VEGETATION DEVELOPMENT FOLLOWING FIRE IN *PICEA MARIANA* (BLACK SPRUCE)–*PLEUROZIUM* FORESTS OF SOUTH-EASTERN LABRADOR, CANADA

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SUMMARY

(1) The pattern of post-fire vegetation development in *Picea mariana* (black spruce)–*Pleurozium* forests in south-eastern Labrador, Canada, is evaluated using palaeoecological methods and vegetation analysis of extant stands.

(2) Macrofossil analysis of mor humus profiles in mature stands yields the following stratigraphy: mineral soil–charcoal–*Polytrichum juniperinum–Cladonia* lichens–*Pleurozium schreberi*–feather mosses and *Sphagnum girgensohnii*. The stratigraphic record of the post-fire dynamics of the vegetation at individual sites strengthens the conclusions obtained from the detailed analysis of a chronosequence of stands.

(3) The pattern of vegetation development, especially of the arboreal species, is significantly different from that reported for the central and western boreal forest in North America. This difference is attributed to the much longer fire cycle in the maritime region of Labrador which allows the accumulation of a thick organic soil layer that is incompletely removed by fire.

(4) Arboreal regeneration is slow due to the limited availability of mineral soil seed-beds. The progressive establishment of black spruce and balsam fir over a 70–100 year period results in an uneven age structure and provides a long period when lichen woodlands cover the landscape.

(5) The majority of the vascular understorey species follow the pattern of initial floristics and resprout rapidly following fire. *Coptis groenlandicum*, *Gaultheria hispidula*, and *Empetrum nigrum* decrease following fire whereas only *Epilobium angustifolium* shows a marked increase.

(6) The cryptogam ground cover undergoes a physiognomic and compositional succession that represents contrasting substrate requirements and the differential response of the major species to a temporally-varying environment.

INTRODUCTION

Fire is a pervasive natural disturbance that controls many structural and functional properties of boreal plant communities, and is the major agent initiating and terminating successions. The interpretation of the successional relationships of these communities has been largely conditioned by the temporal and spatial perspectives adapted by the investigator involved, and by the specific aspect of the vegetation under study. For example, the palaeoecological evidence indicates that at the scale of the plant formation the vegetation in fire-prone boreal regions exhibits stability and uniformity, with no substantial change over several millennia (Swain 1973; Wright 1974; Zackrisson 1977). This evidence is frequently cited to support the view that boreal vegetation is adapted to fire as an integral environmental factor.

At a scale below that of the plant formation, however, the vegetation is clearly non-uniform, and maximum vegetational and floristic diversity is apparently attained when a spectrum of successional communities is maintained within the landscape (cf. Loucks

1970; Heinselman 1973). In a study documenting landscape vegetation patterns and fire history for the 400 000 ha Boundary Waters Canoe Area in northern Minnesota, Heinselman (1973) describes the frequency and extent of fire over a 300-year period. The regional mosaic of vegetation in this area comprises a mixture of successional stages, the pattern of which is largely controlled by the recent fire history.

Within each spatial unit of this vegetation mosaic, the effect of fire on the woody vegetation is primarily as a cycling agent (Methven, Van Wagner & Stocks 1975). The major boreal tree species (*Picea mariana, Pinus banksiana*) establish rapidly by seed released from serotinous cones and, following fire, vigorous even-aged stands generally replace less productive old-age forests. The regeneration behaviour of the trees, coupled with the rapid resurgence of most shrub species from underground parts, has consequently led to a view of succession in boreal ecosystems as a cyclic process involving little overall floristic variation, despite major environmental change resulting from fire (Viereck 1975; Viereck & Schandelmeier 1980).

However, studies concentrating on post-fire changes in cryptogam composition have emphasized the sequential nature of the successional pattern. Four major ground cover types—acrocarpous mosses and crustose lichens, horn and cup lichens (Cladoniae), fruticose lichens (Cladinae) and pleurocarpus mosses—occupy arbitrarily delimited stages in revegetation (Ahti 1959; Kershaw 1978; Johnson 1981). The invasion of cryptogams, therefore, appears to be a response to changes in very local environment and to produce a chronosequence conforming to the traditional concepts of succession (cf. Cooper 1913).

These different viewpoints of the natural role of fire in boreal ecosystems are well illustrated by recent detailed studies of the fire history and phytosociology of the boreal forests of south-eastern Labrador, Canada (Foster 1984a, b). The black spruce–*Pleurozium* community (cf. Foster 1984b) is the predominant vegetation type in this region, and the following account describes the dynamics of this vegetation following fire and examines four questions.

(i) Do the different strata of vegetation (ground cover, understorey, canopy, epiphytes) exhibit similar rates and patterns of regeneration following fire, or are contrasting strategies employed by the different growth forms?

(ii) What are the major environmental factors that control the rate and direction of regeneration, and at what scale do they operate?

(iii) From the stratigraphic evidence contained in the soil organic layer, is it possible to document the vegetation change *in situ*, to confirm that the mosaic of successional communities observed across the landscape provides analogues for the temporal sequence at an individual site?

(iv) How well do the results from this study of a maritime area fit the generalized patterns reported from farther west in the continental boreal region of Canada?

STUDY AREA

Located on the north-eastern coast of Canada, Labrador occupies a portion of the Labrador–Ungava Peninsula. The study area in the south-east extends approximately 300 km from the St Augustin River east to the coast and 160 km from the Mealy Mountains south to the Quebec border at 52°N (Fig. 1).

