

VEGETATION PATTERN AND DIVERSITY IN S.E. LABRADOR, CANADA: *BETULA PAPYRIFERA* (BIRCH) FOREST DEVELOPMENT IN RELATION TO FIRE HISTORY AND PHYSIOGRAPHY

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SUMMARY

(1) The *Betula papyrifera* (paper birch) forest of the wilderness of south-eastern Labrador is described.

(2) *B. papyrifera* forests range in size from less than 1 ha to several km², display sharp borders with the adjoining conifer forests and are restricted to steep slopes that have burned in the previous 110 years.

(3) Floristically, the *B. papyrifera* community is distinguished from conifer forests by the presence of fourteen differential species, by the scarcity of terrestrial cryptogams and by the development of a diverse understorey of vascular plants.

(4) Three minimum conditions are necessary for *B. papyrifera* forest development: (i) moist and well-drained soils, (ii) a nearby seed source, and (iii) an open site.

(5) The nearly exclusive restriction of *B. papyrifera* forest to areas that have burned in the last 110 years indicates that the open-site conditions necessary for stand initiation are largely created by lightning fires.

(6) Age-structure analysis demonstrates that, following fire, regeneration by *B. papyrifera* is rapid and results in the formation of an even-aged overstorey. Gradual invasion of canopy openings by *Picea mariana* and *Abies balsamea* results in the progressive conversion to conifer forest.

(7) Fire maintains *B. papyrifera* and other early post-fire communities in a mosaic pattern and increases regional vegetation diversity. The pattern is not random, but is controlled by species autecologies, the pattern of fires and physiography. The vegetation of south-eastern Labrador is in a state of dynamic equilibrium.

INTRODUCTION

The recognition that disturbance is a prevalent factor in many ecosystems has led to the theory that long-term ecosystem dynamics are frequently a consequence of succession and patterns of periodic disruptions (Bormann & Likens 1979; Heinselman 1981). A corollary of this theory is that perturbations may enhance regional diversity through the creation of a patchwork of successional stages that provide habitats for a diverse flora and fauna (Loucks 1970; Heinselman 1973). However, studies documenting regional-disturbance regimes are needed to examine the general validity of this theory. Research on the phytosociology and fire history of south-eastern Labrador, Canada (Foster 1983b, 1984), provides the background for the investigation presented here on the role of fire in the development of *Betula papyrifera** (paper birch) forests and the implications of this process in terms of regional diversity.

* 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 follow Ahti (1961). Voucher samples of lichens and vascular plants are deposited in the herbarium of the University of Minnesota (MIN). Duplicates of all bryophyte collections are stored in the National Herbarium, National Museum of Canada (CAN).

The landscape of south-eastern Labrador is covered predominantly by a mixed *Picea mariana* (black spruce) and *Abies balsamea* (balsam fir) forest. However, on steep slopes in dissected terrain a vegetation mosaic is created by extensive stands of *Betula papyrifera* that display sharp boundaries with the adjoining conifer forest. The repeated occurrence of hill-slope forests of *B. papyrifera* suggests that there is a common and widespread mechanism for their formation. This mechanism must involve recurrent disturbance, as the shade-intolerant *B. papyrifera* requires open conditions for regeneration.

As little information was available on site preference, origin, or development of *B. papyrifera* forests, a detailed investigation was undertaken to obtain floristic, environmental and historical data on these stands throughout south-eastern Labrador. This information was then used to examine the role of widespread disturbance in the development and maintenance of the stands and in augmenting regional diversity.

STUDY AREA

Labrador comprises the north-eastern extension of the North American boreal region. The study area in south-eastern Labrador is approximately 300×160 km, extending east from St Augustin River to the coast and south from the Mealy Mountains to the Quebec border ($52-53.5^\circ\text{N}$, $55-59^\circ\text{W}$) (Fig. 1).

Labrador forms the eastern portion of the Precambrian Canadian Shield which consists of acidic rocks, primarily quartzo-felspathic gneisses with intrusions of granite and granodiorites (Greene 1974). The entire region was covered by the Laurentide ice sheet during the last glacial period.

The cold Labrador Current exerts a dominant influence on this coastal region, producing a climate characterized by long, cold winters and short, cool summers. Precipitation is amongst the highest of the North American boreal forest; approximately 900 mm is equally distributed through the year (Peach 1975). In southern Labrador convective thunderstorms occur from June to August (Foster 1983b).

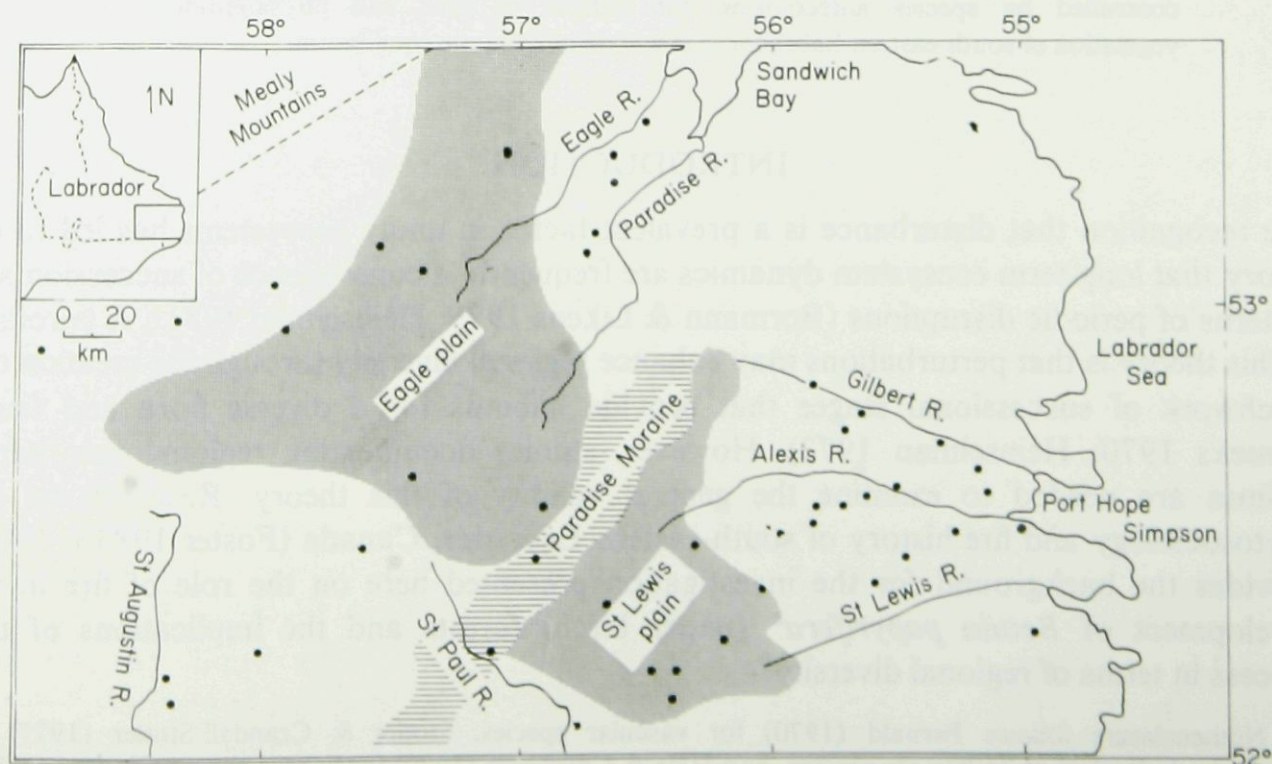


FIG. 1. The study area in south-eastern Labrador. The dots indicate sites visited in the course of field work during the summers of 1979-81.

