



Promoting the Science of Ecology

Vegetation Organization and Dynamics of Lichen Woodland Communities in the Northwest Territories, Canada

Author(s): E. A. Johnson

Source: *Ecology*, Vol. 62, No. 1 (Feb., 1981), pp. 200-215

Published by: Ecological Society of America

Stable URL: <http://www.jstor.org/stable/1936682>

Accessed: 30/12/2008 13:57

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=esa>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

VEGETATION ORGANIZATION AND DYNAMICS OF LICHEN WOODLAND COMMUNITIES IN THE NORTHWEST TERRITORIES, CANADA¹

E. A. JOHNSON

Department of Biology, University of Calgary, Calgary, T2N 1N4 Canada

Abstract. The variances of species abundances from 141 upland stands are partitioned into habitat and fire frequency. Principal components analysis is then performed on each of these partitions. The habitat ordination has a topographic–canopy coverage gradient and a nutrient gradient. The fire frequency ordination has one gradient which orders species according to their temporal response after fire, from shorter lived, faster growing, competitively poor species to longer lived, slower growing, competitively effective species. The fire frequency ordination interacts with the habitat ordination by changing a site's canopy cover for approximately 10 yr after fire. The nutrient gradient is only slightly affected by the fire frequency.

The recovery of vegetation after fire is explained by using the information on the adaptation of species as shown in the two ordinations and from existing life-history information. Most species found in older stands are present in the first years after fire. Recovery by vascular plants, mosses and lichens is by vegetative reproduction and invasion by propagules. Buried viable seeds play little role in recovery. Lichen abundance is best explained by different habitat requirements rather than successional sequences or caribou grazing. Feather mosses are most abundant in specific sites which develop closed canopies and have greater soil nutrients.

The habitat and fire frequency ordinations represent two environmental complexes for which species are adapted, and consequently these are also the two predominant levels of vegetation dynamics. The fire frequency ordination represents shorter term dynamics which cause changes primarily in abundance but not species composition. The habitat ordination represents longer term dynamics which cause major changes in species composition.

Key words: *dynamics; feather mosses; fire; lichens; Northwest Territories, Canada; ordination; Picea glauca; Picea mariana; Pinus banksiana; subarctic; succession; vegetation organization.*

INTRODUCTION

There are two main dimensions in the pattern of vegetation, spatial and temporal. The recognition of different habitats and vegetation types is related to the spatial dimension, and the recognition of pioneer, temporary, ruderal, old growth or pristine vegetation is related to the temporal dimension. Traditionally, in order to study one dimension ecologists have tried to hold the other dimension constant.

In recent years the study of the spatial dimension using geographic transects has been superseded by techniques collectively called gradient analysis or ordination (Whittaker 1967). Ordinations do not presume that the geographic location of a stand or sample is itself of interest, but that the environmental or population variables associated with the location are. Thus the gradients of an ordination are the ordered similarities of the variables and not the ordered geographic locations on a transect. The resulting gradients describe generalized environmental and vegetational trends and are not related to any specific geographic catena.

The purpose of this paper is to describe the spatial and temporal dimensions of upland subarctic vegetation using gradient analysis. The approach differs from

other gradient analysis studies of the temporal dimension (e.g., Goff 1968, Goff and Zedler 1972, Peet and Loucks 1977) in that it uses the ages of the stands since fire as a concomitant variable of the temporal dimension. This collateral variable is used to partition the total variation of the species abundance into spatial and temporal dimensions. Principal components analysis is then performed on both the spatial and temporal partitions separately.

The spatial principal components give results similar to a traditional gradient analysis in which the effect of the temporal dimension in the data has been minimized by choosing stands of similar age since disturbance. The temporal principal component consists of the ordering of species and stands according to the interval between fires, without any reference to habitat difference. It describes the use of the time between fires as a resource.

STUDY AREA

The vegetation sampled is in a 105 000 km² area of the western subarctic forest east of Great Slave Lake, Northwest Territories, Canada, extending from 60°N latitude north to tree line and from longitude 104°W to 112°W (Fig. 1). The bedrock consists mainly of Archaean crystalline basement with Proterozoic intrusives composed primarily of granites, gneisses, and granodiorites. This is overlain by glacial deposits. The

¹ Manuscript received 13 May 1979; revised 4 February 1980; accepted 12 February 1980.

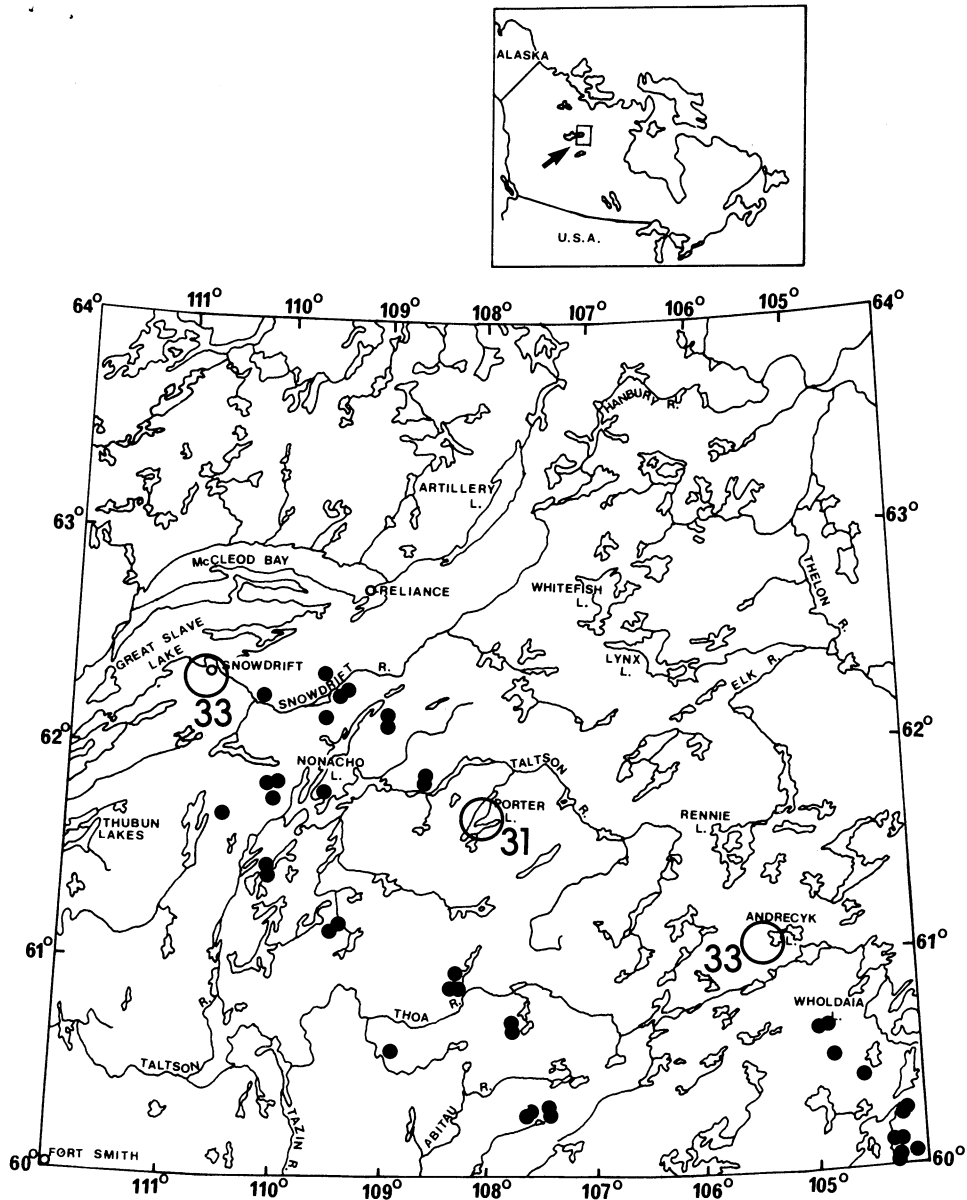


FIG. 1. Map showing the general location of the 141 stands in this study. Circled areas contain the indicated number of stands.

area is divided at approximately 110°W longitude, with a western half covered with thin ablation till and many bedrock exposures and an eastern half covered with thicker till, fewer bedrock exposures, long esker trains, outwash and numerous drumlins.

The region has a humid continental climate with short cool summers, long cold winters and slightly more precipitation during summer than winter. The mean January temperature at Fort Smith is -26° C, the mean July temperature is 17°, and mean annual precipitation is 33 cm. Snow cover usually develops by the first week of October and disappears in late

April or early May. Snow may occur in any month of the year. The mean annual number of days with >2.5 cm of snow is 200 at Fort Smith.

Forest fires are a common natural occurrence (Table 1). Their incidence seems to follow a seasonal pattern, advancing from the southwest towards tree line in the summer and retreating in the fall. This leads to the recurrence of more and larger fires in the southwest and few and smaller ones in the northeast.

The seasonal patterns of lightning fires appear to be related to the conditions associated with air masses and their movements. Lightning storms usually occur

TABLE 1. Summary of forest fires during 1966–1975 for the study area. Month indicated is that in which the fire started.

