer species present and the environmental conditions produced largely by these trees. At the wet end of the moisture gradient there is a similar association of these lichens with the conifer species. The genus *Cladonia* had the largest representation of all the genera in this forest region and for the majority of its species optimum conditions occurred in the dry segment. While a number of foliose species had their greatest development under dry conditions most of these species were recorded in only one or two stands in the dry-mesic, mesic or wet-mesic segments. The number of lichen species with high average per cent presence and average frequency values in the dry segment reappeared in the wet stands with low average per cent presenee and rarely having frequency values.

The forest floor in the open, rocky conifer forests of the region studied supported colonies of *Cladonia rangiferina*, *Cladonia alpestris* and occasional clumps of *Cladonia mitis* and *Cladonia sylvatica*. These open forests were predominantly stands of *Pinus rigida*, *Juniperus virginiana* and *Pinus resinosa*. With the invasion of deciduous trees and greater numbers of herbaceous plants these *Cladinae* appear unable to compete and rapidly decreased. It appears that accumulated mor debris of low pH and sparse ground vegetation are important features in the survival of the *Cladinae* species.

Young stands of *Pinus banksiana* appear to produce conditions similar to those of _Pinus rigida_, _Juniperus virginiana_ and _Pinus resinosa_, but the colonies of _Cladinae_ are usually reduced to small clumps of _Cladonia rangiferina_ only. In such stands the early competition between the trees usually results in a fairly dense forest floor of entangled slowly decompesing stems. These stems are usually of small diameter but support an abundance of _Cladonia_ species, predominantly _Cladonia coniocraea_, _Cladonia chlorophaea_, _Cladonia fimbriata_, _Cladonia gracilis_, _Cladonia cristatella_ and _Cladonia botrytes_. At the same time these and other _Cladonia_ species can be found on the organic debris of needles and twigs. This change in species composition may be due to the reduction of light in these more densely populated stands. To the _Cladinae_ species this reduction in light intensity in all probability is the major reason for their absence in these stands. Stalfelt (1938) gives the compensation point for _Cladonia sylvatica_ in the summer as 1700 Lux at the same time _Umbilicaria pustulata_ has a value of 2000 Lux. Both these species are associated with open areas or areas where tree density is low. _Ramalina farinacea_ a species associated with more mesic conditions where canopies are relatively dense has a compensation point in the summer of 500 L.

The rate of litter decomposition is increased with the invasion of more deciduous species. In addition these tree species reduce the chance of reproduction of shade-intolerant conifer species as the amount of light reaching the forest floor is greatly reduced. This reduction in light energy available drastically affects the growth and distribution of the majority of lichens present.

With the addition of a dense broadleaf litter each autumn and its fairly rapid break-down the following spring the soil becomes unfavourable as a lichen substrate except in isolated areas where few leaves fall and the light intensity at soil level remains fairly high.

The suitable substrates above this active litter layer are the conifer logs. These logs appear frequently in dry-mesic and wet-mesic sites and may support a fairly dense lichen population, although the number of species present is usually reduced. A similar situation to that reported from the Colorado Rockies by McCullough (1948) on Spruce-Fir logs is apparent in the northern conifer-hardwood forests of this region. The early invaders of the decomposing logs were Cladonia species until mosses and herbaceous plants took over.

The decrease in lichen species appears to be due partly to the reduced amount of favourable substrate and the reduction in light energy levels. Moss (1938) reported a reduction in lichen species presence with the reduction in the number of decomposing conifer logs in a conifer stand that was being taken over by Populus tremuloides. Moss concluded that the use of liverworts and lichens as site indicators was evidently complicated by the fact that many were occupying microhabitats and were not influenced markedly by the overall environment within the stand. The present work substantiates this initial observation in the graphs presented to show the change in substrate for these lichen species in the dry-mesic and dry segments and the wet-mesic and wet segments.

This to some extent clarifies the process of lichen species migration from one substrate to another and final disappearance during possible forest succession toward the terminal mesic state. Conditions produced by these conifer logs seem to meet the basic habitat and nutrient requirements of the lichens present, however, no exact information is available on the possible similarity of the dead ground log substrate to the sites where optimum conditions for these lichens occur. Earlier workers have stated that these terricolous lichens are not saprophytic and the conifer logs must form a suitable environment in view of the apparent lack of these Cladonia species on the deciduous logs. It is possible that certain nutrients released by the acid humus and litter on the forest floor of conifer stands are also available from the decomposing conifer logs and that these nutrients are not available from the deciduous logs or the litter in deciduous woods.