The central portion of the study area consists of two broad glacial plains, the St Lewis and Eagle plains, separated by the undulating Paradise moraine (Fig. 1). Towards the coast, where the rim of the plateau is dissected by the St Augustin, Eagle, Paradise, St Lewis, and Alexis Rivers, there are steep bedrock hills separated by deep valleys. The physiography has important influences on the vegetation and environment: the flat interior is dominated by mires and forests of low productivity, whereas the hilly perimeter supports richer, more productive forests and few mires (Foster & King 1984; Foster & Glaser 1986).

The regional vegetation consists mainly of communities dominated by *Picea mariana* and *Abies balsamea*. In addition, *Betula papyrifera*, and to a lesser extent *Picea glauca* (white spruce), are locally important, whereas *Larix laricina* (tamarack) is generally restricted to open peatlands. Across most of the study area a species-poor black spruce–*Pleurozium* forest (cf. Foster 1984; Table 1) forms a nearly continuous cover interrupted only by innumerable mires, lakes, and streams. This forest is characterized by a low ericaceous shrub layer composed, in order of decreasing abundance, of *Ledum groenlandicum*, *Vaccinium angustifolium* and *V. myrtilloides* and sparse herb layer of *Cornus canadensis*, *Gaultheria hispidula*, *Trientalis borealis* and *Empetrum nigrum*. The forest floor is covered by a continuous mat of *Pleurozium schreberi* 5–20 cm thick.

On nutritionally richer sites, especially at low altitudes and on well-drained moist slopes towards the coast, the trees are more luxuriant in a fir–black spruce–feather moss forest. The richer vascular understory includes *Viburnum edule*, *Amelanchier bartramiana* and *Alnus crispa* in the shrub layer and the herbs *Clintonia borealis*, *Maianthemum canadense*, *Trientalis borealis* and *Linnaea borealis*. A deep carpet of mosses is composed of *Sphagnum girgensohnii*, and the feather mosses *Ptilium crista-castrensis*, *Hylocomium splendens* and *Pleurozium schreberi* (Foster 1984).

Lightning is the sole source of fire in this wilderness area (Foster 1983b). 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 mires that serve as very effective fire breaks.

METHODS

Betula papyrifera stands of minimum size 4 ha were located on 1:60 000 aerial photographs and delimited on 1:250 000 topographic maps. A map of stand locations on a 1:10⁶ scale was drawn to illustrate their regional distribution and relationship with fire history, topography and the distribution of mire-dominated terrain. The fire history of the region is based on mapping of fires from aerial photographs and aerial reconnaissance and dating of fire scars on *Picea mariana* (Foster 1983b).

In order to compile maps of topographic roughness and mire distribution, the region was first gridded using the Universal Mercator Transverse grid system with each cell 10 × 10 km. The percentage of each cell occupied by mires was estimated to the nearest 10% from 1:250 000 topographic maps and 1:60 000 black and white aerial photographs. Topographic roughness, an estimate of the amount of relief in an area, was calculated by counting the number of 10-m contour lines crossed by the diagonals of a cell on a 1:250 000 map. Maps were generated from the data arrays using the programs MAPFILE and MAPGEN.

The study sites were selected from the maps, aerial photographs and aerial reconnaissance, on the basis of stand age, fire history and accessibility by float plane. In the field the criteria for the selection of sampling sites included (i) the dominance (>50% cover) of *Betula papyrifera* in the canopy, (ii) the homogeneity of the vegetation and site, and (iii) a minimum size of 1 ha. A total of twenty-six stands were sampled.

The methods of Braun-Blanquet (Mueller-Dombois & Ellenberg 1974) were employed, with plots measuring 20 × 20 m. Cover abundance in each relevé was estimated on the 10-point Domin scale (Birks 1973).

In each plot, four to six of the largest-diameter trees were recorded for height, dbh and age (estimated by the number of growth rings in cores obtained at approximately 15 cm above the mineral soil). The organic layer and mineral soil were examined with the aid of a serrated knife and a soil auger. Other information recorded for each plot included altitude, slope, aspect, and position on the slope.

Two stands, originating from 1889 and 1941 fires (Foster 1983b), were analysed for density and basal area with the point-centred-quarter method (Cottam & Curtis 1956). At least 30 points were established at 10-m intervals along transects across each stand. The age structure of the 1889-origin stand was determined from counts of growth rings of at least fifty trees encountered at increasing distances from the stand centre.

In the 1941-origin stand (relevé 7) a 10 × 10-cm core of the organic layer was cut to the mineral soil and wrapped in plastic and aluminium foil for transport to the laboratory. A similar core was obtained from an adjacent old fir–black spruce–feather moss forest (cf. Foster 1984) for comparison. In the laboratory, the cores were cut in half lengthwise and their gross stratigraphy described. One half was dissected to identify macrofossils, charcoal horizons and the composition of the organic matrix. Samples for pollen analysis were obtained from continuous 5-cm intervals or at distinct horizons. The samples were prepared by the techniques of Faegri & Iversen (1975) as modified by E. J. Cushing (pers. comm.). A minimum of 250 pollen grains were identified from each level and tabulated under a microscope at ×400.

RESULTS

Regional distribution

The regional distribution of *Betula papyrifera* stands forms a distinctive pattern; most stands are located on steep slopes in rugged terrain that has burned within the last 110 years (Figs 2 and 3).

The central portion of the study area, formed by the Eagle and St Lewis plains, is covered by extensive patterned mires and has experienced a very low incidence of fire in the recent past (Foster 1983b). *B. papyrifera* is relatively uncommon, and full-canopied stands do not occur in this area.

In sharp contrast, the dissected uplands towards the periphery of the plateau exhibit a much higher incidence of fire and support extensive *B. papyrifera* forest in addition to productive conifer forest. The greatest concentrations of *B. papyrifera* are found along the St Augustin, Alexis and Eagle Rivers (Figs 1–3). The St Augustin River dissects the south-western plateau to form deep valleys and steep sided bluffs with a local relief exceeding 300 m (Fig. 4). Most of this region was burned in 1880 and 1898, and portions were reburned in 1959 and 1975 (Foster 1983b). Extensive forests of *B. papyrifera*, some exceeding 3 × 1 km, flank the valleys. In general, the valley bottoms support a *Salix*-scrub flood plain community or a conifer forest on the gentle slopes bordering the watercourse.