	April	May	June	July	August	September	Total
Number of man-caused fires	1	5	13	18	13	1	51
Number of lightning-caused fires	0	2	101	150	93	1	347
Total number fires	1	7	114	168	106	2	398
Area of man-caused fires (ha)	5	11	854	83	19	0.5	971
Area of lightning-caused fires (ha)	0	0	102 313	502 956	76 521	0.5	681 791
Total area burned (ha)	5	11	103 166	503 039	76 540	1	682 762

in areas under the influence of maritime Pacific air either in convective systems or along fronts with the Arctic air mass (Johnson and Rowe 1975).

The study area includes parts of the Northwestern Transition (B.27) in the Halliday classification (Rowe 1972). This vegetation belt corresponds to the type Hustich (1949) and Hare (1950) recognized east of Hudson Bay as Open Boreal Woodland or Taiga.

The general physiognomy of the vegetation is as follows. Upland sites are mostly dominated by closed or open forests of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*). White spruce (*Picea glauca*) is common on coarse-textured materials (outwash sand plains and esker ridges), on alluvium adjacent to moving water and on lacustrine deposits adjacent to Great Slave Lake. Aspen (*Populus tremuloides*) is not conspicuous except towards the south. White birch (*Betula papyrifera*), on the other hand, is common throughout the forested area and extends into the tundra. Lowland sites are generally dominated by black spruce, accompanied in considerably less abundance by tamarack (*Larix laricina*). Towards the tree line in the forest-tundra zone, polygonally patterned peaty ground appears.

Little work has been done on the vegetation in the western subarctic. Maimi (1966) studied an island near tree line at the eastern side of the area, Larsen (1971) describes several communities in the Fort Reliance-Artillery Lake area and Argus (1966) briefly lists the plant communities just south of 60°N latitude in Saskatchewan.

Studies of succession in the subarctic are also few. Ritchie (1958, 1959), working in the subarctic of Manitoba, has had perhaps the greatest influence on the thinking of subsequent work on succession. On mesic upland sites he postulates a succession from white birch-willow, to open jack pine, to open pine-black spruce, to mixed spruce-birch. He considers the climax forest to be a closed black spruce forest with a ground cover of feather mosses (*Pleurozium schreberi*, *Hylocomium splendens*, *Ptilium cristacastrensis* and *Dicranum* spp.). He also recognizes edaphic climaxes of jack pine on sand and bedrock. Scotter (1964, 1965, 1968) worked in the Stony Rapids area of Saskatchewan and Taltson River region of the study area. His view of succession is modified from Ritchie

(1958) except that he favors open black spruce as the present self-perpetuating stage. However, he believes that white spruce might be the ultimate climax if fire protection were maintained for a long enough period of time. Maikawa and Kershaw (1976) and Kershaw (1977), working on drumlins in the south central part of the study area, have identified four stages of succession after fire and suggest that the final stage is closed black spruce-feather moss forest.

The only other successional study of interest is by Raup (1930) on the sand plains adjacent to Great Slave Lake near Fort Reliance. He describes the physiographic succession from newly emerged sandy beaches to spruce-lichen woodland on old beach terraces.

SAMPLING METHODS

One hundred and forty-one stands of vegetation were sampled in the present study. Criteria for selection of a stand were: (1) that the vegetation be rooted in mineral soil and/or there be no evidence of standing water in the top 30 cm; (2) that the area sampled be a minimum of 4 ha and the vegetation composition be visually homogeneous; and (3) that burned areas of all ages be sampled but areas disturbed by man (e.g., camp and cabin sites, tree cutting, etc.) be avoided.

For each stand information was collected on vegetation composition and structure, physical environment, and age and fire history. The vegetation was divided into "trees" (≥ 2 cm DBH) and "herbs-shrubs-lichens" (< 2 cm DBH). Trees were sampled with the wandering quarter method (Clausen 1957, Catana 1963, Batcheler 1971), using 10–15 points (50–75 trees), with each point followed by three distances (30–45 distances). The wandering quarter method was used because most of the trees are clumped (Fig. 2). Herbs-shrubs-lichens were sampled for frequency in 10–20 0.06-m² quadrats, located regularly along the transect of the wandering quarter method in each stand. A larger number of quadrats or points was used in younger stands where the abundance of plants was low and hence more samples were needed to reduce the standard error.

The 31 species used in the analysis are those occurring in 25% or more of the stands. The herbs-shrubs-lichens abundance is defined by frequency and the trees abundance by a synthetic index of frequency,



FIG. 2. General view of a black spruce-lichen woodland. The ground is covered with *Stereocaulon paschale* and *Cetraria* sp. The dark patches on the ground are clones of *Empetrum nigrum*. Note the layering around the bases of the black spruce (*Picea mariana*). This stand last burned 153 yr ago.

density and basal area. The synthetic index used here is a linear combination of these three variables, subject to the constraints that the variance of the index be a maximum and that the sums-of-squares correlation between the index and the variable be a maximum (Waugh 1962). This approach should reduce redundancy in the index.

Stand age and fire history were carefully documented. For stands <10 yr old, dates of fires were obtained from Indian and Northern Affairs fire records. For older stands the time since fire was determined by dating several of the largest trees plus the fire scars found on trees in the stand. With some diligence fires could be dated to within 5 yr. In all stands some signs of fire were found. It would appear that very few upland stands escape fire for longer than 200 yr (see Johnson 1979).

The environment was evaluated by slope steepness, position on slope, soil-water-retention capacity (Wilde and Voigt 1955), depth to mottling, gleying and bedrock, stoniness, amount of bedrock exposed, depth to

permafrost (if present), soil texture, humus type (Hoover and Lunt 1952) and soil profile characteristics. Soil was sampled from the top 15 cm (minus the litter layer) in three pits in each stand. These three samples were mixed and a final sample from this mixture removed and air dried. Using standard methods, detailed chemical analyses for pH, conductivity, percent organic matter, nitrate and extractable phosphate, calcium, potassium and magnesium were performed on samples from 23 stands by the Saskatchewan Soil Testing Laboratory, University of Saskatchewan. Topographic location was described using the slope, aspect and geographic location to calculate the potential direct short wave radiation (cf. Furnival et al. 1969, Buffo et al. 1972). Canopy cover was estimated visually over each quadrat.

NUMERICAL METHODS

The first step in the analysis was to partition the abundance of the species populations into two determinants of pattern, namely spatial or habitat, and temporal or interval between fires. Partitioning is necessary; otherwise the ordination, which assumes that the structure in the data is due to one type of pattern, will be confounded.

Ordination techniques are concerned with the relationship *within* a set of variables, i.e., that the data matrix has already been decomposed into a homogeneous set of variables. If multimodality is known to exist or if different kinds of processes are believed to be operating on the variables, then dissection of the frequency distributions into more homogeneous distributions by *between* group univariate or multivariate techniques is in order. When this dissection is not performed before the ordination, the high variation among stands will result in large error variability. In ordinations the mixed population effect is signified by definite clustering of the stands.

In order to partition the species abundance, the "age of each stand since its last fire" is used as a concomitant variable. The removal of this variation is accomplished by the equation:

$$Y = X\Gamma + E$$

where Y is the $n \times s$ matrix of stands (n) by species (s), X is $n \times 1$ vector of stand ages, Γ is a $1 \times s$ vector of regression coefficients, and E is a $n \times s$ matrix of deviations from the regression. The rows (stands) of E are assumed to be independent and the columns (species) to be random normal vectors. The equation implies that the relationship between species abundance and stand age is linear, yet this is not usually the case. However, a higher order equation did not improve the fit enough to justify the added complication with these particular data.

If X and Y are both standardized, their sums of products become correlations which may be partitioned as follows:

$$(XY)'(XY) = \begin{array}{c|c} X'X_{1 \times 1} & X'Y_{1 \times s} \\ \hline Y'X_{s \times 1} & Y'Y_{s \times s} \end{array}$$

stand age correlation stand age × species correlation

$$= \begin{array}{c|c} \text{species} \times \text{stand age} \\ \text{correlations} & \text{species} \\ & \text{correlations} \end{array}$$

The matrix of regression coefficients is:

$$\Gamma = (X'X)^{-1}X'Y$$

and the matrix of residuals (estimated E) is:

$$R = Y'Y - Y'\Gamma X$$

where the $s \times s$ matrix R is a correlation matrix formed from the correlation matrices of Y subtracted from the predicted Y given the stand ages X . Thus R is a species correlation matrix in which the variation due to stand age has been removed from the original Y matrix.

Following a similar argument the residual can be obtained from the unstandardized data, in which case a matrix of stands by species results where the variation due to stand ages has been removed. The residual from both the standardized and unstandardized data will be called habitat.

The second step in the analysis was to perform a principal components analysis on the habitat residual. This analysis is used because it gives both species and stand ordinations and is mathematically (conceptually) understood. The drawbacks and limitations of principal components for vegetation data are well known (Whittaker and Gauch 1973). The data used here consist of species which are found along most of the gradients and are mostly of similar height (physiognomy). Beta diversity along all gradients is low.

The third step in the analysis was to obtain the fire frequency partition. The simplest and most efficient method of doing this is to perform a principal components analysis on the unpartitioned data (the Y in the first equation in this section), and then to subtract species loadings or stand scores from their counterparts in the habitat principal components analysis. However, before the difference of these two principal components can be taken, the habitat principal components analysis is rotated onto the unpartitioned principal components analysis. The rotation ensures the best congruence between the two analyses.

