POST-FIRE RECOVERY OF LICHEN WOODLAND

POST-FIRE RECOVERY SEQUENCE OF
BLACK SPRUCE-LICHEN WOODLAND
IN THE NORTHWEST TERRITORIES

by

Eugene Maikawa, B.Sc.

A Thesis
Submitted to the School of Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree
Master of Science

McMaster University
April 1976

MASTER OF SCIENCE (1976)
(Biology)

MCMASTER UNIVERSITY
Hamilton, Ontario

TITLE: Post-fire recovery sequence of black spruce-lichen woodland in the Northwest Territories.

AUTHOR: Eugene Maikawa, B.Sc. (McMaster)

SUPERVISOR: Professor K.A. Kershaw

NUMBER OF PAGES: ix, 100

ABSTRACT

Tree ring analyses have been used for determining the time since the most recent fire in several areas of burned black spruce-lichen woodland on drumlins in the Northwest Territories. The vegetation on these burns has been described in detail. Analysis of the data by principal component analysis and regression analysis shows that recovery of the ground vegetation after burning follows a general sequence. Topographic factors do not appear to be of much importance. The moss Polytrichum piliferum is very abundant on burns which are less than 25 years of age. For the next 100 years the ground is almost completely covered by lichens, with Stereocaulon paschale dominating the final stages of this lichen phase. After about 150 years, the abundance of S. paschale declines rapidly and is replaced by mosses and vascular plants. This change in species composition with time is accompanied by increases in the depth of organic matter and a slow development of the spruce canopy. Control of this recovery sequence by microclimatic variables is discussed. In addition, the sequence is compared to recovery sequences which have been established for other conifer regions of Canada.

ACKNOWLEDGEMENTS

I am indebted to my friend and supervisor Dr. Kenneth A. Kershaw, for his interest and guidance in the completion of this project. His generosity and understanding have made the period of study a total learning experience. I would also like to extend my sincere thanks to Mr. Herbert Deruyter and Mr. Bryce Kanbara for their enthusiastic assistance in the field under often trying conditions, Ms. Margaret Webber for the organization of field supplies and transportation, Dr. Wayne R. Rouse and Dr. Ann Oaks for their advice and valuable criticisms, and the other members of the laboratory for providing a stimulating working environment. Special thanks are due to Ms. Jocelyn Langendoen for typing the final copy.

This thesis is dedicated to my parents.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Section 1.

INTRODUCTION

The effect of fire in conifer forests of western and northern North America has been the subject of a considerable number of investigations and few who have studied any facet of fire doubt that it has been a recurring event which has influenced the structure and composition of these forests (for example, see the two symposia proceedings edited by Slaughter et al, 1972 and by Wright and Heinselman, 1973). However, in most of the early vegetation studies, many of which are contained in the comprehensive reviews of Lutz (1956) and Ahlgren and Ahlgren (1960), the recovery of vegetation following fire is not examined in relation to a reliable framework of time. The key to understanding the post-fire development of vegetation is accurate knowledge of the starting times for recovery and only recently, through the development of accurate techniques in fire chronology, has the dynamic nature and time scale of the fire factor gained recognition. Tree ring analyses, the most important of which is the fire scar method (Clements, 1910; Spurr, 1954; Frissel, 1973), allow the dates and extents of fires up to three or four hundred years in the past to be identified. In addition, an extension of the fire history to the more distant past is possible through radiocarbon analysis of charcoal in soils (Bryson et al, 1965) and the analysis of pollen and charcoal in lake sediments (Swain, 1973).

Very few generalizations can be made regarding post-fire recovery sequences of the ground vegetation for various parts of the northern conifer zone of Canada. Ahti (1959) and Bergerud (1971) recognize a five stage recovery sequence for lichen woodland in Newfoundland. Cladonia lichens and the shrubs Kalmia angustifolia L., Vaccinium angustifolium Ait. and Rhododendron canadense (L.) Torr. are the most abundant species during recovery. The final stage, dominated by Cladonia stellaris (Opiz.) Pouz. & Vezda, commences 80 years following fire. In northern Ontario, Shafi and Yarranton (1973) distinguish four phases in a post-fire recovery sequence involving primarily vascular plants and covering less than 60 years. In addition, Scotter (1964), working in northern Saskatchewan, identifies a three phase sequence of recolonization. During the first 10 post-fire years, crustose lichens and Polytrichum mosses are most abundant. The second phase is dominated by Cladonia lichens while in the final phase, starting 50 years after fire damage, both Cladonia lichens and a variety of feather mosses become the most abundant components. A comparison of these reports indicates large differences between the recovery sequences with respect to both rates of recovery and the species involved and it is clear that other factors in addition to the actual burning may complicate the primary effects of fire. Differing geomorphological, climatic and floristic characteristics of the different geographical areas are probably the most important of these factors. Thus, before generalizations applicable to widespread fire-affected regions can be made, detailed examinations of the effects of fire in many different regions are necessary in order to determine features common to all.

Johnson and Rowe (1975) have examined fire reports prepared by the Northwest Forestry Service, Department of Indian and Northern Affairs for a region of subarctic forest (104° to 112°W, 60°N to the tree line) which lies to the east of Great Slave lake in the Northwest Territories (N.W.T.). During the period 1966 to 1972, a total of 273 fires were reported. They show that fires burn about 0.9 percent of the area annually and that the majority of fires are caused by lightning. They also show that there is a seasonal pattern of fires in both time and space which may be explained by the interaction of two air masses, a cold, dry arctic air mass and a warmer, moister one from the Pacific. During spring, the incidence of fire is high in the southwest section of the study area. In the early summer, this zone of high fire incidence shifts progressively towards the treeline to the northeast, and then retreats from the treeline in late summer and autumn.

Although the findings of Johnson and Rowe (1975) indicate that fire is a normal event in the region to the east of Great Slave lake, very little is known about the recovery of vegetation following fire in this region. The region is dominated by spruce-lichen woodland which occurs on a wide range of geomorphological features (cf region B27 of Rowe, 1972). Aerial photographs available for the area show eskers, gravel-sand outwash areas, drumlins, river alluvial plains and outcrops of bedrock which are all dominated by spruce-lichen woodland displaying a patchiness that is very characteristic of fire affected vegetation. The objectives of this thesis are to study the post-fire recovery sequence of spruce-lichen woodland in this region and second, to study the patterns of vegetation within individual burns. This study involves the accurate aging of previously burned areas and the quantitative determination of the structure of the vegetation on these burns.

The primary objective, to study the recovery of spruce-lichen woodland following fire, necessitated the examination of a number of burns of different ages. Since geomorphological variation may complicate the primary effects of fire, it was essential that the examination of burns be confined to a single feature of fairly uniform structure. A large field of drumlins in the Abitau-Dunvegan lakes area was selected as a study area and offers a number of advantages. The drumlins were relatively constant in size, shape and orientation in contrast to the highly variable nature of the other features. This allowed topographic control during the examination. The large number of uniform drumlins and the high density of burns on the drumlins relative to other land forms facilitated sampling replication.

Recently, much interest has been directed towards the contention that fire is a contributing factor in the decline in numbers of barren-ground caribou in northern Canada through the destruction of slow growing lichen forage (Scotter, 1964). The drumlin field has an abundance of caribou trails with shed antlers and is within the winter foraging range for the Beverly and Kaminuriak barren-ground caribou herds (Thomas, 1969). Thus the information from this study is particularly relevant to the problem of caribou management.

Description of the Research Area

The research area (60°21'N, 106°54'W) is situated in the Abitau-Dunvegan lakes region in N.W.T. approximately 135 km northeast of Uranium City, Saskatchewan in the centre of a drumlin field which covers about 4100 km^2 (Figure 1). Based on climatic data from Uranium City during the period 1931 to 1960, the area is very dry with a total annual precipitation of only 30.4 cm and has mean January and July temperatures of -28°C and 15°C respectively (Table 1).

The drumlins (Figure 2) represent the most outstanding topographic feature in the area although eskers (Figure 3), rocky outcrops, boulder fields (Figure 4), small streams and numerous long, narrow lakes are also present. The elongate drumlins are generally uniform in size and shape. They are

Figure 1. Location of the Abitau Dunvegan lakes research area in N.W.T. The inset, which is 10 km by 15 km, shows the precise location of base camp ($60^{\circ}21'N$, 106° $54'W$).

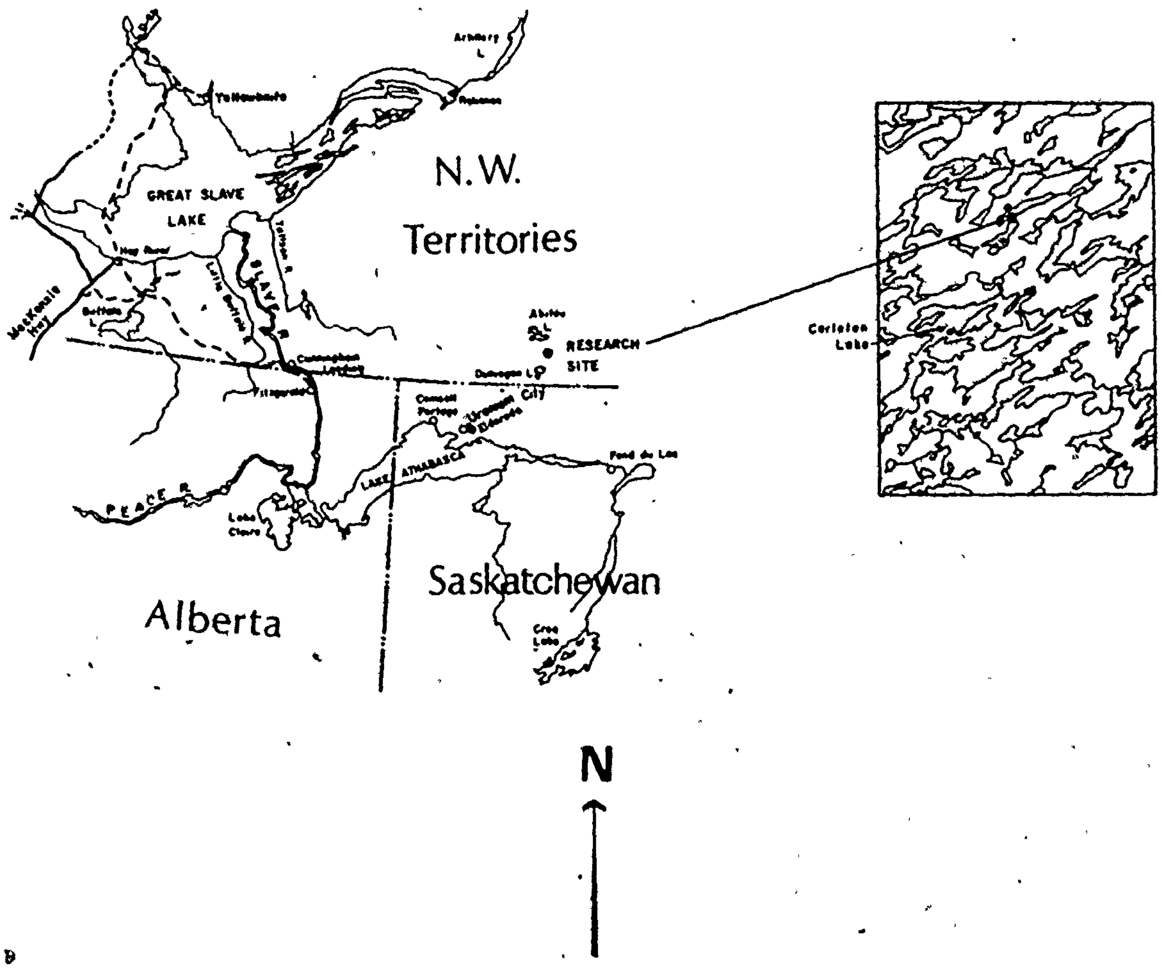

N.W.
Territories
GREAT SLAVE
LAKE
RESEARCH
SITE
Carleton
Lake
LAKE ATHABASCA
PEACE R.
Saskatchewan
Alberta
N

Table 1. Climatic data for Uranium City, Sask. based on the period 1931 to 1960 (courtesy of W.R. Rouse, Dept. of Geography, McMaster University)

Month	Mean Daily Temperature (°C)	Mean Daily Maximum Temp. (°C)	Mean Daily Minimum Temp. (°C)	Mean Monthly Precipitation (cm)	Mean Daily Global Solar Radiation (cal cm^{-2} day^{-1})
J	-27.8	-22.5	-32.5	1.0	40
F	-24.4	-20.0	-30.0	1.0	125
M	-16.1	-12.5	-22.5	1.0	270
A	-5.0	-1.1	-12.5	1.0	450
M	4.4	10.0	-1.9	2.5	600
J	10.0	15.6	5.0	3.0	550
J	15.0	20.0	8.9	5.1	510
A	13.3	18.3	6.7	4.1	400
S	6.1	10.0	1.1	4.3	220
O	-2.5	0.0	-6.4	2.8	115
N	-11.9	-12.5	-17.5	2.3	40
D	-22.5	-18.9	-27.5	2.3	25
Annual	-5.0 mean			30.4 total	278 mean

Figure 2. Oblique aerial view of Dunvegan lake showing a portion of the drumlin field.

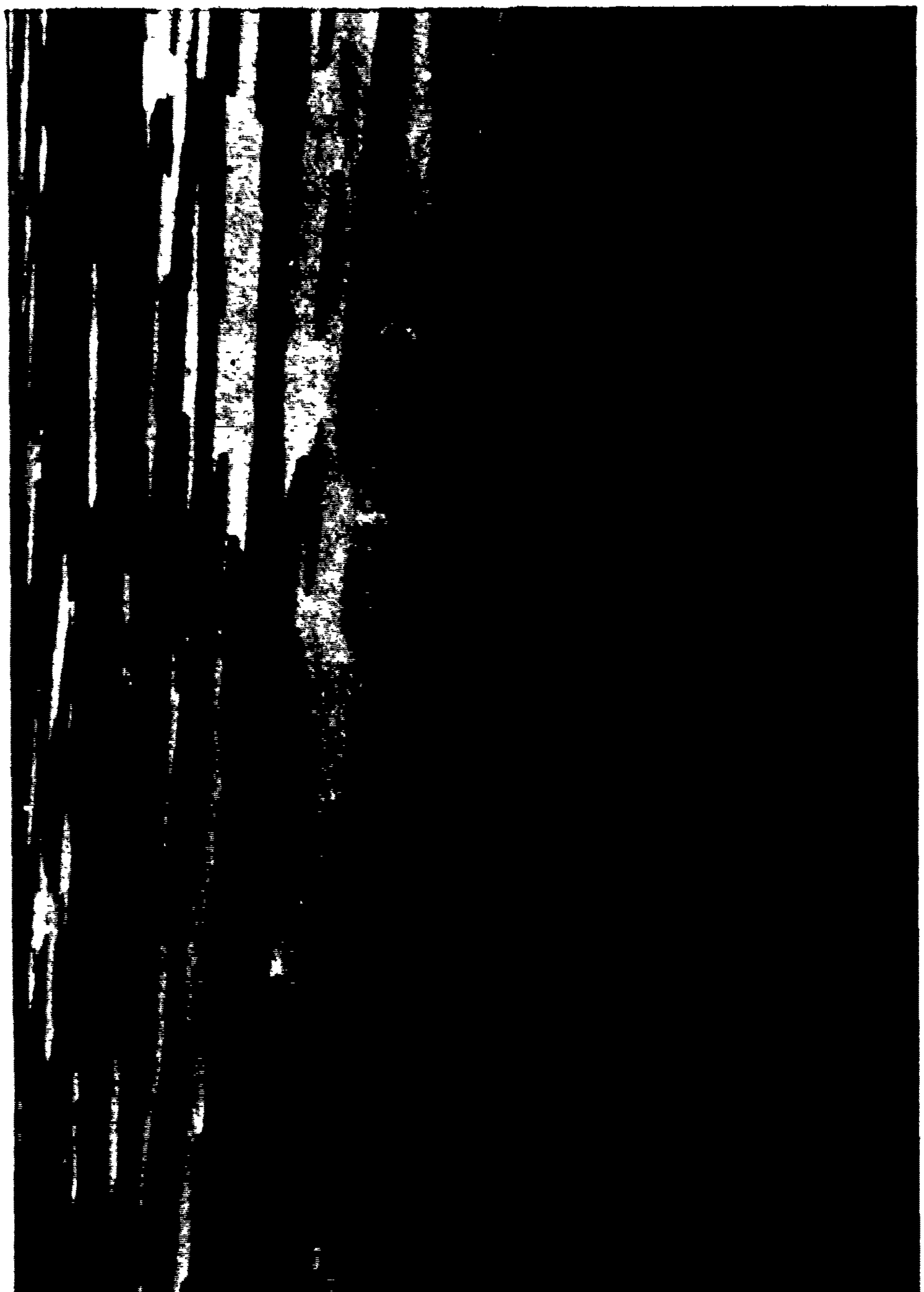


Figure 3. Oblique aerial view of a typical esker.

Figure 4. Ground level view of a boulder field at the edge of a small lake.

approximately 3 km long, 0.5 km wide and rise steeply to a height of 30 m from flat, wet margins (Figure 5). The substrate of the drumlins, a sand and gravel mixture, also appears to be uniform for the drumlins in the area. Boulder-filled sinkholes are present on many of the drumlin crests. The pattern of water drainage and the orientation of the drumlins and lakes indicate that movement of glacial ice was predominantly in a northeast to southwest direction.

Black spruce (Picea mariana (Mill.) BSP.) is the most important component of the tree canopy on the drumlins. The only other components of the tree canopy of importance are Betula papyrifera Marsh., Alnus rugosa (Du Roi) Spreng. and Pinus banksiana Lamb. The latter, although thinly scattered on most drumlins, can be found in pure stands on some drumlins to the southwest of base camp and on eskers. Betula papyrifera is most abundant on recent burns. In contrast, the wet margins surrounding the drumlins are occupied by dense stands of stunted Picea mariana with scattered individuals of Betula papyrifera and Larix laricina (Du Roi) K. Koch.

The ground vegetation on the drumlins is dominated by lichens. The most important components of the lichen mats, which rarely exceed 4 or 5 cm in depth, are Cladonia stellaris (Opiz.) Pouz. & Vezda and Stereocaulon paschale (L.) Hoffm. These mats are mixed with varying amounts of moss and shrub species. The most important of these is the vascular plant Vaccinium vitis-idaea L. The flora of the wet margins surrounding

Figure 5. Oblique aerial view of a typical drumlin.

the drumlins is much richer in vascular species and is dominated by Ledum groenlandicum Oeder, Myrica gale L., Chamaedaphne calyculata (L.) Moench, Empetrum nigrum L., Vaccinium oxycoccus L. and Rubus chamaemorus L. together with carpets of Sphagnum spp.

Although the dry warm climate and extended periods of daylight during summer months are conducive to the drying of all vegetated surfaces, the influence of fire is most evident on the drumlins. The presence of charred stumps, pieces of charcoal scattered on the ground, fire scarred trees and the high density of various size patches of woodland (Figure 6) whose irregular boundaries are often distinct due to differences in tree density and ground layer vegetation (Figures 7 and 8), all indicate that the drumlins are very fire susceptible. The high fire susceptibility on the drumlins is probably due to the efficient drainage of the sand-gravel substrate and their steep slopes. In addition, the lichen dominated surface cover is extremely flammable when dry. Only rarely does fire appear to affect the low wet margins surrounding the drumlins.

Figure 6. A small section of an aerial photograph (3 km by 1.5 km) showing the high density of various size patches of lichen woodland, which gives the drumlins a mottled appearance. Lakes are shown in black.

Figure 7. The size and shape of this burn is fairly distinct from the air due to differences in tree density and ground vegetation. The perimeter of the burn, which is about 2 hectares in size, is indicated with arrows.

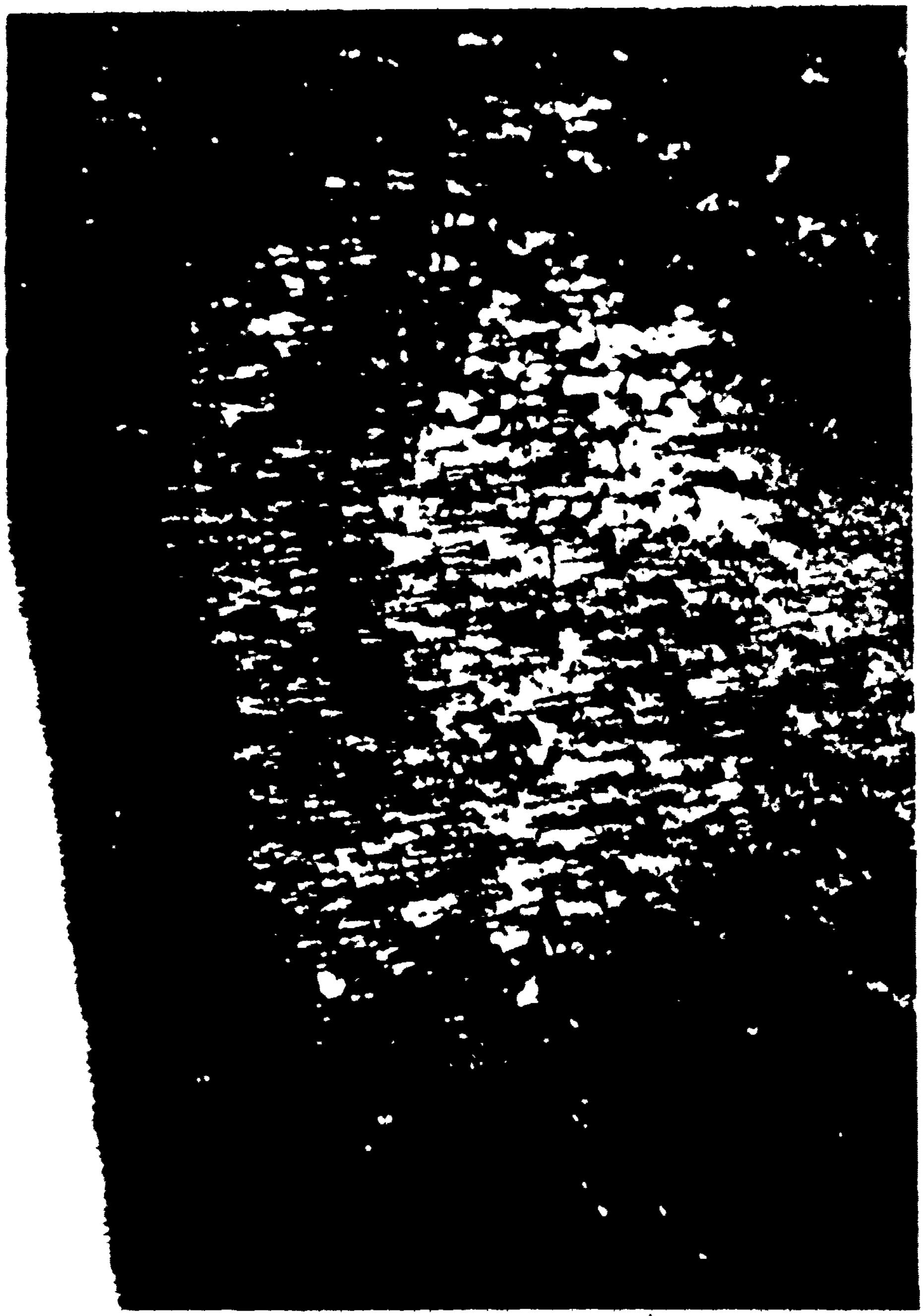


Figure 8. Oblique aerial view of a recently burned area. The burn, which is about 5 hectare's in size, is indicated by an arrow.