Geologically, Labrador forms the eastern part of the Precambrian Canadian Shield. In south-eastern Labrador the bedrock is predominantly quartzo-felspathic gneisses with intrusions of granite and granodiorites (Greene 1974). The entire region was covered by
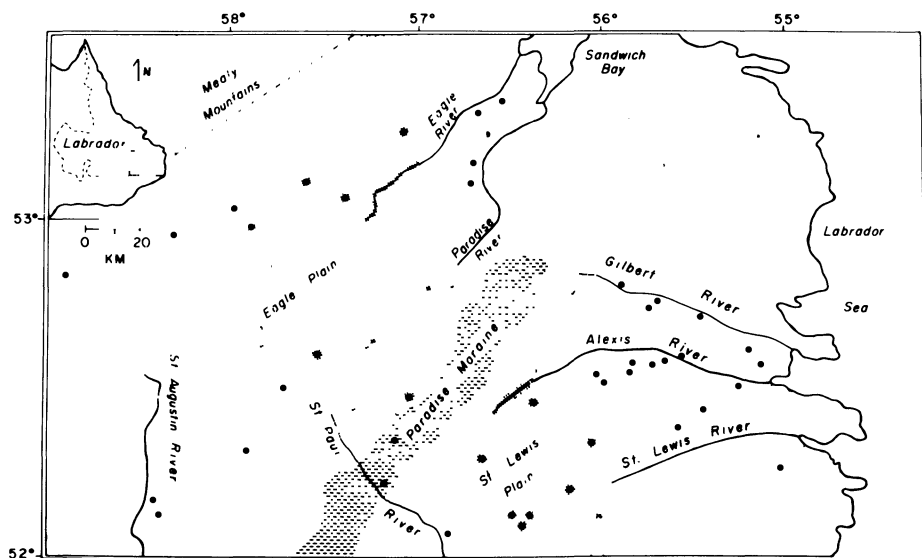
FIG. 1. The study area in south-eastern Labrador showing the major physiographic features in the region. The dots represent sites visited in the course of field work during the summers of 1979–81.

the Laurentide ice sheet; retreat from coastal positions commenced approximately 12 000 B.P. (Ives 1978).

The climate is characterized by long, cold winters and short, cool summers, with a mean annual temperature of approximately 0 °C. Approximately 1100 mm precipitation is distributed evenly through the year, and is among the highest for the North American boreal forest (Peach 1975).

Phytogeographically the area has a depauperate flora, and many of the important boreal tree species are absent or rare (Foster 1984b). Jack pine (*Pinus banksiana*) does not occur in Labrador and, in the south-east, white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*) and balsam popular (*Populus balsamifera*) are uncommon.

The black spruce (*Picea mariana*)–*Pleurozium* forest community is the most widespread vegetation type in southern Labrador, and occupies a wide range of sites from poorly-drained outwash plains to convex slopes and hill crests (Foster 1984b). The tree canopy is uneven and composed of narrow-crowned and slow-growing black spruce and balsam fir (*Abies balsamea*) 8–12 m high. The discontinuous shrub layer is composed of ericaceous species, including *Kalmia polifolia*, *Ledum groenlandicum*, *Vaccinium angustifolium*, and *V. vitis-idaea*. Common herbs are *Cornus canadensis*, *Deschampsia flexuosa*, *Empetrum nigrum*, *Gaultheria hispidula* and *Rubus chamaemorus*. The ground cover consists of a nearly continuous carpet of *Pleurozium schreberi*, accompanied by more mesic bryophytes (*Hylocomium splendens*, *Ptilium crista-castrensis* and *Sphagnum girgensohnii*) and foliose and fruticose lichens.

Fire-history studies have shown that lightning is the sole ignition source in this area (Foster 1984a). The fire rotation (*sensu* Heinselman 1973) is approximately 500 years, which is 3–10 times longer than that estimated for the drier, continental portions of the North American boreal region (Heinselman 1981). The long fire rotation in south-eastern Labrador is attributed to the very high precipitation and to the predominance of extensive

PLATE 1. Open and uneven appearance of a 57-year-old lichen woodland in south-eastern Labrador. *Cladonia rangiferina* and *C. stellaris* form the ground cover and the low shrub layer is comprised of *Vaccinium angustifolium, V. vitis-idaea* and *Ledum groenlandicum.*

mires that serve as very effective fire breaks. Following fire there is a period of 75–100 years during which lichen woodland vegetation occupies the site before the formation of a closed canopy forest (Plate 1).

METHODS

Seventy-six successional and mature stands in the black spruce–*Pleurozium* community were selected on the following criteria: (i) stand homogeneity over a minimum area of approximately 40 × 40 m; (ii) apparent uniformity of the physical environment, including continuous aspect and slope and absence of local disturbance; (iii) inclusion of the available range of stand ages. The fire history of the study area and the stand ages had been documented previously by growth ring counts of fire scars on black spruce (Foster 1984a) and it was possible to select a series of stands that had been burnt at intervals of approximately 15 years, over a period of 150 years.

Vegetation analysis for the project utilized the semi-quantitative methods of Braun-Blanquet (Mueller-Dombois & Ellenberg 1974) as employed in previous studies (Foster 1983, 1984b; Foster & King 1984). Complete floristic lists of cryptogam and vascular species were made for standard 20 × 20 m relevé plots, and cover abundance values were assigned on the 10-point Domin scale (Birks 1973). Epiphytic lichen cover was estimated as a vertical projection onto the floor of the plot. Nomenclature follows Fernald (1970) for vascular species, Stotler & Crandall-Stotler (1977) for liverworts, Ireland *et al.* (1980) for mosses, and Hale & Culberson (1970) for lichens except *Cladonia*, which follows Ahti (1961).

Data were compiled from a total of thirty-seven relevés located in areas burned in 1975 and in the adjacent unburned stands to examine the response of the vascular understorey species to fire. As only 5 years had elapsed since the sites had burned, it was possible to match burned and unburned stands on the basis of overstorey composition, tree age and density, as well as on undergrowth characteristics, topography, soils, slope, and aspect. The magnitude of the change in the frequency of nineteen common vascular species after burning was calculated as log (frequency burned/frequency unburned). In the two cases where frequency values were zero, values of 1% were substituted for computational purposes. Therefore, the range of possible values for the magnitude of change in frequency extends from −2 to +2.

Quantitative estimates of temporal changes in abundance for the prominent ground-layer species (bryophytes and lichens) were derived from the cover–abundance estimates of the seventy-six relevés forming the time-series. For each species the abundance in each stand was plotted against time since the last fire, and then smoothed curves were drawn through the points (individual species scatterplots are contained in Foster (1983)). Stands exceeding 90 years in age were grouped either as closed forest or as lichen woodland (open stands with a lichen cover greater than 30% and a very discontinuous canopy). Qualitative data (presence–absence) was used to document when the various minor cryptogams colonize following fire.