It would appear that the compensation points of the majority of fruticose species is reached long before the conifer species have been completely suppressed by the deciduous trees. A study of the per cent canopy figures will show that the amount of light reaching the forest floor is already greatly reduced in the dry-mesic and wet-mesic stands. High light energy and the conditions produced by coniferous species would appear to be important factors related to lichen distribution.

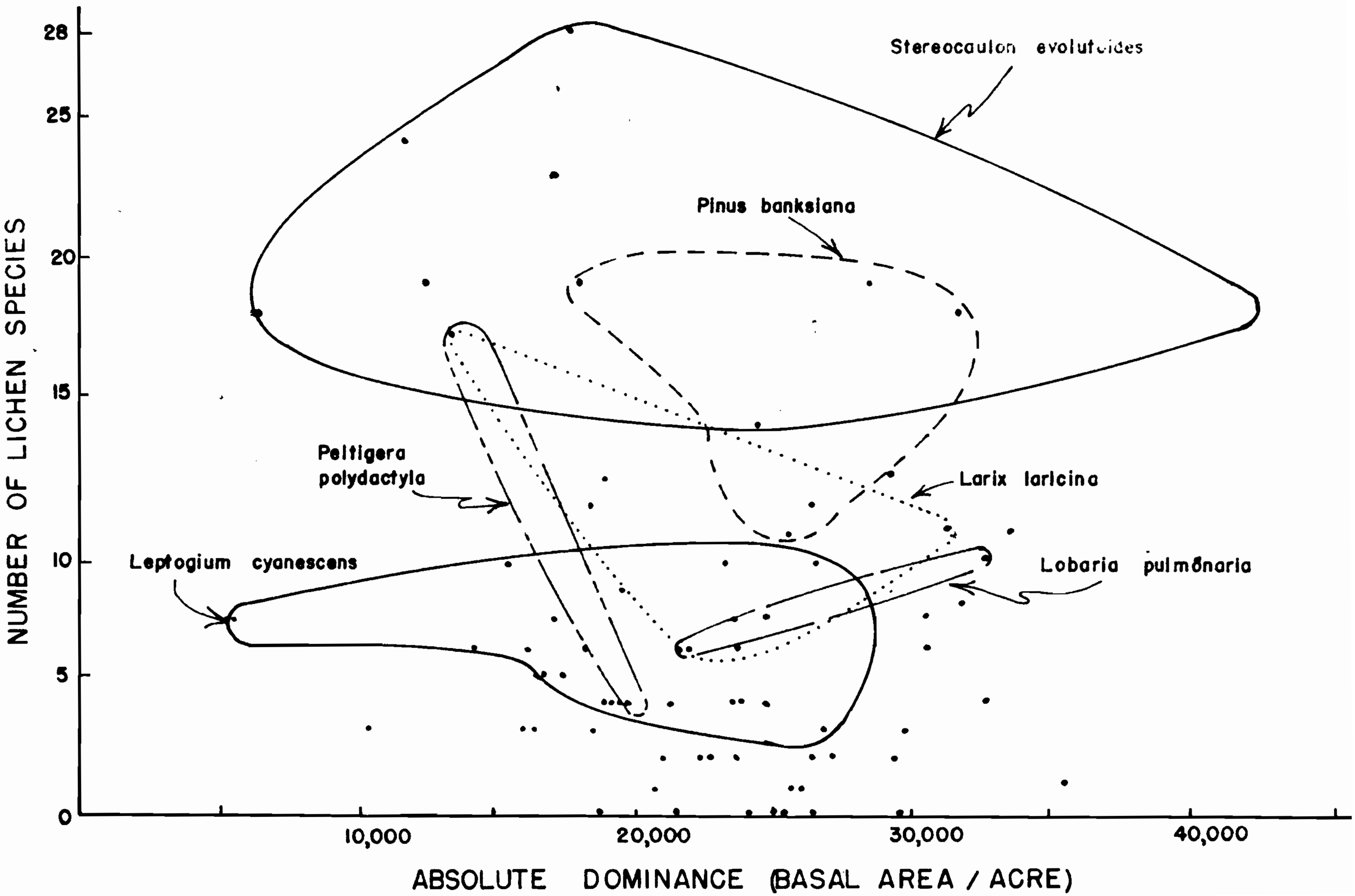
The majority of foliose species recorded in the dry segment of the moisture gradient seem to react in a similar manner to that of the fruticose species in that they were associated with the conditions produced in the coniferous stands. They were seldom recorded on substrate other than logs or tree bases, and were absent when that substrate was missing. Foliose species recorded in the mesic stands were seldom associated with conifers. They were either on live deciduous tree bases or rocks with the exception of Peltigera canina on soil. The three Cladonia species in the mesic segment were the only species recorded on logs and in all probability conifer logs, and in one case each on rocks and soil. Peltigera canina was the only species that had a high presence value on soil in the mesic woods, usually at the base of trees. The compensation point of Peltigera canina seems considerably lower than the majority of lichen species recorded in this study.