The linear transformation (rotation) of the habitat species loadings onto the unpartitioned species loadings used was:

$$\beta = (L^H L^H)^{-1}(L^H L^U)$$

where β is a matrix of transformation coefficients, L^H is a matrix of components by species for the habitat

partitioned loadings and L^U is a matrix of species by components for the unpartitioned loadings.

By multiplying the habitat species loading by the transformation coefficients, the rotated species loadings of the habitat partitioned data are obtained.

$$L^H = L^H \beta$$

where L^H is the matrix of species by components for the rotated habitat species loadings. A correlation coefficient of 0.93 (significant at $\alpha = .01$) for both components between the rotated habitat partitioned species loadings and the unpartitioned species loadings indicates the efficiency of the transformation and also the configurational similarity. This large similarity indicates the greater importance, in accounting for the variation in the species abundance, of the habitat ordination than of the fire frequency ordination.

RESULTS

Habitat principal components analysis

The habitat principal components ordination gives a triangular-shaped distribution of both species and stands (Figs. 3 and 4). The first component has stands with high loadings for lichens (*Cladonia*, *Cetraria* and *Stereocaulon*) at one end and low loadings for *Ceratodon purpureus* and *Epilobium angustifolium* at the other end. The center of the first component is then drawn out by the second component, with the negative end of the first having high loadings for *Epilobium angustifolium*, *Hylocomium splendens*, *Ceratodon purpureus*, and *Picea mariana*. The four tree species are found generally on the three sides of the triangle, with *Picea mariana* and *Picea glauca* close together on the left side, *Betula papyrifera* on the bottom and *Pinus banksiana* on the right side (Fig. 3). Fig. 4 gives an approximate division of the stand ordination by canopy and understory dominants. Community types are readily separated. The tree canopy (as measured in percent cover) is unrelated to stand age ($r = .03$).

The presence of burned stands on the left of Fig. 4 indicates the interaction of the fire frequency ordination with the habitat ordination. The stands demarcated as burned <10 years since fire in this figure have *Epilobium*, *Ceratodon* and *Polytrichum* with high loadings. The remaining species in these stands represent an eclectic group which seems to reflect survival and regeneration from the prefire vegetation. The interaction can best be demonstrated by examining in Fig. 5 the change in stand position between the habitat ordination and the ordination of the unpartitioned data (i.e., Y in the Numerical Analysis). The first component of the habitat ordination is replaced in the unpartitioned data ordination by a division into young stands (<10 yr) on the left and all other stands on the right. The second component of the habitat ordination remains more or less unaffected on the unpartitioned data ordination. The unpartitioned data ordination



FIG. 3. The species loadings of the habitat principal component analysis. The loadings are determined by differences in variation among species due to the habitat and not variation related to interval between fires. Numbers correspond to species listed below: (1) *Picea glauca* (Moench.) Voss. (2) *Betula papyrifera* Marsh. (3) *Pinus banksiana* Lamb. (4) *Picea mariana* (Mill.) Britt., Sterns and Pogg. (5) *Cladonia amaurocraea* (Forke.) Shaer. (6) *Cladonia arbuscula* (Wallr.) Rabh. (7) *Cladonia coccifera* (L.) Wield. (8) *Cladonia cornuta* (L.) Hoffm. (9) *Cladonia gracilis* (L.) Willd. (10) *Cladonia mitis* Sondst. (11) *Cladonia rangiferina* (L.) Hoffm. (12) *Stereocaulon paschale* (L.) Hoffm. (13) *Cetraria islandica* (L.) Ach. (14) *Cetraria nivalis* (L.) Ach. (15) *Peltigera malacea* (Ach.) Funck. (16) *Ceratodon purpureus* (Hedw.) Brid. (17) *Dicranum fuscenscens* Turn. (18) *Dicranum polysetum* Sw. (19) *Hylocomium splendens* (Hedw.) BSG (20) *Pleurozium schreberi* (Bridg.) Mitt. (21) *Polytrichum juniperinum* Hedw. (22) *Polytrichum piliferum* Hedw. (23) *Ptilidium ciliare* (L.) Hampe. (24) *Picea mariana* (Mill.) Britt., Sterns & Pogg. (seedling) (25) *Geocaulon lividum* (Richards) Fern. (26) *Empetrum nigrum* L. (27) *Epilobium angustifolium* L. (28) *Arctostaphylos uva-ursi* (L.) Spreng. (29) *Ledum groenlandicum* Oeder. (30) *Vaccinium uliginosum* L. (31) *Vaccinium vitis-idaea* L.

shows the pronounced clustering of stands characteristic of mixed population effects.

Component 1 describes an environmental gradient of topographic position, direction and substrate. In order to evaluate the direction and angle of slopes on which stands were found, the potential direct short-wave radiation was calculated (cf. Geiger 1965, Buffo et al. 1972). As can be seen in Fig. 6 the average solar radiation values are low for all parts of the gradient as is to be expected for a region 61°N latitude and 50–150 km from tree line. The open canopy black spruce-lichen and jack pine-lichen communities (divisions 1–4) are found on horizontal surfaces or south-facing slopes, whereas black spruce-white birch-lichen and black spruce-white spruce-feather moss communities (divisions 5–7) are found on northerly slopes. Divisions 8 to 10 contain mostly burned stands <10 yr old. They occupy a diversity of slope positions, directions

and angles as is indicated by their large confidence intervals.

Soil texture and landforms change on component 1 (Fig. 6) from sandy outwash and till in open black spruce-lichen and open jack pine-lichen, to loamy sand till in open black spruce-glandular birch-lichen, to sandy loam till in open black spruce-birch-lichen, to silt loam till and lacustrine in closed black and white spruce-feather moss. Again, the burned stands of divisions 8–10 contain a range of textures and landforms.

Stand slope position (Fig. 7) changes from flat to convex upper slopes in open black spruce-lichen and jack pine-lichen, to concave upper and middle slopes in open black spruce-birch-lichen, to concave lower slopes in closed black and white spruce-feather moss.

In summary, component 1 is a gradient from open canopy black spruce, jack pine-lichen communities on

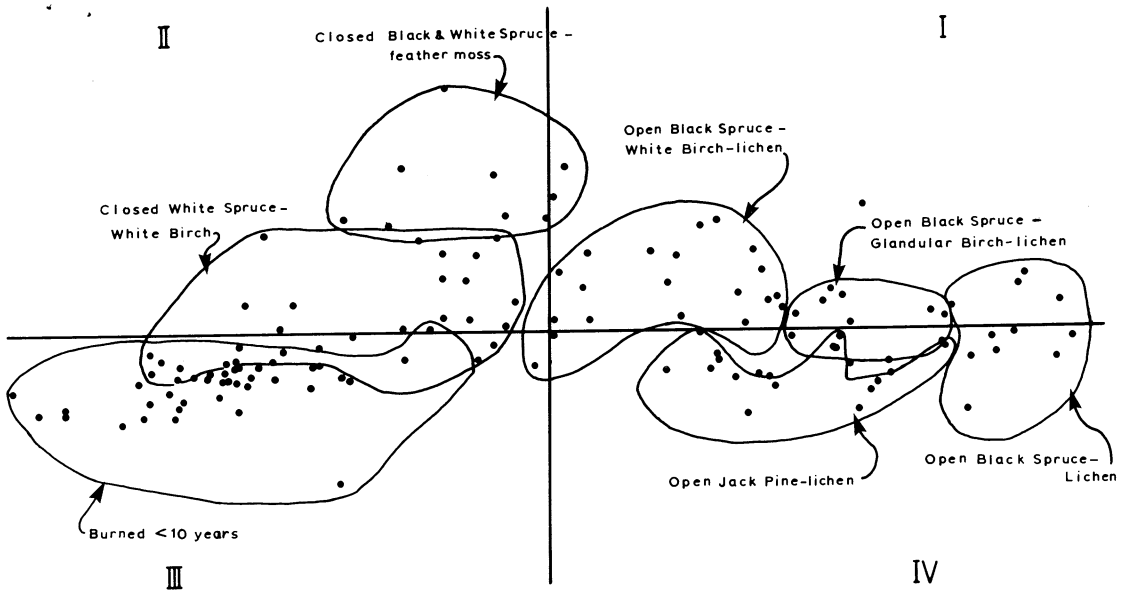


FIG. 4. The stand scores on the first two gradients of the habitat principal components analysis. The classification into communities is an arbitrary means of dividing up the gradients for ease of discussion; the divisions are based on the most abundant canopy and understory species.

upper slopes of flat or convex landforms with porous substrate and larger solar radiation input (due to slope direction and angle), to closed canopy black and white spruce-lichen communities on lower slopes of concave landforms with more impermeable substrate and lower solar radiation input.

shows the relationship of average percent organic matter, pH, conductivity, available phosphate, calcium and nitrate for 23 samples spread along the gradient. The feather moss communities are located in division 1 and 2 and show much higher nutrient levels with high organic content in the surface 15 cm, higher nitrate, phosphate, calcium concentration, conductivity