Under moist, cool and acid conditions unfavourable to processes of decomposition, plant remains, particularly of the ground layer, are incorporated in the organic soil layer in conifer forests. Stratigraphic analysis of the organic soil profile should therefore reveal temporal changes in stand composition. In all relevé plots 10 × 10 cm monoliths of the organic layer were cut down to the mineral soil with a serrated knife and the gross stratigraphy was described. Monoliths from five stands with fires in 1959, 1898, 1959 and 1898, *c.* 1750, and pre-1750 were selected for detailed analysis. Analysis in the laboratory consisted of a description of the gross stratigraphy and detailed examination of individual horizons, including the microscopic identification of plant remains and charcoal at 10–20× magnification (Watts 1978; Birks 1980). Moss leaf fragments were determined at 400× magnification and intact lichen thalli were identified to species utilizing standard chemical and morphological criteria (Hale 1982).

Detailed age-structure analysis of three stands of different ages (36, 140 and >230 years) was utilized to investigate the recruitment pattern of trees following fire. Within a dense spruce–*Pleurozium* forest exceeding 230 years old, and a 140-year-old stand, all trees within 3 m of an arbitrary line were aged by tree-ring counts from sections taken at ground level, and the basal diameters were measured. In a 36-year-old stand, each individual tree within a circular plot 30 m in diameter was aged and measured in a similar fashion. In each stand at least forty individuals were analysed.

RESULTS

Mor humus profiles

The 21-year-old woodland (1959 fire) supports scattered black spruce and balsam fir up to 2-m tall, and low ericaceous shrubs. The lichen cover is loosely attached to a substrate of conifer litter and *Polytrichum juniperinum* that is interspersed with the crustose lichen *Lecidea granulosa*. The humus profile (Fig. 2a) contains a thin layer of Cladinae podetia (*Cladonia mitis*, *C. uncialis*) extending to 10 cm depth. At the base of the profile a layer approximately 0·5 cm thick consists of charcoal fragments (>0·1–2·0 cm) that overlie an ash-grey A_2 mineral soil horizon.

Profile 2 (Fig. 2b) is from an adjacent stand that burned in 1898 and 1959. The present vegetation is an open and nearly treeless expanse, with a ground cover of *Polytrichum juniperinum*, *Cladonia arbuscula*, *C. mitis* and *C. uncialis*, and low shrub cover of *Ledum groenlandicum*, *Vaccinium angustifolium* and *V. cespitosum*. The organic layer records
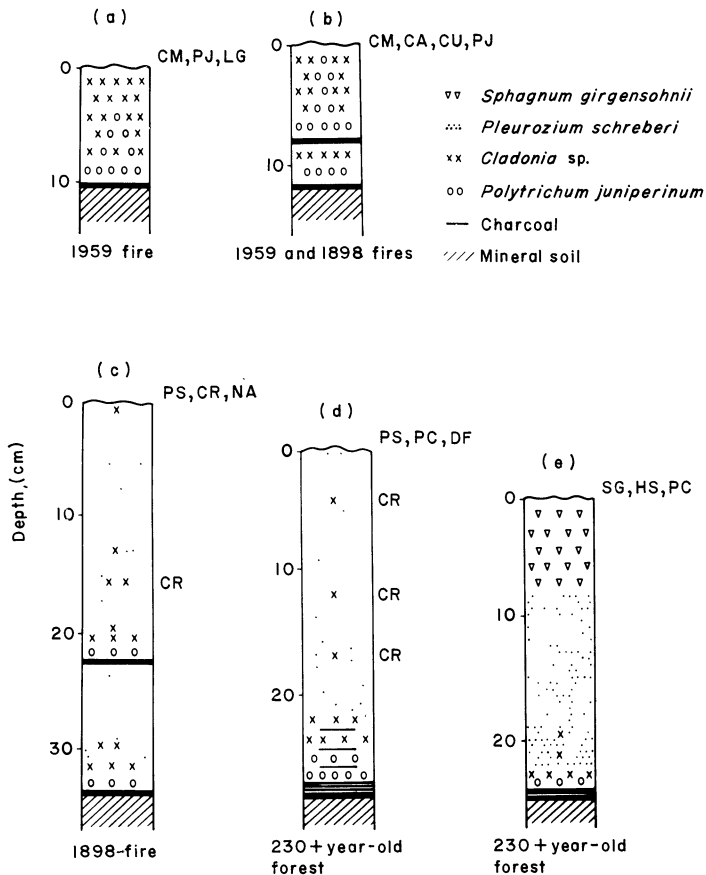

FIG. 2. Mor-humus profiles from five sites of contrasting fire history in south-eastern Labrador. Species abbreviations at the top of each profile indicate the present ground cover: CA, *Cladonia arbuscula*; CM, *C. mitis*; CR, *C. rangiferina*; CU, *C. uncialis*; DF, *Dicranum fuscescens*; HS, *Hylocomium splendens*; LG, *Lecidea granulosa*; NA, *Nephroma arcticum*; PC, *Ptilium crista-castrensis*; PJ, *Polytrichum juniperinum*; PS, *Pleurozium schreberi*; SG, *Sphagnum girgensohnii*.

both fires. The upper part of the profile is very similar to Profile 1 (Fig. 2a) in detail, but is underlain by a charcoal horizon and a lower profile of *Polytrichum juniperinum* and well-decomposed lichen thallus fragments (cf. *Cladonia*) resting on charcoal and mineral soil. The site was evidently developing to an open lichen woodland following the 1898 fire when it was reburned in 1959. The bulk of the humus profile was not burned in 1959, and therefore the record of previous vegetation change was left intact.

In the next stand, last burned in 1898, black spruce trees cover 65%, accompanied by occasional balsam fir. Ericaceous shrubs cover 30% of the area, and *Pleurozium schreberi* is the dominant ground cover, with large patches of *Cladonia stellaris* and *C. rangiferina* persisting in canopy openings. The organic layer, sampled in the moss carpet, extends 22 cm to a charcoal horizon (Fig. 2c). Approximately 4 cm of green *Pleurozium* at the surface grades downward into yellow and then moderately humified remains, which extend an additional 15 cm. Below, *Cladonia* spp. and *Polytrichum juniperinum* form a well-humified matrix overlying a dense mat of *Polytrichum* rhizomes and 1·5 cm of wood and charcoal. A very similar although truncated sequence, which represents the development of the forest consumed by the 1898 fire, extends from 22 cm to 34 cm and terminates in mineral soil.