Section 2.

METHODS

(2.1) Aging of burns

Numerous burns were chosen by examining air photo coverage available for the study area and from low altitude examinations of burned areas from bush planes.

The fire scar method (Clements, 1910; Spurr 1954; Frissel, 1973) is the most accurate of the tree ring analyses for dating burns. Fire scars (Figure 9) may form on tree trunks whenever the bark is heated sufficiently to kill some but not all of the cork cambium. If the tree recovers, the surviving cambium lays down annual rings which gradually overgrow the scar thus allowing an estimate of the time since fire damage. As all trees are usually killed through crown damage in areas where the fire is intense (Van Wagner, 1970), scarred trees are most often situated on the perimeter of burns and on the edges of stringers, which are unburned patches within burns, where creeping ground fires are more probable (Figure 10).

The method is not without problems. Some low intensity fires may not scar any trees. Areas such as these were not examined if possible. In addition, other agents than fire can cause scarring, such as bears, rodents, freeze damage and windthrow of neighbouring individuals, and some of these scars can closely mimic the effects of burning. To eliminate the problem of distinguishing fire damage from these other agents,

Figure 9. A typical fire scar on the trunk of a black spruce tree.

Figure 10. Oblique aerial view (200m by 75m) at the edge of a burn showing stringers within the burned area. The edge of the burn is indicated with large arrows while the main stringers are indicated with smaller arrows.

several criteria which are characteristic of fire scars were used (Rowe et al, 1973-74). A vertically elongate patch of exposed wood positioned low on the trunk, charcoal on the scarred wood (Figure 11), an increase in annual ring width immediately following the fire (Figure 12) and replicate scars on the same side of several trees, all indicated fire damage.

For each burn, as many scarred trees as possible were located and cut down so that cross-sections of the annual ring development could be examined. The number of years since fire damage was determined for each section by counting the number of annual rings from the scarred ring to the bark. Occasionally, a cross-section showed more than one scar or the ages of the scars for a single burn were divided into more than one age group. Both phenomena indicate a recurrence of fire. For each burn, the time since the most recent fire was estimated from an average of the elements of the youngest age group.

Fire scars were absent for four burns. It was obvious that one of these areas was recently burned. Since shrubs such as _Salix_ spp. re-establish themselves rapidly from the basal sections of stems and underground roots (Lutz, 1956; Smith and Sparling, 1966; Tucker and Jarvis, 1967), the age of this burn was estimated from several age determinations of _Salix_ spp. which were obtained from annual ring counts of cross-sectioned stems. In the other three areas, the organic layer was up to 15 cm thick, mosses and vascular plants were abundant, and the

Figure 11. Cross-section through a fire scar. Note the charcoal on the scarred wood.

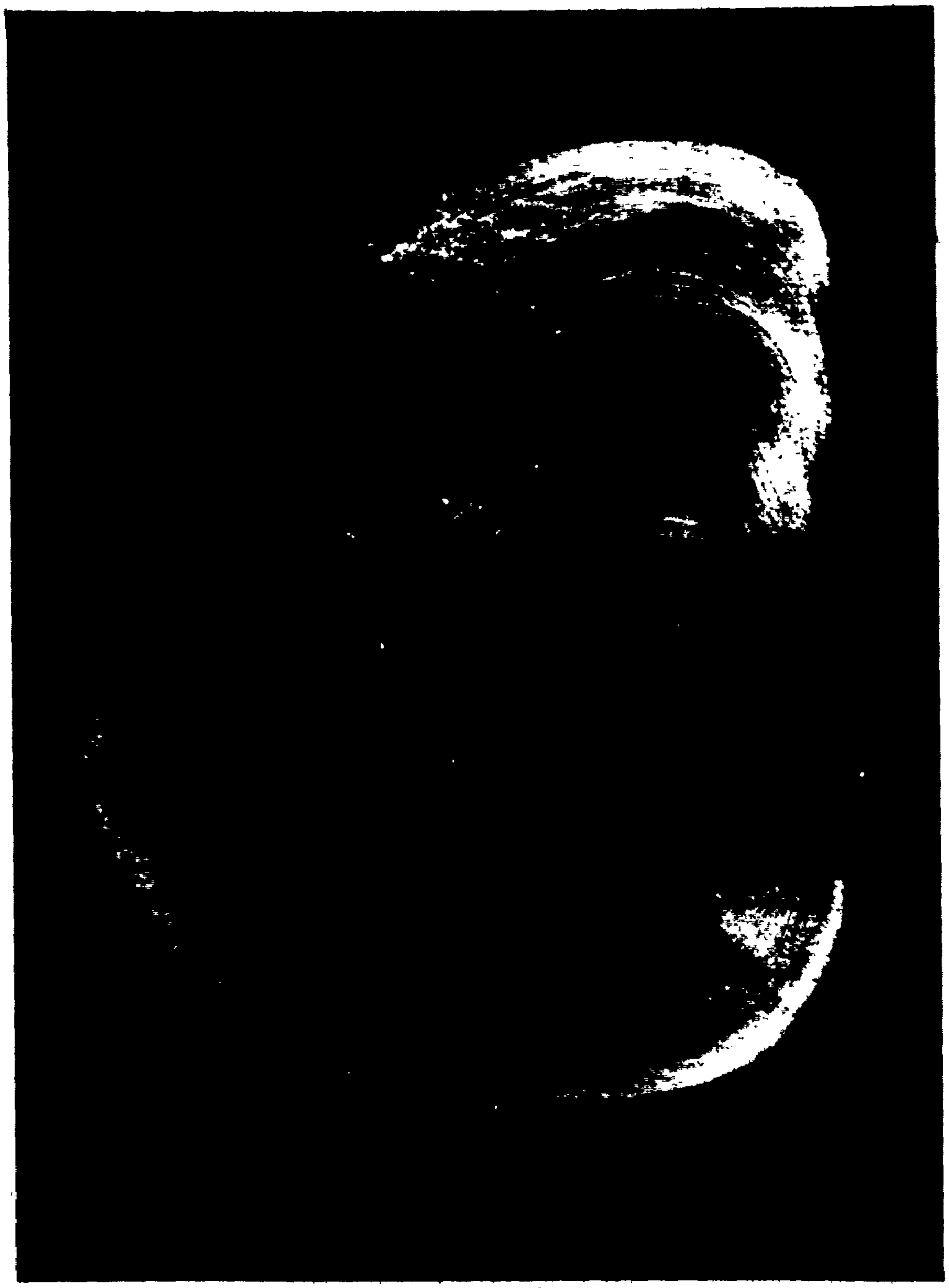


Figure 12. Close up of a cross-sectioned scar showing an increase in annual ring width immediately following fire damage.

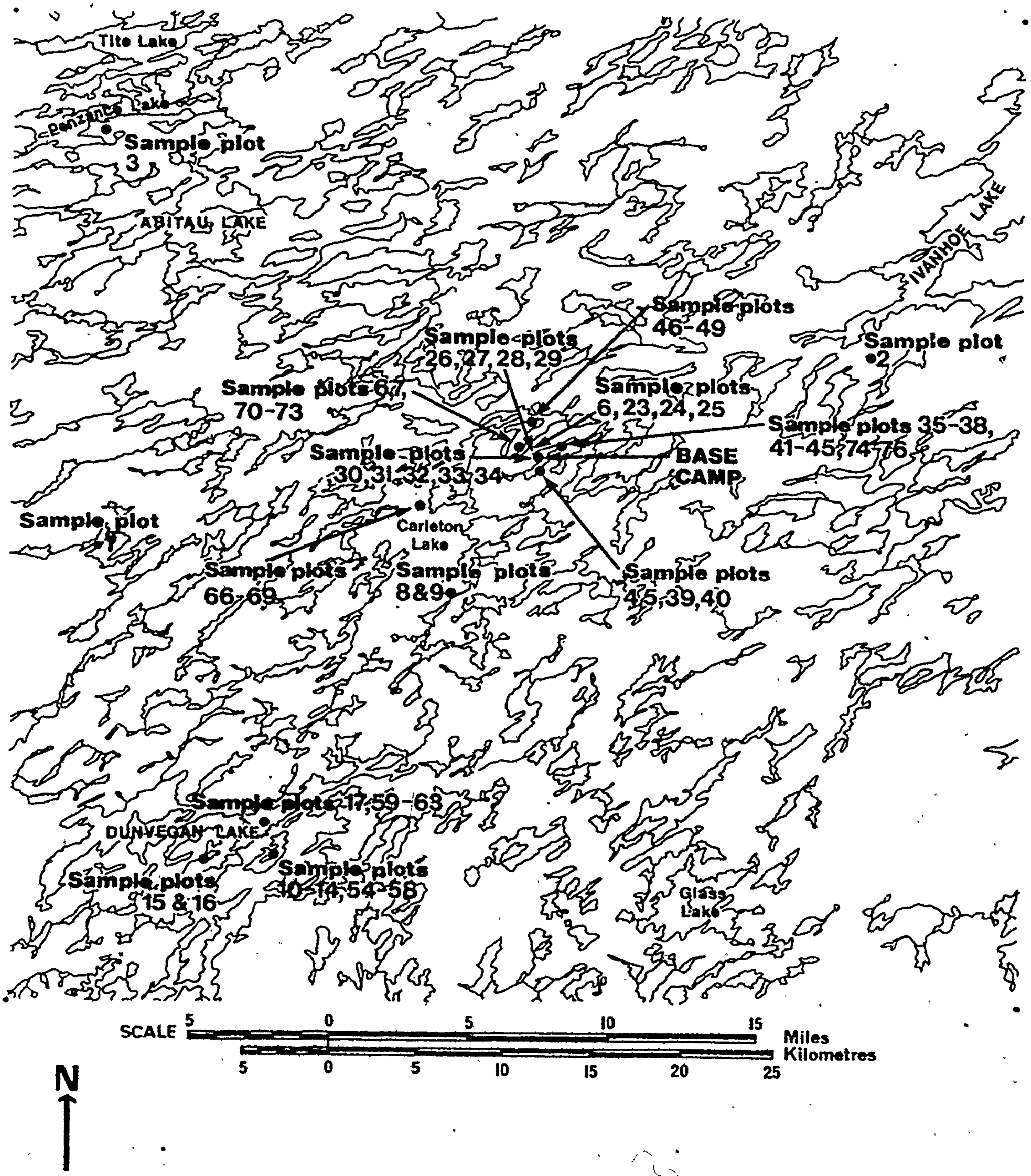
trees were comparative large and dense. These characteristics suggested that the absence of scarred trees was due to a long fire-free period. To determine the minimum possible age of these burns, fifteen of the oldest looking trees were aged from annual ring counts of core samples obtained using an increment borer, and an estimate was made from the age of the oldest tree. This approach is not as accurate as the fire scar method, since the length of time required for the establishment of trees may be variable. In addition, the approach is inaccurate when all trees are not killed by the last fire.

After the burns were aged, nineteen were chosen for examination. This included only burns with reliable age estimates, and gave a wide range of different age burns from a large number of widely distributed drumlins. Thus, the results are characteristic of the Abitau-Dunvegan lakes area as a whole.

(2.2) Sampling procedure

To sample the ground vegetation, seventy 10 m by 10 m sites were distributed over the 19 burns (Figure 13). All burns could not be equally replicated due to the small size of some of the burns. Replicate sample sites were positioned well within the perimeter of each burn and away from stringers to eliminate any burn edge effects. To be able to account for differences in the ground layer vegetation due to topography,

Figure 13. The location of sample sites (plots) in the Abitau Dunvegan lakes drumlin field.


Tite Lake
Penzance Lake
Sample plot 3
ABITAU LAKE
IVANHOE LAKE
Sample plots 46-49
Sample plots 26,27,28,29
Sample plot •2
Sample plots 67, 70-73
Sample plots 6,23,24,25
Sample plots 35-38, 41-45,74-76
Sample plots 30,31,32,33,34
BASE CAMP
Sample plot 1
Carleton Lake
Sample plots 66-69
Sample plots 8&9
Sample plots 4,5,39,40
Sample plots 17,59-63
DUNVEGAN LAKE
Sample plots 15 & 16
Sample plots 10-14,54-58
Glass Lake
SCALE
5 0 5 10 15 Miles
5 0 5 10 15 20 25 Kilometres
N

the slopes of sites were measured using an inclinometer. Whenever possible, replicate sites were placed on the crest, northwest and southeast facing slopes of the drumlins. The total number of trees were recorded for each site as indication of tree canopy development. Within each of the seventy 10 m by 10 m sites, twenty replicate 1 m by 1 m quadrats were randomly positioned using pairs of random numbers as coordinates. Percent cover is an estimation of the area covered by a given species (Kershaw, 1964). It is more sensitive to variation in species abundances than local frequency and has been used in low, prostrate, lichen dominated vegetation where individuals are impossible to define with satisfactory results (Larson and Kershaw, 1974). The percent cover of each species within each quadrat was estimated from 5 random drops of a pin frame containing 10 point samples each. At the same time, the depth of the organic layer, measured from the bottom of the living portion of the lichens to the underlying sand and gravel surface, was measured from an exposed profile at the centre of each quadrat. The distance from the centre of each quadrat to the nearest tree and the circumference of its trunk at ground level were measured. In addition, the age of the nearest tree was determined for each quadrat from an annual ring count of a core sample obtained using an increment borer. All quadrat data were averaged to give mean values for each site. This allowed analysis of the data at the 1 m by 1 m quadrat scale as well as the 10 m by 10 m site scale.

(2.3) Data analyses

The main method of data analysis used was principal component analysis, an ordination technique which has been shown to be efficient in summarizing large bodies of data. Its applicability as an ecological tool has been illustrated by a number of workers (Gittins, 1965; Orloci, 1967; Kershaw, 1968; Neal and Kershaw, 1973a,b; Kershaw and Rouse, 1973). The particular analysis used operates on a plot by plot variance-covariance matrix derived from the percentage cover values of the species and ordinates sample areas. The results of the analysis are presented graphically with each sample area represented by a point and having coordinates on three orthogonal axes representing linear uncorrelated components in the solution of the matrix (Kershaw and Shepard, 1972). The distance between any two points is related to the similarity in species composition of a pair of sample areas. The first axis accounts for the greatest proportion of total variance in the data, with successive axes accounting for decreasing amounts of variance. These ordination diagrams are overlayed with environmental data or species abundances and can be fitted with contour lines to emphasize any relationships present (Austin and Orloci, 1966).

To examine variation in the species composition of the ground layer vegetation among burns, principal component analysis was carried out using species cover values for each of the seventy 10 m by 10 m sites and values of burn age, depth of the organic layer and tree canopy characteristics, as well as species abundances, were overlayed. The resulting ordination showed that a large proportion of the variation along the second axis was attributable to six sites from the youngest burns. As this may have been obscuring some relationships present within the sites from the older burns, the data from the six sites were removed and the analysis was repeated using mean species cover values for each of the remaining sixty four sites. Ordination diagrams were hand fitted with contour lines where relationships were visually apparent.

To examine variation within burned areas which were 23, 49, 67, 78, 92, 138, 150, >190 and 215 years of age, the analysis was repeated nine additional times using cover values for each of eighty 1 m by 1 m quadrats every time. Again, overlays of burn age, depth of the organic layer and tree canopy characteristics were made. However, they did not reveal any apparent relationships for any of the nine ordinations. Thus further analysis at the quadrat scale was not made.

Throughout the principal component analyses, burn age, depth of the organic layer and tree canopy characteristics were all treated as independent variables. The relationships between pairs of these parameters were examined through scatter diagrams using values for each site. This was followed by linear regression analysis and the calculation of correlation coefficients or curvilinear regression analysis and the calculation of coefficients of determination.

The relationships between site mean values of the independent variables and cover values of six of the most abundant species were examined through scatter diagrams. This was again followed by linear regression analysis and the calculation of correlation coefficients or curvilinear regression analysis and the calculation of coefficients of determination. In addition, correlation coefficients were calculated between the cover values of the six most abundant species and all other species to examine species associations.

Section 3.

RESULTS

(3.1) Burn ages

The ages of the fifteen burns estimated from fire scars and the distribution of the 58 sample sites over these burns are presented in Table 2a. For each burn the age estimate was made from a mean of at least 4 replicate cross-sectioned scars. The standard errors of the means do not exceed ± 2.3 years.

The distribution of 13 sample sites over the four burns for which fire scarred trees were absent and their corresponding ages are presented in Table 2b. The very recently burned area was estimated at 3 years old from age determinations of *Salix* spp. growing on the burned site. In addition, the ages of the three old burns, which represent minimum possible times since fire damage, and the tree age determinations from which the estimates were made, are also presented.

A number of general features are evident from Table 2. First, the number of 10 m^2 sample sites per burn ranges from 1 to 6 and reflects the variation in size of the burns. Second, a wide range of burn ages, from 3 to over 200 years is present in the sample. Third, there is a high proportion of burns less than 100 years of age.

(3.2) Independent variables

The number of trees is correlated with age of the

Table 2. Results of Burn age determinations

a) based on fire scars

No. of Sample Sites	Time Since Fire Damage For Cross-sectioned Scars (yrs)	Estimated Age of Burn (yrs)	Standard Error of Mean
1	12 12 11 12 12 12 12	12	0.1
4	25 22 23 24 23 23 23 23 23	23	0.3
6	30 33 32 31 32 32	32	0.4
3	40 43 45 42 38	42	1.2
4	44 45 48 45 42 44	45	0.8
2	45 47 47 47 47 48	47	0.4
5	52 48 50 48 49 49	49	0.6
4	69 67 67 67 67	67	0.4
2	71 70 72 73 72	72	0.5
4	74 83 83 81 73 76	78	1.9
6	93 89 92 92 93	92	0.7
3	98 98 94 98 99 98	97	0.7
4	139 138 134 139	138	1.2
5	140 148 150 150 155 155	150	2.3
4	219 215 213 215 217 214 212 218	215	0.9

b) based on tree ages

No. of Sample Sites	Ages of Oldest Trees -Scarred Trees Absent (yrs)	Estimated Minimum Age of Burn (yrs)
5	106 111 101 100 112 115 113 102 110 111 103 116 104 102 104	116
3	178 163 164 173 119 161 179 187 168 152 178 163 182 186 188	188
4	164 187 184 171 166 168 182 184 149 174 177 190 161 186 185	190
1	3*	3

* from age determinations of <u>Salix</u> spp.

burn as shown in Figure 14. The relationship appears to be linear and although there is a considerable scatter of points, the regression and correlation coefficients shown in Table 3 indicate that the relationship is statistically significant. The relationship between quadrat-to-tree distance and number of trees is shown in Figure 15. These two variables show an inverse curvilinear relationship. The regression coefficients and coefficient of determination presented in Table 3 indicate that this relationship is also statistically significant. Quadrat-to-tree distance shows a similar inverse curvilinear relationship with burn age (Figure 16, Table 3). These results indicate that the density of trees on the burns increases with time following a fire.

Depth of the organic layer shows a linear relationship with age of the burn (Figure 17, Table 3). This increase in the organic layer with increasing burn age is also related to the size and density of trees (Table 3). However, it is most strongly related to tree density and Figure 18 shows the nature of the relationship. Again, the plots show a substantial scatter of points.

Significant relationships were not indicated

Figure 14. Scatter diagram - number of trees per site vs burn age. Axes are on linear scales.