Component 2 describes a nutrient gradient. Fig. 8

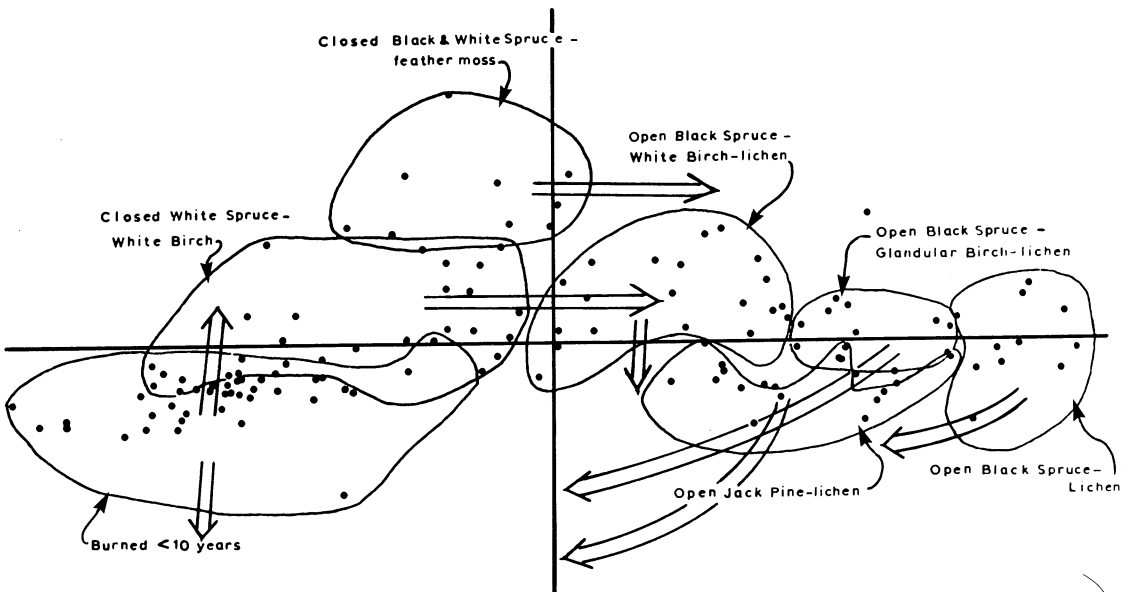


FIG. 5. A schematic diagram in which the large arrows indicate the changes in stand positions between the habitat principal components analysis (origin of arrows) and the principal component analysis of the data before the differences in stand ages had been removed. Note the relatively larger change in the stand ordering of habitat component one and lesser change in component two.

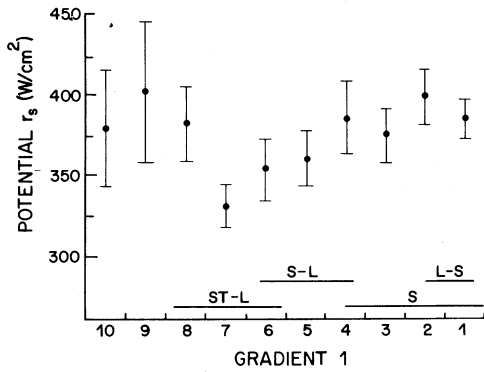


FIG. 6. The average potential shortwave radiation (r_s) (June equinox) with 90% confidence intervals, and ranges of soil texture along divisions of the first habitat gradient. The divisions on the gradient go from left to right on gradient 1 in Fig. 4, i.e., divisions 8, 9 and 10 include "Burned < 10 years" stands and "Closed White Spruce-White Birch" stands. ST-L:silt loam; S-L:sandy loam; L-S:loamy sand; S:sand.

and pH. Evidently their generally basal slope position results in more seepage water and consequently in a better supply of nutrients. The higher organic content may also be indicative of slower decomposition. Higher soil exchange capacities allow the retention of more nutrients.

At the other end of the gradient (divisions 3-5) the soil is more sandy. The stands consequently have low pH and conductivity and relatively low nutrient availability. These communities are dominated by black spruce and jack pine with a ground cover of lichens.

Fire frequency principal component analysis

This ordination gives a one-dimensional distribution of both species loadings and stand scores (Figs. 9 and

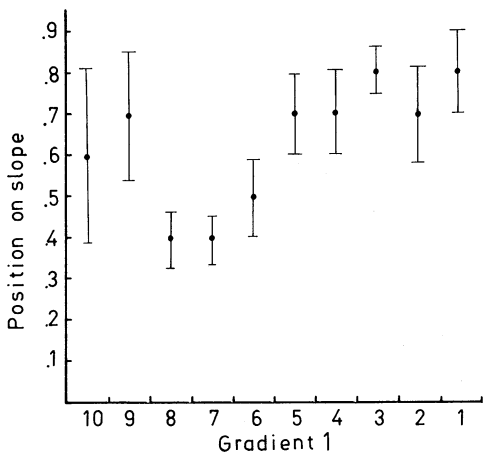


FIG. 7. The average slope position with 90% confidence intervals on the first habitat gradient; 0.1 represents the base of the slope; 0.9 represents either top of slope or level. See Fig. 6 for meaning of gradient divisions.

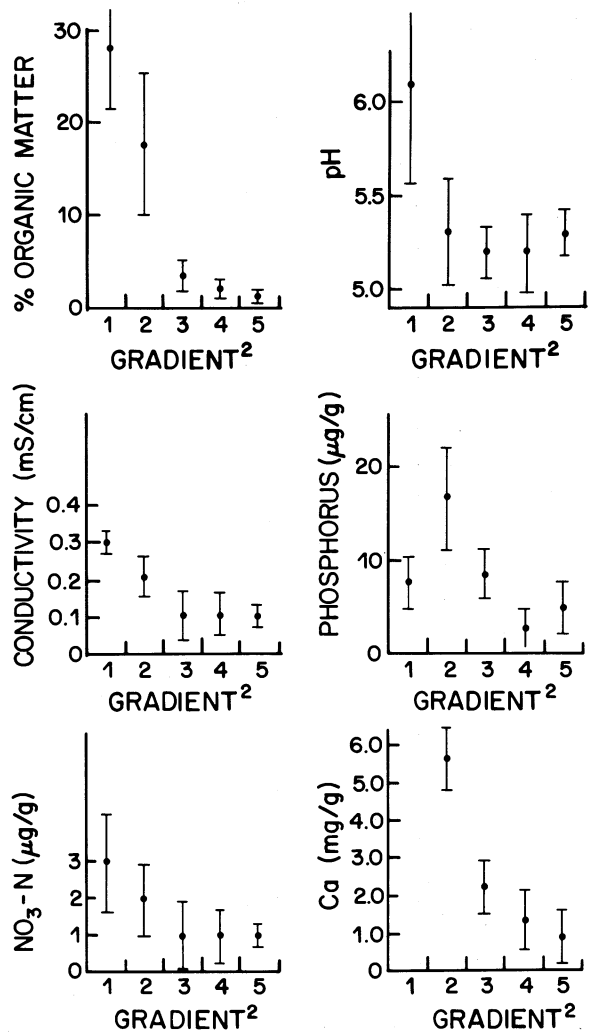


FIG. 8. Substrate characteristics across the second habitat gradient. The divisions on the gradient go from top to bottom on gradient 2 in Fig. 4; i.e., divisions 1 and 2 include the closed spruce-feather moss forests. Bars give 90% confidence intervals.

10). Species at the top of Fig. 9 have abundance patterns which show rapid recovery after fire and then decline. The loadings at the bottom of the figure are species adapted to slow recovery after fire. The remaining parts of the component form a gradient of recovery strategies between these extremes. In order to aid in the interpretation of the species loadings, the chronosequences of some species have been inserted on Fig. 9. A more complete set of chronosequences is shown in Fig. 11.

The stand ordination (Fig. 10) gives the relative position of stands determined by the sum of the species abundance in the stand multiplied by their loadings. Thus stands in quadrant III of Fig. 10 have species of the "fast recovery" strategy in greater abundance. Note that the small graphs in Fig. 10 are derived from