The mature spruce–*Pleurozium* forest contains black spruce exceeding 230 years old and the organic soil layer is 28 cm thick. Despite the great difference in age between the stands, the humus profiles of the 230- and 82-year-old forests (Fig. 2d, c) are remarkably similar. The profile from the older forest contains a thicker layer of *Pleurozium schreberi* and mixed *Pleurozium–Cladonia*.

Figure 2e depicts the stratigraphy found in a *Sphagnum* carpet in an old-age (230+ year-old) spruce–*Pleurozium* forest. Green *Sphagnum girgensohnii* forms a moist layer 5 cm thick, overlying humified remains that extend an additional 3 cm. Beneath an abrupt transition the stratigraphy *Pleurozium*/*Pleurozium–Cladonia*/*Polytrichum juniperinum*/ charcoal/mineral soil is found. *Pleurozium schreberi* ranges from slightly humified just below the *Sphagnum* to well-humified and nearly indistinguishable at lower levels. *Polytrichum juniperinum* is poorly preserved, although the characteristic radiculose stems and inflexed and entire leaf margins are retained. The *Cladonia* spp. comprise a gelatinous matrix of broken thalli interspersed with mosses, and have lost their secondary chemicals.

Forest age-structure analysis

Age-structure analyses are presented from a renegerating black spruce–lichen woodland 35 years old (Fig. 3) and from 140-year-old (Fig. 4) and 230+ year-old closed spruce–*Pleurozium* forests (Fig. 5). Extensive observations and tree borings from the seventy-six relevés indicate that these three stands are representative of age–size relationships of forests across the region.

The youngest stand is an open lichen woodland composed of a mixture of multi-aged black spruce and fir, with some trees dating to the years immediately following the 1945 fire (Fig. 3). Individuals range in size from saplings to trees exceeding 20 cm in basal diameter and 7 m in height. Seedlings, especially of black spruce, are still establishing on the open site. From the size distribution it is apparent that individuals which established in the past 25 years have grown more slowly than those which commenced growth in the preceding 10 years.

Analysis of the 140-year-old forest documents a progressive establishment of black spruce and balsam fir that has led to the gradual formation of a closed canopy (Fig. 4). The largest and oldest spruce have straight boles, an indication of development from
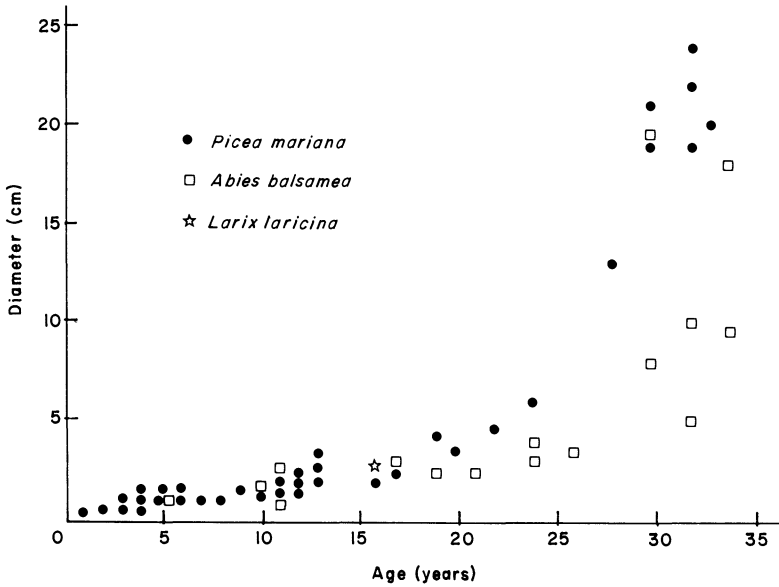
FIG. 3. Age-structure analysis of a 36-year-old *Picea mariana* (black spruce) lichen woodland in south-eastern Labrador.
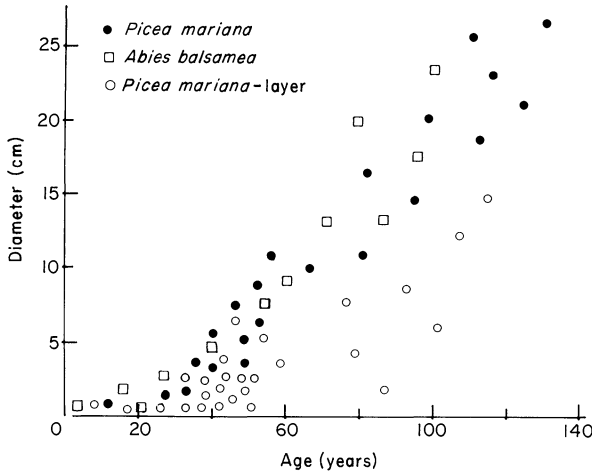

FIG. 4. Age-structure of a 140-year-old *Picea mariana* (black spruce)–*Pleurozium* forest in south-eastern Labrador.

seedlings. In contrast, many of the smaller, slower-growing spruce have strongly curved boles and frequently form circular clones. These are layers produced through vegetative reproduction (cf. Hustich 1968). Fir lagged behind spruce in establishment following the fire, but is now reproducing more successfully.

Within the mature forest the black spruce provide a minimum stand age of 230 years (Fig. 5). Balsam fir is well-represented in all age-classes and exhibits slightly faster growth
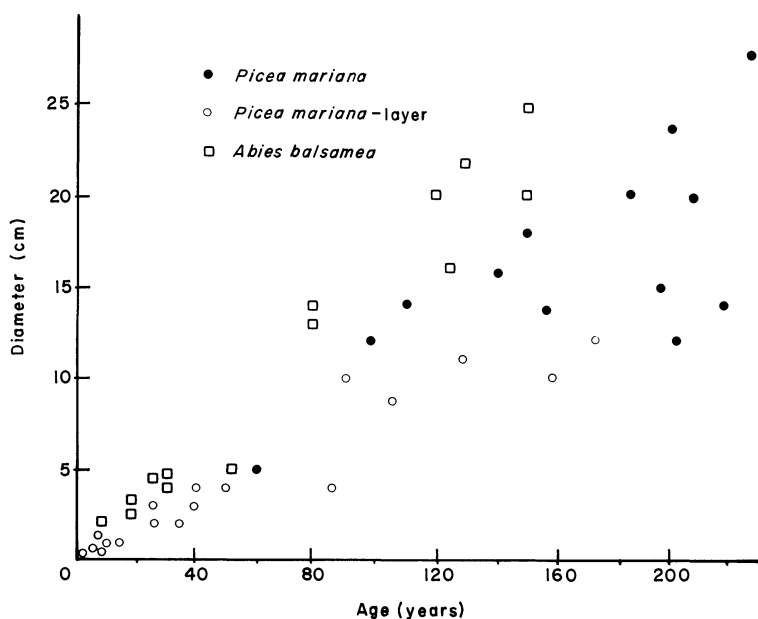
FIG. 5. Age-structure analysis of a 230+ year-old *Picea mariana* (black spruce)–*Pleurozium* forest in south-eastern Labrador.

than spruce. The stand is multi-aged, and the abundance of balsam fir seedlings and layered black spruce stems suggests that adequate replacement of senescent individuals is occurring to maintain a closed canopy.