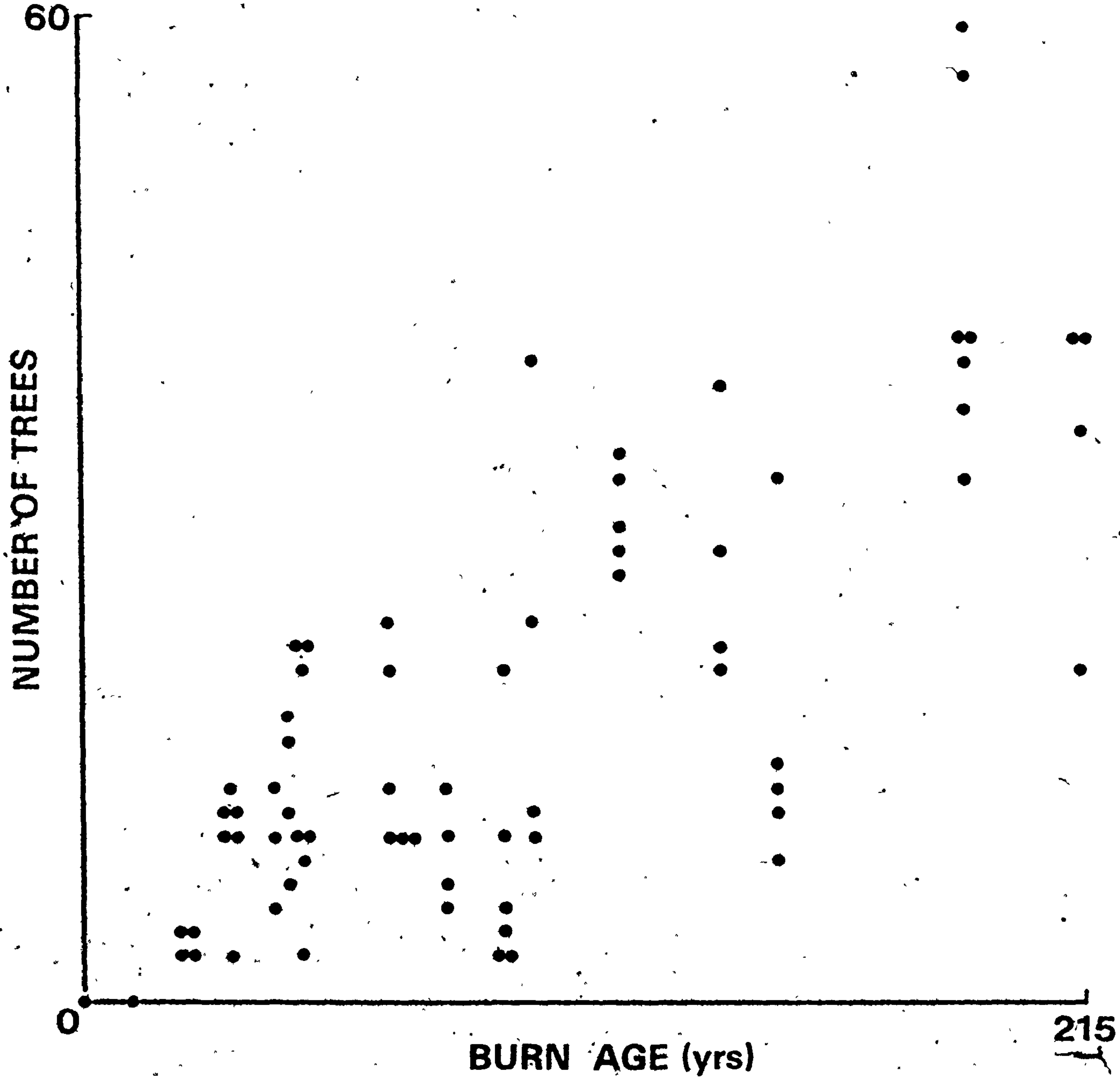

60
NUMBER OF TREES
0
215
BURN AGE (yrs)

Table 3. Regression results for site values of independent variables.

a) Linear regression (y = a + bx) and correlation (r) coefficients which are significant at the P = .001 level.

y variable	x variable	a	b	r
depth of organic layer (cm)	burn age (yr)	0.66	0.03	0.68
no. tree/plot	burn age (yr)	2.35	0.17	0.75
depth of organic layer (cm)	no. trees	0.61	0.17	0.81
depth of organic layer (cm)	trunk circumference (cm)	7.06	0.20	0.56
depth of organic layer (cm)	quadrat-tree distance (cm)	20.65	-1.78	-0.63

b) Curvilinear regression ($y=a+bx+cx^2$) coefficients which are significant at the P = .001 level. Coefficients of determination (r^2) are also shown.

y variable	x variable	a	b	c	r^2
quadrat-to-tree distance (cm)	no. trees	261.92	-8.76	-0.10	0.61
quadrat-to-tree distance (cm)	burn age (yr)	212.04	-0.69	0.00030	0.32

Figure 15. Scatter diagram - site values of quadrat-to-tree distance vs number of trees. Axes are on linear scales.

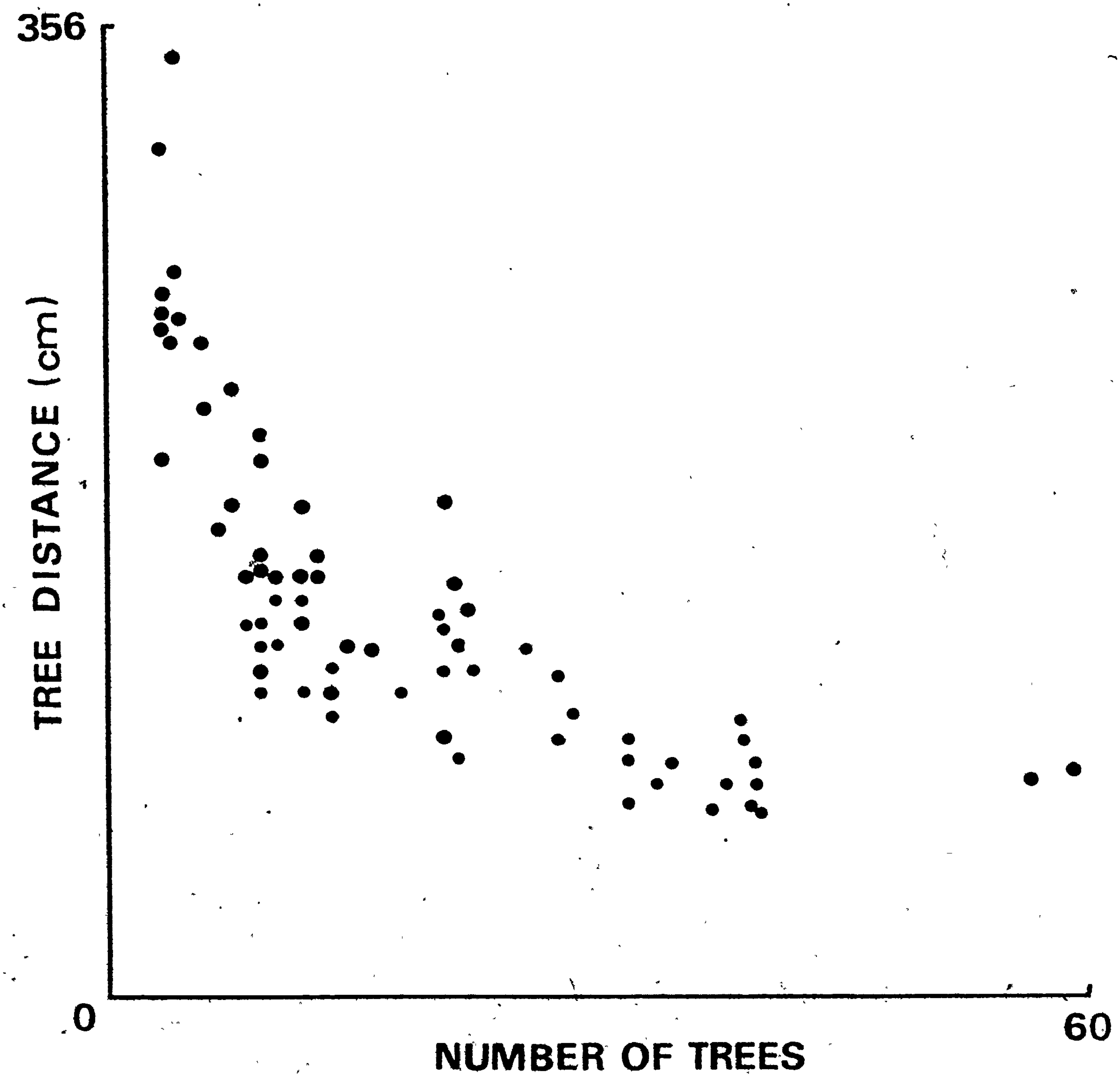

356
TREE DISTANCE (cm)
0
60
NUMBER OF TREES

Figure 16. Scatter diagram - site values of quadrat-to-tree distance vs burn age. Axes are on linear scales.

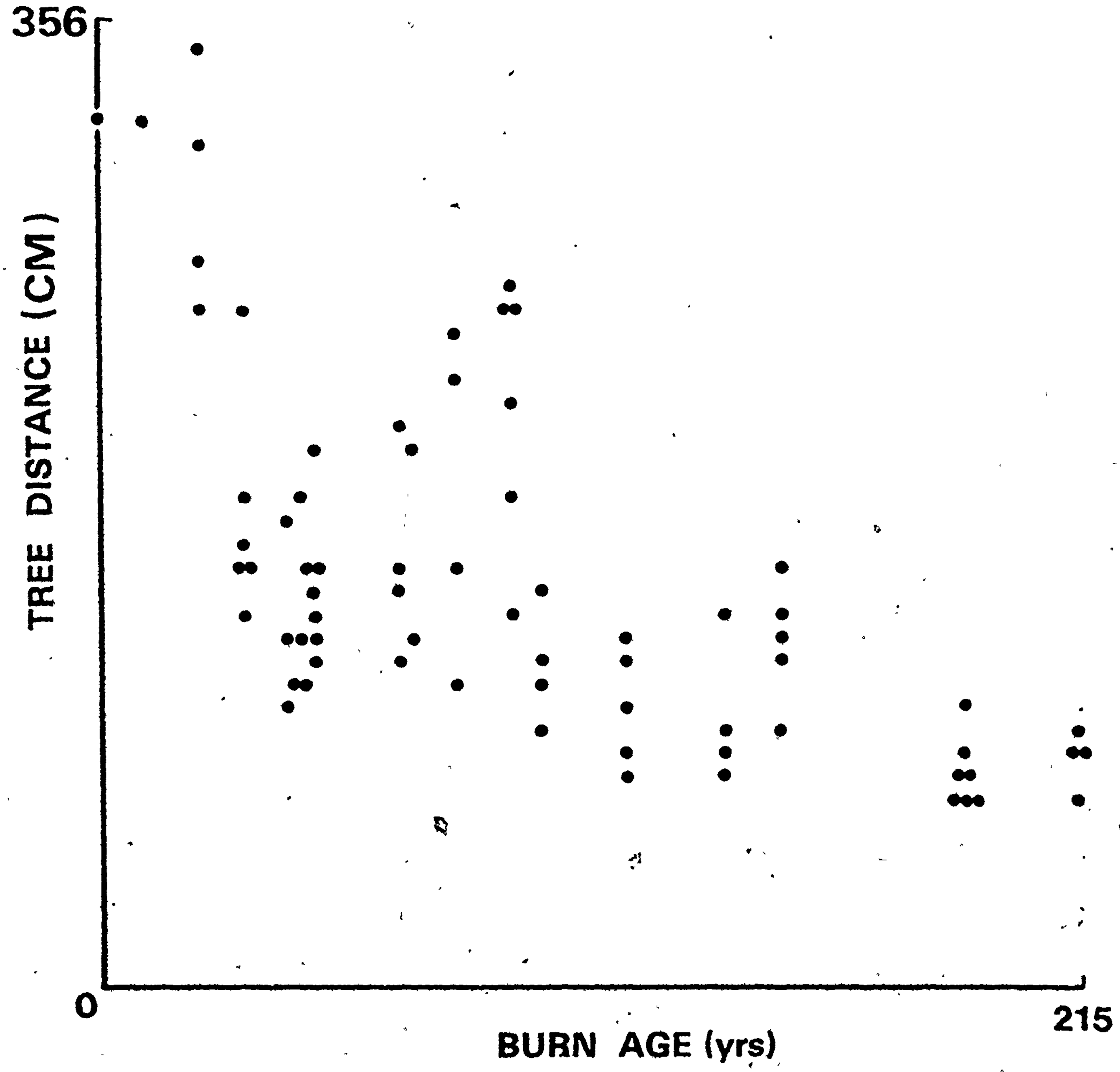
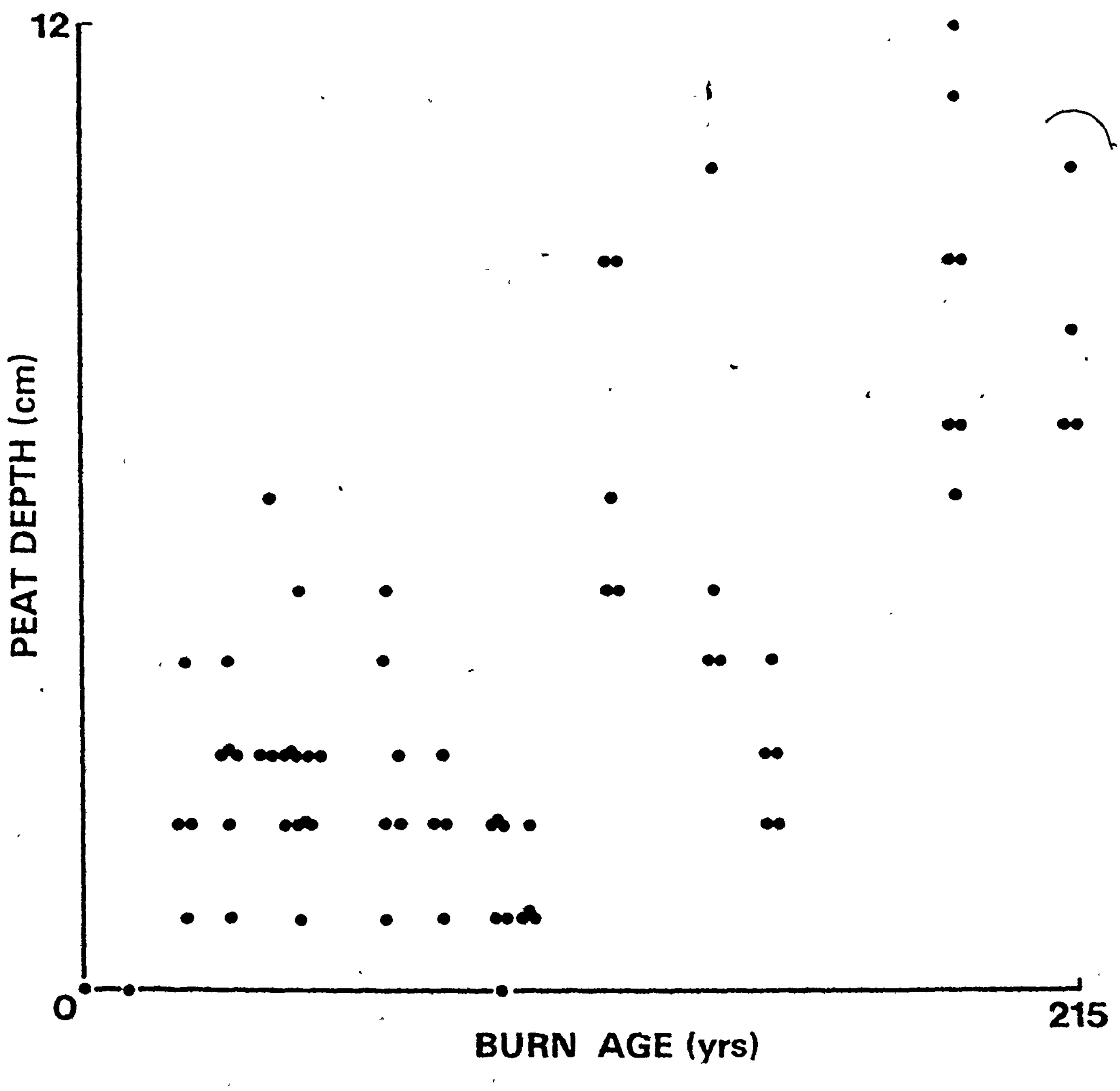

356
TREE DISTANCE (CM)
0
215
BURN AGE (yrs)

Figure 17. Scatter diagram - site values of depth of organic layer (peat) vs burn age. Axes are on linear scales.


12
PEAT DEPTH (cm)
0
215
BURN AGE (yrs)

between slope of the site and tree age, tree size, tree density or depth of the organic layer.

(3.3) Ground vegetation

(3.3.1) Species Abundances

A list of species encountered during the sampling program and their abundances are presented in Table 4. The list includes 22 species of lichens, 8 species of mosses, liverworts and lycopods and 6 species of vascular plants. Two additional categories, bare ground and litter, account for any unvegetated surfaces.

The ground surface is dominated by lichens, primarily Stereocaulon paschale and Cladonia stellaris which together make up almost 40 percent of the vegetation cover. The only other species of major abundance is the vascular plant Vaccinium vitis-idaea with 15 percent cover. Although cover of the ground is close to complete with only about 3 percent of the ground being bare, litter accounts for approximately 20 percent of the total percent cover.

(3.3.2) Ordination Results

In both ordinations of 10 m^2 sites, greater than 65 percent of the total variance in the data was accounted for

Figure 18. Scatter diagram - site values of depth of organic layer (peat) vs number of trees. Axes are on linear scales.

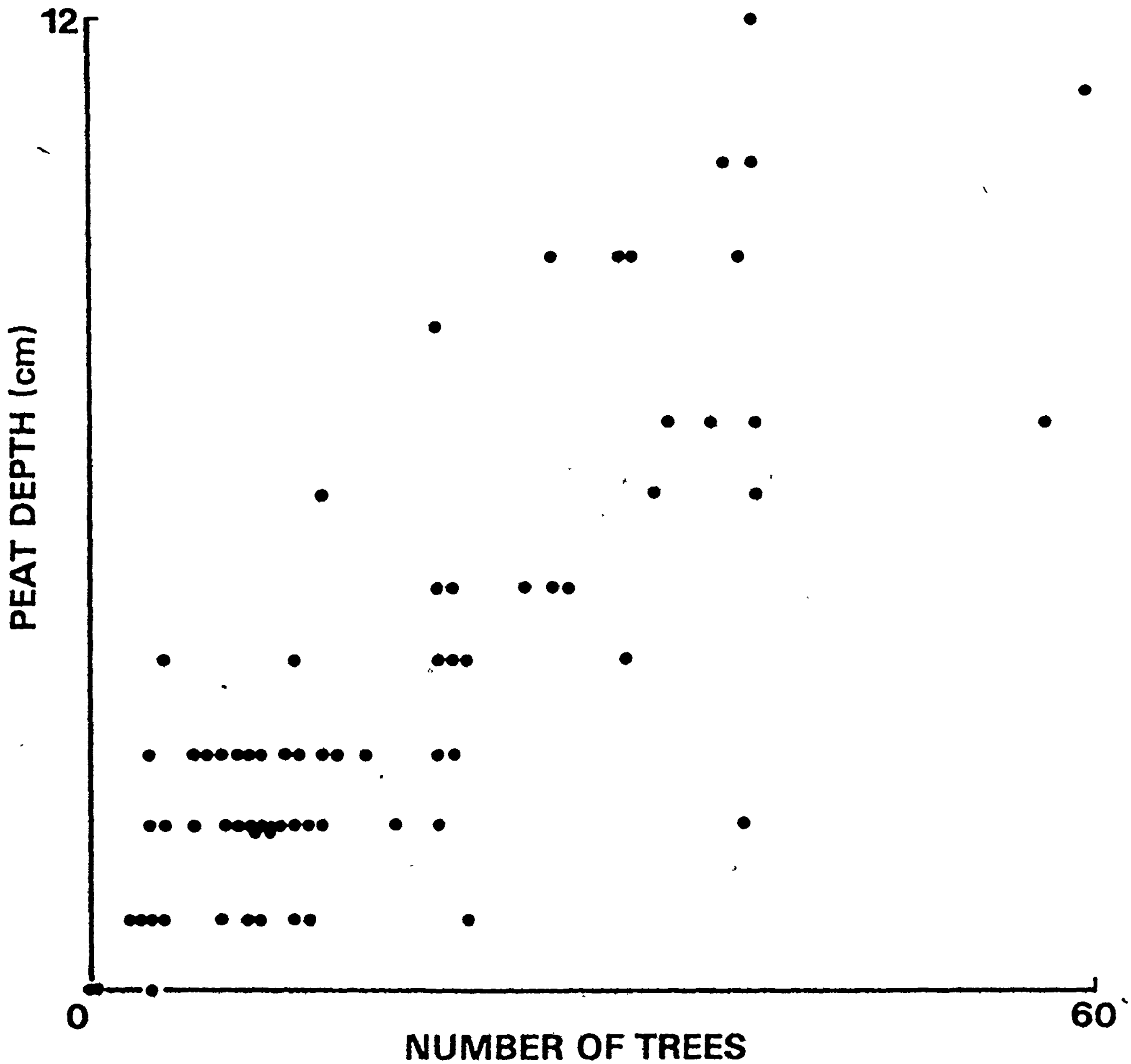

12
PEAT DEPTH (cm)
0
60
NUMBER OF TREES

Table 4. Species abundances averaged from percent cover estimates in 70 sample sites.

Species	site mean % cover value	standard deviation
a) lichens		
Cladonia stellaris (Opiz.) Pouz. & Vezda	17.31	9.78
C. uncialis (L.) Wigg.	8.48	5.34
C. amaurocraea (Flörke) Schaer	4.17	3.80
C. gracilis (L.) Willd.	2.15	2.98
C. mitis (Sandst.)Hale & W. Culb.	0.73	2.09
C. botrytes (Hag.) Willd.	0.10	0.33
C. gonecha (Ach.) Asah	0.83	0.82
C. cristatella Tuck.	0.11	0.35
C. cornuta (L.) Hoffm.	1.46	1.43
C. coccifera (L.) Willd.	0.78	0.71
C. macrophylla (Schaer.) Stenham.	0.39	0.43
C. subulata (L.) Wigg.	0.04	0.10
C. crispata (Ach.) Flot.	1.50	1.71
C. rangiferina (L.) Harm.	1.01	1.77
Cetraria islandica (L.) Ach.	1.54	1.37
C. nivalis (L.) Ach.	9.16	9.37
Stereocaulon paschale (L.) Hoffm.	22.03	24.13
Peltigera aphthosa (L.) Willd.	0.08	0.22
P. scabrosa Th. Fr.	1.06	1.38
Nephroma arcticum (L.) Torss.	0.10	0.36
Lecidea uliginosa (Schrad.) Ach.	0.85	1.94
Lecidea granulosa (Ehrh.) Ach.	1.40	2.80
b) mosses, leverworts and lycopods		
Ptilium crista-castrensis (Hedw.) De Not.	0.26	1.22
Polytrichum piliferum Hedw.	4.13	13.62
Polytrichum juniperinum Hedw.	0.87	1.93
Dicranum spp.	0.46	1.06
Hylacomium splendens (Hedw.) BSG	0.31	0.72
Pleurozium schreberi (Brid.) Mitt.	1.26	2.79
Ptilidium ciliare (L.) Hampe	4.40	6.02
Lycopodium spp.	0.09	0.36
c) vascular plants		
Arctostaphalos uva ursi (L.) Spreng.	0.08	0.35
Ledum groenlandicum Oeder	2.77	2.85
Vaccinium vitis-idaea L.	15.26	7.19
Vaccinium uliginosum L.	1.85	2.57
Vaccinium myrtilloides Michx.	0.58	1.10
Geocaulon lividum (Richards.) Fern.	0.98	1.34
d) remainder		
litter	19.75	10.32
bare ground	3.39	11.32

by the first three axes (Table 5). Both ordinations indicate that the species composition of the ground vegetation is strongly related to burn age. The ordination using cover data for each of the seventy sites with burn age overlayed (Figure 19), shows a distinct separation of the 3, 12 and 23 year old burns along axis 2, which extracts 19 percent of the total variance. This distinct separation is indicative of the dissimilarity in species composition of the three very recently burned areas from the older burns in the sample. In the same way, the ordination with the 3, 12 and 23 year old burns removed shows a trend with age of the burn again along axis 2 (Figure 20), which extracts 18 percent of the total variance. In this case, the hand fitted contour lines are more tenuous indicating that there is considerable variability in the relationship. However, the relationships of burn age with tree canopy characteristics and with depth of the organic layer shown by the regressions are not indicated by overlaying the values of these parameters on either ordination. In addition, measurements of slope and aspect are not related to any of the axes.