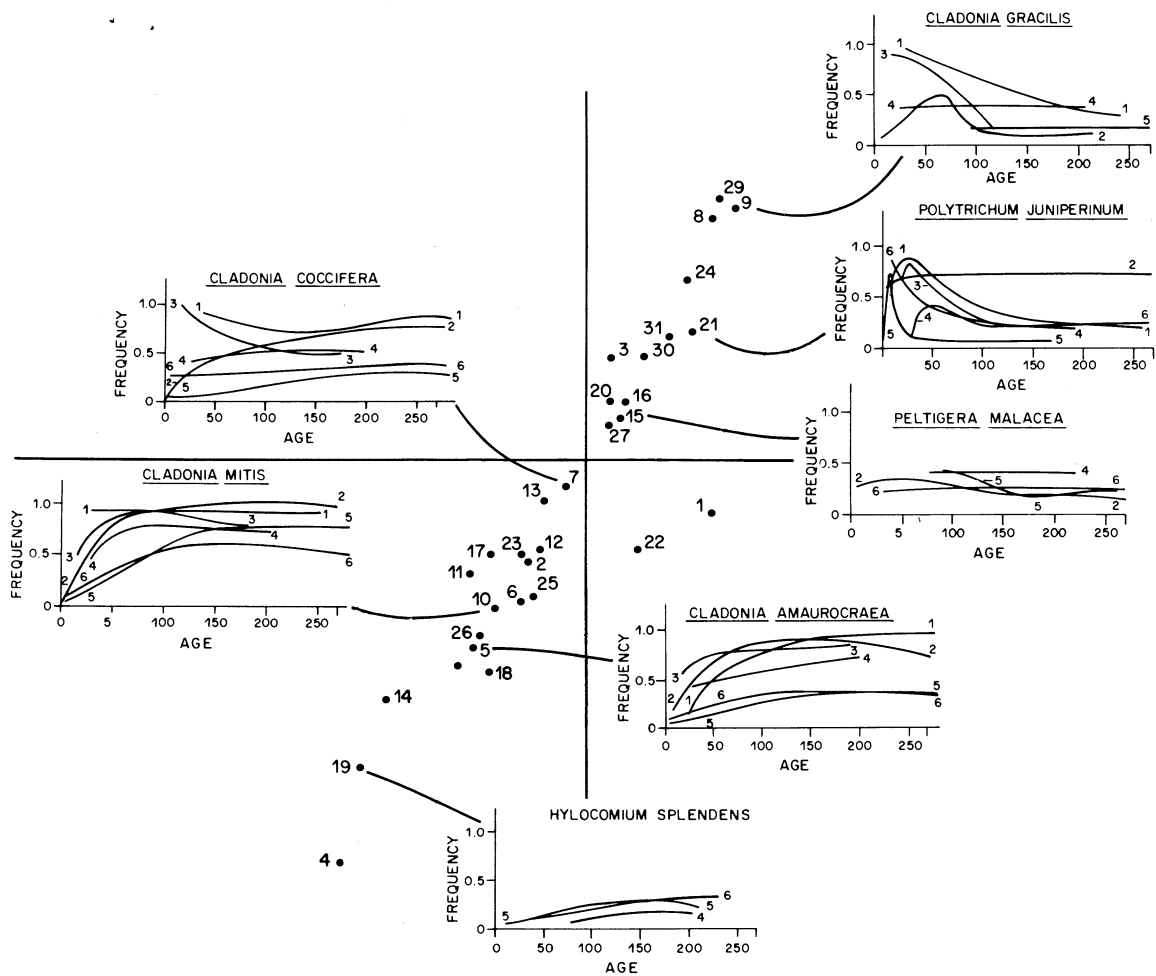


FIG. 9. The species loadings on the fire frequency principal components analysis, calculated from the differences between the principal components analysis in which the variation due to the age of the stand has been removed (habitat ordination) and the principal components analysis in which differences due to stand ages are still present (unpartitioned data). Numbers on the chronosequences correspond to the following communities: 1. Open black spruce-lichen. 2. Open jack pine-lichen. 3. Open black spruce-glandular birch-lichen. 4. Open black spruce-white birch-lichen. 5. Closed black spruce-white spruce-feather moss. 6. Closed white spruce-white birch. The numbers beside the points correspond to the species in Fig. 3.

the stand ordination and are not separate interpretations as are the chronosequences in Fig. 9.

DISCUSSION

The vegetation which occupies a site after fire can come from three sources: (1) vegetative reproduction (sprouting), (2) viable seeds buried in the soil, and (3) invasion by propagules. Add to these the differences in species growth and recovery rates, and many (but not all) of the changes in composition and abundance associated with secondary succession can be rationalized.

Of the species that increase in abundance quickly after fire (top of Fig. 9), many regenerate vegetatively. Of the 18 species of woody shrubs, 81% have some means of vegetative reproduction. The three shrubs

which occur in more stands than any other vascular plants (*Ledum groenlandicum*: 57% of the stands; *Vaccinium uliginosum*: 43%; and *V. vitis-idaea*: 93%) all have efficient means of vegetative reproduction. Of the six major trees, half reproduce vegetatively after fire: *Betula papyrifera*, *B. glandulosa* and *Alnus crispa*. All of these woody vascular species show a quick response after fire, with either a decline or a constant abundance for some years after.

Among the bryophytes, *Ceratodon purpureus* and *Polytrichum* spp. are the most efficient at vegetative reproduction. These species show effective sprouting and spread from underground protonemata after their tops have been destroyed or buried (Leach 1931, Marsh and Koerner 1972). These species show a response in time similar to their vascular counterparts.

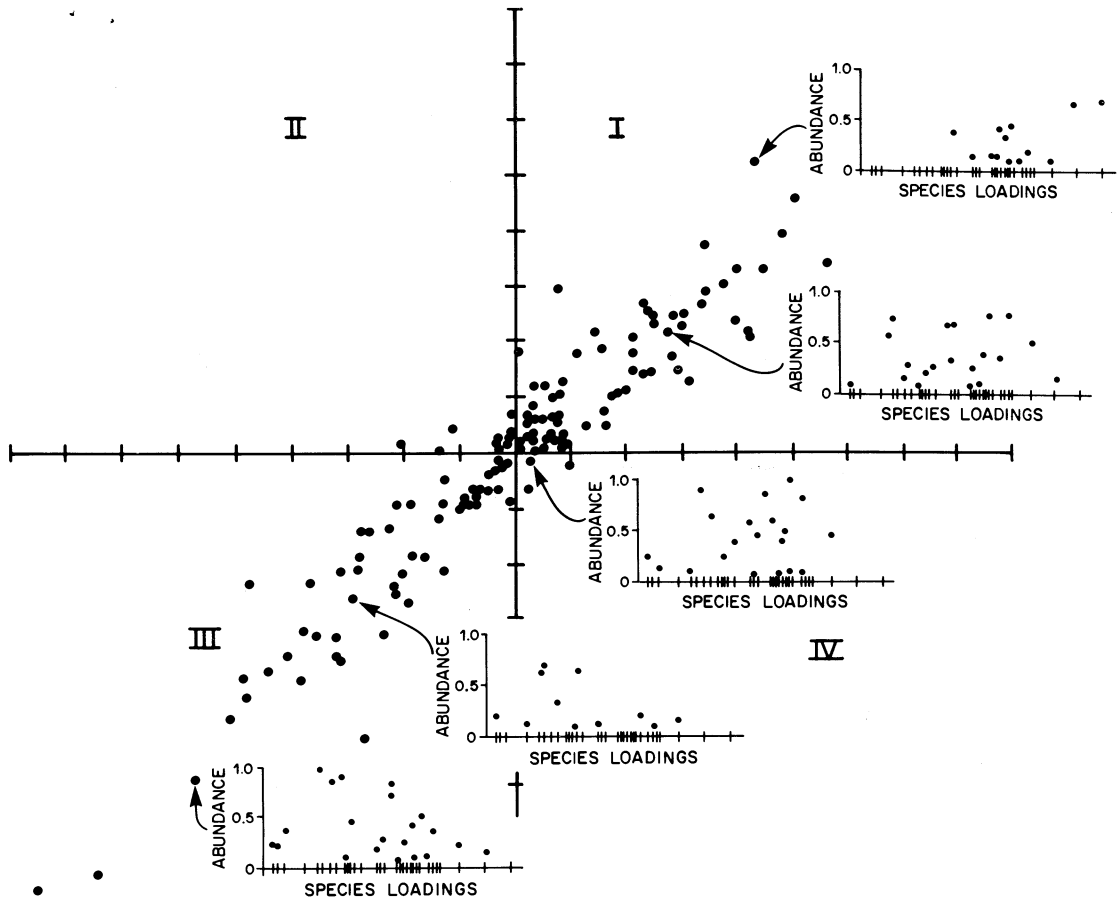


FIG. 10. The stand scores on the fire frequency principal components analysis. Stand scores are a characterization of the abundance of species of each recovery strategy present in the stand. The small figures display this abundance distribution for species ordered (on the ordinate) by their different recovery strategies (i.e., species loadings). The unevenly spaced abscissa marks indicate the position of the species loadings and the dots are the stand abundances of the species. Points on the left of the abscissas of the small figures represent species adapted for rapid recovery after fire; those on the right are species that recover more slowly.

Vegetative reproduction need not always represent a "rapid recovery" strategy. A comparison of some of the life-history traits of white birch and black spruce demonstrates this. White birch (*Betula papyrifera*) uses vegetative reproduction along with rapid growth to recover quickly after fire. In this way it can retain its position in the stand until the next fire. Black spruce reproduces exclusively by seed after fire and grows slowly. It uses layering to maintain and increase its density only in older stands.

After a fire, areas between sprouts are open to colonization. In old stands these spaces are filled with lichens and a few herbaceous and woody species. Plants that produce abundant, light seeds or spores (e.g., *Epilobium* spp., *Corydalis* spp., *Carex* spp., *Calmagrostis* spp., *Poa glauca*, *Agrostis scabra*, *Ceratodon purpureus*, *Polytrichum* spp.) invade this open habitat early. These species have rapid growth rates. They mature, flower, fruit and die out or are greatly

reduced in abundance after 5–10 yr. As a group, these species can stand little crowding and thus are present only for the brief period immediately after fire.

Most ground lichens invade in the first years after fire by thallus fragments, sporeidia and apothecia. They are often overlooked because of their very small size. Their increase in abundance after invasion varies with species (Fig. 11), e.g., from fast increases in abundance by *Cladonia cornuta* (dispersed by soredia) and *C. coccifera* (soredia) to slower increases in abundance by *C. mitis* (fragmentation) and *C. rangiferina* (fragmentation). Ground lichens are adapted to all parts of the fire gradient in Fig. 9 from *Cladonia cornuta* and *C. gracilis* at the top to *C. mitis*, *C. amaurocraea* and *C. rangiferina* at the bottom.