Early post-fire changes in vascular understorey composition

Table 1 provides the frequency of nineteen common vascular species in burned (5-year-old) and unburned spruce–*Pleurozium* stands. The range of possible values for the magnitude of change in frequency extends from −2 to +2 (see Methods). The extremes realized in the data were −1·79 for *Empetrum nigrum* and 1·93 for *Epilobium angustifolium*. Species are arranged in order of increasing magnitude of change.

Three major response patterns are identified, and species are separated into three groups (with arbitrary cut-off values set at |0·40|). The majority of the species exhibit little change in frequency following fire, and are termed 'sprouters', as they display prolific resurgence from underground organs. Four species—*Coptis groenlandicum*—*Empetrum nigrum*, *Gaultheria hispidula* and *Kalmia angustifolia*—decrease significantly in frequency and abundance following fire and are grouped as 'decreasers'. *Empetrum nigrum*, although a very common and relatively abundant shrub in old forests, is never found on recently burned sites (1976, 1975, and 1967 burns) and was only occasionally noted on some 1959 burns. *Epilobium angustifolium*, although not found on adjacent old-age sites, was recorded in 84% of burned plots and was the only 'increaser'.

Cryptogam succession following fire

One year following a fire the blackened surface is devoid of plants, except for the resprouting vascular species. By 5 years, *Lecidea granulosa* has formed a crust-like surface on burned humus and reaches peak expression (15–50% cover) by 20 years (Fig.

TABLE 1. Post-fire changes in the understorey composition of *Picea mariana* (black spruce) – *Pleurozium* forests in Labrador.

	Frequency (%)		Magnitude of change*
	Unburned	Burned	
Decreasers			
Empetrum nigrum	61·1	—	−1·79
Kalmia angustifolia	22·2	5·0	−0·65
Gaultheria hispidula	100·0	36·8	−0·43
Coptis groenlandicum	66·7	26·3	−0·40
Sprouters			
Rubus chamaemorus	50·0	21·1	−0·37
Linnaea borealis	83·3	52·6	−0·20
Alnus crispa	55·5	36·8	−0·18
Equisetum sylvaticum	27·8	21·1	−0·12
Cornus canadensis	100·0	89·5	−0·05
Lycopodium annotinum	55·5	52·6	−0·02
Vaccinium vitis-idaea	55·5	52·6	−0·02
Ledum groenlandicum	94·4	100·0	0·03
Deschampsia flexuosa	38·9	42·1	0·05
Smilacina trifolia	22·2	26·3	0·07
Kalmia polifolia	27·8	36·8	0·12
Vaccinium cespitosum	44·4	63·1	0·15
Vaccinium angustifolium	22·2	47·4	0·33
Increasers			
Epilobium angustifolium	—	84·2	1·93
	$n = 18$	$n = 19$	

$$* \log \left(\frac{\text{frequency burned}}{\text{frequency unburned}} \right).$$

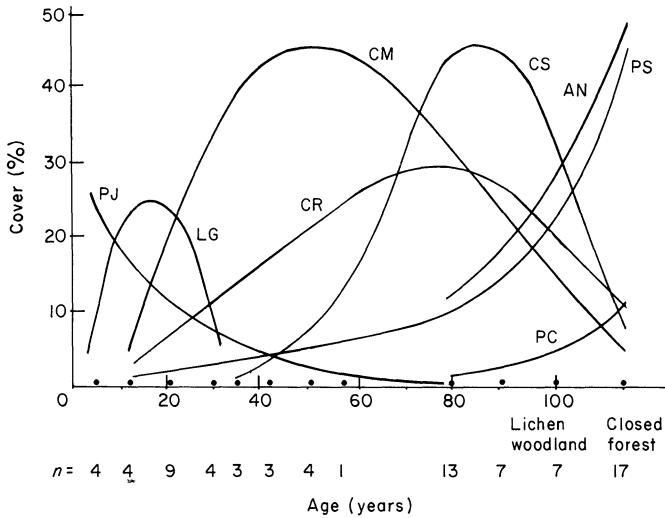$n = $ 4 4 9 4 3 3 4 1   13 7 7 17

FIG. 6. The pattern of revegetation of the dominant cryptogams after fire in south-eastern Labrador. Stands exceeding 90 years old are grouped into either lichen woodlands or conifer forest (see text for distinction). n = number of plots sampled in forests of a given age. Species abbreviations: AN, *Alectoria nigricans*; CM, *Cladonia mitis*; CR, *C. rangiferina*; CS, *C. stellaris*; LG, *Lecidea granulosa*; PC, *Ptilium crista-castrensis*; PJ, *Polytrichum juniperinum*; PS, *Pleurozium schreberi*.

6). In the face of competition for space and light with the taller *Cladonia* spp., *Lecidea* rapidly declines to residual levels and is absent from nearly all locations by 40 years.

Ceratodon purpureus and *Polytrichum juniperinum* form dense patches in depressions and in the mineral hollows created by windthrows immediately following a fire. *Ceratodon* exhibits behaviour similar to that of *Lecidea*, decreasing rapidly in the early years following fire, whereas *Polytrichum* persists for a longer period (Fig. 6).

Horn and cup lichens (*Cladonia chlorophaea*, *C. coccifera*, *C. cornuta*, *C. gracilis*, *C. macrophylla*, *C. pleurota* and *C. sulphurina*) are first seen on 10- to 12-year burns, and are restricted mainly to decaying wood and humus mounds where they never exceed 5–10% total cover (Fig. 7). In later years these species are often restricted to bleached snags of *Picea mariana*.