Overlays of species abundances on both ordinations of 10 m^2 sites express the trend in species composition in terms of individual species. Six of the more abundant

Table 5. Percent of total variance extracted by the first three axes for ordinations of sample sites.

No. of Sites Ordinated	Axis	Percent of Total Variance
70	1	46.1
	2	19.1
	3	12.4
64	1	61.0
	2	17.8
	3	7.1

Figure 19. Ordination of the site data on the first three component axes with burn age overlayed. Classes: I<23 years; II>23 years.

ORDINATION OF BURN AGES

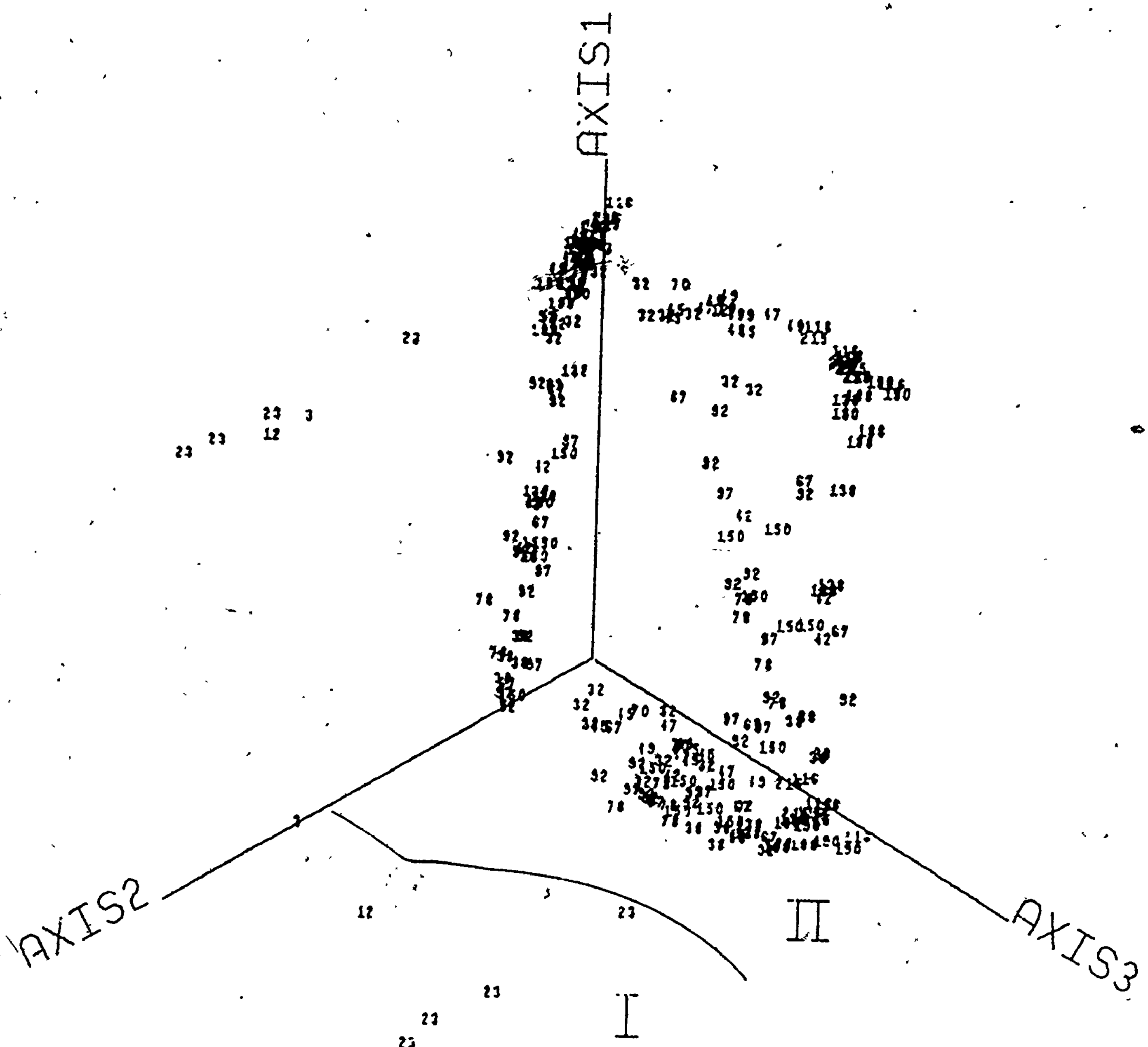
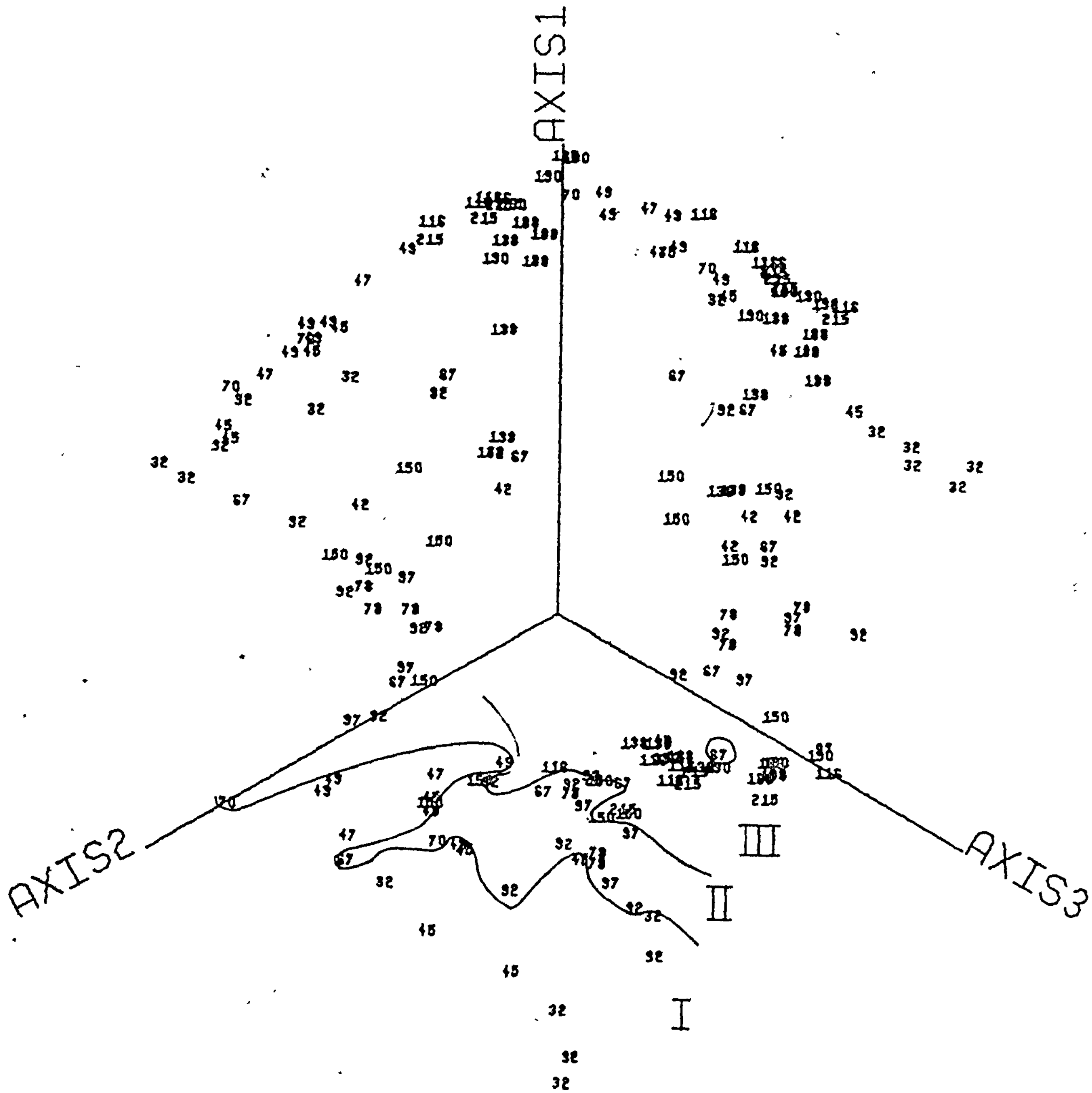


Figure 20. Ordination of sites greater than 23 years of age on the first three component axes with burn age overlayed. Classes: I<50 years; II 51-100 years; III >100 years.

ORDINATION OF BURNS > 23 YEARS OF AGE



species illustrate the trend most effectively. Polytrichum piliferum is most abundant on the 12 and 23 year old burns where it comprises up to 77 percent of the vegetation cover but is present only in very low levels on burns of other ages (Figure 21). Cetraria nivalis, showing a trend between axes 2 and 3 (Figure 22), is only partly related to burn age and is most abundant on intermediate age burns. Cladonia stellaris is most abundant on intermediate age burns (Figure 23) while Stereocaulon paschale attains maximum abundance on intermediate to older age burns (Figure 24). Vaccinium vitis-idaea and Ptilidium ciliare increase in abundance with increasing burn age and become most abundant on the oldest burns (Figures 25 and 26).

(3.3.3) Regression Results

The relationship between the abundances of the six species and age of the burn are shown in Figure 27 and Table 6. The abundances of the six species are also significantly related to several of the independent variables (Table 6) while Table 7 show that each of the six species are significantly associated with several of the other species.

Polytrichum piliferum forms extensive carpets which account for 43 percent cover on burns less than 25 years of age. It is present in conjunction with Cladonia botrytes.

Figure 21. Ordination of the site data on the first three component axes with the percent cover of Polytrichum piliferum overlayed. Classes I<10%; II> 10%.

ORDINATION OF POLYTRICHUM PILIFERUM

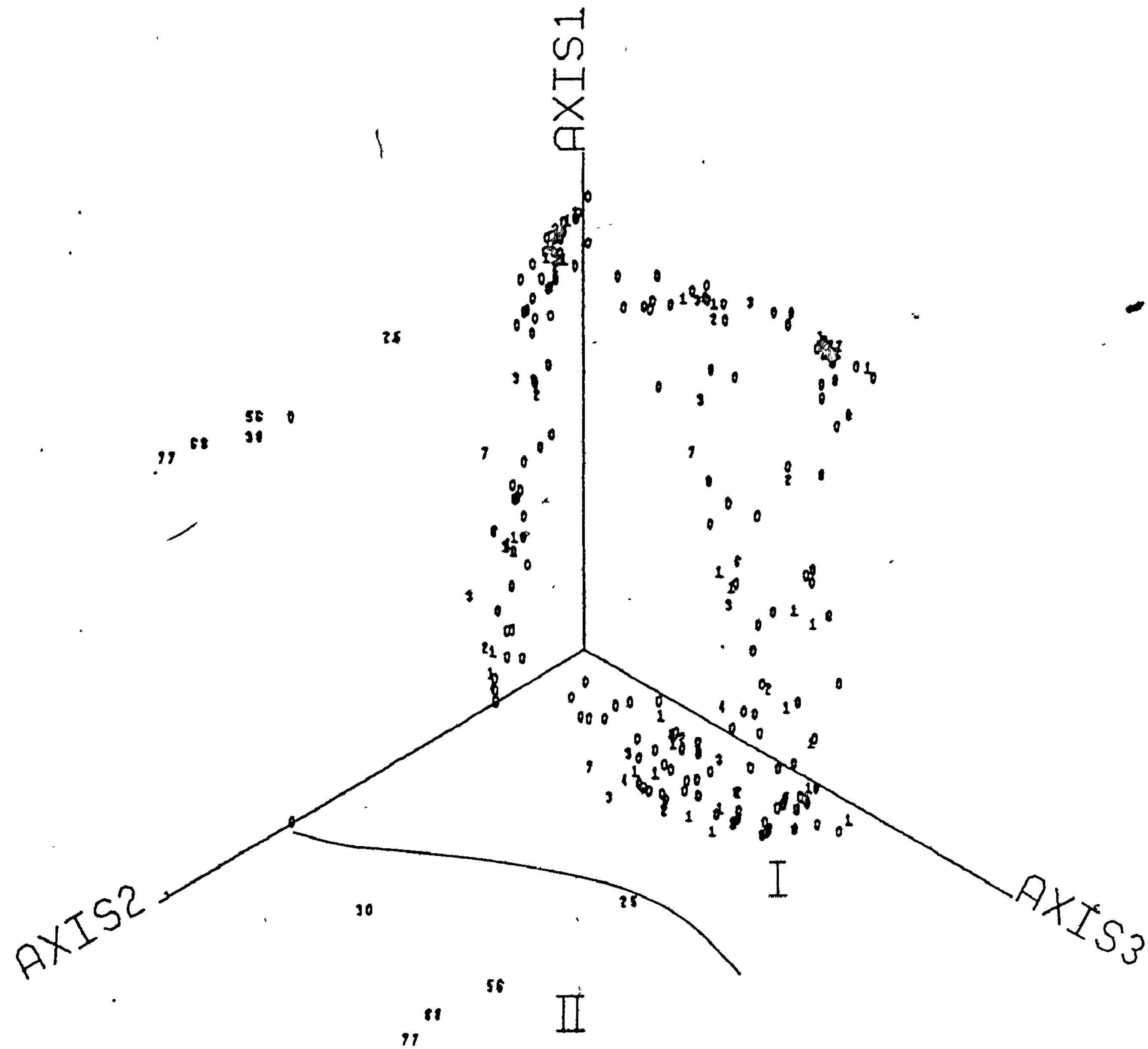


Figure 22. Ordination of sites greater than 23 years of age on the first three component axes with the percent cover of <u>Cetraria</u> <u>nivalis</u> overlayed. Classes: I<10%; II 11-20%; III>20%.

ORDINATION OF CLADONIA STELLARIS

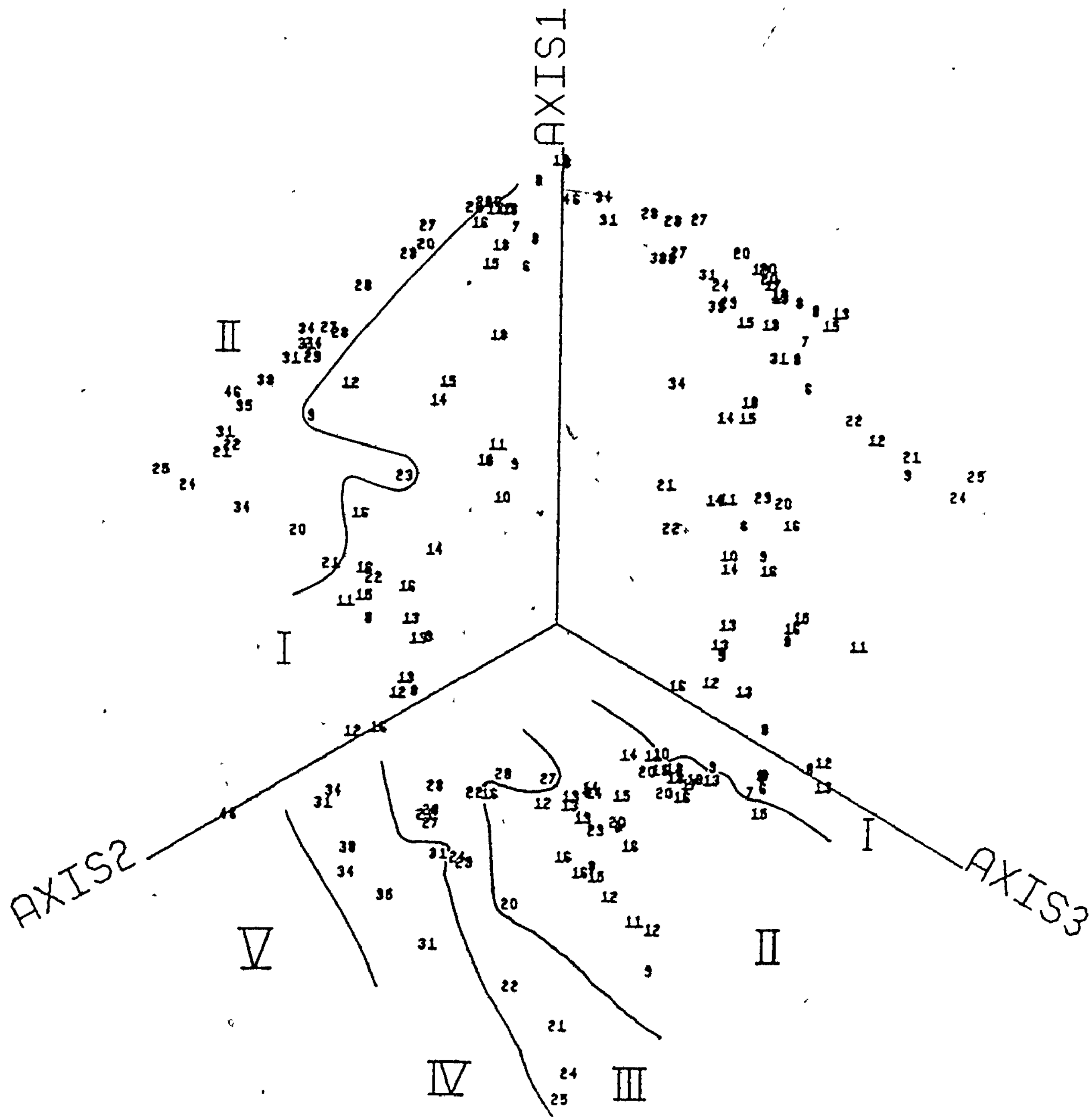


Figure 23. Ordination of sites greater than 23 years of age on the first three component axes with the percent cover of Cladonia stellaris overlayed. Axis 1 classes: I<19%; II>19%. Axis 2 classes: I 10%; II 11-20%; III 21-30%; IV 31-40%; V>40%.

ORDINATION OF CETRARIA NIVALIS

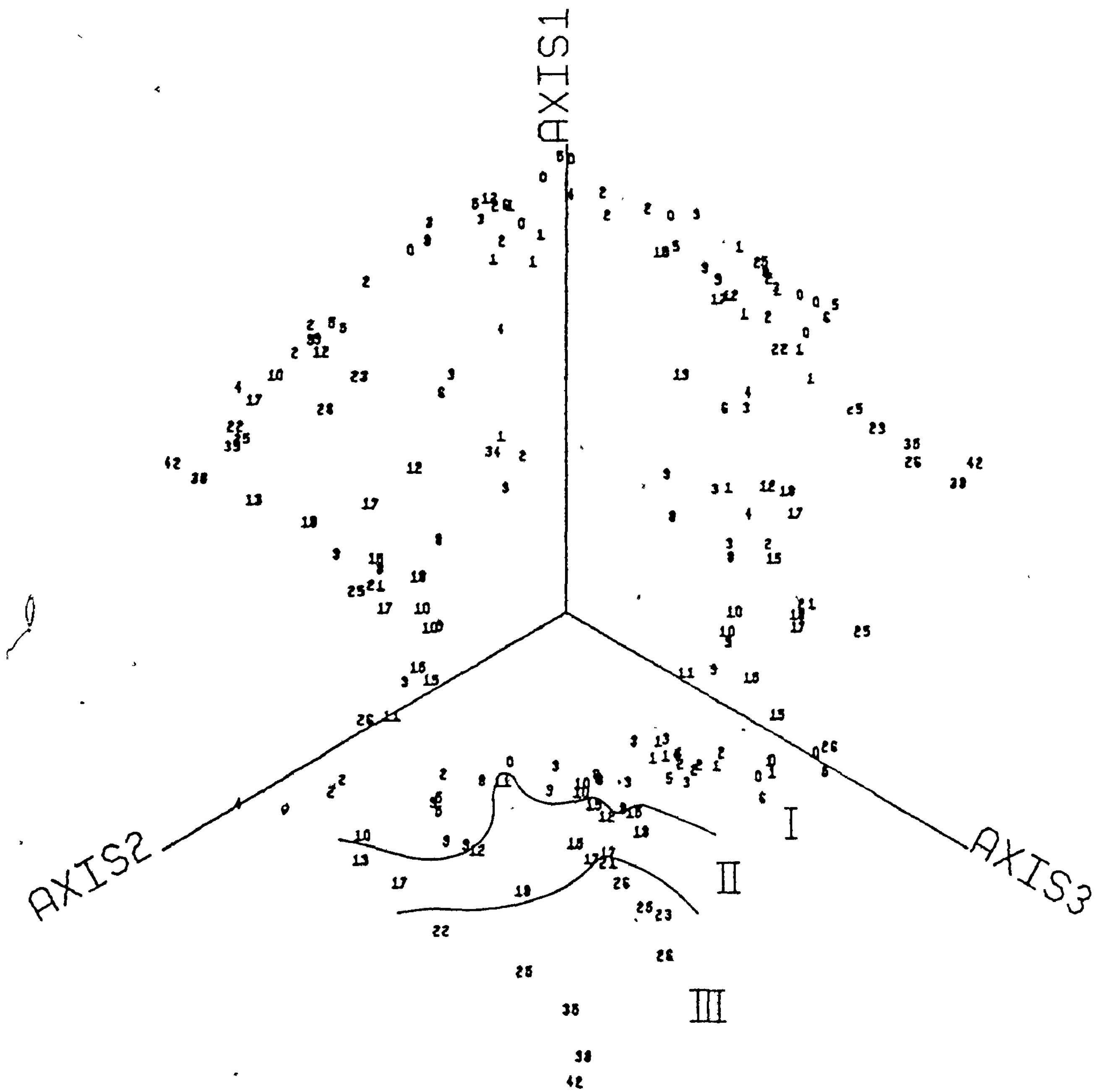


Figure 24. Ordination of sites greater than 23 years of age on the first three component axes with the percent cover of *Stereocaulon paschale* overlayed. Axis 1 classes: I<10%; II 11-30%; III 31-50%; IV>50%. Axis 2 classes: I≤20%; II>20%.