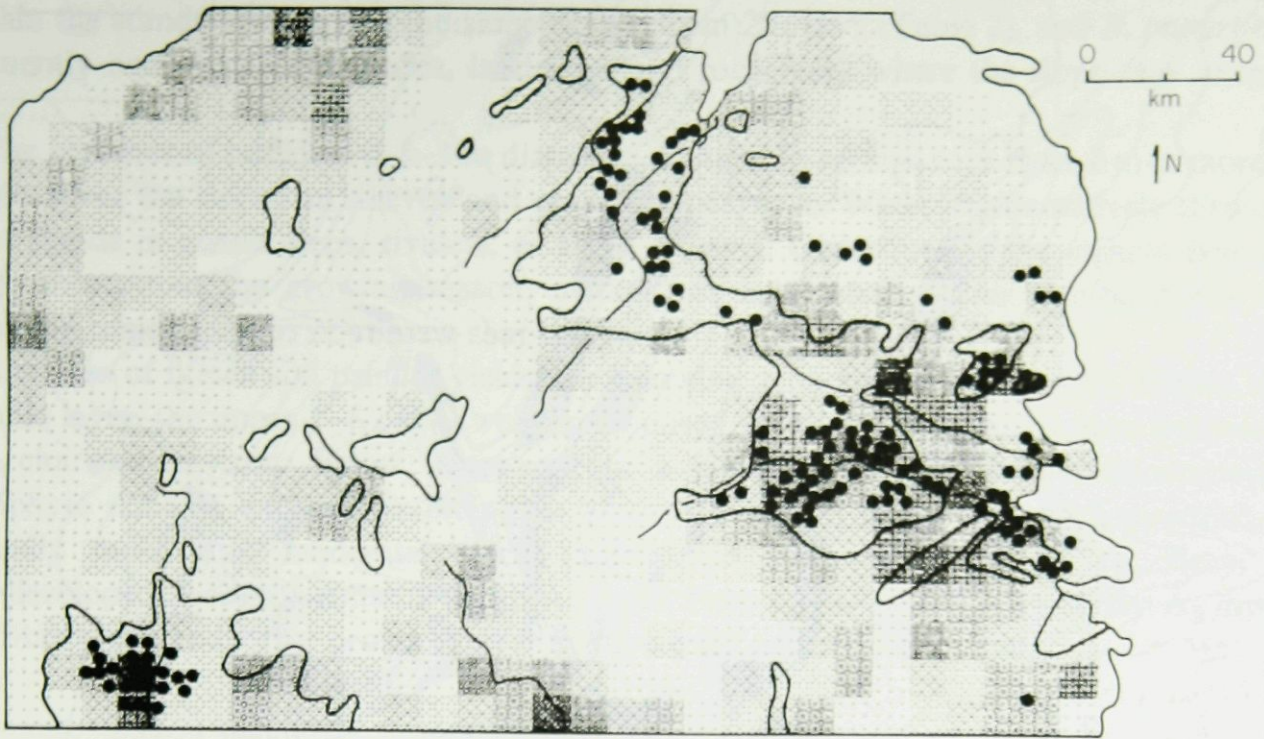


FIG. 2. The relationship between fire history, topography and the distribution of *Betula papyrifera* forests in south-eastern Labrador. Symbols: (●), *B. papyrifera* stands; areas enclosed by solid lines were burned during 1870–1980; (□–■), topographic surface roughness, from least to most.

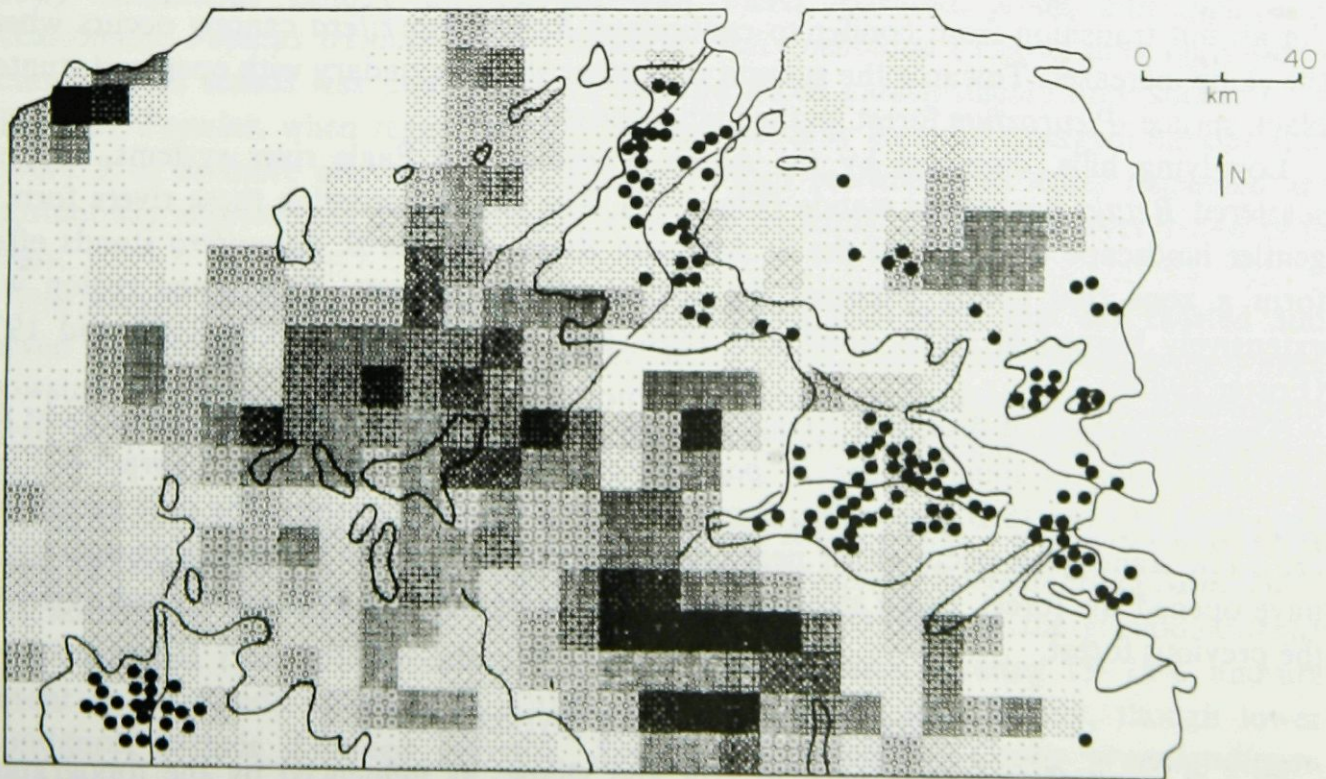


FIG. 3. The relationship between fire history, the distribution of mires and the distribution of *Betula papyrifera* forests in south-eastern Labrador. Symbols: birch forests and fires as in Fig. 2; (□–■), percentage of mires in the landscape, from <10% to 90–100%.



FIG. 4. Distribution of *Betula papyrifera* forests (black areas) on the hillslopes and canyon walls of the St Augustin River Valley, south-eastern Labrador.

An abrupt transition from conifer to continuous *Betula papyrifera* canopy occurs where the slope increases. Towards the summit is another sharp boundary with open and stunted black spruce–*Pleurozium* forest on the high, exposed hills.

Low-lying hills, dissected by the Alexis, Paradise and Eagle river systems, support scattered *Betula papyrifera* stands (Figs 1–3). The slopes bordering these rivers form a gentler landscape than that of the St Augustin River, and the *B. papyrifera* stands often form a zone that nearly encircles the spruce-covered hilltops. This broad region was extensively burned in 1870, 1889 and 1898, and again in 1941, 1959, 1975 and 1976 (Foster 1983b).

The coincidence of dissected terrain and fire within the past 110 years can account for the distribution of most of the *B. papyrifera* stands in south-eastern Labrador. Field inspection of over 35 *B. papyrifera* forests confirms this relationship. The only exceptions are a few stands that occur either near coastal settlements, where small logging operations have opened the forest, or on steep slopes where avalanches or rock slides have removed the previous forest.

Description of Betula papyrifera stands

The *B. papyrifera* stands vary in size and shape, as influenced by the topography, drainage and local pattern of fire. Patches less than 0.5 ha are scattered across many of the low coastal hills or are confined to narrow seepages, whereas those that exceed 750 ha occur along the broad canyons of the St Augustin River.

Generally, the stands are located on steep slopes with southern exposures (Fig. 4). Within the stands investigated the slope ranges from 2 to 25° (Table 2), and *B. papyrifera* frequently occurs on talus slopes, landslides and rock faces where the slope may exceed 30°.

The presence of boulders 0.5–3 m diameter, along with vertical rock faces 3 m or more in height, gives the slopes an uneven and rugged appearance. Water drains actively through most stands in gentle seeps, rivulets, or small streams. Consequently the ground is quite moist throughout the growing season, in contrast to the soil in the conifer stands on adjoining ridges, hilltops or convex-shaped slopes.