Buried viable seeds seem to play a relatively unimportant role in this part of the subarctic (Johnson 1975). Seeds were present in the soil but most proved to be nonviable. This almost complete lack of viable

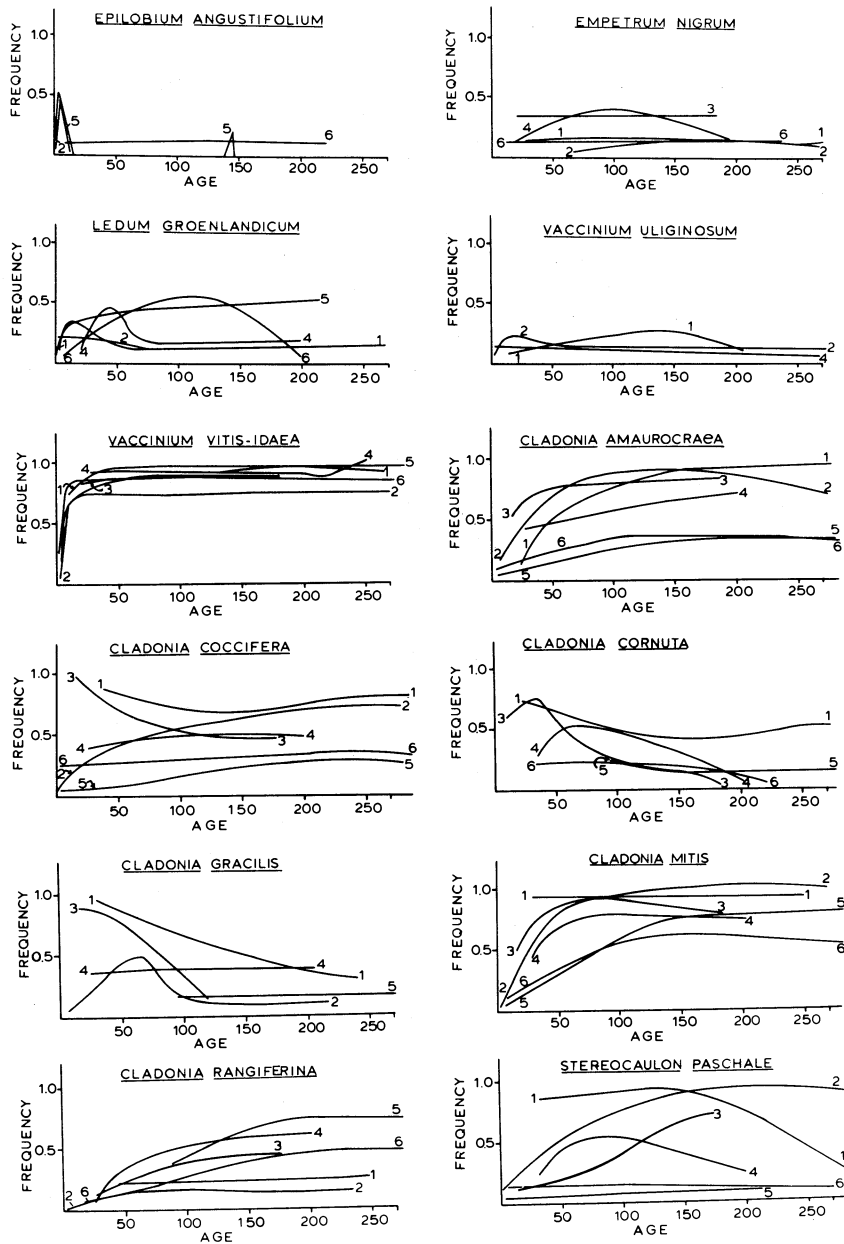


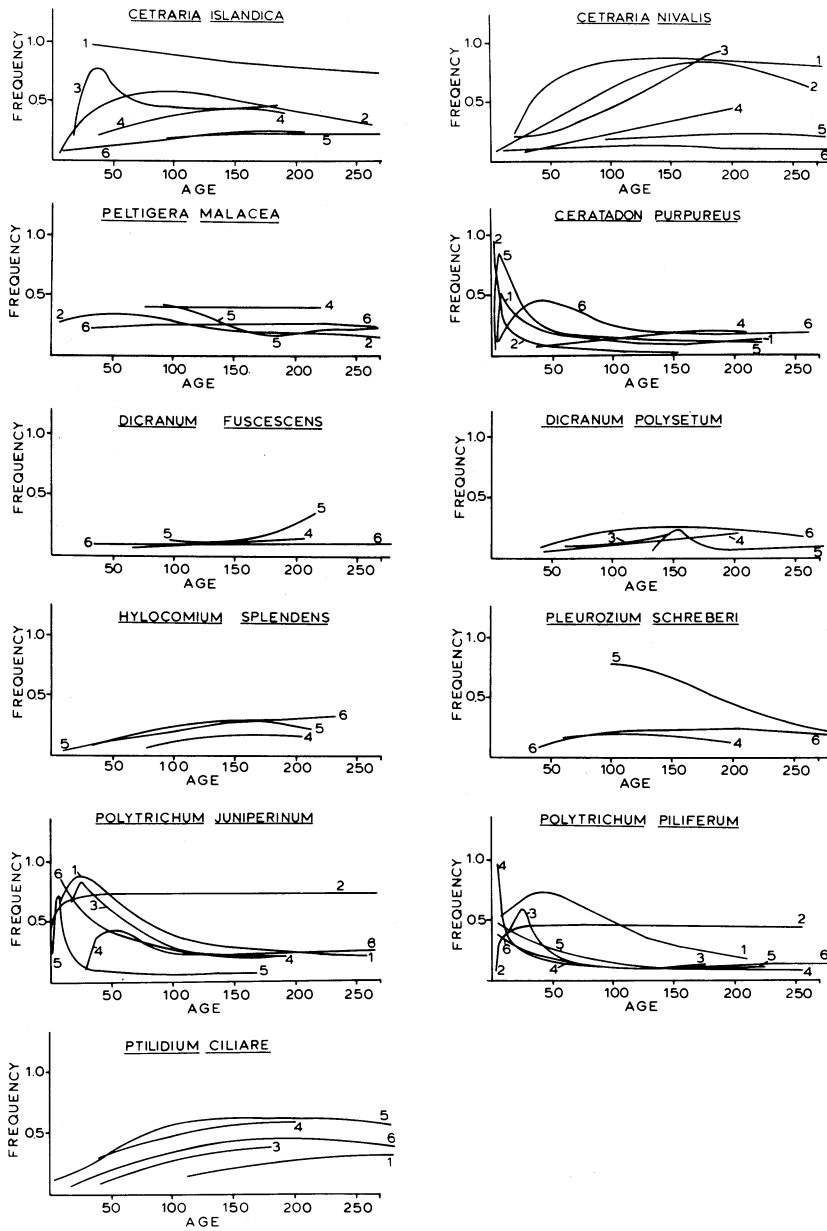
FIG. 11. Chronosequences of species abundance after fire in different community types. If a species has not been found in more than a few stands in one community type it was not plotted. An assortment of computer-fitted functions was used to give the best least squares fit to the points for these graphs. The numbers correspond to the communities listed in the legend of Fig. 9.

germinable seeds appears to be part of a northward decline in the buried viable seed populations. The shortened growing season probably selects seeds that germinate rapidly as soon as conditions are favorable, so that seedlings can make full use of the reduced growing season.

The serotinous cones of jack pine and black spruce can be considered a form of "buried" viable seeds. However, unlike seeds buried in the soil which ger-

minate on an environmental signal caused by disturbance (see e.g., Marks 1974), these two trees shed their seeds on the stimulus of heat from a forest fire.

Regional precipitation, habitat moisture and energy budgets are important in understanding the drying of the lichen mat and in turn the assimilation and growth rate of lichens (Ahti 1959, Ahti and Hepburn 1967, Kershaw and Rouse 1971, Kershaw 1977). For example, *Cladonia rangiferina*, often considered a cli-



max species, grows best in mesic environments, which on upland sites are closed spruce-ferner moss forests. Furthermore, the rate of increase and maximum abundance of *C. rangiferina* in different community types (in Fig. 11) shows this habitat influence.

The abundance of ground lichens such as *Stereocaulon paschale* had been attributed to caribou grazing (Ritchie 1959, Scotter 1964, Ahti and Hepburn 1967). Unfortunately in the western subarctic, direct observation of grazing effects has been limited. However, it seems that, except in local habitats during the spring

thaw, little severe grazing occurs (see also Miller 1972, 1976, Bergerud 1974). It is therefore difficult to ascribe either the large areas covered with *Stereocaulon paschale* to heavy caribou grazing, or the very limited areas covered with *Cladonia alpestris* and *C. rangiferina* to light caribou grazing. It is simpler to suggest that the abundance patterns of these lichens are due primarily to their habitat requirements.