ORDINATION OF STEREOCAULON PASCHALE

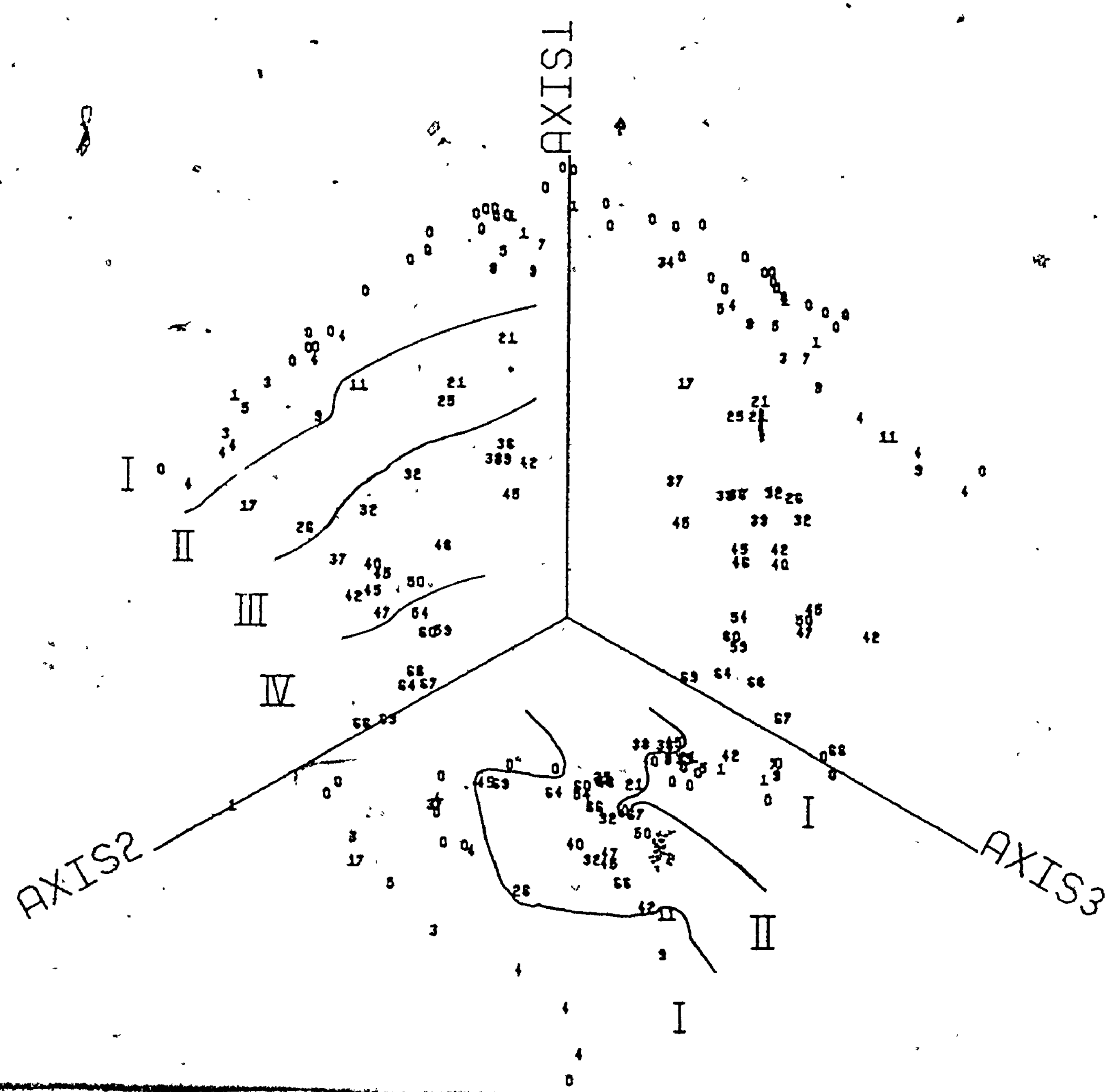


Figure 25. Ordination of sites greater than 23 years of age on the first three component axes with the percent cover of Vaccinium vitis-idaea overlayed. Classes: I< 15%; II>15%.

ORDINATION OF VACCINIUM VITIS—IDEAE

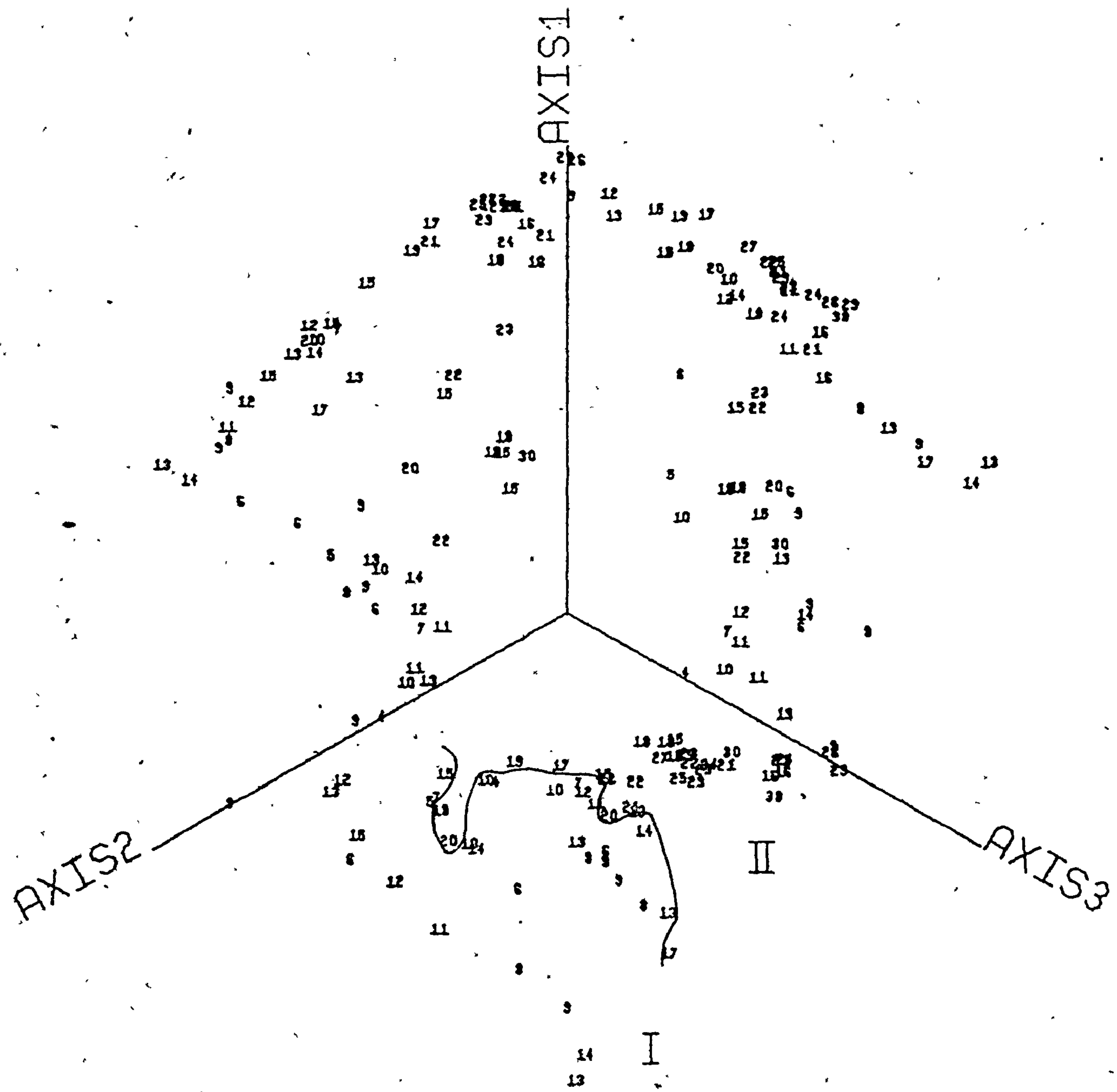


Figure 26. Ordination of sites greater than 23 years of age on the first three component axes with the percent cover of Ptilidium ciliare overlayed. Classes: I<5%; II>5%.

ORDINATION OF PTILIDIUM CILIARE

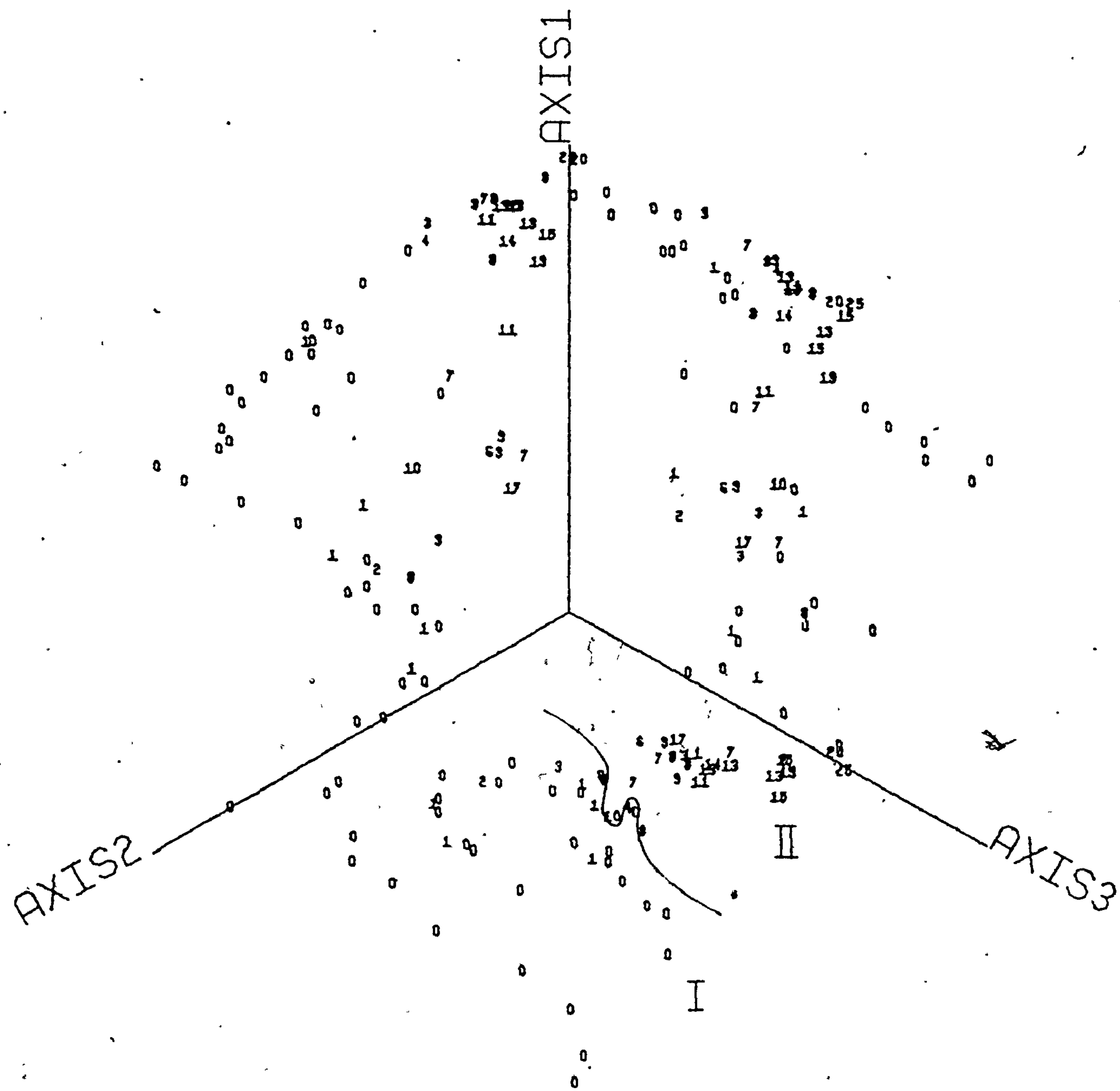
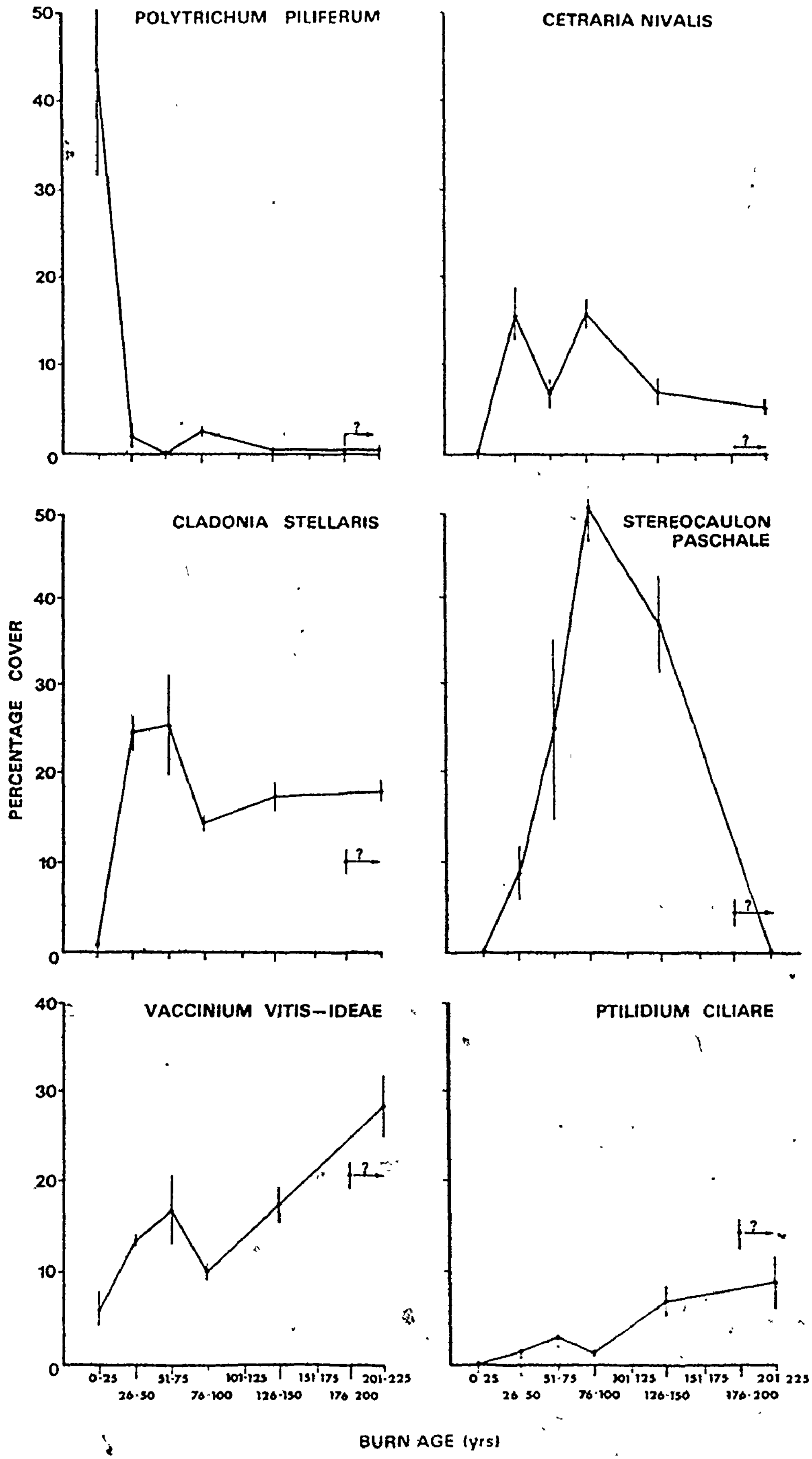


Figure 27. Changes in the abundance of six selected species with burn age. Age classes: 0-25 years; 51-75 years; 76-100 years; 101-150 years; 151-200 years; 201-250 years. A minimum age is indicated by "?".



POLYTRICHUM PILIFERUM
CETRARIA NIVALIS
CLADONIA STELLARIS
STEREOCAULON PASCHALE
VACCINIUM VITIS–IDEAE
PTILIDIUM CILIARE
PERCENTAGE COVER
0
10
20
30
40
50
0-25
26-50
51-75
76-100
101-125
126-150
151-175
176-200
201-225
BURN AGE (yrs)

Table 6. Regression results for site values of six species abundances and independent variables.

a) Linear regression ($y = a+bx$) and correlation (r) coefficients which are significant at the P = 0.001 level.

y variable (% cover)	x variable	a	b	r
Vaccinium vitis-idaea	burn age	8.32	0.07	0.58
Ptilidium ciliare	(yr)	-2.14	0.07	0.67
Vaccinium vitis-idaea	depth of	7.96	2.10	0.65
Ptilidium ciliare	organic layer (cm)	-1.58	1.62	0.74
Vaccinium vitis-idaea	no. trees	8.01	0.37	0.69
Ptilidium ciliare		-2.28	0.37	0.80
Polytrichum piliferum	quadrat-to-tree distance(cm)	-38.68	0.74	0.50
Polytrichum piliferum	tree age (yr)	17.67	-0.14	-0.44

b) Curvilinear regression ($y=a+bx+cx^2$) coefficients which are significant at the P = .001 level. Coefficients of determination (r^2) are also shown.

y variable (% cover)	x variable	a	b	c	r^2
Vaccinium vitis-idaea	quadrat-to-tree distance (cm)	93.35	-1.32	0.0058	0.44
Ptilidium ciliare	quadrat-to-tree distance (cm)	70.87	1.55	0.0079	0.53
Cetraria nivalis	depth of organic layer (cm)	17.58	-2.61	0.087	0.29

Table 7. Correlation coefficients between site percent cover values of six selected species and other species which are significant at the P = .001 level.

Species	Species	Correlation Coefficient
Polytrichum piliferum	Cladonia botrytes	.68
	Lecidea uliginosa	.61
	Cladonia cristatella	.48
	Lecidea granulosa	.45
Cetraria nivalis	Cladonia amaurocraea	.68
Cladonia stellaris	Cladonia uncialis	.73
	Cladonia gracilis	.63
	Cetraria islandica	.62
	Cladonia cornuta	.54
	Cladonia crispata	.49
	Cladonia coccifera	.42
	Cladonia gonecha	.41
Stereocaulon paschale	Vaccinium myrtilloides	.39
Vaccinium vitis-idaea	Ptilidium ciliare	.70
	Cladonia rangiferina	.51
	Ledum groenlandicum	.45
	Pleurozium schreberi	.41
	Hylocomium splendens	.40
Ptilidium ciliare	Vaccinium vitis-idaea	.70
	Hylocomium splendens	.63
	Pleurozium schreberi	.62
	Cladonia rangiferina	.58
	Dicranum spp.	.53
	Ledum groenlandicum	.45
	Peltigera scabrosa	.39
	Ptilium crista-castrensis	.38

C. cristatella, Lecidea uliginosa and Lecidea granulosa (Table 7). The decrease in abundance on burns greater than 25 years of age is related to the increase in tree density and tree age on these burns (Table 6).

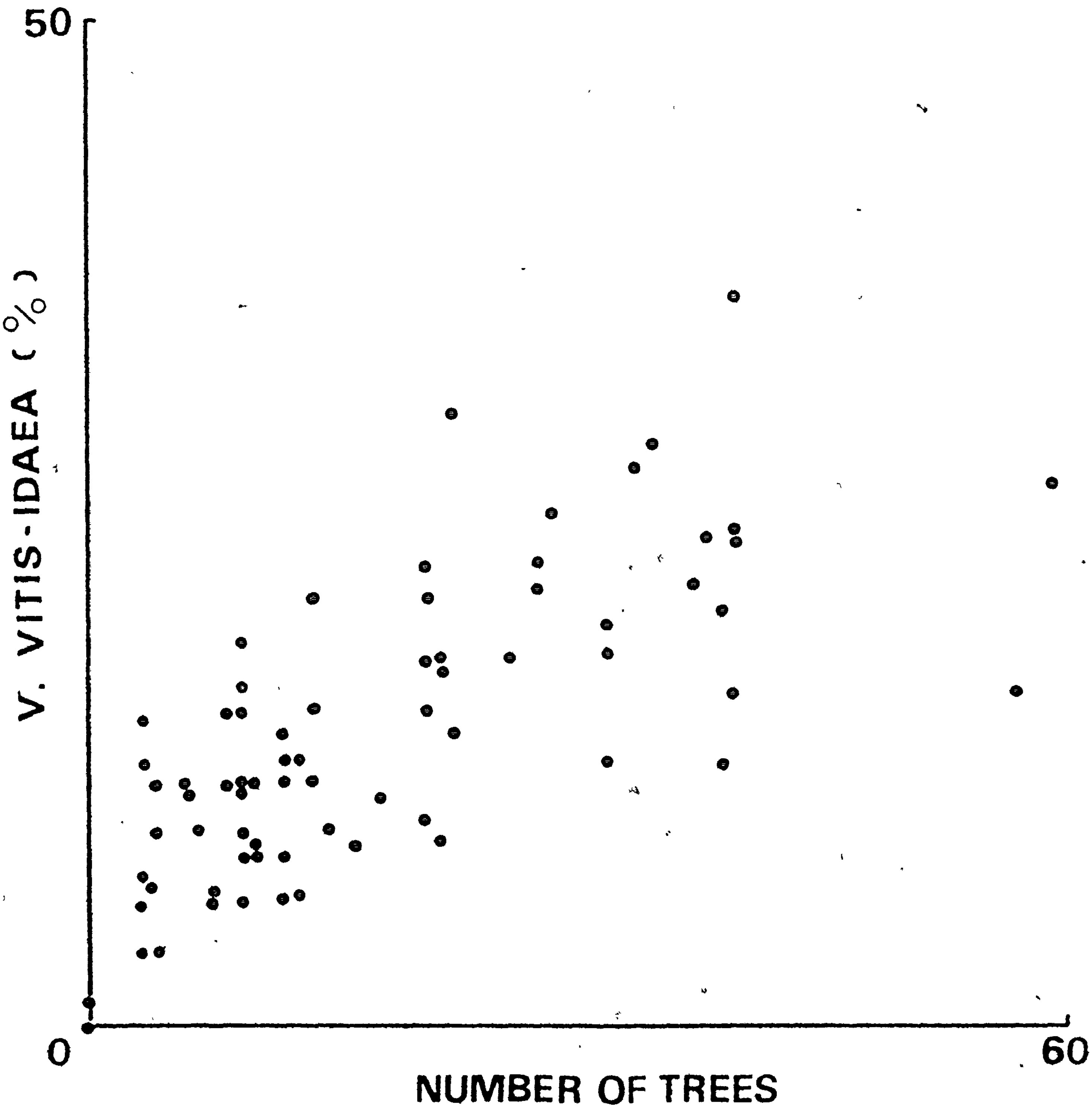
Cetraria nivalis is absent on burns less than 25 years of age. It is most abundant on burns between 26 and 100 years old where it is associated with Cladonia amaurocraea (Table 7). The cover values of Cetraria nivalis are inversely related to depth of the organic layer (Table 6).