Analyses of fifteen soil profiles yields the following generalized stratigraphy. Within the organic layer, the upper 1–8 cm of well-decomposed deciduous litter and humus overlies a thin charcoal horizon. Below, there occurs a layer of partially to well-decomposed bryophyte remains and conifer litter that extends 5–25 cm to the mineral soil, which is typically moist and moderately well drained. In soils exceeding 15 cm deep, a well-developed spodosol consists of an A₁ layer 1-cm thick, an ash-gray sandy A₂ layer 5–15-cm thick, and a rust-brown B layer overlying the coarser parent material.

Floristic analysis and vegetation description

The *Betula papyrifera* community is distinctive among the forest types of south-eastern Labrador in physiognomy, composition, vascular species diversity and floristic integrity. The prominence of a well-developed shrub understory, the lush and species-rich herbaceous ground cover, and the minor importance of bryophytes distinguish it from the conifer communities (Table 1). The differential species in this community are strikingly apparent in the field.

In aggrading (*sensu* Bormann & Likens 1979) and mature forests, *B. papyrifera* forms a nearly continuous canopy interspersed with *Picea mariana*, *Abies balsamea* and, occasionally, *Populus tremuloides*. In addition, *Salix bebbiana* (willow) may be a minor component in stands less than 50 years old and *Picea glauca* occurs only sporadically (Table 2). *Populus*, when regenerating from suckers, may form an emergent canopy that towers 5 m or more above the main canopy. *Picea mariana* and *Abies balsamea* are substantially shorter than the deciduous trees and frequently comprise a layer 1.5–6 m in height.

The *Betula papyrifera* are generally multi-stemmed with boles that are twisted and curved in a downslope attitude. The multiple stems result from sprouting following winter browsing by moose (*Alces alces* (Clinton)) and snowshoe rabbit (*Lepus americanus* (Erxleben)). Conifers, killed in the previous fire, fall against the *Betula* saplings and deform them.

A discontinuous shrub layer 1.5–3 m high includes *Alnus crispa*, *Viburnum edule*, *Salix bebbiana*, *Sorbus decora*, *Prunus pennsylvanica* and *Amelanchier bartramiana* (Table 2).

A floristically rich herbaceous layer generally covers 75–90% of the ground. *Cornus canadensis* and *Trientalis borealis* are generally predominant, covering 15–75%, and are present in all stands investigated. Other species exhibiting high fidelity, though lower abundance, include *Linnaea borealis*, *Solidago macrophylla*, *Coptis groenlandicum*, *Maianthemum canadense*, *Lycopodium annotinum*, *Dryopteris spinulosa* and *D. disjuncta* (Table 2).

Cryptogams are restricted to less than 10% cover beneath the *B. papyrifera* canopy. *Pleurozium schreberi*, *Polytrichum juniperinum*, *Dicranum fuscescens* and the lichens

TABLE 1—continued

| Vegetation Species | Birch | | Fir-spruce- feather moss | | Spruce-fir | | Spruce- <i>Pleurozium</i> | | Spruce- <i>Sphagnum fuscum</i> | |
|--------------------------------|-------|---------------|-----------------------------|---------------|------------|---------------|------------------------------|---------------|-----------------------------------|---------------|
| | MV* | Frequency (%) | MV | Frequency (%) | MV | Frequency (%) | MV | Frequency (%) | MV | Frequency (%) |
| VII { <i>Mylia anomala</i> | | | | | | | | | 2 | 47 |
| <i>Chamaedaphne calyculata</i> | | | | | | | | | 4 | 80 |
| <i>Smilacina trifolia</i> | 2 | 4 | 2 | 10 | | | 2 | 25 | 2 | 67 |
| <i>Kalmia polifolia</i> | | | 1 | 5 | 1 | 7 | 2 | 17 | 2 | 100 |

Cover abundance values: 1, <3%; 2, 3–10%; 3, 10–35%; 4, >35%. * MV, modal value is shown.

† Roman numerals refer to species groups, identified in Foster (1984).

Cladonia mitis, *C. rangiferina*, *C. chlorophaea* and *C. cornuta* occur where leaf litter is sparse and on stumps, dead conifer wood, tree bases and humus-covered rock. *Sphagnum girgensohnii* is common in depressions and bordering streams.

A striking characteristic of the older *Betula papyrifera* stands is that there is little between-stand variability in floristic composition; the same species in similar abundances occur throughout the region.

B. papyrifera stands 0–20 years old generally contain a few additional cyryptogam species. As noted on the 1975 burns (Relevés 1 and 2, Table 2) *Epilobium angustifolium*, *Marchantia polymorpha*, *Funaria hygrometrica* and *Polytrichum juniperinum* reach peak abundance 5–10 years immediately following fire. *Polytrichum juniperinum* remains abundant in older stands, whereas the other species decrease rapidly in abundance within 20 years of the stand origin (Table 2).

Organic soil stratigraphy

Evidence of the role of fire in the genesis of *B. papyrifera* forests is preserved in the humus stratigraphy. The pollen stratigraphy and composition of the organic soil layers in a 41-year-old *B. papyrifera* forest and the adjoining mature fir-spruce-feather moss forest are depicted in Fig. 5. The mosaic of vegetation indicates that a 1941 fire swept across the middle and upper slopes of this south-facing watershed, leaving the conifer forest on the lower slope unburned. The *B. papyrifera* forest forms a block approximately 100 × 50 m across the middle of the slope.

The basal horizon of the soils in both forests consists of well-decomposed conifer and bryophyte remains interspersed with abundant, small (≤ 1 -mm diameter) charcoal fragments. This layer represents repeated episodes of forest growth interrupted by fire, spanning an unknown period of time. Above, the profiles contain a well-decomposed matrix of moss remains (mainly *Pleurozium schreberi* with some *Ptilium crista-castrensis*), and needles and cones of *Picea mariana* and *Abies balsamea*. The degree of humification decreases towards the top of the profiles and, in the conifer forest, the material grades into a surface layer of *Pleurozium schreberi*, *Ptilium crista-castrensis* and conifer litter (Fig. 5a).