Mesic stands sampled were not favourable sites for terricolous lichens, and it would seem that the corticolous species are also restricted. Hale (1955) concluded that the pioneer oak openings and climax maple woods had completely different cryptogamic vegetation. The majority of the cryptogams were most frequent in stands dominated by Quercus and usually rare or absent in more mesic stands. It seems likely that the absence of terracolous lichens can be associated with this general absence of conifers. The presence of standing conifer trees and decomposing logs on the ground can from the preceeding analyses be associated with the presence of terricolous lichens, especially Cladonia species. The three major Cladonia species seem to tolerate unfavourable environmental conditions in the stands preceeding the mesic condition and when a conifer substrate is absent are able to survive on a rock habitat. The remaining Cladonia species would therefore seem unable to compete with the three major Cladonia species for suitable substrate. Additionally the reduced light energy and the possibly high compensation points of these species in all probability contributes to their extinction. The possibility that lichens were present at one stage in stands where they are now absent is not to be overlooked. While no quantitative data on actual logs present on the forest floor were collected it would be reasonable to assume that their presence was at a minimum.

High numbers of lichen species were recorded in two deciduous dominated stands in the dry segment. In one, Populus grandidentata had become established on a burned over Pinus banksiana site. The high lichen count here would resemble very closely that for the Populus stand studied by Moss (1938). The reduction in numbers of lichen species some twenty years after his initial visit was related to a reduction in log substrate. An open stand of Quercus rubra on Precambrian outcrop showed similar ground features to those recorded in the Pinus rigida stands. This stand had a very low conifer importance value index, and would seem to disprove the thought that only conifer stands are optimum for terricolous lichens in the region. One can only speculate as to past history of the site with the thought that as oak is a slow growing tree the site would seem optimum only for this tree species. The thick oak leaves are very slow to decompose and in conjunction with the high light

FIGURE 30

Distributional patterns of 4 lichens and two tree species illustrating the independant occurrences of individual organisms in stands ordinated on the basis of important habitat features.



Stereocaulon evolutoides
Pinus banksiana
Peltigera polydactyla
Larix laricina
Leptogium cyanescens
Lobaria pulmonaria
NUMBER OF LICHEN SPECIES
28
25
20
15
10
5
0
10,000
20,000
30,000
40,000
ABSOLUTE DOMINANCE (BASAL AREA / ACRE)

intensity possibly due to the openness of the stand, favorable conditions are present for lichen establishment and growth.

In the results of the analyses the continuous aspects of the northern conifer-hardwood vegetation is clearly indicated. The quantitative analyses showed that trees and lichen species occupied a specific segment of the moisture gradient. The patterns of the majority of both these life forms appear as normal curves with no two species occupying exactly similar positions. At the same time lichen species appear in the two extreme moisture segments suggesting that they can survive and reproduce under differing environmental conditions.

The increase in deciduous tree species in the mesic segments of the moisture gradient results in environmental conditions unsuitable for the majority of the lichen species recorded in this study. The increase in per cent canopy values reduces the total amount of light energy available at the forest floor. The increase in broadleaf litter and the increase in rate of turnover of organic matter reduces the majority of suitable substrates for species that find their apparent optimum in the wet and dry segments. A number of lichens present in the mesic segments were not recorded in the wet and dry segments. Extremely low values for these species did not allow a graphic representation to illustrate their position.

In Figure 30, absolute dominance and number of lichen species in all 71 stands has been plotted to show light, conifer and moisture. A group of lichens and trees with narrow ecological tolerances have been plotted to emphasize the affect of the above factors on their distribution.

The entire assemblage of tree and lichen species can be said to represent a vegetational continuum in which all species interact and position themselves in environmental situations most suited for their existance.