Cladonia stellaris is the second most abundant species (Table 4) and most characteristic of burns between 26 and 75 years old but maintains a moderate level of abundance thereafter. It is most strongly associated with Cladonia uncialis, C. gracilis, C. cornuta, C. crispata, C. coccifera, C. gonecha and Cetraria islandica (Table 7). The cover values are not significantly related to tree density, tree age, tree size or depth of the organic layer.

Stereocaulon paschale is the most abundant species in the area representing 22 percent of the total vegetation cover in the sample data (Table 4). Although it is present in significant amounts on burns between 26 and 150 years of age, it attains a maximum abundance of 51 percent cover on 76 to 100 year old burns where it is associated principally with *Vaccinium myrtilloides* (Table 7). In addition, the cover values are not significantly related to any of the independent variables.

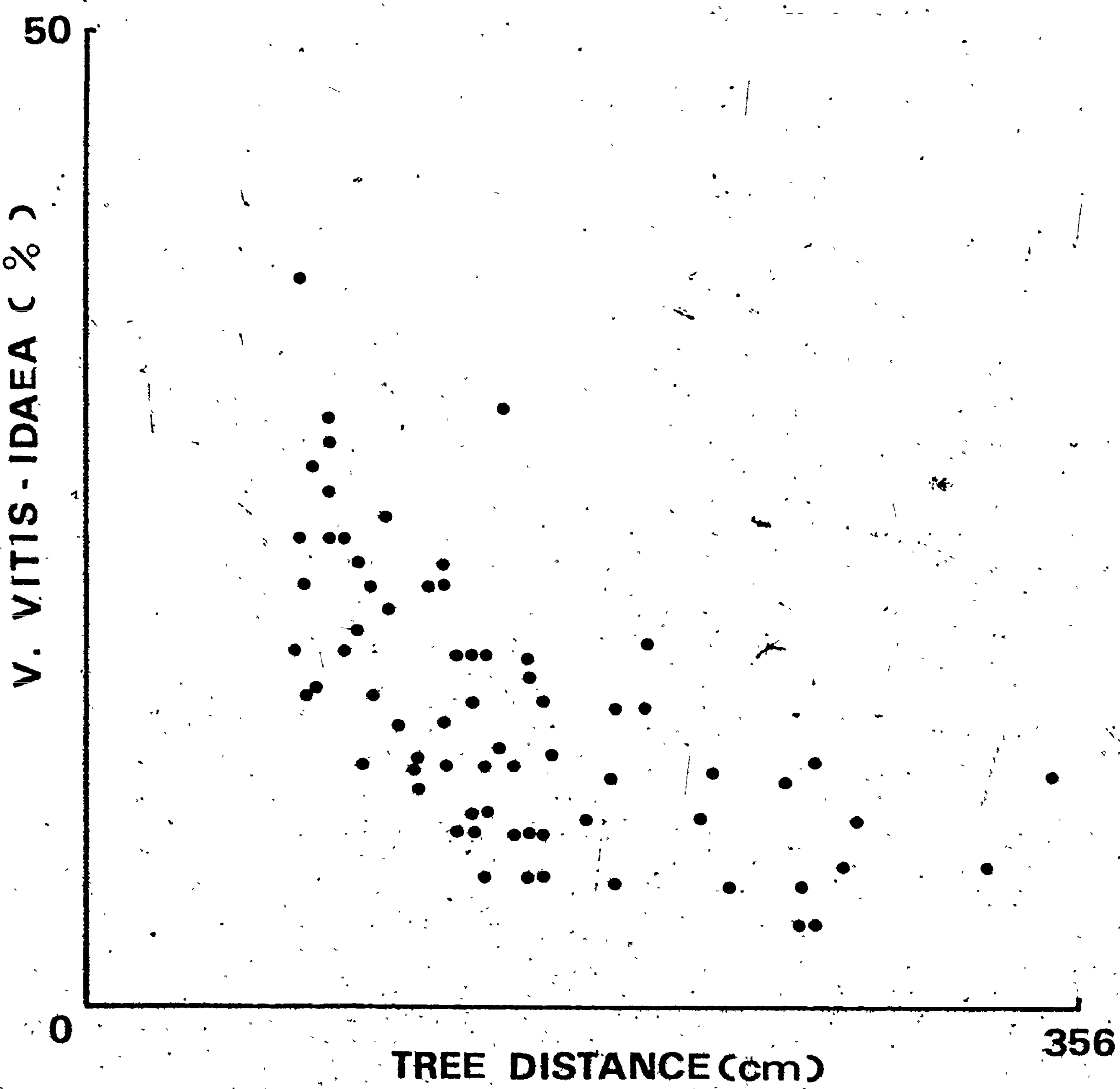
Although *Vaccinium vitis-idaea* is far more abundant than *Ptilidium ciliare*, both of these species increase in abundance with increasing age of burn. These distributions are strongly related to the high tree density and depth of organic layer values of the old woodland (Figures 28, 29, 30 and 31, Table 6). In addition, both species are most significantly associated with *Hylocomium splendens*, *Pleurozium schreberi*, *Cladonia rangiferina* and *Ledum groenlandicum* (Table 7).

Figure 28. Scatter diagram - site values of percent cover of Vaccinium vitis-idaea vs number of trees. Axes are on linear scales.



50
V. VITIS-IDAEA (%)
0
60
NUMBER OF TREES

Figure 29. Scatter diagram -site values of percent cover of *Vaccinium vitis-idaea* vs quadrat-to-tree distance. Axes are on linear scales.



50
V. VITIS - IDAEA (%)
0
356
TREE DISTANCE (cm)

Figure 30. Scatter diagram - site values of percent cover of Ptilidium ciliare vs number of trees. Axes are on linear scales.

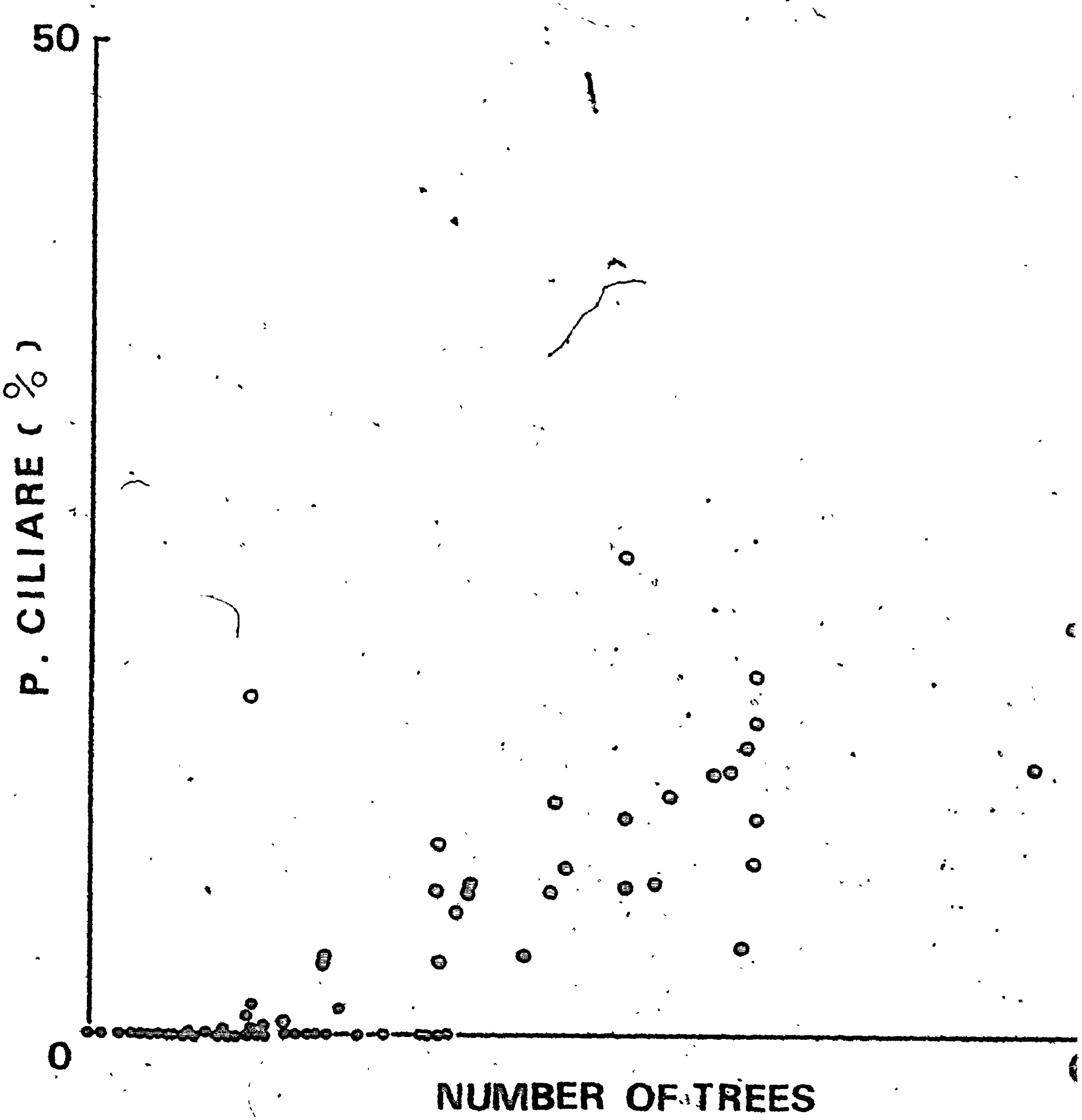
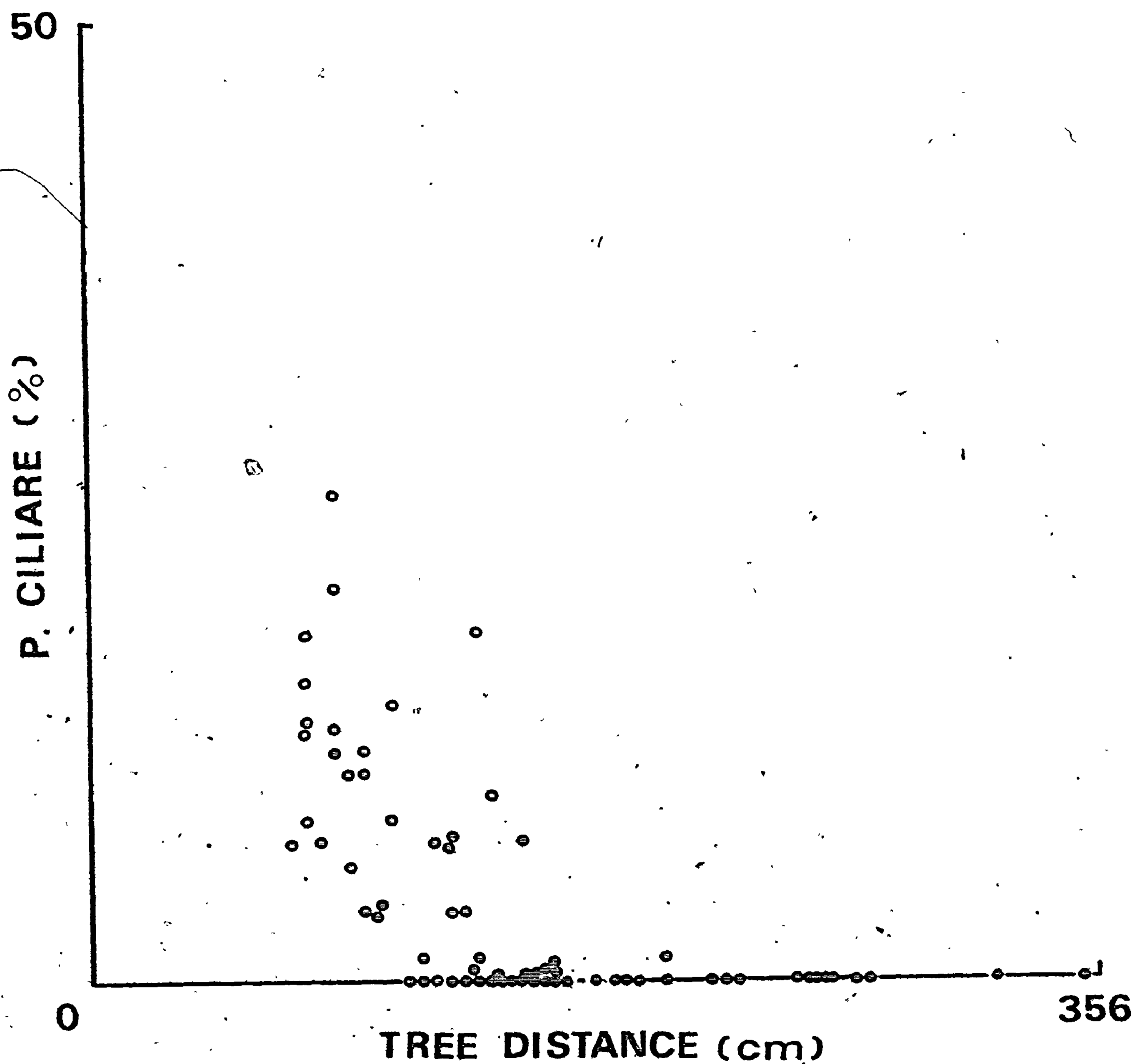

50
0
P. CILIARE (%)
NUMBER OF TREES

Figure 31. Scatter diagram - site values of percent cover of Ptilidium ciliare vs quadrat-to-tree distance. Axes are on linear scales.


50
P. CILIARE (%)
0
356
TREE DISTANCE (cm)

Section 4.

DISCUSSION

(4.1) The dates and extents of fires on the drumlins

A reliable temporal basis is absolutely essential to study the post-fire recovery of vegetation. In this study, the fire scar method has been the most valuable of the tree ring analyses used, for identifying definite starting times for recovery on the burns. Use of the method was limited only by the location of an adequate number of replicate scars for each burn, by inaccuracies involved in determining the exact scarred ring from which to begin counting for each sectioned scar and in the actual counting of the annual rings themselves. Despite the fact that some of the estimates were based on means from as few as 4 or 5 replicate scars, the small standard errors of these means, which are less than ±2.3 years, indicate that a high degree of reliability in the estimated ages has been attained. In addition, the very recently burned area estimated to be three years old is also reliable since only *Salix* plants which had re-established themselves following fire from basal sections of stems or underground roots were aged. However, for the three areas of old woodland where fire scars were absent, only minimum possible times since burning could be made from the age of the oldest tree. Thus, with the exception of these three burns, the burn age estimates are accurate and form a reliable time sequence, extending from 3 to over 200 years, for examining the recovery sequence.

Although a wide range of different age burns are present, a large proportion of these burns are less than 100 years old. There are two possible explanations of this result. Either many of the old burns were not as visually apparent as the young burns due to the indistinctness of their boundaries and therefore were not examined, or there are very few areas of woodland greater than 100 years old. MacLean and Bedell (1955) comment that most parts of the northern Ontario Clay Belt were burned at least once in the last 130 to 140 years, while Viereck (1973) suggests that nearly all forest stands in Alaska are less than 150 years old with most representing earlier stages of fire recovery. Furthermore, Day (1972) approximates the probability of fire in more fire susceptible areas of Canada's forests as once every 100 years. From these and the observations in this study, it is concluded that there are very few areas of old spruce-lichen woodland on the drumlins and the average reburn interval is less than 100 years.

Few of the burns exceed 0.25 km^2 in size and the majority of burns are only a couple hectares. The limited extent of these burns is typical of fire in most parts of Canada although fires can sweep for many kilometers in some areas. For example, Hare and Taylor (1956), from aerial photographs of Ungava and Labrador, comment upon the widespread occurrence of sporadic small burns. Scotter (1970) found that 60 percent of the fires in subarctic sample were less than 4 hectares in size. In all Canada from 1961 to 1967, 85 percent of all fires were 4 hectares or less in size (D.E. Williams, from Rowe and Scotter, 1973). Although many factors are undoubtedly responsible for the limited extents of these fires, such as the exhaustion of fuel, a change in the weather, topography and the presence of natural fire breaks, these figures suggest that the patchiness of vegetation in the Abitau-Dunvegan lakes area is a common feature.

(4.2) Variation between sample sites

Principal component analysis has been efficient in extracting the major proportion of variation in the species composition of the ground layer vegetation among 10 m^2 sites. The first three principal components account for greater than 65 percent of the total variance in both ordinations of 10 m^2 sites. However, in both cases, although burn age is correlated with the second principal component, the first and third components are not correlated with any of the independent variables measured. In addition, a considerable amount of variability is evident within relationships. The contour lines of the ordination overlays are often tenuous and substantial variability is present in many of the scatter diagrams. Thus, a considerable proportion of the variation among 10 m^2 sites is not accounted for.

This unaccounted for variation among sites may be due to a number of factors which may affect the actual recovery of vegetation following any individual fire. The intensity of fire will be important in determining the number of trees killed, whether the cones and their seed on fire killed trees remain viable (Ahlgren, 1959) and the extent to which the organic layer is destroyed. Lutz (1956) reports variation of 0 to 100 percent destruction of the organic layer on burns in Alaska. In addition, the frequency of fire and preburn vegetation on the site, the climate for several years following a fire, the size and shape of the fire which may be important in determining the early colonizing species, the season of the fire which will largely affect the availability and success of propagules, and the intensity of local grazing by caribou, may also be factors which have complicated the sequence of recovery on the burns, with recovery taking varied courses and progressing at different rates. These factors may also complicate the patterns of vegetation within individual burns. No control of these factors during the sampling program was possible.

The ordination results, although providing an excellent summary of the data which indicates that recovery does follow a general sequence on the drumlins, have not uncovered any additional relationships. This may in fact be due to the degree of variation present in the data and to the structure of the data. Inherent in the use of principal component analysis is the unrealistic assumption that the relationships between the abundances of a species and its controlling factors are linear. In actual fact, there is most often a non-linear relationship between the two variables and the unsatisfactory nature of the ordination results may also be partly due to the presence of non-linearity within the data.

(4.3) Post-fire development of the spruce canopy and organic layer

Increases in the age, size and density of trees result in progressive development of the black spruce canopy. This is accompanied by a slow increase in the depth of organic matter. Although both crown and surface fires kill black spruce readily in relation to other conifer species, the ability of black spruce to recolonize burned areas subsequent to fire is well known (eg. Holman and Parker, 1940; Lutz, 1956; Zasada, 1971). Black spruce have semiserotinous cones that disseminate seed slowly and continuously over a period of at least two or three years and are partially opened by heat. Thus there is always some seed available for recolonization after burning from the tops of snags, which are fire killed trees. Only in a few cases is the fire intense enough to destroy the uppermost cones and their seed (Le Barron, 1940; Ahlgren, 1959; Horton and Lees, 1961; Zasada, 1971). Even in these cases, although the maximum seed dispersal distance for black spruce is only about 300 feet (Anon., 1939b), seed from surrounding stands may be blown on snow into very large burns (MacArthur and Gagnon, 1959). In Newfoundland, Wilton (1963) found that for the first 60 days following burning of a black spruce stand, 0.6 million seeds per hectare were dispersed, which indicates that extremely large quantities of seed are immediately available.

Although an improvement in seedbed conditions by burning has been suggested (Haig, 1938; Little, 1953), quantitative data concerning the germination requirements for black spruce and the requirements for subsequent growth are lacking. Ahlgren (1959) finds that seedlings seldom become established on severely burned sites before two or three years have passed and Place (1955) also finds that on dry sandy soils, low, open growing *Polytrichum* mosses provide a favourable environment for germination. Linteau (1957) confirms the advantages of *Polytrichum* invasion of bare mineral soil in the establishment of black spruce seedlings. He reports a rather superficial root system in one to seven year old seedlings growing on mineral soil, with an average depth of only 2 inches and roots sent out in only two or three directions. On the same mineral soil, but covered with mosses dominated by *Polytrichum* species, rooting depth varied from 2 to 6 inches and averaged 3.5 inches. In addition, those on moss-covered soil had secondary and tertiary roots showing substantially more development. Thus, on the drumlins, initial germination and establishment of black spruce seedlings on the young burns are likely favoured by the development of extensive *Polytrichum* mats on these burns. The dramatic decrease in intertree distance as treeless young burns are colonized by seedlings explains the non-linearity of the relationship between site mean quadrat-to-tree distance and the number of trees per site.

The optimum tree age for seed production is about 150 years (Anon., 1948b). However, spruce trees begin producing seed at the early age of 10 to 15 years (MacArthur and Gagnon, 1959; Horton and Lees, 1961). It is thus very likely that continuing increases in tree density with burn age on the drumlins are supported by seed from the earliest colonizing trees. In addition, it appears that further increases in tree density in the oldest woodland are primarily due to vegetative reproduction by the older trees, which is usually referred to as layering (eg. Johnson, 1956; Stanek, 1961b), and only infrequently through the establishment of seedlings. This observation is consistent with Place (1955) who suggests that Dicranum spp., Pleurozium schreberi, Hylocomium splendens and Ptilium crista-castrensis, which are components of the ground vegetation on these old burns, are poor seedbeds for the germination of black spruce seed. Decreased light intensities in the older woodland may inhibit the growth of seeds which do germinate. Logan (1961) grew seedlings in pots for 3 years with an adequate supply of moisture and at 4 light levels, 13, 25, 45 and 100 percent of the light in the open. He found root growth, seedling weight, shoot weight, root weight and length of root severely reduced in seedlings grown at light levels of 45 percent or less. Vincent (1965) suggests that layering tends to become more important in the reproduction by older trees as soil moisture increases but the stands remain open enough to allow the lower branches to remain alive.