An examination of the graphs in Fig. 11 reveals that in general most of the species found in older stands are present in the first years after fire (for similar re-

sults see Kéever 1950, Egler 1954, Niering and Egler 1955, Hack and Goodlett 1960, Sigafos and Hendricks 1969, Ohmann and Ream 1971, Purdie and Slatyer 1976). However, due to differences in growth rates, species become prominent at different times in a stand's recovery. This is particularly obvious with the trees. For example, on mesic sites where both white birch and black spruce make up the older forests, the density of black spruce is similar to that of white birch in young stands, but birch is more prominent in the latter because it sprouts and grows faster than does black spruce. A similar relationship exists on drier sites between jack pine and black spruce, where jack pine has a faster growth rate and is more prominent in young stands. There is consequently little evidence of a species-replacement series.

Apparent exceptions to this rule are the feather mosses (*Hylocomium splendens*, *Dicranum* spp., *Pleurozium schreberi*). These mosses usually appear in stands 30–50 yr after fire in mesic higher nutrient habitats and quickly become the most abundant ground cover. Their occurrence in old, closed-canopy, mesic stands rich in species has led to the opinion that they are indicators of stable, end stages of succession (Ritchie 1959, Scotter 1964, Maikawa and Kershaw 1976). The succession is believed to be one of canopy closure mainly by extensive layering of the spruce. The increased shade eliminates the intolerant lichens and allows the dominance of the shade-tolerant feather mosses after about 200 yr. Kershaw (1977) states that this would occur on sandy soils if fire were withheld. The stages of this succession are similar to the sequence of communities recognized in the habitat ordination.

There are at least three objections that can be raised to this viewpoint. First, quantitative estimates of the average fire recurrence for this region are 70–100 yr and the survivorship of stands is <1% by 200 yr (Johnson 1979). Also the fire recurrence appears to be controlled by the air mass climate (Johnson and Rowe 1975). Consequently fire is a part of the climate of the region and any discussion which must require the lengthening of the fire frequency must also require a major change in other climatic parameters. Furthermore, the present frequency of fires does not allow enough time for the perpetuation of a stand composition for more than one generation of trees.

Second, appearance of feather mosses in older closed canopy communities can be explained by favorable water and nutrient conditions of certain sites, and hence is not a good indicator of an advanced stage of succession. Tamm (1953, 1964) has shown that the distribution of the feather-moss *Hylocomium splendens* is determined by the need for shade, moderate water, and high nutrient levels. Feather mosses are not "rooted" in the substrate like *Polytrichum* and *Ceratodon*. Consequently, they are nearly independent of the substrate's nutrient and water supply. This

explains why feather mosses quickly dry up and die when the canopy cover is not adequate to prevent high evaporation. Also, because they absorb few nutrients from the substrate they are dependent on rain drip from the canopy for nutrients. Thus good site quality is necessary to assure a high nutrient level in the canopy foliage and a richer rain leachate for the moss to absorb. After fire, with canopy cover lacking, invasion by feather moss is prevented. Furthermore, the lack of attachment to substrate prevents vegetative regeneration from a surviving below-ground portion, as in species like *Polytrichum juniperinum*.

However, given a shady, humid, high-nutrient environment as is found on the cool, basal slopes of black spruce-white spruce-feather moss stands, the feather mosses are very effective competitors against other species. They can quickly spread over and weaken or eliminate other ground plants such as lichens (except the nitrogen-fixing and faster growing *Peltigera* species) and *Polytrichum* mats. Feather mosses are not confined exclusively to old, closed, mesic stands but can be found in dry, nutrient-poor open black spruce-lichen stands in suitable areas at the base of birch and black spruce.

Finally, there is no evidence in stand ages or structure that the canopy closure gradient of the habitat ordination is a succession sequence.

Community dynamics

Up to this point I have considered mostly community organization and how it can be utilized to understand vegetation recovery after fire. I conclude by presenting an hypothesis on the relationship of community organization to dynamics and some of the possible implications of this line of reasoning.

The preceding analysis has identified environmental gradients to which species are adapted in the subarctic. These have tentatively been called fire frequency and habitat. I suggest that these environmental gradients also represent the two predominant levels for understanding vegetation dynamics—shorter term (fire frequency) and longer term (habitat) (cf. Swain 1978).

Shorter-term dynamics are not just the changes in species abundance that follow fire but the whole period over which the frequency of fires is stationary. Thus it includes from one to several fire-recovery cycles. What is important is that the interval between fires has a statistically definable length (Johnson 1979) and that this length does not significantly change over the centuries. Consequently it is this stationary interval between fires that selects the species for those adapted in growth and reproduction to the time interval available.

The interval between fires in this part of the subarctic is short, from 70–100 yr (Johnson 1979), and seems to be important in determining the predictability of the recovery sequence and the great similarity of

species between the old pre-fire and early postfire communities. Species appear to accommodate their life histories to the fire frequency by utilizing different life spans, growth rates and reproductive strategies (vegetative growth, serotinous cones, buried viable seeds, and reproductive effort, etc). A comparison of vegetation from before and after fire reveals a change primarily in abundance and not in species composition.

Shorter-term dynamics in this part of the subarctic seem to remain stationary for an average of 400–500 yr. This estimate is based on paleoecological data presented by Bryson and Larsen (1965) and Nichols (1967, 1975). Between these periods are transitional intervals during which the fire frequency and other environmental parameters change rapidly (Nichols 1975). These transitions are usually associated with change in the atmospheric circulation (Bryson and Wendland 1968, Lamb 1972, Webb and Bryson 1972, Wendland and Bryson 1974, Bryson 1974). However there are situations in which other longer term mechanisms, e.g., species invasions, pedogenesis, pathogen, geomorphological changes, may be involved (Iverson 1964, West 1964, Cushing 1965, Davis 1976, Wright 1977).

The magnitude of these longer term changes is such that they involve significant changes in a site's water, energy and nutrient budget as well as the species adapted to these regimes. Consequently the dynamics involve not only changes in abundance but changes in species. Sites are thus converted from an assemblage of species adapted to the prior environment to an assemblage of somewhat different species adapted to the present environment. The best historical record of longer term dynamics is in macro- and microfossils of lake sediments (see e.g., Janssen 1967, Whitehead et al. 1973, Swain 1978). One point which is clearly shown by these studies is the apparent freedom by which species are recombined after each transition.

Inspection of the pattern of these longer term dynamics (for the subarctic see Nichols 1975) seems to indicate that the direction of change is not predictable. If this hypothesis can be supported, it has several interesting implications. Orderly development of communities over the longer term could not have been the rule except in the sense that history in retrospect always appears to be directional (Heinselman 1963). Species appear in the longer term to be assembled into communities largely independent of each other (Davis 1976). Selection must have been for species that could reliably be reassembled into communities in a very short time, that is, species which can easily be rehabilitated.

Thus, models of community organization as presented here contain most of the information needed to study vegetation dynamics. The major components of the shared shorter term changes are reflected in the adaptation of the species in the fire ordination (Figs.

9 and 10). Because the fire frequency stabilizes the composition, the changes in the vegetation are *mostly* in abundance and are easily rationalized from the ordination. The major components of the shared longer term changes are reflected in the adaptation of the species in the habitat ordination (Figs. 3 and 4). Because the habitat changes appear to be unpredictable as to direction, the only statement that can be made of the future is that change will always be to some relatively nearby assemblage of species.

ACKNOWLEDGMENTS

I should most like to thank J. W. Sheard and O. L. Loucks for their help and encouragement. I should also like to thank M. A. Jasieniuk, S. J. B. Johnson, P. L. Marks, B. R. Neal, H. E. Wright and J. S. Rowe for criticism of the research and drafts. Collection of data in the field was assisted by A. Bossort, W. Harris, M. Jasieniuk, S. Johnson, R. Godwin, A. Lincoln, T. Trotter and K. Traynor.

I thank Indian and Northern Affairs, particularly Howard Gray, John Gilmour, and Eddy Powder for their cooperation in the field. Financial support for this study was provided by Environment Canada and Indian and Northern Affairs. The author also held an Institute for Northern Studies Scholarship during part of this work.

LITERATURE CITED

- Ahti, T. 1959. Studies on the caribou lichen stands of Newfoundland. *Annales Botanici Societatis Zoologicae Botanicae Fennicae 'Vanamo'* 30:1–43.
- Ahti, T., and R. L. Hepburn. 1967. Preliminary studies on woodland caribou range, especially on lichen stands, in Ontario. Wildlife Number 74, Department of Lands and Forests Ontario Research Report, Toronto, Ontario, Canada.
- Argus, G. W. 1966. Botanical investigation in northeastern Saskatchewan: the subarctic Patterson-Hasbala Lakes region. *Canadian Field-Naturalist* 80:119–143.
- Batcheler, C. L. 1971. Estimation of density from a sample of joint point and nearest-neighbor distances. *Ecology* 52:703–709.
- Bergerud, A. T. 1974. Relative abundance of food in winter for Newfoundland caribou. *Oikos* 25:379–387.
- Bryson, R. A. 1974. A perspective on climatic change. *Science* 184:753–760.
- Bryson, R. A., and J. A. Larsen. 1965. Radiocarbon and soil evidence of former forest in the southern Canadian tundra. *Science* 147:46–48.
- Bryson, R. A., and W. M. Wendland. 1968. Tentative climatic patterns for some late glacial and post-glacial episodes in central North America. Pages 271–298 in W. J. Mayer-Oakes, editor. *Life, land and water*. University of Manitoba Press, Winnipeg, Manitoba, Canada.
- Buffo, J., L. J. Fritschen, and J. L. Murphy. 1972. Direct solar radiation on various slopes from 0 to 60 degrees North Latitude. Forest Service Research Paper PNW-142, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.
- Catana, H. J. 1963. The wandering quarter method of estimating population density. *Ecology* 44:349–360.
- Clausen, J. J. 1957. A phytosociological ordination of the conifer swamps of Wisconsin. *Ecology* 38:638–645.
- Cushing, E. J. 1965. Problems in the Quaternary phytogeography of the Great Lakes Region. Pages 403–416 in H. E. Wright, Jr. and D. G. Frey, editors. *The Quaternary of the United States*. Princeton University Press, Princeton, New Jersey, USA.
- Davis, M. B. 1976. Pleistocene biogeography of temperate

