

# Phytosociological description of the forest vegetation of southeastern Labrador

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A floristic analysis of the forest vegetation of southeastern Labrador was conducted using the phytosociological methods of Braun-Blanquet and a phytosociological table was constructed with the FORTRAN program TWINSPAN, which produces hierarchical classifications by two-way indicator species analysis. A total of 88 relevés incorporating 77 species are grouped into five major assemblages: birch, fir – spruce – feather moss, spruce–fir, spruce–*Pleurozium*, and spruce – *Sphagnum fuscum* communities. The five communities, as arranged from birch to spruce – *Sphagnum fuscum*, display decreasing trends in productivity, site quality, and richness of vascular flora, and increasing prominence of oligotrophic species, primarily cryptogams and ericaceous shrubs. Black spruce and balsam fir comprise more than 95% of the forest canopy in this region, whereas paper birch is restricted to moist and well-drained slopes, and white spruce, aspen, and balsam poplar are rare. Factors suggested as responsible for the limited productivity and depauperate vascular flora of the forests in this region include: semipermanently frozen soil, short growing season, nutrient-deficient mineral substratum, and intensive root competition in the poorly aerated soil. The low incidence of fire in this maritime climate is responsible for the old and uneven age structure of the conifer forests and the development of a thick bryophyte cover and deep organic humus that limit stand productivity.

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L'auteur a effectué une analyse floristique de la végétation forestière du sud-est du Labrador par les méthodes phytosociologiques de Braun-Blanquet; un tableau phytosociologique a été construit à l'aide du programme FORTRAN TWINSPAN: ce programme produit des classifications hiérarchiques par une analyse à deux voies des espèces indicatrices. Un nombre total de 88 relevés comprenant 77 espèces sont répartis en cinq groupes principaux de communautés, soit des communautés à bouleau, à sapin – épinette – mousses hypnacées, à épinette–sapin, à épinette–*Pleurozium*, et à épinette – *Sphagnum fuscum*. Ces cinq communautés, dans l'ordre ci-dessus, montrent des tendances vers une diminution de la productivité, de la qualité des sites et de la richesse en espèces vasculaires, et vers une augmentation des espèces oligotrophes, surtout des cryptogames et des arbustes éricacés. L'épinette noire et le sapin baumier forment plus de 95% du couvert forestier dans cette région, tandis que le bouleau blanc est restreint aux pentes humides et bien drainées et que l'épinette blanche, le tremble et le peuplier baumier sont rares. Les facteurs qui pourraient être responsables de la productivité limitée et de la flore vasculaire appauvrie des forêts de cette région comprennent un sol gelé d'une façon semi-permanente, une courte saison de croissance, un substrat minéral pauvre en éléments nutritifs et une compétition racinaire intense dans un sol peu aéré. La faible fréquence des incendies sous ce climat maritime explique que les forêts conifériennes soient âgées et inéquiennes, et est responsable de la présence d'un couvert dense de bryophytes et d'un humus organique épais qui limitent la productivité des peuplements.

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## Introduction

General phytogeographical and floristic descriptions of Labrador comprise part of many of the early geographical and biological explorations of this region (Low 1896; Fernald 1925; Abbe 1936; Tanner 1944; Rousseau 1952, 1968). The most comprehensive classification of the forest vegetation is provided by Hustich (1939, 1949a, 1949b, 1951), a member of the original Tanner expedition. Following the Finnish system of A. K. Cajander, Hustich groups the main forest types into moisture series. This simple classification was intended to facilitate the comparison of the vegetation of Labrador and northern Europe and has been the basis for much of the subsequent forestry and phytogeographical work undertaken in Labrador. According to this scheme, dry series forests and wet series forests, which include lichen woodland and muskeg, respectively, are depauperate in species, are highly unproductive, and occupy extreme habitats. Moist series forests include various conifer – feather moss forests, are rich in species, represent the most productive forests in Labrador, and occupy favorable sites, generally moist but well-drained lower slopes. Hustich does not consider the successional forest types,

including birch forests, in his classification.

Hustich did not investigate southeastern Labrador, but his classification scheme is generally applicable there and has been adapted by foresters in describing the region (Wilton 1959, 1965). Wilton's is the only work that includes numerous sites in the southeast. He broadens the classification scheme of Hustich to include "fire types" that are successional varieties of mature upland forest communities. His emphasis, however, is primarily on forest productivity and timber yield, and it therefore lacks detailed floristic information. His sites are located predominantly in the productive forest zone towards the coast and along the lower valleys of the major rivers.

The phytosociological classification of the forest vegetation of southeastern Labrador has two purposes. As part of an investigation of vegetation history and forest dynamics, this work was undertaken to provide an understanding of the upland flora and plant communities of the region. This study provides the foundation for work on fire history and vegetation development following fire, and for further investigations of specific plant communities.