(4.4) Post-fire recovery sequence of the ground vegetation

Concurrent with the development of the spruce canopy and organic layer is a change in species composition of the ground vegetation with increasing age of burn on the drumlins. A fairly rapid rate of change occurs over the initial 25 years which is followed by a more gradual one on the older burns. Topographic factors, such as slope and aspect, do not appear to be of much importance to the recovery of vegetation on the drunlins. They are, however, of special importance in the post-fire distribution of vegetation and soils in interior Alaska (Krause et al, 1959; Viereck, 1973). For example, Krause et al (1959) compare the soil and vegetation on north- and south-facing slopes of an upland site burned 115 to 130 years previously and find an open black spruce-*Sphagnum* stand growing on wet peaty soil with permafrost on the north slope contrasting with a dense white spruce-*Hylocomium splendens* stand growing on the south slope. This marked difference in the importance of topography in the two geographical regions is most likely due to the steeper slopes of the upland site in Alaska. This will result in larger differences in micro-climatic conditions between slopes of the upland site than the drumlins. This effect may be augmented by differing macroclimatic, geomorphological and floristic characteristics of the two regions.

Six of the most abundant species, Polytrichum piliferum, Cetraria nivalis, Cladonia stellaris, Stereocaulon paschale, Vaccinium vitis-idaea and Ptilidium ciliare, show different temporal distributions and are the major contributors to the trend in species composition of the ground vegetation with time following fire. Although a number of workers (eg. Hustich, 1951; Lutz, 1956; Ahti, 1959; Scotter, 1965) have reported several of these species as components of the ground vegetation in fire affected lichen woodland and give general descriptions of their habitats, the critical factors which control their post-fire ecology have not yet been identified.

Polytrichum piliferum, which is frequently mentioned as colonizing soon after fire (Hustich, 1951; Lutz, 1956; Scotter, 1964), is a very abundant up to 25 years following fire but is virtually absent on older burns. Its distribution contrasts with the lengthier temporal distributions of the other abundant species which are absent on burns which are less than 25 years old. This largely accounts for the extreme dissimilarity in species composition of the young burns in comparison to the older burns. The ability of Polytrichum piliferum to quickly colonize burned surfaces may be facilitated by the survival of fragments in the soil and not by spore dispersal (Lutz, 1956). It begins to form extensive carpets by about 12 years following fire. These carpets appear to be favourable for the establishment of lichens, mostly Cladonia species, as well as the germination of black spruce seeds. Its dramatic decline on burns greater than 25 years of age is correlated with the increases in age and density of trees.

Cetraria nivalis becomes most abundant on burns which are 25 to 100 years of age and gradually declines in abundance on older burns. In an inverse fashion, Vaccinium vitis-idaea and Ptilidium ciliare require at least 25 years for establishment and become most abundant on the oldest burns where they are found in conjunction with the mosses Pleurozium schreberi, Hylocomium splendens and Ptilium crista-castrensis. Fraser (1956) speculates that the shade intolerance of lichens which are abundant in open woodland results in their disappearance under closed canopy conditions and Hustich (1951) and Ahti (1959) give habitat descriptions implying the preference of these mosses for damp, shaded conditions of closed canopy woodland. Since the abundance of C. nivalis is correlated with the depth of organic layer and the abundances of V. vitis-idaea and P. ciliare are correlated with changes in tree density and depth of organic layer, light and moisture may be factors which are important in controlling their temporal distributions.

Cladonia stellaris and Stereocaulon paschale, the two most abundant components of the ground vegetation, attain maximum abundances on burns which are 26 to 75 and 76 to 100 years of age respectively. The lack of significant relationships between the abundances of C. stellaris or S. paschale and other independent variables may again be due to the variation in the data and to the structure of the data.

Cladonia stellaris, which is one of the most widely occurring and abundant species of lichen in northern lichen woodlands (Hustich, 1951; Fraser, 1956; Ahti, 1959, 1964; Ahti and Hepburn, 1967; Lambert and Maycock, 1968; Lechowicz and Adams, 1974a), has been described in relation to intermediate and older burned areas by Ahti (1959) and Bergerud (1971) in Newfoundland, Yarranton (1975) in northern Ontario and Scotter (1964) in northern Saskatachewan. Yarranton (1975) has examined the growth rates and reproductive characteristics of C. stellaris on burns and suggests that its appearance on burns greater than 25 years of age is controlled by the development of a humus layer and soil nutrients and not poor dispersal abilities while its subsequent increase in abundance over 30 years is influenced by light, water availability and physical interference by other species. Stereocaulon paschale, although equally extensive in distribution being found in Newfoundland (Hustich, 1951), N.W.T. (Scotter and Thompson, 1966), Ontario and B.C. (Ahti et al, 1967), comprises a dominant component of the ground vegetation only in a restricted geographical zone about 200 miles wide and extending from Great Slave lake, east along the 60th parallel, to Churchill, Manitoba (Ritchie, 1959; Argus, 1966; Johnson, 1975). In addition, it has yet to be described in relation to a post-fire recovery sequence. However, Ritchie (1959) finds S. paschale as a dominant ground component in northern Manitoba woodland and suggests that the intensive local grazing and trampling by caribou repress the Cladonia and favour the more rapidly growing S. paschale. Tengvall (1928, from Hustich, 1951) and Kärenlampi (1971) offer the only comparative growth rate studies which could be located. Tengvall (1928) finds the annual growth rate of S. paschale to be about double that of C. stellaris in Sweden while Kärenlampi (1971) finds no significant difference in Finland. Hustich (1951) also suggests that its rapid growth rate explains in part the recolonization in Labrador by Stereocaulon after disturbance by caribou or man. Furthermore, in the lichen forests of Finland, the temporary dominance of S. paschale has been accounted for in terms of caribou grazing by Du Rietz (1925) from Ritchie 1959 and

Kalliola (1932) from Ritchie, 1959. In the lichen woodland in the Abitau-Dunvegan lakes region, although S. paschale was found on or near old trails, entire drumlins are often covered by almost pure S. paschale-black spruce woodland and for this reason, it seems very unlikely that the presence of S. paschale is only the result of grazing of the Cladonia stellaris-Cetraria nivalis mats. Conversely, extensive grazing of the S. paschale mats themselves was also evident which points to its importance as a source of winter fodder for the herds of caribou using the area. Visual inspection of the snow-covered drumlins in early April of 1975 showed numerous areas with recent caribou cratering activity. S. paschale was very often the most abundant lichen component beneath the snow (Figure 32). This is in agreement with Kareev (1968), who also notes the importance of S. paschale as a winter fodder for caribou in Russia. It is obvious that more detailed information is required concerning both the ecology of S. paschale and the fodder preferences of the caribou herds utilizing the drumlin field as a winter foraging range, before the importance of grazing by caribou to the sequence of recovery can be critically assessed.

(4.5) The microclimate of burned surfaces and the subsequent time dependent changes

The development of the black spruce canopy and an

Figure 32. Caribou crater showing an uncovered patch of *Stereocaulon paschale.*

organic cover are most responsible for the changes in microclimatic conditions recorded by Kershaw, Rouse and Bunting (1974) and Rouse (1976) at the Abitau-Dunvegan lakes research site. They examine the summer radiation balance over burns which are 0, 1, 2, 24 and 81 years old. The radiation balance or net radiation, Q*, can be expressed in the form

$$Q^* = K\downarrow (1-\alpha) + L\downarrow - L\uparrow$$

where $K\downarrow$ is incoming solar radiation, α is the albedo representing the ratio of outgoing to incoming solar radiation, $L\downarrow$ is the incoming longwave radiation and $L\uparrow$ is the outgoing longwave radiation. They find that burning leads to an immediate reduction in net radiation of 15 percent which lasts for at least 24 years (Table 8). Since incoming short and longwave radiation are common for all five surfaces averaging 530 and 492 cal cm^{-2} day^{-1} respectively and the albedos of the 0, 1, 2, 24 and 81 year old burns average 5.0, 6.5, 9.0, 15.6 and 20.4 percent respectively, differential surface heating, which directly affects outgoing longwave radiation, must be important in determining the radiation balance during the summer months.

Net radiation is important as it defines the amount of energy available to heat the soil, to heat the air and for evapotranspiration. Kershaw et al (1974) and

Table 8. Measured radiation fluxes (cal cm^{-2} day^{-1}) for mainly clear days in July and August. Data include daily totals of Q* for 5 sites and the ratio of Q* for each of the burns to Q* for the 81 year old lichen woodland (Q^*_{β}/Q^*_{lw}) (from Rouse, 1976).

Date	Period (hrs)	K↓	L↓	Q*					Q^*_{β}/Q^*_{lw} (%)				
				0	1	2	24	81	0	1	2	24	81
July 10	04-18	671	494	337	337	329	334	410	82	82	80	81	100
July 16	04-19	639	514	321	315	300	318	384	84	82	78	83	100
July 17	04-18	407	445	243	232	203	218	272	89	85	75	80	100
July 31	04-19	479	469	250	261	249	267	312	80	84	80	86	100
Aug. 1	04-19	484	500	262	258	233	262	293	89	88	80	89	100
Aug. 4	04-20	603	502	295	290	279	280	352	84	82	79	80	100
Aug. 9	04-20	431	523	253	256	260	239	282	90	91	92	85	100
Ave.		530	492	280	278	265	274	329	85	85	81	83	100

Rouse (1976) also examine mid-summer surface temperatures, soil temperatures, soil moisture and evapotranspiration for the five surfaces. They find that freshly burned surfaces have the highest surface temperatures and the most extreme diurnal surface temperature fluctuations both of which decrease with time following fire (Table 9). Fire creates a 70 percent increase in the mean daily surface temperatures which remain 40 percent warmer even after 24 years. The average diurnal surface temperature ranges for the 0, 1 and 2 year old burns are extreme at about 46°C but decrease substantially to 37°C on the 24 year old burn and 28°C on the 81 year old burn. The subsurface soils of the fresh burns are also warmer and have larger vertical soil temperature gradients than the older burns (Table 10). Furthermore, although the average soil moistures are not greatly different, the 0 year old burn is very wet in the surface layers, the 24 year old burn is the driest at all depths and the 81 year old burn is the wettest at all depths. However, the 0 and 81 year old burns show the largest seasonal variation in soil moisture (Figure 33). This variation may be explained by the high rates of evaporation from the wet surface layers of the 0 year old burn and the high rates of evapotranspiration on the 81 year old burn

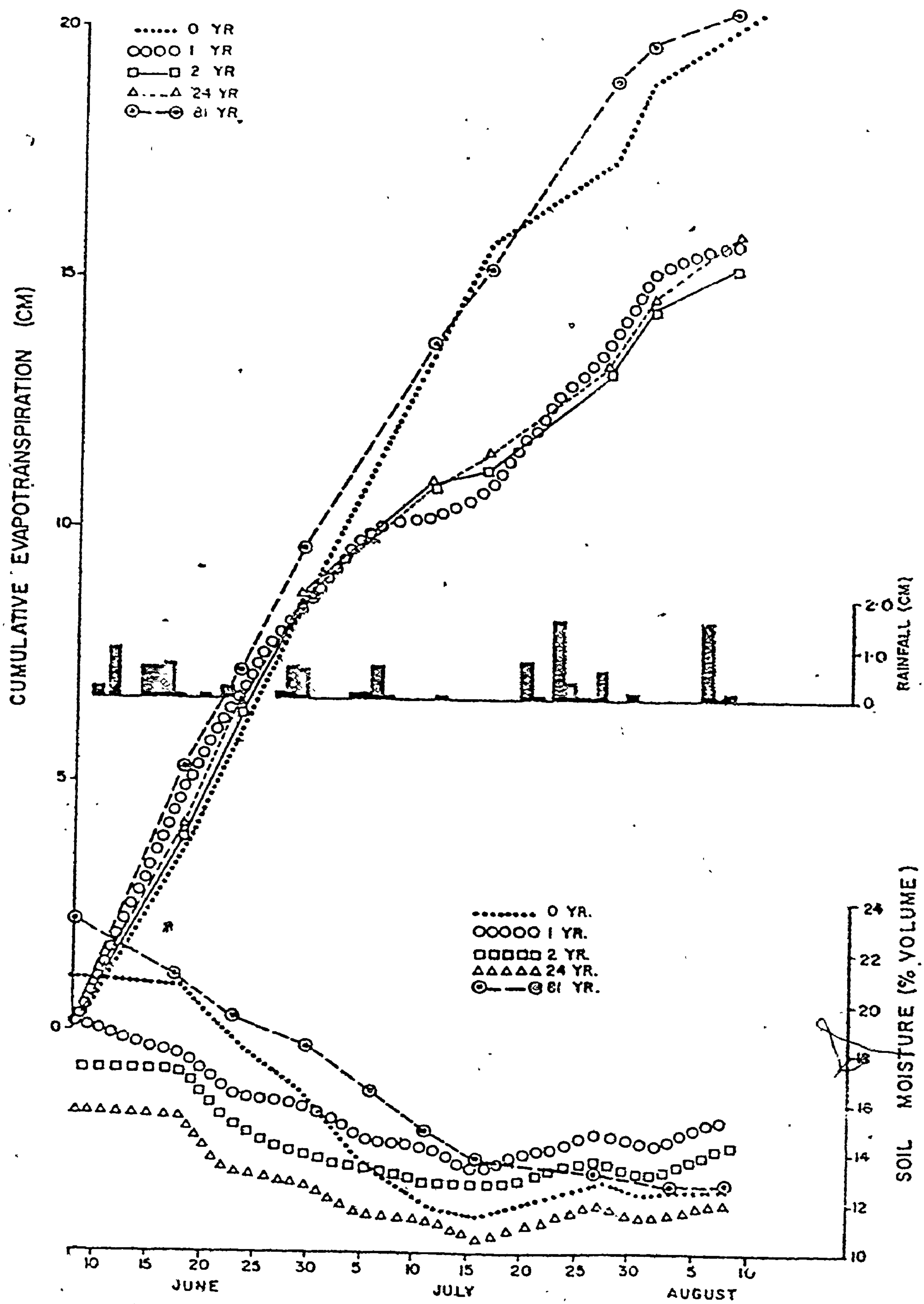
Table 9. Radiative surface temperatures for the daily interval (0400-2000 h) during July and August. All values in °C. The ratio of surface temperature for the burned surfaces to that for the 81 year old lichen woodland is given in ($T_o\beta/T_o lw$) (from Rouse, 1976).

Date	Mean Daily					Daily Maximum					Daily Minimum				
	0	1	2	24	81	0	1	2	24	81	0	1	2	24	81
July 10	48.5	47.6	46.5	41.8	29.3	65.1	64.3	62.7	52.6	39.4	19.6	19.6	19.6	20.8	13.2
July 16	43.9	44.0	46.3	37.4	25.9	62.7	61.1	68.2	52.6	36.4	14.6	15.8	15.8	13.2	10.6
July 17	35.6	36.4	38.5	33.6	23.7	50.8	49.9	53.4	43.3	32.2	15.8	15.8	17.1	15.8	10.6
July 31	35.5	33.3	33.2	28.2	19.6	56.9	55.2	54.4	43.3	33.2	9.2	8.0	9.5	9.5	6.4
Aug. 1	32.9	32.4	34.0	28.6	20.9	52.6	53.4	55.2	41.4	39.4	2.2	2.2	2.2	0.8	0.8
Aug. 4	36.3	34.2	35.3	31.4	20.8	57.9	57.0	57.0	49.0	32.2	2.2	2.2	2.2	0.8	0.8
Aug. 9	26.4	25.3	23.4	23.3	15.8	49.9	49.0	45.2	40.4	27.8	2.2	2.2	2.2	2.2	2.2
Ave.	37.0	36.2	36.7	32.0	22.3	56.6	55.7	56.6	46.1	34.4	9.4	9.4	9.8	9.0	6.4
$T_o\beta/T_o lw$	1.7	1.6	1.6	1.4	1.0	1.6	1.6	1.6	1.3	1.0	1.5	1.5	1.5	1.4	1.0

Table 10. Average subsurface soil temperature (°C) at different depths. The ratio of temperature for the burned surface to that for the 81 year old lichen woodland is given in (T_B/T_{lw}) (from Rouse, 1976).

Depth (cm)	0 Yr.	1 Yr.	2 Yr.	24 Yr.	81 Yr.
5	15.1	15.3	17.2	13.8	10.2
10	13.4	15.1	16.3	13.5	9.6
20	12.4	13.8	14.9	12.2	9.6
40	10.8	12.2	14.3	11.4	7.9
80	8.5	9.6	10.2	9.2	5.1
160	6.1	5.4	6.0	5.9	3.1
Ave.	11.1	11.9	13.2	11.0	7.6
T_B/T_{lw}	1.5	1.6	1.7	1.4	1.0

Figure 33. The seasonal patterns of soil moisture, precipitation and cumulative evapotranspiration at each site (From Rouse 1976).

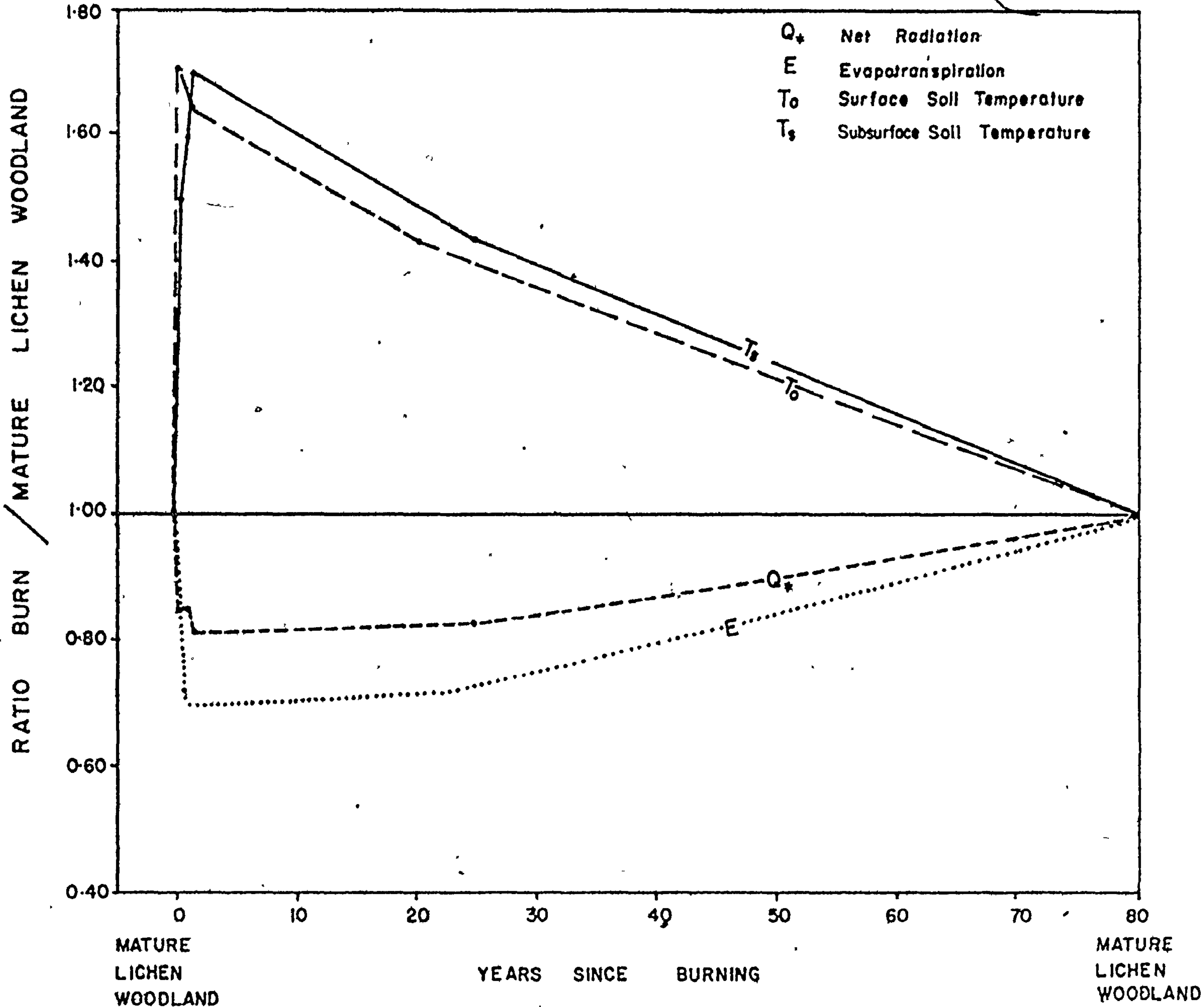


0 YR
1 YR
2 YR
24 YR
81 YR
CUMULATIVE EVAPOTRANSPIRATION (CM)
RAINFALL (CM)
SOIL MOISTURE (% VOLUME)
0 YR.
1 YR.
2 YR.
24 YR.
81 YR.
JUNE
JULY
AUGUST

induced by the transpiring spruce canopy, relative to the dry 1, 2 and 24 year old burns with their lack of transpiring vegetation. These microclimatic differences are summarized in Figure 34 which shows the micro-climatic trends with time following fire.

These trends in microclimatic variables with burn age are probably the most important factors in controlling the recovery sequence of vegetation on the drumlins. During summer months, the diurnal temperature extremes of the freshly burned surfaces may allow only those species with relatively wide temperature tolerance levels to colonize, although these surfaces probably possess adequate levels of moisture in the surface layers to meet the requirements of many species. _Polytrichum_ mosses are the most important colonizers of these surfaces and their subsequent development into extensive mats after about 24 years is primarily responsible for dampening the temperature fluctuations on these charred surfaces. In addition this development is accompanied by a general drying of the soil. These are conditions which may be more favourable for the germination and establishment of black spruce seeds and the establishment of lichens than for vascular plants. As the spruce seedlings mature, the trees will become more important in influencing the ground surface microclimate. The development of the canopy is accompanied by a decrease in surface and soil

Figure 34. The time sequence of surface and subsurface soil temperatures, net radiation and evapotranspiration from the 81 year old lichen woodland through various stages of recovery bark to the lichen woodland phase (from Rouse 1976).