- deciduous forest. Louisiana State University, Geoscience and Man 13:13-26.
- Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition—a factor in old field vegetation development. *Vegetatio* 4:412-417.
- Furnival, G. M., W. D. Reifsnnyder, E. Wyler, and T. G. Siccama. 1969. Solar climate calculator. Pages 181-187 in *Proceedings of the Third Forest Microclimate Symposium*. Kananaskis Forest Experiment Station, Seebe, Alberta, Canada.
- Geiger, R. 1965. *The climate near the ground*. Harvard University Press, Cambridge, Massachusetts, USA.
- Goff, F. G. 1968. Use of size stratification and differential weighting to measure forest trends. *American Midland Naturalist* 79:402-418.
- Goff, F. G., and P. H. Zedler. 1972. Derivation of species succession vectors. *American Midland Naturalist* 87:397-412.
- Hack, J. T., and J. C. Goodlett. 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. Professional Paper 347, United States Geological Survey, Washington, District of Columbia, USA.
- Hare, F. K. 1950. Climate and zonal divisions of the boreal forest formation in eastern Canada. *Geographical Review* 40:615-635.
- Heinselman, M. L. 1963. Forest sites, bog processes and peatland types in the Glacial Lake Agassiz Region, Minnesota. *Ecological Monographs* 33:327-374.
- Hoover, M. D., and H. A. Lunt. 1952. A key for the classification of forest humus types. *Soil Science of America Proceedings*, 1952:368-370.
- Hustich, I. 1949. On the forest geography of the Labrador Peninsula: a preliminary synthesis. *Acta Geographica* 10:1-63.
- Iverson, J. 1964. Retrogressive vegetational succession in the post-glacial. *Journal of Ecology* 52(Supplement):59-70.
- Janssen, C. R. 1967. A postglacial pollen diagram from a small *Typha* swamp in northwestern Minnesota, interpreted from pollen indicators and surface samples. *Ecological Monographs* 37:145-172.
- Johnson, E. A. 1975. The buried seed populations in the subarctic forest east of Great Slave Lake, N.W.T. *Canadian Journal of Botany* 53:2933-2941.
- . 1979. Fire recurrence in the subarctic and its implications for vegetation composition. *Canadian Journal of Botany* 57:1374-1379.
- Johnson, E. A., and J. S. Rowe. 1975. Fire in the wintering grounds of the Beverley caribou herd. *American Midland Naturalist* 94:1-14.
- Keever, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. *Ecological Monographs* 20:229-250.
- Kershaw, K. A. 1977. Studies on lichen dominated systems. XX. An examination of some aspects of the northern boreal lichen woodlands in Canada. *Canadian Journal of Botany* 55:393-410.
- Kershaw, K. A., and W. R. Rouse. 1971. Studies on lichen-dominated systems. II. The growth pattern of *Cladonia alpestris* and *Cladonia rangiferina*. *Canadian Journal of Botany* 49:1401-1410.
- Lamb, H. H. 1972. *Climate: present, past and future*. Methuen, London, England.
- Larsen, J. A. 1971. Vegetation of Fort Reliance, N.W.T. *Canadian Field-Naturalist* 85:147-178.
- Leach, W. 1931. On the importance of some mosses as pioneers on unstable soils. *Journal of Ecology* 19:98-102.
- Maikawa, E., and K. A. Kershaw. 1976. Studies on lichen-dominated systems. XIX. The postfire recovery sequence of black spruce-lichen woodland in the Abitau Lake Region, N.W.T. *Canadian Journal of Botany* 54:2679-2687.
- Maini, J. S. 1966. Phytoecological study of sylvo-tundra at Small-Tree Lake, N.W.T. *Arctic* 19:220-243.
- Marks, P. L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability and northern hardwood ecosystem. *Ecological Monographs* 44:73-88.
- Marsh, W. M., and J. M. Koerner. 1972. Roles of moss in slope formation. *Ecology* 53:489-493.
- Miller, A. R. 1972. Feeding behavior of barren-ground caribou on taiga winter ranges. International Conference on the Behavior of Ungulates in Relationship to Management. Calgary, Alberta, Canada.
- . 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 3. Report Series Number 36, Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Nichols, H. 1967. The post-glacial history of vegetation and climate at Ennadai Lake, Keewatin and Lynn Lake, Manitoba (Canada). *Eiszeitalter und Gegenwart* 18:176-197.
- . 1975. Palynological and paleoclimatic study of the late Quaternary displacement of the boreal forest-tundra ecotone in Keewatin and Mackenzie, N.W.T., Canada. Occasional Paper Number 15. Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado, USA.
- Niering, W. A., and F. E. Egler. 1955. A shrub community of *Viburnum lantana* stable for twenty-five years. *Ecology* 36:356-360.
- Ohmann, L. F., and R. A. Ream. 1971. Wilderness ecology: virgin plant communities of the Boundary Waters Canoe Area. Forest Service Research Paper NC-63, North Central Forest Experiment Station, St. Paul, Minnesota, USA.
- Peet, R. K., and O. L. Loucks. 1977. A gradient analysis of southern Wisconsin forests. *Ecology* 58:485-499.
- Purdie, R. W., and R. O. Slatyer. 1976. Vegetation succession after fire in sclerophyll woodland communities in south-eastern Australia. *Australian Journal of Ecology* 1:223-236.
- Raup, H. M. 1930. The vegetation of the Fort Reliance sand plain. *Annals of the Carnegie Museum* 20:9-38.
- Ritchie, J. C. 1958. A vegetation map from the southern spruce forest zone of Manitoba. *Geographical Bulletin (Canada)* 12:39-46.
- . 1959. The vegetation of Northern Manitoba, III: studies in the subarctic. Technical Paper Number 3, Arctic Institute of North America, Montreal, Quebec, Canada.
- Rowe, J. S. 1972. Forest regions of Canada. Publication Number 1300, Canadian Forestry Service, Department of Environment, Ottawa, Ontario, Canada.
- Scotter, G. W. 1964. Effects of forest fires on the winter range of barren-ground caribou in northern Saskatchewan. *Wildlife Management Bulletin Series 1, Number 18*, Canadian Wildlife Service, Northern Affairs and National Resources, Ottawa, Ontario, Canada.
- . 1965. Study of the winter range of the barren-ground caribou with special reference to the effects of forest fires. Unpublished report, CWSC Number 1129, Canadian Wildlife Service, Ottawa, Ontario, Canada.
- . 1968. Effects of forest fires on the lichen winter ranges of barren-ground caribou in northern Canada. Dissertation. Utah State University, Logan, Utah, USA.
- Sigafoos, R. S., and E. L. Hendricks. 1969. The time interval between stabilization of alpine glacial deposits and establishment of tree seedlings. United States Geological Survey Professional Paper 650-B:89-93.
- Swain, A. M. 1978. Environmental changes during the past 2000 years in North-Central Wisconsin: analysis of pollen, charcoal and seeds from varved lake sediments. *Quaternary Research* 10:55-68.
- Tamm, C. O. 1953. Growth, yield and nutrition in carpets of forest mosses (*Hylocomium splendens*). *Meddelanden fran Statens Skogsforskningsinstitut (Stockholm)* 43:1-140.

- . 1964. Growth of *Hylocomium splendens* in relation to tree canopy. *Bryologist* 67:423–426.
- Waugh, F. V. 1962. Factor analysis: some basic principles and an application. *Agricultural Economics Research* 14:77–80.
- Webb, T., III, and R. A. Bryson. 1972. Late- and postglacial climatic change in the northern Midwest, U.S.A.: quantitative estimates derived from fossil pollen spectra by multivariate statistical analysis. *Quaternary Research* 2:70–115.
- Wendland, W. M., and R. A. Bryson. 1974. Dating climatic episodes of the Holocene. *Quaternary Research* 4:9–24.
- West, R. G. 1964. Inter-relations of ecology and Quaternary palaeobotany. *Journal of Ecology* 52(Supplement):47–57.
- Whitehead, D. R., H. Rochester, Jr., S. W. Rissing, C. B. Douglas, and M. C. Sheehan. 1973. Late glacial and post-glacial productivity changes in a New England pond. *Science* 181:744–747.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Biological Review* 49:207–264.
- Whittaker, R. H., and H. G. Gauch. 1973. Evaluation of ordination techniques. *Handbook of Vegetation Science* 5:287–321.
- Wilde, S. A., and G. K. Voigt. 1955. Analysis of soils and plants for foresters and horticulturalists. J. W. Edwards, Ann Arbor, Michigan, USA.
- Wright, H. E., Jr. 1977. Quaternary vegetation history—some comparisons between Europe and America. *Annual Review of Earth and Planetary Sciences* 5:123–158.