Related Approaches

In North America no similar investigation using quantitative methods has been undertaken in the study of terricolous lichens. Brinkman (1934) attempted to evaluate the lichens of the Spruce-Fir Forests of northern Alberta in relation to the forest site values. He was able to show that with increase in wood volume and age of stands the number of lichen species was reduced. In lower value sites lichens were invariably present on the forest floor but with increase in age of the trees they appeared on logs in greater numbers. As the site values increase there is a corresponding decrease in number of lichen species. Some species were found to range through all forest types, although, Brinkman gave no details of the sites. The thought that certain genera found in all sites would show a species difference was suggested, and that a closer study might prove them to have an indicator value. Brinkman further suggested that there was considerable room for more study and results should be compared with other areas. In the present study the migration of lichens from soil to log substrates has been confirmed and presented in graphic form. Where presence and frequency values were high enough species were plotted to show their distribution on the four types of substrate. A definite trend was seen in which the Cladonia species showed a migration from soil to log substrate with deciduous tree invasion.

The only other study of terricolous lichens has been that of Robinson (1959) on lichen succession in abandoned old fields of North Carolina. The lichens, all Cladonia species, were sampled and frequency recorded in 12 old fields ranging in age from 1 year to 120 years. Three groups of lichens were distinguished by their occurrence in various successional stages. During the first few years of abandonment no lichens were found and only one was found at the terminal stage of the study. The dominant trees throughout the successional stages were the Pines. During these intermediate stages 12 lichen species were recorded, some being present for a period of sixty years while others for only four years. Robinson concluded that the "variation in the nature of the organic debris during the succession is the major factor controlling the composition of the lichen vegetation". The results in the present study show that the high presence and frequency values were recorded in dry Pine dominated stands and that with successional development these values decrease. The reduction in suitable substrate, i.e. a slowly decomposing needle and twig litter that is very acidic, is a major factor as suggested by Robinson. But this is in conjunction with an increase in deciduous leaf litter and the reduction in light energy due to a more dense canopy. Robinson recorded no <u>Cladonia</u> species in the climax Oak-Hickory stands whereas in this investigation three <u>Cladonia</u> species were shown to be present in mesic woods.

A search of pertinent literature has failed to reveal any quantitative studies on terricolous lichens of mixed Northern Temperate Forests of Europe. Many studies have been carried out in timber line zones in relation to alpine woodlands and the lichenous, heath forests in Scandinavia. Studies have been undertaken in Europe on corticolous lichens, but have been related mainly to those trees with lichens present. A review of these studies has been given by Hale (1955).

Hale (1955) and Culberson (1955), (1955) were the first to develop a quantitative approach to the study of corticolous cryptogams in North America. An attempt was made to show the relation of the cryptogamic vegetation to the forest types and to particular tree species together with interrelations of the cryptogams themselves. Hale was able to demonstrate that in the southern forests of Wisconsin there was a definite association between lichen species and total forest composition with a strong element of host specificity. Certain species were more common in the dry stands than the mesic stands, others were present on one tree species and not on others. Culberson also showed similar relationships in respect to lichens of the northern forests of Wisconsin. A paper by Culberson (1955) on the geographical distribution of the corticolous lichens of Wisconsin showed that there was a definite line from northwest to southeast across the the state separating the northern and southern lichen species. Certain species ranges overlapped, but their optimum geographical site was either in the north or the south. Other species were restricted to either north or south of the boundary clearly showing the geographical affinity. In the same paper Culberson reported that the bark vegetation on Pinus strobus and Pinus banksiana in stands from southern Wisconsin increased in the northern forests. By plotting average number of species per quadrat and average frequency a very appreciable gradient, increasing from south to north was shown in the species richness of the bark communities on Pine.

As the present study of terricolous lichens is the first of its kind no detailed comparisons may be made to other regional forest types. It is hoped that this investigation will be only the beginning of such studies and that an understanding of the terricolous lichens in further forest communities will be forthcoming. Future work will enable regional comparisons similar to that of Culberson (1955) to be made in respect of terricolous lichens of temperate and boreal forests.

SUMMARY

Quantitative data on trees and terricolous lichen composition were collected in 71 stands selected randomly throughout the Northern Conifer-Hardwood Region of central eastern Canada.

Three major treatments were performed. The first was an attempt to understand the distribution and the relationship of the tree vegetation. Similarly the second was to understand the distribution and relationship of the lichen vegetation. The third treatment was to compare and relate these two analyses in the overall vegetational complex.