Q* Net Radiation
E Evapotranspiration
To Surface Soil Temperature
Ts Subsurface Soil Temperature
Ts
To
Q*
E
1·80
1·60
1·40
1·20
1·00
0·80
0·60
0·40
RATIO BURN / MATURE LICHEN WOODLAND
0
10
20
30
40
50
60
70
80
MATURE LICHEN WOODLAND
YEARS SINCE BURNING
MATURE LICHEN WOODLAND

temperatures, a slight increase in soil moisture and undoubtedly results in a decrease in light at the floor of the woodland and these conditions may be important in the replacement of lichens by feather mosses and vascular plants. However, changes in nutrient status with burn age may prove to be equally important in controlling the post-fire species distributions as well as the germination of spruce seed and establishment and growth of seedlings. Kayll (1968) reviews the existing literature pertaining to soil nutrients after burning and suggests that fire frees the nutrient capital in soils which he terms a "frozen asset". Lutz (1956) and Scotter (1964) report increases in nitrogen, exchangeable calcium and to a lesser degree potassium and phosphorus which are accompanied by a decrease in acidity in the surface layers following fire in Alaska and northern Saskatchewan respectively, and Heilman (1966,1968) finds a decrease in nitrogen, potassium and phosphorus with age of stand in Alaska.

(4.6) General conclusions - geographical control of recovery sequences

Post-fire recovery sequences for the ground vegetation have been established for several different regions of northern Canada but large differences between these sequences and the Abitau-Dunvegan lake situation (Table 11) are evident. For example, Ahti (1959) and Bergerud (1971) independently examine mixed black spruce and balsam fir (Abies balsamea)-lichen woodland in Newfoundland. They recognize a five stage recovery sequence of the ground vegetation. The ground is bare up to 3 years. Between 3 and 10 years after fire, crustose lichens, primarily Lecidea spp., are most abundant with the shrubs Kalmia angustifolia, Rhododendron canadense and Vaccinium angustifolium becoming abundant and remaining so up to 60 years. Cladonia crispata, C. deformis and C. cristatella are most abundant between 10 and 25 years which is followed by lichen mats dominated by Cladonia mitis, C. rangiferina and C. mitis up to 80 years after burning. Cladonia stellaris is the last to achieve dominance forming mats with feather mosses in woodland greater than 80 years old. In the Abitau-Dunvegan situation, the species of the tree canopy, vascular plants and cryptograms are very different. Polytrichum piliferum Stereocaulon paschale and Vaccinium vitis-idaea are very abundant in the N.W.T. but are unimportant in the lichen woodland in Newfoundland. In addition, the Cladonia stellaris mats in the older woodlands in Newfoundland are much more luxuriant, attaining thicknesses averaging 13.2 cm compared

Table 11. A summary of the recovery sequence of the ground layer vegetation on the drumlins.

Post-fire Time Interval (yrs)	Dominant Species	Associated Species
0-25	Polytrichum piliferum	Cladonia botrytes Lecidea uliginosa Cladonia cristatella Lecidea granulosa
26-75	Cetraria nivalis Cladonia stellaris	Cladonia amaurocraea Cladonia coccifera Cladonia uncialis Cetraria islandica Cladonia gracilis Cladonia cornuta Cladonia crispata Cladonia gonecha
76-175	Stereocaulon paschale	Vaccinium myrtilloides
>176	Vaccinium vitis-idaea Ptilidium ciliare	Peltigera scabrosa Cladonia rangiferina Dicranum spp. Pleurozium schreberi Hylocomium splendens Ptilium crista-castrensis Ledum groenlandicum

with about 3 or 4 cm on the drumlins. These differences, as well as the apparently faster rate of recovery in Newfoundland, are probably due to differences in flora, geomorphological features and climate. The terrain of Newfoundland, with mountains up to 2700 feet high in the west and decreasing to 700 feet above sea level in the east, is much rougher than the Abitau-Dunvegan Lake region. In addition, the climate of Newfoundland, with a mean annual temperature of 0 to 5°C, an annual temperature range of only 20°C and an annual precipitation ranging from 150 cm in the south to 75 cm in the north, is oceanic and contrasts with the continental type climate in the N.W.T.

As one further example, Scotter (1964), working only 100 miles to the southwest of the Abitau-Dunvegan lakes area in northern Saskatchewan (50° to 60°N, 104° to 106°W), identifies a three phase sequence of recolonization following fire (Tables 12, 13 and 14) which is clearly different from the sequence currently reported. On the drumlins, the earlier stages of recovery are dominated by _Polytrichum piliferum_ and _P. juniperinum_ whereas Scotter's early stage of recovery includes a variety of additional bryophyte species, for example _Ceratodon purpureus_ and _Marchantia polymorpha_, which are absent on young burns on the drumlins. In addition, there are far greater

Table 12. Dominant bryophytes present in three successional stages following forest fires (from Scotter, 1964).

First stage (1 to 10 years)

Ceratodon purpureus	Polytrichum piliferum
Polytrichum juniperinum	Marchantia polymorpha
Polytrichum juniperinum var. alpestre	

Second state (11 to 50 years)

Aulacomnium palustre	Pleurozium schreberi
Ceratodon purpureus	Polytrichum commune
Hedwigia ciliata	

Third stage (51 or more years)

Dicranum elongatum	Ptilium crista-castrensis
Dicranum rugosum	Sphagnum capillaceum
Hylocomium splendens	Sphagnum capillaceum var. tenellum
Pleurozium schreberi	
Polytrichum commune	Ptilidium ciliare

Table 13. Dominant lichens present in three successional stages following forest fires. (from Scotter, 1964).

First Stage (1 to 10 years)

Crustose
- Baeomyces rufus
- Lecidea cuprea
- Lecidea granulosa

Foliose
- Peltigera canina var. spuria

Second Stage (11 to 50 years)

Crustose
- Baeomyces rufus
- Lecidea cuprea
- Lecidea granulosa
- Ochrole hia frigida

Foliose
- Peltigera canina
- Peltigera canina var. rufescens
- Peltigera canina var. spuria

Fruticose
- Cetraria crispa
- Cetraria nivalis
- Cladonia alpicola
- Cladonia amaurocraea
- Cladonia bacillaris
- Cladonia botrytes
- Cladonia carneola
- Cladnnia coccifera
- Cladonia cornuta
- Cladonia cristatella
- Cladonia deformis
- Cladonia gracilis
- Cladonia mitis
- Cladonia pyxidata
- Cladonia pyxidata var. neglecta
- Cladonia verticillata

Third Stage
First phase (51 to 120 years)

Foliose
- Peltigera aphthosa
- Peltigera canina

Fruticose
- Cetraria crispa
- Cladonia alpestris
- Cladonia amaurocraea
- Cladonia gracilis
- Cladonia mitis
- Cladonia multiformis
- Cladonia rangiferina
- Cladonia turgida
- Cladonia uncialis
- Stereocaulon alpinum
- Stereocaulon tomentosum

Second Phase (120 or more years)

Foliose
- Nephroma arcticum
- Peltigera aphthosa
- Peltigera canina
- Peltigera canina var. ulorrhiza
- Peltigera malacea
- Peltigera pulverulenta

Fruticose
- Cladonia alpestris
- Cladonia mitis
- Cladonia rangiferina

Table 14. Dominant vascular plants in three successional stages following fire in black spruce forests (from Scotter, 1964).

First Stage (1 to 10 years)

Agrostis scabra	Equisetum sylvaticum
Calamagrostis canadensis	Poa glauca
Carex aenea	Prunus pensylvanica
Carex canescens	Ribes glandulosum
Carex deflexa	Rubus idaeus var. aculeatissimu
Corydalis sempervirens	Salix spp.
Epilobium angustifolium	
Epilobium glandulosum	

Second Stage (11 to 30 years)

Alnus crispa	Lycopodium annotinum
Arctostaphylos uva-ursi	Lycopodium companatum
Cornus canadensis	Lycopodium obscurum
Geocaulon lividum	Ribes oxyacanthoides
Juniperus communis	Salix spp.
Ledum groenlandicum	Vaccinium uliginosum
	Vaccinium vitis-idaea var. minus

Final Stage (30 or more years)

Alnus crispa	Ledum palustre var. decumbens
Cornus canadensis	Rubus chamaemorus
Empetrum sp.	Salix bebbiana
Geocaulon lividum	Vaccinium oxycoccus
Ledum groenlandicum	Vaccinium vitis-idaea var. minus

numbers of vascular species in Scotter's early stage, the most abundant being *Epilobium angustifolium* which comprises up to 60 percent of the biomass on recent burns in northern Saskatchewan. Furthermore, in the Abitau-Dunvegan situation, intermediate age burns are dominated by lichens, primarily *Cladonia* species and *Stereocaulon paschale* with the contribution by bryophytes being negligible. In Scotter's middle stage, however, although *Cladonia* lichens are also dominant and *Stereocaulon alpinum* and *S. tomentosum* are present in small amounts, *Stereocaulon paschale* appears to be rare and bryophytes common. All species occurring on the oldest burns on the drumlins are present in Scotter's final stage but again there are more species of bryophytes, lichens and vascular plants in Scotter's final stage. This contrast between the recovery sequences is not due to climate. Scotter indicates that a mean annual temperature of $-4.7^{\circ}C$ and a total annual precipitation of 32.4 cm averaged from Beaverlodge, Saskatchewan and Brochet, Manitoba for 1956, are typical of his study area and these are identical to those presently reported for the Abitau-Dunvegan area. These differences are most likely due to geomorphological differences of the two study areas and their examination. Scotter's study area can be divided into two broad types. The southwest is occupied by a monotonous flat Precambrian sandstone plain covered with glacial sand deposits while the northeast is rugged, with 300 foot high hills and ridges of exposed Pre-cambrian bedrock separated by elongated valleys containing bogs, lakes and streams. Scotter's sequence is very general as it applies to fire affected black spruce-lichen woodland growing on all of these features whereas this study examines the recovery of vegetation on one geomorphological type, drumlins, which are not nearly so numerous in northern Saskatchewan. Thus the differences between Scotter's recovery sequence and the one for the drumlins in the Abitau-Dunvegan lakes region appear to be mainly due to the geomorphological types examined. On the other hand, the contrast between the post-fire recovery of lichen woodland in Newfoundland and the N.W.T. may be due to geomorphological, climatic and floristic differences of the two areas. These comparisons emphasize the importance of considering the effects of fire in different geographical regions separately.

REFERENCES

Ahlgren, C.E. 1958. Some effects of fire on forest reproduction in northeastern Minnesota. J. Forestry 57: 194-200.

Ahlgren, I.F. and C.E. Ahlgren. 1960. Ecological effects of forest firest. Bot. Rev. 26: 483-533.

Ahti, T. 1959. Studies on the caribou lichen stands of Newfoundland. Ann. Bot. Soc. Zool. Bot. Fenn 'Vanamo', 30, I.

Ahti, T. 1964. Macrolichens and the zonal distribution in boreal and arctic Ontario, Canada. Ann. Bot. Fenn., 1, I.

Ahti, T. and R.L. Hepburn. 1967. Preliminary studies on woodland caribou range, especially on lichen stands in Ontario. Dept. Lands For. Ont. Res. rep. Wildlife, No. 74.

Anon. 1948b. Black spruce seed is a limited air traveller. U. S.D.A., Lake States F.E.S. Techn. Note No. 147.

Anon. 1948b. Woody-plant seed manual. U.S.D.A., Misc. Pub. No. 654.

Argus, G.W. 1966. Botanical investigations in Northeastern Saskatchewan: The subarctic Patternson-Hasbala Lakes region. Can. Field Nat. 78: 139-149.

Austin, M.P. and L. Orloci. 1966. Geometric models in ecology. II. An evaluation of some ordination techniques. J. Ecol. 54: 217-227.

Bergerud, A.T. 1971. Abundance of forage on the winter range of Newfoundland caribou. Can. Field Nat. 85: 39-52.

Bryson, R.A., W.N. Irving and J.A. Larson. 1965. Radiocarbon and soil evidence of former forest in the southern Canadian tundra. Science 147 (3653): 46-48.

Clements, F.E. 1910. The life history of lodgepole burn forests. U.S. Forest Service, Bull. 79: 56.

Day, R.J. 1972. Stand structure, succession, and use of southern Alberta's Rocky Mountain forest. Ecology 53 (3): 472-478.

Fraser, E.M. 1956. The lichen-woodlands of the Knob Lake area of Quebec/Labrador. McGill Subaractic res. paper, I,3.

Frissel, S.S. Jr. 1973. The importance of fire as a natural ecological factor in Itasca State Park, Minnesota. Quat. Res. 3: 397-407.

Gittins, R. 1964. Multivariate approaches to a limestone grassland community. I. A stand ordination. J. Ecol. 53(2): 385-401.

Haig, I.T. 1938. Fire in modern forest management. J. Forestry 36: 1045-1051.

Hare, F.K. and R.G. Taylor. 1956. The position of certain forest boundaries in southern Labrador-Ungava. Geographical Bulletin No. 8.

Hielman, P.E. 1966. Change in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. Ecology 47: 826-831.

Heilman, P.E. 1968. Relationship of availability of phosphorus and cations to forest succession and bog formation in interior Alaska. Ecology 49(2): 331-336.

Holman, H.L. and H.A. Parker. 1940. Spruce regeneration. The Prairie Provences. Forestry Chron. 16: 79-83.

Horton, K.W. and J.C. Lees. 1961. Black spruce in the foothills of Alberta. Can. Dept. Forestry, For. Res. Br. Techn. Note. No. 110.

Hustich, I. 1951. The lichen woodlands in Labrador and their importance as winter pastures for domesticated reindeer Acta Geogr. 12, I.

Johnson, H.J. 1956. Some aspects of black spruce reproduction in the central Boreal Forest Region of Manitoba. Can. Dpt. Nth. Aff. and Nat. Res., For. Br. For. Res, Div. Mimco S. and M. 56-3.

Johnson, E.A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. Can. J. Bot. 53(24): 2933-2941.

Johnson, E.A. and J.S. Rowe. 1975. Fire in the wintering ground of the Berley Caribou Herd. Am. Midl. Nat. 94: 1-14.

Kareev, G.T. 1968. Reindeer fodder resources. In P.S. Zhigunox editor. Reindeer Husbandry. 129-176.

Kärenlampi, L. 1971. Studies on the relative growth rate of some fruticose lichens. Rep. Kevo Subarctic Res. Stat. 7: 33-39.

Kayll, A.J. 1968. The role of fire in the boreal forest of Canada. Canada Department of Forestry and Rural Development, For. Br., Petawawa Forest Experiment Station Information Report PS-X-7.

Kershaw, K.A. 1964. Quantitative and dynamic plant ecology. Edward Arnold, London.

Kershaw, K.A. 1968. Classification and ordination of Nigerian savanna vegetation. J. Ecol. 56: 467-482.

Kershaw, K.A. and W.R. Rouse. 1973. Studies on lichen-dominated systems. V. A primary survey of a raised-beach system in northwestern Ontario. Can. J. Bot. 51: 1285-1307.

Kershaw, K.A., W.R. Rouse and B.T. Bunting. 1975. The impact of fire on forest and tundra ecosystems. INA publication No. QS-8038-000-EE-A1.

Kershaw, K.A. and R.W. Shepard. 1972. Computer display graphics: principal component analysis and vegetation ordination studies. Can. J. Bot. 50: 2239-2250.

Krause, H.H., S. Rieger and S.A. Wilde. 1959. Soil and forest growth on different aspects in Tanana watershed of interior Alaska. Ecology 40: 492-495.

Lambert, J.D.H. and P.F. Maycock. 1968. The ecology of terricolous lichens of the Northern Conifer - Hardwood forests of central Eastern Canada. Can. J. Bot. 46: 1043.

Larson, D.W. and K.A. Kershaw. 1974. Studies on lichen-dominated systems. VII. Interaction of the general lichen-heath with edaphic factors. Can. J. Bot. 52: 1163-1176.

Le Barron, R.K. 1940. The role of forest fires in the reproduction of black spruce. Minn. Acad. Sci., Proc. 7; 10-14.

Lechowicz, M.J. and M.S. Adams. 1974a. Ecology of Cladonia lichens. I. Preliminary assessment of the ecology of terricolous lichen-moss communities in Ontario and Wisconsin. Can. J. Bot. 52: 55.

Linteau, A. 1957. Black spruce reproduction on disturbed soil conditions. Can. Dept. Nth. Aff. and Nat. Res., For. Br. Tech. Note No. 54.

Little, S. 1953. Prescribed burning as a tool of forest management in the northeastern states. J. Forestry 51: 496.

Logan, K.T. 1961. Progress report on Project P-388. Response of tree seedlings to four light intensities. Can. Dept. Forestry, Petawawa F.E.S., File Report.

Lutz, H.J. 1956. Ecological effects of forest fire in the interior of Alaska. U.S. Forest Service Technical Bulletin 1133: 121.

MacArthur, J.D. and D. Gagnon. 1959. Some observations of forest conditions after fire in the Gaspe Peninsula. Can. Dept. Nth. Aff. and Nat. Res., For. Br., For. Res. Div. Mimeo 59-14.

MacLean, D.W. and G.H.D. Bedell. 1955. Northern Clay Belt growth and yield survey. Can. Dept. Nth. Aff. and Nat. Res., For. Br. Techn. Note. No. 20.

Neal, M.W. and K.A. Kershaw, 1973a. Studies on lichen-dominated systems. III. Phytosociology of a raised beach system near Cape Henrietta Maria, northern Ontario. Can. J. Bot. 51: 1115-1125.

Neal, M.W. and K.A. Kershaw. 1973b. Studies on lichen-dominated systems. IV. The objective analysis of Cape Henrietta Maria raised-beach systems. Can. J. Bot. 51: 1177-1190.

Orloci. L. 1967. Data centering: a review and evaluation with reference to component analysis. Syst. Zool. 16: 208-212.

Persson, A. 1964. The vegetation at the margin of the receding glacier Skaftafèllsjökull, SoutH eastern Iceland. Bot. Notiser 117: 323.

Place, I.C.M. 1955. The influence of seedbed conditions on the regeneration of spruce and balsam fir. Can. Dept. Nth. Aff. and Nat. Res., For. Br. Bull. 117.

Ritchie, J.C. 1959. The vegetation of northern Manitoba III. Studies in the subarctic. Arctic Institute of North America Technical Paper No. 3.

Rouse, W.R. 1976. Microclimatic changes accompanying burning in subarctic lichen-woodland. Arctic and Alpine Res. (In press).

Rowe, J.W. 1972. Forest regions of Canada. Dept. Environ. Can. For. Serv. Publ. 1300.

Rowe, J.S., J.L. Bergsteinsson, G.A. Padbury and R. Hermesh. 1973-74. Fire studies in the Mackenzie Valley. Dept. Ind. Aff. and Nth. Dev., Nth. Econ. Dev. Br., Arctic Land Use Res. Program.

Rowe, J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quat. Res. 3: 444-464.

Scotter, G.W. 1964. Effects of forest fires on the winter range of barren-ground caribou in northern Sask. Can. Wildlife Service, Wildlife Management Bulletin, Series 1, No. 18.

Scotter, G.W. 1970. Wildfires in relation to the habitat of
of barren-ground caribou in the taiga of northern Canada. In "Proceedings,Tenth Annual Tall Timbers Ecology Conference" (E.V. Komarek, Ed.) 85-105. Tallahassee, Florida.

Scotter, G.W. and J.W. Thompson. 1966. Lichens of the Thelon River and Kaminuriak Lake regions, Northwest Territories. The Bryologist 69(4): 497-502.

Shafi, M.I. and G.A. Yarranton. 1973. Vegetational heterogeneity during a secondary (post-fire) succession. Can. J. Bot. 51: 73-90.

Slaughter, C.W., R.J. Barney and G.M. Hansen (eds). 1972. Fire in the northern environment - a symposium. U.S. For. Serv. Pac. Northwest For. Range Exp. Stn. 275.

Smith, D.W. and J.H. Sparling. 1966. The temperatures of surface firest in jack pine barren. I. The variation in temperature with time. II. The effects of vegetation cover, wind speed, and relative humidity on fire temperatures. Can. J. Bot. 44: 1285-1298.

Spurr, S.H. 1954. The forests of Itasca in the nineteenth century as related to fire. Ecology 35: 21-25.

Stanek, W. 1961b. Natural layering of black spruce in northern Ontario. Forestry Chron. 37: 245-258.

Swain, A.M. 1973. A history of fire and vegetation in north-eastern Minnesota as recorded in lake sediments. Quat. Res. 3: 383-396.

Thomas, D.C. 1969. Population estimates of barren-ground caribou March to May, 1967. Can. Wildlife Service Report, Series No. 9.

Tucker, R.E. and J.M. Jarvis. 1967. Prescribed burning in a white spruce-trembling aspen stand in Manitoba. Woodlands Review (July): 333-335.

Van Wagner, C.E. 1970. Fire and red pine. Proc. 10th Annual Tall Timbers Fire Ecol. Conf. 211-214.

Viereck, L.A. 1973. Wildfire in the taiga of Alaska. Quat. Res. 3: 465-495.

Vincent, A.B. 1965. Black spruce - a review of its silvics, ecology and silviculture. Can. Dept. of Forestry Publication No. 1300.

Wilton, W.C. 1963. Black spruce seedfall immediately following fire. Forestry Chron. 39: 477-478.

Wright, H.E.,jr. and M.L. Heinselman (eds.) 1973. The ecological role of fire in natural conifer forests of western and northern America - a symposium. Quat. Res. N.Y. 3: 317-513.

Yarranton, G.A. 1975. Population growth in Cladonia stellaris (Opiz.) Pouz. and Vezda. New Phytol. 75: 99-110.

Zasada, J.C. 1971. Natural regeneration of interior Alaska forests - seed, seedbed and vegetative reproduction considerations. In "Proceedings, fire in the northern environment - a symposium": 231-246. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.