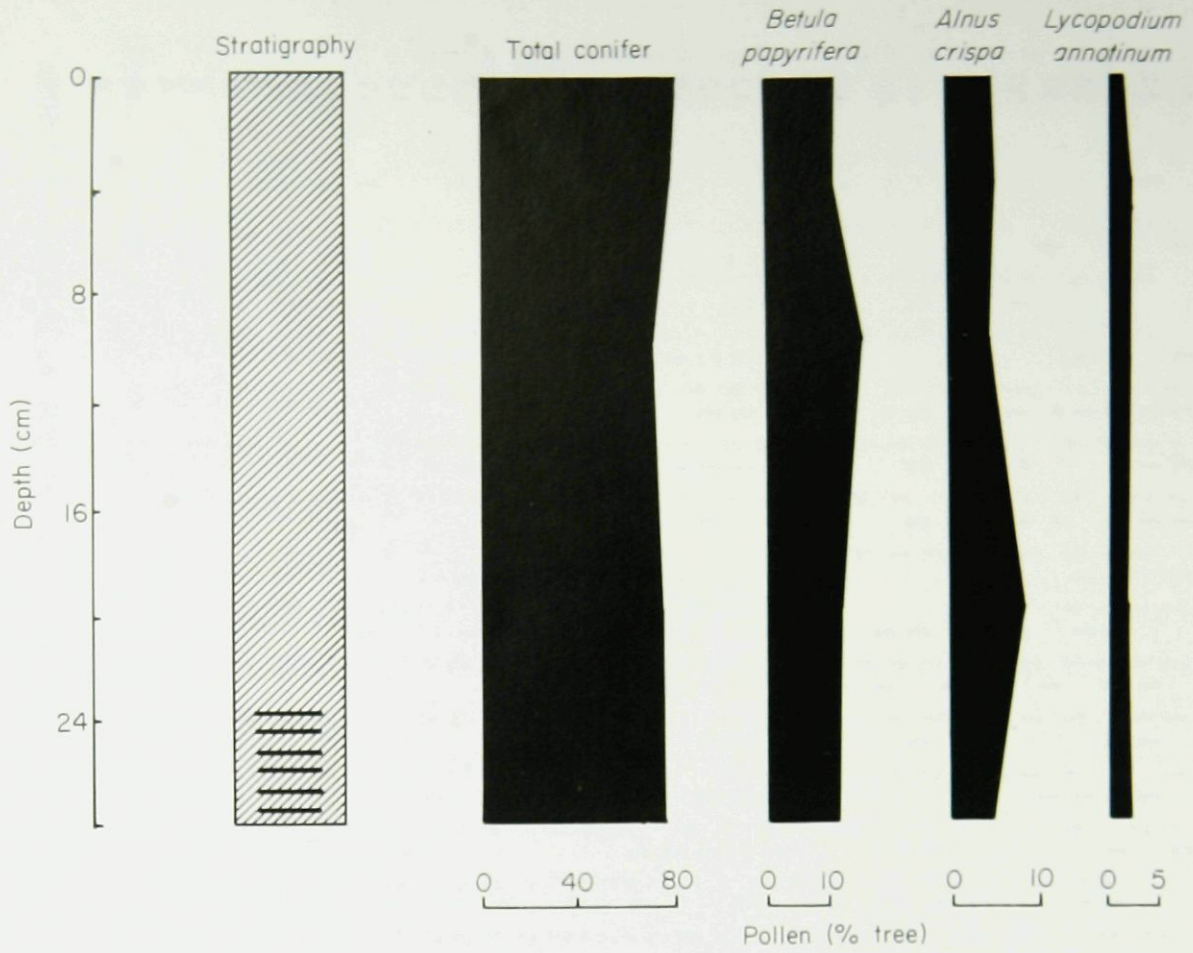
Beneath the *B. papyrifera* canopy the organic profile exhibits an abrupt break from this pattern above a charcoal horizon at a depth of 5.5 cm. This layer, composed of charred wood and needles of *Picea mariana*, represents the 1941 fire. Above it there is a 5-cm layer of deciduous humus and leaf litter.

TABLE 2. Floristic table of *Betula papyrifera* stands in south-eastern Labrador. Relevés are arranged in order of increasing stand age, species are arranged in decreasing frequency of occurrence.