Relative frequency, relative density and relative dominance were calculated for all tree species in all stands. An importance value index was obtained by summing all three relative values.

All quantitative standdata were related to the influence of moisture. To determine the effect of moisture the stands were assigned moisture categories in the field. The five categories were dry, dry-mesic, mesic, wet-mesic and wet. All quantitative data for the trees were averaged for each moisture segment. To aid in the interpretation of these average values a series of graphs were prepared for selected species. When these average values were plotted the results in many cases were normal curves. These curves were considered to represent the ecological tolerances of species to moisture conditions. The peaks of these curves are related to the situation of optimum development. Groups of species with narrow ranges and broad ranges were included and the species of each group were shown to exhibit similar reactions to moisture conditions.

On the basis of all the importance values of each tree and the position on the moisture gradient the dominant trees for each moisture segment were determined. Acer saccharum, a mesic species had the highest importance value of all species and was the dominant tree in 28 stands. Ulmus americana was dominant in 7 and Acer saccharinum was dominant in 6 stands and these were the leading trees in the wet segment. Pinus strobus was dominant in 6 stands at the dry end of the moisture gradient.

The total assemblage of species on the moisture gradient resembled an intergrading series of normal curves in which no two species possessed the same amplitudes of tolerance. The continuous nature of the forests of the region therefore seems to be undisputable as illustrated by the patterns of individual species along the moisture gradient.

Analysis of the lichen data was initially based upon the same moisture gradient. Quantitative values were averaged for individual lichens for each moisture segment. When these values were plotted normal curves resulted for the majority of lichens. For the majority of species narrow ranges of tolerance were exhibited. The remainder of the curves were bowl-shaped in that two peaks of tolerance were evident, one usually of greater magnitude than the other. These curves were considered to represent the situations of optimum development. Groups of lichens were shown to react in a similar manner to moisture conditions as the trees.

For the species that exhibited broad ranges of tolerance the relation to moisture was not clear. These species showed high values in the dry, dropped out in the mesic and reappeared in the wet segment. with reduced values. Moisture conditions therefore, appeared to have less of an influence on the distribution of these lichens than on the majority.

These results illustrated that the lichen communities of the region were continuous and that many species showed different responses to the environment. Following these two analyses, an analysis of the lichens in relation to tree vegetation was made which emphasized the continuum hypothesis.

Correlations with numbers of lichen species in each stand were separately made with average per cent canopy, importance value of conifer and absolute dominance for each stand. The interpretation of all these graphs lead to the conclusion that the number of lichen species present is greatest in dry stands dominated by conifer and deciduous trees, but that wet stands dominated by conifer produce conditions for establishment and survival on a greatly reduced scale. The lichen species present in the wet and dry moisture segments emphasize their broad ranging nature and ability to survive under different environmental conditions. Non-optimum sites were the deciduous dominated stands of the mesic and wet segments. Here a dense canopy that restricted light penetration, a smothering litter that is quickly incorporated into the A_1 layer and the lack of suitable substrates are the usual conditions.

Continuous vegetational patterns are evident in the entire forest complex when the quantitative data for both trees and terricolous lichens are correlated. These patterns influence the availability of substrate, the type of litter and light energy at the extremes of the moisture gradient. Thus the trees respond to conditions of the environment; lichens respond to these conditions, but in turn are conditioned by the influence of the trees in the environment.

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APPENDIX

List of 87 lichen species,6 varieties,and 33 forms encountered in stands.