Cladonia mitis and *C. rangiferina* become established on 10- to 12-year-old sites. *Cladonia mitis* expands more rapidly, reaches a maximum of 50–75% cover, and may persist as a dominant for 40–60 years (Fig. 6). *Cladonia rangiferina* is more abundant on moister sites and demonstrates greater shade tolerance than *C. mitis* (cf. Ahti 1959).

Cladonia stellaris gradually increases in cover following establishment in 35-year-old stands and assumes a maximum cover of 50–75% in 80- to 90-year-old woodlands (Fig. 6). On sandy outwash plains and river terraces the forest canopy may never close because of the edaphic conditions, and *Cladonia stellaris* may persist as the dominant ground cover until the next fire.

Beneath the expanding conifer canopy that forms with time, there occurs progressive establishment and expansion of forest cryptogams, primarily bryophytes, at the expense of
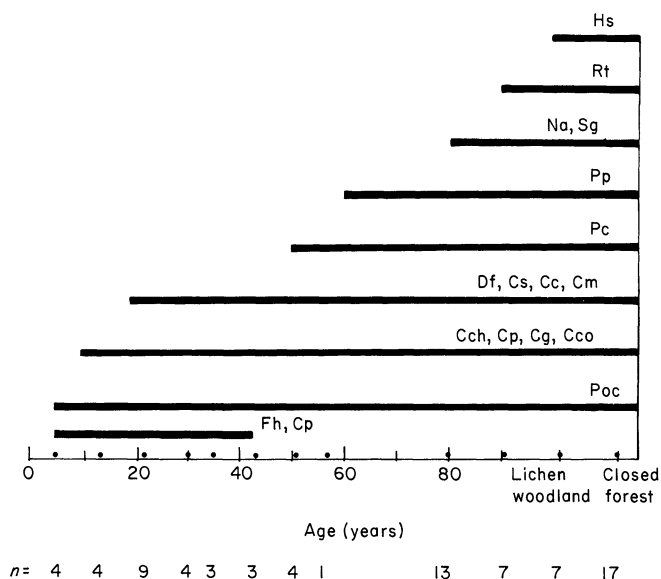

FIG. 7. Successional sequence of minor cryptogams after fire in south-eastern Labrador. Species are arranged in order of establishment as determined from frequency data from seventy-six relevés. Age scale as in Fig. 6. Species abbreviations: Cc, *Cladonia cristatella*; Cch, *C. chlorophaea*; Cco, *C. coccifera*; Cg, *C. gracilis*; Cm, *C. macrophylla*; Cp, *C. pleurota*; Cs, *C. sulphurina*; Df, *Dicranum fuscescens*; Fh, *Funaria hygrometrica*; Hs, *Hylocomium splendens*; Na, *Nephroma arcticum*, Pc, *Ptilidium ciliare*; Poc, *Polytrichum commune*; Pp, *Peltigera polydactyla*, Rt, *Ramalina thrausta*; Sg, *Sphagnum girgensohnii*.

the lichen cover (Fig. 7). The shade produced by clones of black spruce, which may exceed 5 m in diameter, provides a mesic habitat conducive to the growth of *Pleurozium schreberi*. Increase in the cover of this moss roughly parallels tree cover, and is approximately inversely proportional to the abundance of lichens. Forest cryptogams, including *Nephroma arcticum*, *Ptilium crista-castrensis* and *Peltigera* spp., enter after tree cover exceeds 30–50%. *Hylocomium splendens* and *Sphagnum girgensohnii* establish after 80 years and remain at relatively low abundance in all but very old and moist stands.

Three groups of lichens—fruticose and foliose arboreal epiphytes and foliose epigaeic species—are found only in late successional forests and increase beneath or within the conifer canopy. The most important arboreal species—*Alectoria nigricans*, *Hypogymnia physodes*, *Platismatia glauca* and *Ramalina thrausta*—assume prominence in old forests, as the black spruce decrease in vigour and the canopy opens somewhat. *Nephroma arcticum* and *Peltigera* spp. (*P. aphthosa*, *P. polydactyla*, *P. scabrosa*), although never abundant, are a conspicuous part of the ground cover of closed forests (Foster 1984b).

DISCUSSION

Mor humus stratigraphy

As a result of excess moisture, cool temperatures, and the resistant nature of the lignified and acidic forest litter, decomposition rates are slow in boreal forests, and the organic layer frequently accumulates to considerable depth (Moore 1981). Plant micro- and macro-fossils in this layer provide a stratigraphic record of the vegetation *in situ* which may be traced from the surface to assemblages at lower levels that represent progressively earlier stages in vegetation development.

The advantages of having a stratigraphic record of vegetation change *in situ* are manifold for a study of community development. Without this record it would be speculative and possibly quite erroneous to infer that vegetation of different ages in the present landscape represent stages in the temporal sequence of vegetation change following fire (cf. Egler 1976; McIntosh 1980). The preserved and albeit incomplete history of the recent vegetation at each site strengthens the conclusions concerning vegetation dynamics that are drawn from detailed analysis of extant stands.

In south-eastern Labrador the forest stands found on burns of different ages provide excellent analogues for the stratigraphic record contained in mor humus profiles. A generalized scheme of vegetation development following fire depicts progressive changes in ground cover concomitant with an increasing cover of conifer trees (Fig. 8). The interval between consecutive fires determines how far this sequence progresses at a given site.

The presence of charcoal at the base of every humus layer, and of multiple charcoal horizons in some profiles, documents the historical importance of fire in this region. In Labrador the extensive area of old forest gives the false impression that some stands have totally escaped fire (Foster 1984a). This is not borne out by stratigraphic analysis.

Pattern of arboreal regeneration

From the data and observations made across south-eastern Labrador it is apparent that tree establishment is slow and progressive, commencing the season following fire and continuing into the closed forest stage several decades later (Figs 3–5) (Foster 1984a). In the early years after fire the landscape is nearly barren of seedlings, and only scattered regeneration occurs on 20- and 30-year-old burns.