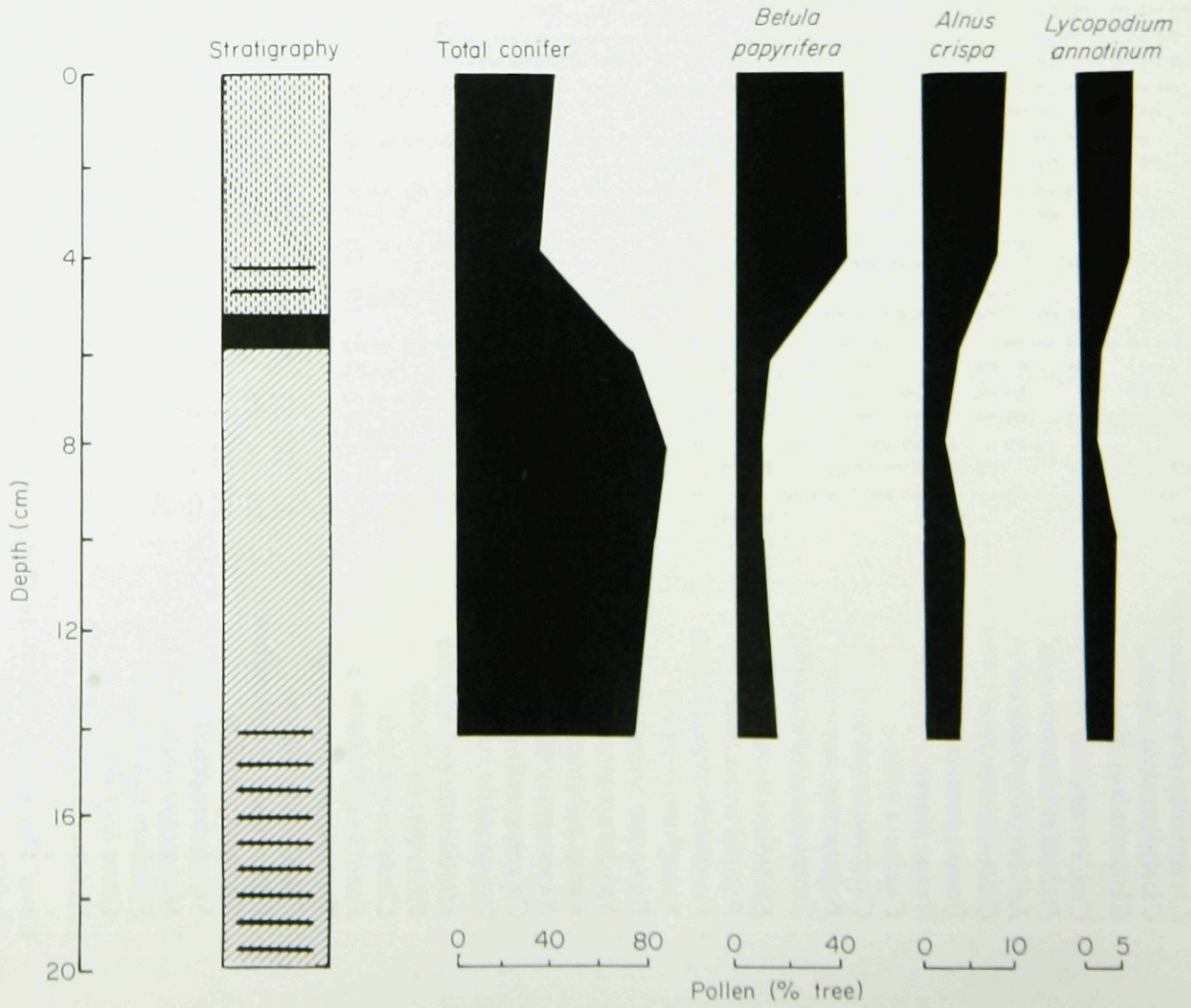
| Relevé | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | Mean | |
|--------------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|------|-----|
| Altitude (metres × 0.1) | 19 | 19 | 18 | 18 | 10 | 10 | 21 | 20 | 18 | 22 | 18 | 15 | 37 | 36 | 37 | 12 | 25 | 21 | 20 | 18 | 24 | 18 | 14 | 12 | 12 | 68 | | |
| Aspect (degrees × 0.1) | 16 | 15 | 35 | 35 | 9 | 9 | 20 | 22 | 0 | 0 | 18 | 16 | 5 | 5 | 20 | 18 | 20 | 20 | 20 | 20 | 22 | 20 | 20 | 16 | 15 | 17 | 16 | |
| Slope (°) | 15 | 25 | 15 | 10 | 10 | 10 | 2 | 2 | 15 | 8 | 20 | 15 | 10 | 5 | 2 | 8 | 5 | 15 | 10 | 10 | 8 | 5 | 15 | 15 | 5 | 11 | | |
| Age (years) | 6 | 6 | 14 | 14 | 22 | 22 | 41 | 41 | 41 | 41 | 50 | 65 | 82 | 82 | 82 | 82 | 82 | 82 | 82 | 82 | 82 | 82 | 91 | 91 | 91 | 100 | 61 | |
| Number of species | 25 | 28 | 33 | 36 | 31 | 32 | 34 | 33 | 34 | 37 | 41 | 47 | 36 | 36 | 32 | 29 | 36 | 31 | 30 | 36 | 37 | 42 | 35 | 31 | 30 | 26 | 34 | |
| <i>Betula papyrifera</i> | 2 | 3 | 9 | 9 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 8 | 10 | 10 | 10 | 10 | 9 | 9 | 10 | 10 | 4 | 10 | 10 | 10 | 10 | 10 | 100 |
| <i>Alnus crispa</i> | 3 | 4 | * | 4 | 6 | 4 | 5 | 4 | 6 | 7 | 6 | 6 | 3 | 6 | 7 | 7 | 8 | 7 | 7 | 7 | 8 | 2 | 7 | 3 | 7 | 5 | 100 | |
| <i>Cornus canadensis</i> | 6 | 6 | 6 | 5 | 3 | 4 | 6 | 5 | 3 | 7 | 6 | 4 | 2 | 4 | 7 | 8 | 8 | 4 | 4 | 4 | 4 | 3 | 5 | 6 | 5 | 4 | 100 | |
| <i>Trientalis borealis</i> | 4 | 4 | 3 | 3 | 3 | 4 | 3 | 4 | 4 | 4 | 4 | 3 | 2 | 4 | 5 | 5 | 6 | 3 | 4 | 3 | 2 | 3 | 4 | 5 | 3 | 3 | 100 | |
| <i>Polytrichum juniperinum</i> | 8 | 6 | 5 | 4 | 5 | 3 | 3 | 3 | 2 | 3 | 3 | 2 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | * | 1 | 3 | 1 | 2 | 2 | 100 | |
| <i>Ribes glandulosum</i> | 3 | 2 | 2 | 2 | 3 | 4 | 2 | 1 | 2 | 3 | 3 | 2 | 2 | 3 | 4 | 4 | 2 | 4 | 2 | 3 | 5 | 1 | 5 | 5 | 2 | 2 | 100 | |
| <i>Pleurozium schreberi</i> | 1 | 1 | 1 | 2 | 4 | 3 | 3 | 3 | 2 | 2 | 2 | 3 | 2 | 3 | 3 | 2 | 2 | 2 | 2 | 2 | 6 | 7 | 3 | 2 | 2 | 3 | 96 | |
| <i>Linnaea borealis</i> | 1 | 3 | 3 | 3 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 4 | 4 | 3 | 2 | 2 | 96 | |
| <i>Picea mariana</i> | 2 | 1 | 2 | 3 | 3 | 3 | 5 | 4 | 5 | 3 | 3 | 3 | 2 | 4 | 4 | 5 | 4 | 5 | 5 | 5 | 3 | 7 | 4 | 5 | 5 | 3 | 92 | |
| <i>Solidago macrophylla</i> | 2 | 3 | 7 | 5 | 3 | 3 | 1 | 3 | 2 | 4 | 4 | 3 | 2 | 4 | 4 | 2 | 2 | 5 | 3 | 5 | 2 | 2 | 2 | 2 | 1 | 6 | 85 | |
| <i>Abies balsamea</i> | | | 2 | 2 | 1 | 1 | 4 | 5 | 3 | 3 | 3 | 2 | 7 | 4 | 2 | 2 | 2 | 4 | 1 | * | 3 | 8 | 1 | 4 | 3 | 4 | 80 | |
| <i>Viburnum edule</i> | 3 | 1 | 3 | 2 | 3 | 3 | 3 | 2 | 3 | 3 | 4 | 2 | 1 | 6 | 4 | 3 | 2 | 3 | 2 | 5 | 2 | 4 | 5 | 2 | 2 | 2 | 81 | |
| <i>Dryopteris disjuncta</i> | | | 3 | 1 | 2 | 1 | 2 | 2 | 1 | 3 | 3 | 3 | 2 | 2 | 2 | 2 | 3 | 2 | 2 | 2 | 3 | 1 | 2 | 1 | 3 | 4 | 81 | |
| <i>Dryopteris spinulosa</i> | 5 | 5 | 4 | 2 | 2 | 4 | 7 | 5 | 2 | 3 | 3 | 4 | 3 | 1 | 2 | 2 | 3 | 3 | 3 | 7 | 4 | 3 | 3 | 1 | 4 | 4 | 81 | |
| <i>Vaccinium myrtilloides</i> | 2 | | | * | 1 | 1 | 1 | 1 | 3 | 2 | 3 | 3 | 3 | 1 | 1 | 1 | 4 | 3 | 5 | * | 3 | 3 | 4 | 3 | 2 | 2 | 77 | |
| <i>Sorbus decora</i> | | | 1 | 2 | 2 | 1 | 1 | 3 | 2 | 2 | 2 | 3 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 4 | 77 | |
| <i>Dicranum fuscescens</i> | 2 | 2 | 2 | * | 2 | 4 | 2 | 1 | 2 | 1 | * | 1 | 3 | 3 | 4 | 5 | 2 | 1 | 3 | 2 | 2 | 3 | 2 | 3 | 3 | 3 | 77 | |
| <i>Salix bebbiana</i> | 3 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 2 | 1 | 2 | 2 | * | 3 | 3 | 73 | |
| <i>Deschampsia flexuosa</i> | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 3 | 3 | * | 1 | 2 | 2 | 2 | 2 | 1 | 73 | |
| <i>Gaultheria hispidula</i> | | | 3 | 3 | 2 | 3 | 2 | 3 | 2 | 2 | 2 | 5 | 1 | 4 | 3 | 5 | 1 | 4 | 8 | 7 | 3 | 3 | 9 | 6 | 5 | 5 | 73 | |
| <i>Lycopodium annotinum</i> | 2 | 2 | 2 | 3 | 3 | 2 | 3 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 4 | 1 | 1 | 2 | 2 | 2 | 69 | |
| <i>Ledum groenlandicum</i> | 2 | | | 1 | 1 | 2 | 2 | 3 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 69 | |
| <i>Ptilidium ciliare</i> | | | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 2 | 3 | 1 | 1 | 1 | 1 | 3 | 2 | 2 | 4 | 3 | * | 3 | 3 | 3 | 65 | |
| <i>Maianthemum canadense</i> | | | 1 | 2 | 3 | 3 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 65 | |
| <i>Cladonia rangiferina</i> | | | 3 | 1 | 1 | 1 | 2 | 2 | 3 | 2 | 2 | * | 2 | 2 | 2 | 1 | 1 | 1 | 2 | * | 2 | 2 | 2 | 2 | 1 | 1 | 61 | |
| <i>Coptis groenlandicum</i> | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | * | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 61 | |
| <i>Amelanchier bartramiana</i> | | | 3 | 2 | 1 | 1 | 1 | 1 | 3 | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | * | 2 | 1 | 1 | 1 | 2 | 1 | 3 | 61 | |

Betula forest development in Labrador

(a) Old forest



(b) 1941-origin forest



The pollen assemblages from the two profiles exhibit contrasting trends that corroborate the abrupt transition from conifer to *Betula papyrifera* following fire. Whereas the conifer pollen percentages remain relatively constant in the fir–spruce–feather moss forest profile (Fig. 5a), in the *B. papyrifera* stand there occurs a pronounced increase in *Betula* and *Alnus crispa* pollen and of *Lycopodium annotinum* spores, with a concomitant decrease in conifer (*Picea* and *Abies*) pollen above the charcoal horizon (Fig. 5b). This sequence documents the conversion of a predominantly conifer forest to a *Betula papyrifera* forest along with associated changes in the understory following the fire.

Stand development




The post-fire development of *B. papyrifera* stands is different from that of conifer forests in southern Labrador. In most conifer stands the initial density of seedlings is low (generally $<50 \text{ ha}^{-1}$) and the burned areas depend on sustained recruitment over a period of 40–100 years for complete restocking. Regenerating conifer forests thus often persist as an open-lichen woodland for nearly a century (Foster 1983a, 1985).