Actinogyna muhlenbergii (Ach) Scholander.
Alectoria nidulifera Norrl.
Bacidia chlorococca (Graewe.) Lett.
Bacidia fusca (Mass.) Du Rietz
Bacidia incompta (Born.) Anzi
Candelaria concolor (Dicks.) Arn.
Cetraria ciliaris Ach.
Cetraria oakesiana Tuck.
Cetraria pinastri (Scop.) S.Gray
Cetraria tuckermanii Oakes
Cladonia alpestris (L.) Rabenh.
Cladonia bacillaris (Ach.) Nyl.
 form clavata (Ach.) Vainio
 form reagens
Cladonia botrytes (Hag.) Willd.
Cladonia cenotea (Ach.) Schaer.
Cladonia chlorophaea (Floerke.) Spreng.
 form carpophora (Floerke.) Anders
 form prolifera (Wallr.) Arn in Rehm.
 form simplex (Hoffm.) Arn.
Cladonia coccifera (L.) Zopf.
Cladonia coniocraea (Floerke) Sandst.
 form ceratodes (Floerke.) Dalla Torre & Sarnth.
 form truncata (Floerke.) Dall Torre & Sarnth.
Cladonia crispata (Ach.) Flot.
Cladonia cristatella Tuck.
 form abbreviata
 form Beauvoisii (Del.) Vainio
 form degenerata Robbins
 form ochrocarpia Tuck.
 form pleurocarpia Robbins
 form ramosa Tuck.
 form squamosissima Robbins
 form vestita Tuck.
Cladonia cylindrica Evans
Cladonia deformis (L.) Hoffm.
Cladonia delicata (Ehrh.) Floerke.
 form quercina (Pers.) Vainio
Cladonia digitata Schaer.
Cladonia farinacea (Vain.) Evans
Cladonia fimbriata (L.) Fr.
Cladonia furcata (Huds.) Schrad.
 var.pinnata form foliolosa (Del.) Vainio
 var.pinnata form truncata (Floerke.) Vainio
Cladonia gracilis (L.) Willd.
 var.dilatata (Hoffm.) Vainio
Cladonia macilenta Hoffm.
 form styracella (Ach.) Vainio
 form granulosa Aigret

Cladonia mitis Sandst.
Cladonia multiformis Merr.
Cladonia nemoxyna (Ach.) Nyl.
Cladonia ochrochlora Floerke.
Cladonia pleurota (Floerke.) Schaer.
form decorata Vainio
Cladonia pyxidata (L.) Fr.
var.neglecta (Floerke.) Mass.
var. neglecta form simplex (Ach.) Harm.
var. neglecta form carpophora
Cladonia rangiferina (L.) Web.
Cladonia scabriuscula (Del.) Leight.
Cladonia squamosa (Scop.) Hoffm.
form clavariella
Cladonia subtenuis (des Abbayes) Evans
Cladonia subulata
Cladonia sylvatica (L.) Hoffm.
Cladonia turgida (Ehrh.) Hoffm.
form scyphifera Vainio
form corniculata Floerke.
Cladonia uncialis (L.) Webb.
form dicraea (Ach.) Vainio
Cladonia verticillata (Hoffm.) Schaer.
form evoluta (Th.Fr.) Stein in Cohn
Crocynia membranacea (Dicks.) Zahlbr.
Crocynia neglecta (Nyl.) Hue
Evernia mesomorpha Nyl.
Lasallia papulosa Ach. Llano
Lecanora pallescens (L.) Mass.
Lecanora subfuscata Magn.
Leptogium cyanescens (Ach.) Kocher.
Lobaria pulmonaria (L.) Hoffm.
Microphiale diluta (Dicks.) Zahlbr.
Nephroma bellum (Spreng.) Tuck.
Parmelia aurulenta Tuck.
Parmelia caperata (L.) Ach.
Parmelia conspersa (Ach.) Ach.
Parmelia fronifera Merr.
Parmelia lusitana
Parmelia physodes (L.) Ach.
Parmelia plitti Gyel.
Parmelia rudecta Ach.
Parmelia stenophylla (Ach.) Heug.
Parmelia subaurifera Nyl.
Parmelia subtilis
Parmelia sulcata Tayl.
Parmeliopsis ambigua (Wuff.) Nyl.
Parmeliopsis hyperopta (Ach.) Vain.
Peltigera canina (L.) Willd.
var.canina
Peltigera canina var. spuria (Ach.) Schaer.
Peltigera canina var. rufescens form innovans (Korber.) Thomson
Peltigera evansiana Gyel.
Peltigera horizontalis/polydactyla
Peltigera polydactyla (Neck.) Hoffm.

Peltigera canina var.spuria form sorediata
Pertusaria sp. DC.
Physcia adscendens (Th.Fr.) Hampe.
Physcia aipolia (Ehrh.) Hampe.
Physcia ciliata (Hoffm.) Du Rietz
form fibrillosa
Physcia millegrana Degelius
Physcia orbicularis (Neck.) ~~Thomson~~ Poetsch
form rubropulchia
Physcia phaea (Tuck.) Thomson
Pyxine sorediata (Ach.) Mont.
Ramalina intermedia Nyl.
Ramalina obtusata (Arn.) Bitt.
Rhizocarpon geographicum (L.) DC.
Stereocaulon evolutoides (Magn.) Frey.
Umbilicaria deusta (L.) Baumg.
Umbilicaria mammulata (Ach.) Tuck.
Xanthoria polycarpa (Ehrh.) Rieb.