In view of the semi-serotinous cones of black spruce and the abundant seed fall
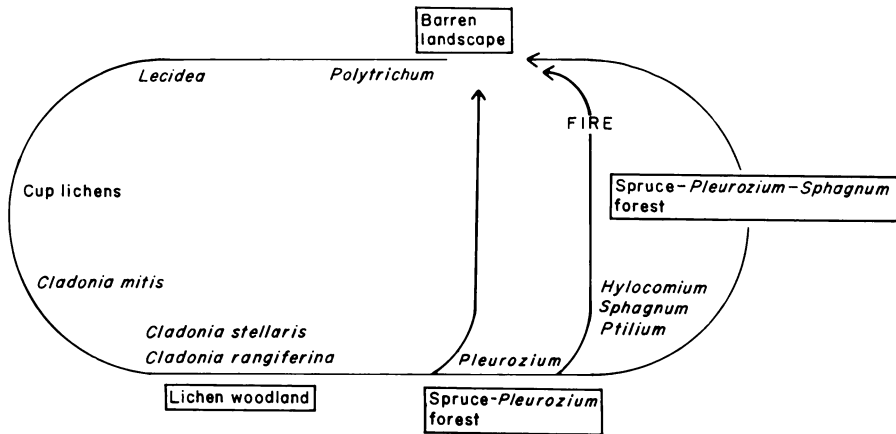
FIG. 8. Schematic representation of the post-fire development sequence of the *Picea mariana* (black spruce)—*Pleurozium* forest in south-eastern Labrador.

observed following fire (Heinselman 1957), the poor tree reproduction is at first surprising. Moisture appears to be the limiting factor as seedlings are largely restricted to depressions, the edges of watercourses, and exposed mineral soil, and are absent on the charred humus that blankets the uplands (Plate 2).

During the first season of growth the radicle of black spruce elongates 2 cm or less and seedlings are restricted to seedbeds of relatively constant moisture supply (Heinselman 1957). Charred humus is known to present a highly unfavourable microsite; as a
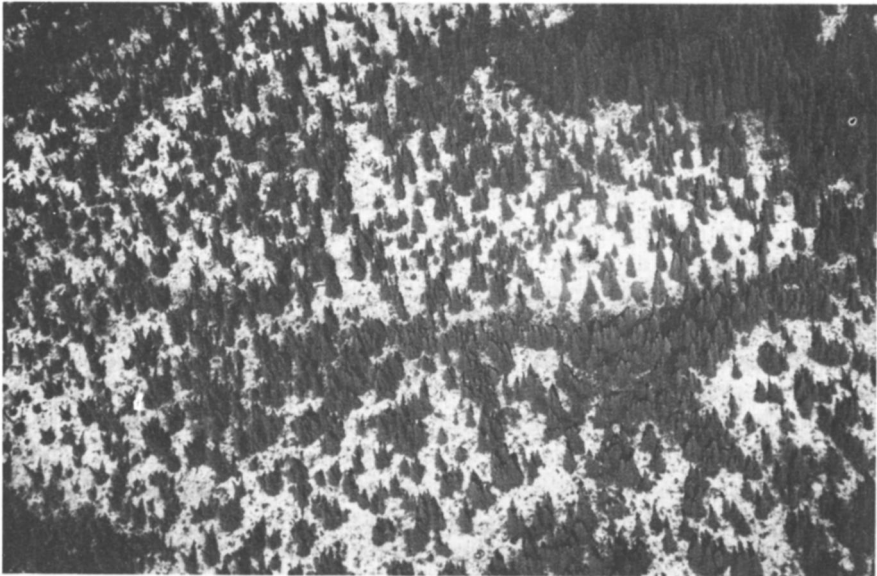

PLATE 2. Aerial photograph of a 57-year-old lichen woodland on a 1927 fire in south-eastern Labrador. Widely scattered black spruce (*Picea marina*) and balsam fir (*Abies balsamea*) are separated by intervening areas of ericaceous shrubs and *Cladonia* lichens. The density of trees is much greater in moist depressions and seepages than on the adjacent uplands.

consequence of the low albedo and low density the blackened surface organic layers undergo rapid and extreme fluctuations in moisture content (Vincent 1966; Kershaw 1977). The charred organic material that covers the landscape following fire in south-eastern Labrador thereby extends the period of seedling establishment, and produces a multi-age forest very different from that described elsewhere in the boreal forest.

In the western and central boreal region of Canada the shorter fire cycle and the drier summer climate may facilitate the complete removal of the organic layer and the consequent exposure of the mineral soil by fire. This favourable seedbed, coupled with abundant seed fall, produces the even-aged and dense stands of black spruce characteristic of burns in Alaska (Lutz 1953; Viereck 1973), the Northwest Territories (Scotter 1964; Rowe & Scotter 1973), Alberta (Moss 1955), Manitoba (Richie 1960), Minnesota, U.S.A., (Heinselman 1957, 1973), and Ontario and Quebec (Shafi & Yarranton 1973).

The slow and progressive regeneration of black spruce and balsam fir in Labrador has important ecological consequences. First, the rate of reforestation is highly dependent on the size and pattern of burns. As initial stocking densities are low, subsequent seedling establishment is largely dependent on propagules that are dispersed from the unburned forest at the periphery of the burn or from unburned enclaves within the burn. Seed dispersal falls off rapidly with distance, and thus the centres of large burns are especially slow to restock. The few initially established trees may therefore assume special importance as an 'internal' seed source during later years of succession on large burns. In view of the long period of reforestation and the large size of many of the fires (Foster 1984a), the rapidly growing saplings of black spruce and balsam fir, which begin producing cones within 10–15 years, may provide the bulk of the seed source for stand regeneration.

Perhaps the most significant result of slow reforestation is the extended period available for cryptogam succession, lichen dominance and the maintenance of a woodland vegetation composed of open-grown trees and shrubs. As explained above, the feather mosses depend on shade provided by the tree canopy; the amount of tree cover governs the relative abundance of bryopyte versus lichen cover. The period of 80–100 years during which lichen woodlands dominate the burned landscape in southern Labrador is unusual for the boreal forest region and is more typical of the subarctic region (Rowe & Scotter 1973; Kershaw 1977; Johnson 1981).