In contrast, observations in *B. papyrifera* stands of 1975–76, 1967 and 1959 origin demonstrate that the initial density of *B. papyrifera* is quite high and accounts for most of the individuals that will be present in the mature forest. Rapid establishment probably results from the favourable moisture conditions on protected, moist slopes and from abundant seed production from nearby stands. Extensive field observations confirm that in south-eastern Labrador the root crowns of *B. papyrifera* are killed by even light surface fires and, therefore, seldom sprout. On the 1975–76 fire sites *B. papyrifera* saplings were densely packed and averaged about 1 m in height. After 10–20 years the saplings reach a height of 2–4 m and their density probably reaches a maximum.

In the 41-year-old (1941 origin) forest, an upper canopy 8–11 m high is composed of *B. papyrifera* 10–18 cm dbh and scattered *Picea mariana* and *Abies balsamea* less than 10 cm dbh. Conifer saplings range from 0.3 to 8.0 m tall and *Betula papyrifera* seedlings are quite sparse. The total tree density exceeds 7000 stems ha^{-1} and the relative density of species is *B. papyrifera* (0.65), *Abies balsamea* (0.17), *Salix* spp. (0.10), *Picea mariana* (0.05) and *Prunus pensylvanica* (0.03) (Table 3).

TABLE 3. Density data for two *Betula papyrifera* stands in south-eastern Labrador.

| Origin (date A.D.) | 1941 | | 1889 | |
|-----------------------------------|------------------|---|------------------|---|
| Basal area (m ha^{-1}) | 38.0 | | 20.7 | |
| Density (stems ha^{-1}) | 7484 | | 783 | |
| Species | Relative density | Actual density (stems ha^{-1}) | Relative density | Actual density (stems ha^{-1}) |
| <i>Betula papyrifera</i> | 0.65 | 4734 | 0.71 | 561 |
| <i>Salix bebbiana</i> | 0.10 | 729 | 0.17 | 131 |
| <i>Abies balsamea</i> | 0.17 | 1275 | 0.05 | 39 |
| <i>Picea mariana</i> | 0.05 | 364 | 0.03 | 20 |
| <i>Populus tremuloides</i> | — | — | 0.04 | 33 |
| <i>Prunus pensylvanica</i> | 0.03 | 182 | — | — |

FIG. 5. Pollen stratigraphy of the organic soil layer in (a) an old age fir–spruce–feather moss forest, and (b) 1941-origin *Betula papyrifera* stand that developed following fire in a conifer forest. No pollen was found in the humus and charcoal layers below 14 cm in (b). Stratigraphy symbols: , charcoal; , mor humus; , mull humus.

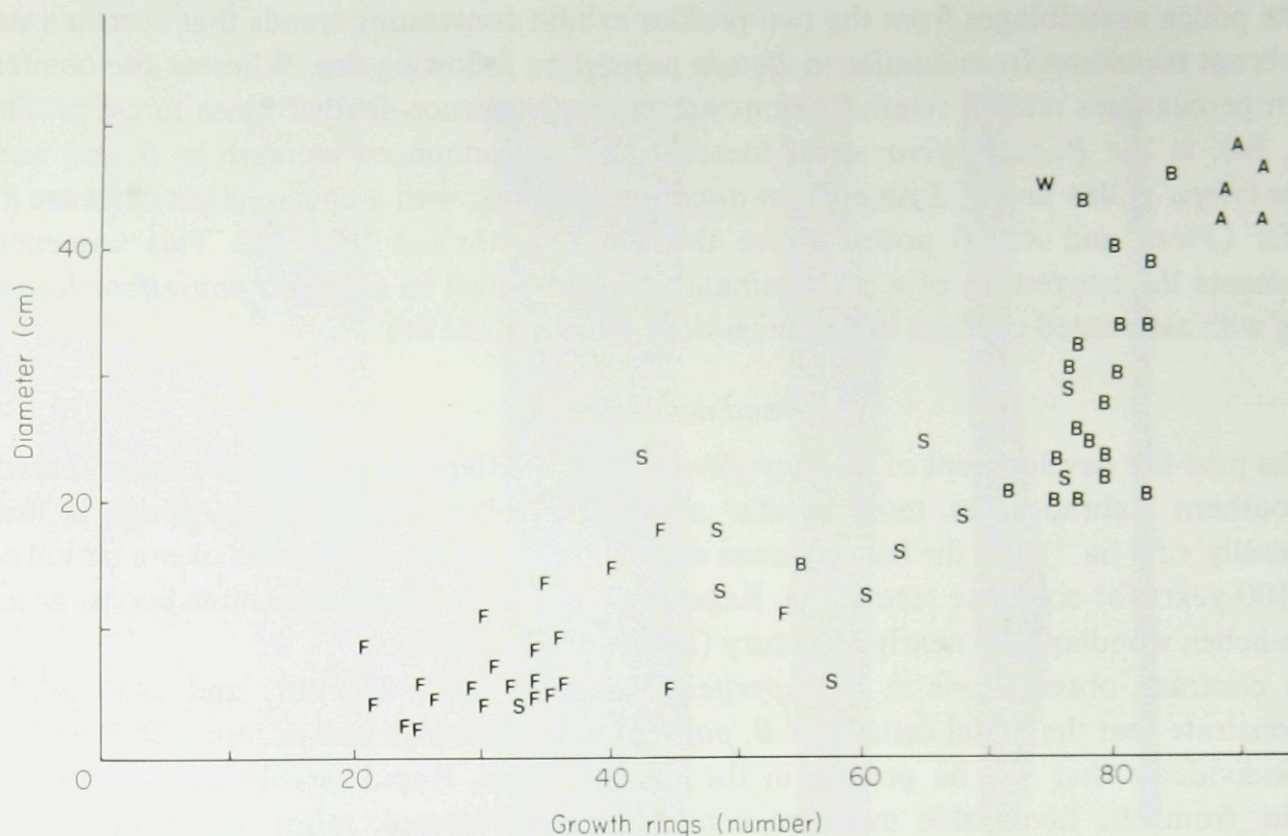


FIG. 6. Age structure of an 1889-origin *Betula papyrifera* forest. Symbols: (A), *Populus tremuloides*; (B), *Betula papyrifera*; (F), *Abies balsamea*; (S), *Picea mariana*; (W), *Picea glauca*. Annual rings counted in 1983.

In contrast the 92-year-old (1889 origin) stand has only 7813 stems ha^{-1} and a total basal area more than twice that of the 1941 stand ($21 \text{ m}^2 \text{ ha}^{-1}$ v. $38 \text{ m}^2 \text{ ha}^{-1}$). Age-structure analysis of the 1889-origin forest reveals a pattern of establishment and stand development that is typical for *Betula papyrifera* stands (Fig. 6). The trees cluster into four distinct groups of decreasing age: *Populus*, *Betula*, *Picea* and *Abies*. *Picea mariana* exhibits the greatest age span—30–76 growth rings. *Populus tremuloides* trees have the largest diameter and greatest number of growth rings as a result of their ability to produce rapidly growing root suckers following disturbances. The *Betula papyrifera*, which presumably all established by seed, date to within 15 years of the fire. With one exception, subsequent establishment has been lacking and no saplings occur in the understory to continue the dominance of *B. papyrifera*.

The understory is composed predominantly of conifer saplings and suppressed stems. Some *Picea mariana* establish soon after the fire and limited regeneration occurs in subsequent years. *Abies balsamea* establishes prolifically 40–50 years following a fire and appears to be the species most capable of reproducing under a closed canopy. The results suggest that, with time and the absence of large-scale disturbance, *A. balsamea* will become the dominant tree in the stand.

The signs of *Betula papyrifera* stand deterioration first appear in stands 75–100 years old. The tops of trees start to die, leaving a broken upper canopy and a lower, bushy sublayer. With the gradual opening of stands, conifer dominance increases.

DISCUSSION

Site conditions and floristic composition

Observations of *Betula papyrifera* communities across Labrador, from the Quebec border to Port Hope Simpson on the east coast, indicate that the composition, physiognomy and site conditions of this vegetation type are remarkably consistent.

Soil conditions, especially nutrient availability, pH and aeration, are probably the important site differences between the floristically rich *B. papyrifera* forests and the depauperate conifer forests. Downslope water movement through the well-drained soils increases the availability of nutrients to the rooting zone, and may provide a favourable environment for decomposition and root growth. Moreover, deciduous litter provides a relatively nutrient-rich and readily decomposed substrate of near-neutral pH (Damman 1971; Page 1974).

The seasonal nature of the deciduous canopy may be another factor contributing to the rich development of the undergrowth. Open canopy conditions in spring result in greater light, as well as higher soil temperatures, than in the closed conifer forests. An early burst of growth under such favourable conditions may result in enhanced productivity for numerous understory species.

Stand origin and the fire regime of south-eastern Labrador

From the results of the field studies it is apparent that three minimum conditions are necessary for the establishment of extensive *B. papyrifera* stands: (i) moist and well-drained soils, (ii) a nearby seed source, and (iii) an open site.

The regional distribution and local conditions of the stands are evidence of the micro-environment favoured for *B. papyrifera* establishment. Its absence from level, dry or waterlogged sites suggests that it benefits from the relatively warm and productive conditions present on the south-facing slopes in the topographically dissected areas.

A seed source is an absolute requirement; vegetative reproduction serves as only a very minor mechanism for stand development. This observation is in contrast to numerous literature reports from other regions (Lutz 1956; Ahlgren 1959; Heinselman 1973). An adequate seed source may be provided by an adjacent unburned *B. papyrifera* stand or by scattered individuals within an unburned conifer forest. The pattern of seed production and relatively great dispersal of its propagules favours rapid establishment on open sites (Marquis 1969, Marquis, Solomon & Bjorkbom 1969).

Finally, the shade intolerance of *B. papyrifera* necessitates broad-scale disturbance of the closed conifer canopy for the development of large *B. papyrifera* forests. Rock slides and avalanches open the forests on steep slopes and observations around coastal villages indicate that stands may develop after clearcut logging. However, throughout the vast interior wilderness of south-eastern Labrador, lightning fires provide the predominant disturbance for stand development.

The role that fire plays in the origin of *B. papyrifera* stands is documented by the large number of extensive stands found in areas burned within the last 110 years (Figs 2 and 3) and is corroborated by field studies. The frequent recurrence of fire through the watersheds of the St Augustin, Alexis, Paradise and Eagle Rivers has maintained abundant young and vigorous *B. papyrifera* forests. In contrast, across the broad St Lewis and Eagle Plains, where fire frequency is extremely low (Foster 1983b) and suitable sites are rare, *B. papyrifera* forests are not found.

The historical evidence contained in the organic profile of *B. papyrifera* stands and the examination of young stands on recent burns detail a pattern of rapid invasion of open, favourable sites following the destruction of the previous forest cover by fire. The burned forest that gives rise to *B. papyrifera* stands is generally conifer-dominated, predominantly fir–spruce–feather moss forests that contain only scattered *B. papyrifera*. In all the *B. papyrifera* forests examined the presence of standing conifer snags and the thick conifer humus beneath the uppermost charcoal horizon support the observation that few if any forests originate after burning of *Betula*-dominated ($\geq 50\%$ cover) forests. The explanation for this may be found in an understanding of the fire regime and relative inflammability of the different forest types.

Whereas the conifer vegetation is quite prone to fire, the full-canopied *B. papyrifera* forest is the least inflammable forest cover type in the study area; on most burns the fire generally sculpts around dense *B. papyrifera* forests (Fig. 7). In many places the path of an intense crown fire in conifer forest can be followed to a large *B. papyrifera* stand, which is burned only on the edges; the main body of the *B. papyrifera* forest remains unscathed, having itself provided an effective fire break.

The low inflammability is a result of the high moisture content of the canopy and the lush shrub and herb layers (Van Wagner 1969). *Betula papyrifera* stands burn only under special conditions, such as in early spring before bud-burst, following an unusually severe drought, or late in stand history when the proportion of conifers has increased.

An additional factor increasing the effectiveness of *B. papyrifera* stands as fire breaks is their position in deep valleys and on steep slopes. As the base of many of these slopes terminates in a lake or stream, fires tend to enter the valleys from the top of the slope and burn slowly downslope rather than sweep through and up the valley. Fire moving downslope has a low momentum and is readily suppressed by a barrier of vegetation of low inflammability.

There are three possible fates of developing *B. papyrifera* forests. First, in the absence of disturbance the conifers increase in density and cover at the expense of *B. papyrifera*, which is unable to regenerate. Concomitantly there occurs a gradual shift to a more acidic soil as conifer litter and moss production increase. The predominance of the herb and shrub layer would decrease as soil conditions change and the conifer canopy closes. Secondly, in the event of an intense fire, *B. papyrifera* forests, especially if small, may be consumed, resulting in the local elimination of the species. This has been observed in some locations on 1959 and 1975 fires. The third possibility is for fire to open an area adjacent to an existing *B. papyrifera* forest without consuming it. In this situation, the unburned stand can serve as a seed source for the establishment of new stands on adjacent favourable sites and a mosaic of deciduous stands can be maintained amidst the predominantly conifer vegetation.

Fire and vegetation dynamics in south-eastern Labrador

The results of this study illustrate the effects of fire on the long-term vegetation dynamics in south-eastern Labrador. Fire not only creates a mosaic pattern of conifer stands of different age, structure and composition (Foster 1985) but also maintains the distinctive *B. papyrifera* forests in the region. Without fire, forests of *B. papyrifera* and other early post-fire communities (e.g. lichen woodlands) would be gradually eliminated from the landscape and replaced by closed-canopy conifer forests.

The mosaic pattern of vegetation present in the region today will change with time but within the constraints imposed by fire behaviour, species autecologies and regional



FIG 7. Burn pattern on the 1975 Alexis River fire. Fire sculptures around full-canopied *Betula papyrifera* forests, selectively burning the surrounding conifers. (Photograph by D. R. Foster.)

topography. Some areas (e.g. Eagle plain) may never have supported *B. papyrifera* stands during the late Holocene or ever will, as their relief and organic soils are not suited for this species even if a fire were to open the forest canopy. Conversely, other areas (e.g. Alexis River valley) have a high probability of maintaining *B. papyrifera* as the requirements for stand development (well-drained soils, seed source and frequent fire) are met. The local distribution of *B. papyrifera* stands will change in these regions, but their overall frequency may not vary much.

On a regional scale, the vegetation of south-eastern Labrador appears to be in a dynamic equilibrium, with the overall pattern of forest composition and age remaining unchanged with time, as Heinselman & Wright (1973) suggest. In fact, vegetation history studies in the region show that the overall composition of the forests in the region has changed little in the last 4000 years (Lamb 1980; Engstrom & Hanssen 1985).

This and other studies in south-eastern Labrador (Foster 1983a,b, 1985) support the general theories explaining long-term ecosystem dynamics as in large part a function of their disturbance regimes (Heinselman 1973). In south-eastern Labrador and in other northern ecosystems, fire, in general, is the dominant disturbance influencing the distribution of vegetation. However, the effects of fire are not independent of other landscape features such as soils, topography and vegetation type. These features interact with fire to produce the mosaic but non-random pattern of vegetation present in northern ecosystems today.

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