Response of the vascular understorey to fire

In contrast to the arboreal species, the majority of the vascular understorey species are well-adapted for survival and rapid regeneration following fire. In south-eastern Labrador resurgence through sprouting or suckering from underground organs is the predominant mode of regeneration. Growth is rapid following fire, undoubtedly because of favourable environmental conditions including abundant light and enhanced soil temperatures, increased decomposition rates, and increased nutrient availability (Viereck & Schandelmeier 1980). The result is a dramatic increase in flower production and abundance to levels greatly exceeding pre-burn levels for such common species as *Cornus canadensis*, *Deschampsia flexuosa*, *Equisetum sylvaticum*, *Ledum groenlandicum*, *Rubus chamaemorus*, *Vaccinium angustifolium*, and *V. cespitosum*.

That some species are susceptible to fire or to the associated changes in environmental conditions is evident by the group of 'decreasers'. Within this group *Coptis groenlandicum*, *Empetrum nigrum* and *Gaultheria hispidula* have shallow root systems and may therefore be particularly sensitive to burning. *Empetrum nigrum* is reported to be absent following burning of blanket bogs in Europe (Bell & Tallis 1973).

The observation that only one vascular species (*Epilobium angustifolium*) increases following fire is remarkable when compared to the central and western boreal forest, where the list includes such common forms as *Aralia hispida*, *Corydalis sempervirens*, *Geranium bicknellii*, *Polygonum cilinode* (Ohmann & Grigal 1979; Viereck & Schandelmeier 1980) and the graminoids *Calamagrostis canadensis*, numerous *Carex* spp. and *Poa glauca* (Heinselman 1973). *Epilobium angustifolium* is seldom found growing in mature forests, but can regenerate from buried root stalks (Moss 1936) or disperse rapidly with light wind-carried seed. Once established, it spreads prolifically by extensive rhizome systems and seed reproduction.

Cryptogam succession

In general, the vegetation development of the ground cover follows the classic physiognomic trends (Cooper 1913). Low and appressed crustose and foliose lichens and acrocarpous bryophytes are succeeded by the taller fruticose lichens and ultimately by the weft- and tuft-forming pleurocarpous mosses.

The establishment sequence suggests a decreasing gradient of habitat instability and environmental severity and a continual diversification of the available habitats with time following fire. The recently burned landscape presents a harsh environment subject to frequent disturbance, and the initial colonizers—*Ceratodon purpureus*, *Funaria hygrometrica*, *Lecidea granulosa* and *Polytrichum juniperinum*—are species characteristic of temporally unstable sites, especially charred surfaces (Crum 1979; Hale 1979). Substrate stability increases with time as a result of the gradual development of the vascular plant cover.

Overriding environmental changes are induced by tree establishment and growth. Shaded regions beneath conifers provide distinct habitats that increase in size with time. On these sites the amelioration of temperature and moisture extremes is accompanied by decreased light intensity and enhanced humidity. Under this environmental regime forest cryptogams are competitively favoured over the sun-loving fruticose lichens. In open woodlands *Pleurozium schreberi* forms a dense carpet that neatly matches the shaded areas beneath conifer branches, whereas the intervening areas between trees remain dominated by lichen cover. Many of the pleurocarpous mosses have been shown to depend on throughfall from the conifer canopy for nutrients (Tamm 1953; Reilly, Richards & Bebbington 1979), and studies in lichen woodlands demonstrate that the soil surface around spruce trees shows increased nutrient availability (Moore 1981).

Ecological significance of ground-cover succession

In terms of ecosystem structure and function, the early successional cryptogams may be considered relatively insignificant. When compared with the vascular component, the lichens and acrocarpous mosses contribute little to total community biomass or production and are a relatively minor factor in biogeochemical cycles (cf. Rencz & Auclair 1978).

The ground cover, however, exerts an influence on the rate and course of later stages of vegetation development. In the absence of an extensive vascular ground layer, the lichens and *Polytrichum juniperinum* may help to stabilize the charred substrate and decrease erosion. The crust-like surface formed of *Lecidea granulosa* is succeeded by a 5–15 cm layer of *Cladonia* podetia that intercepts rainfall and reduces surface-water flow (Jack 1935).

The extensive *Cladonia* mat may inhibit the germination and seedling establishment of the conifers and thereby increase the time necessary for reforestation (Hustich 1951; Ahti

1959). The fruticose growth form of these species presents a substrate similar to burned duff in its susceptibility to rapid and extreme fluctuation in moisture content, and seedlings have difficulty penetrating the lichens to moist soil. There is also preliminary evidence that lichens secrete secondary chemicals inhibitory to germination and growth of vascular seedlings (S. Cowles personal communication).

As a consequence, conifer seedlings are largely restricted to seedbeds projecting above the lichen mat, such as rotting stumps and fallen, dead trees, to exposed mineral soil on windthrows, and to moist moss-filled depressions. The narrow (0·1–2·0 cm) desiccation cracks that separate the lichen mat into irregular-shaped polygons also present moist seedbeds in the humus. By decreasing the availability of sites open to conifer establishment the early successional lichens serve to prolong vegetation development.

Thus, the pattern observed during vegetation development following fire on the spruce–*Pleurozium* forests of south-eastern Labrador is heterogeneous, and results from the individualistic behaviour of the various species and growth forms involved. Different species and life forms operate within different sets of morphological and physiological constraints, and respond to environmental regimes that operate at contrasting temporal and spatial scales within the community. The response and regeneration of the vascular understorey corresponds well with Egler's (1954) concept of initial floristics. The post-fire community consists largely of species found in the unburned forests that exhibit changes in abundance and in energy allocation to growth and reproduction.

Whereas fire serves as a recycling agent in the understorey, it may eliminate trees locally and reduce their density over a wide area. For the conifers, regeneration occurs progressively over a long period. Subtle and important changes in post-fire seedbed conditions that exert little effect on the deeply rooted understorey species largely control the rate and pattern of seedling establishment. In addition to harsh edaphic conditions, the rapid establishment of a deep lichen cover inhibits regeneration. The early-successional species serve to prolong succession and deter the entry of late-successional species (Niering & Goodwin 1974).

The cryptogams follow a more traditional succession in terms of physiognomic changes and exhibit a stepwise establishment sequence (Kershaw 1978; Johnson 1981). Differential growth rates, competitive ability, and environmental tolerance result in species ordination along a temporal gradient of gradual amelioration in environmental extremes. The major factor that mediates conversion of lichen woodland to bryophyte-dominated forest is shade provided by the canopy cover.

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