In addition, this study is intended to describe one extreme in the continuum of boreal vegetation that stretches across northern North America. A detailed floristic description and classification of the forest vegetation of southeastern Labrador has

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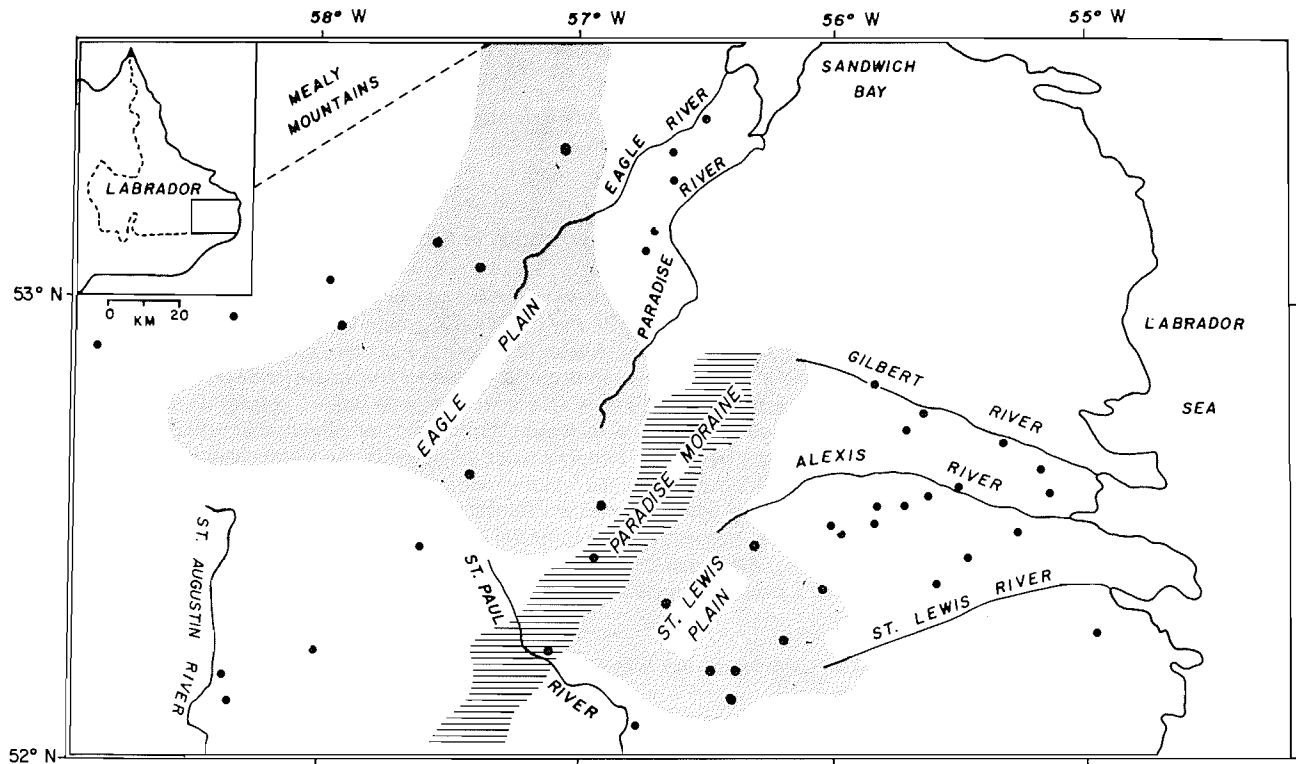


FIG. 1. The study area in southeastern Labrador showing the major physiographic features mentioned in the text. The dots represent sites visited in the course of the field work during the summers of 1979 to 1981.

never been undertaken. Much of the interior of this broad area is botanically unexplored, and the relationship of the vegetation across the southeast with the rest of Labrador and the main boreal forest to the west is largely unknown.

### The study area

Located on Canada's northeastern coast, Labrador belongs politically to the province of Newfoundland and geographically occupies a portion of the Labrador-Ungava Peninsula, which it shares with the province of Quebec. The study area in the southeast forms a rough rectangle, approximately  $300 \times 600$  km, extending from the St. Augustin River east to the coast and from the Mealy Mountains south to the Quebec border at  $52^\circ\text{N}$  (Fig. 1).

Labrador occupies the eastern part of the Precambrian Canadian Shield. In southeastern Labrador the bedrock is predominantly quartzofelspathic gneisses with intrusions of granite and granodiorites (Greene 1974). The entire region was covered by the Laurentide ice sheet during the last glacial period; retreat from coastal positions commenced approximately 12 000 years B.P. (before present) (Ives 1978).

The cold Labrador current and Arctic air masses exert a dominant influence on this coastal region, producing a climate characterized by long cold winters and short cool summers. Precipitation levels are among the highest for the North American boreal forest. Approximately 100 cm precipitation is equally distributed through the year (Peach 1975).

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

### Methods

The field work occupied approximately 7 weeks during each summer from 1979 through 1981. A total of 45 locations across southeast-

ern Labrador were visited during this period (Fig. 1). Sites for vegetation analysis were selected to provide broad geographical coverage, to sample the full range of mature forest vegetation (>80 years old), and to facilitate access to recent fires for the second portion of the study (Foster 1984). Aerial photographs (1:60 000: 1968 series, Canadian National Air Photo Library) were used to determine the recent fire history and major vegetation of an area; aerial observation enabled a closer inspection of the area and was the final step in the selection process. Access was by float plane, which was the only restriction in the selection process. To maximize the efficiency of air travel, lakes were chosen that offered watersheds with the greatest variety of vegetation, generally two or more age-classes and numerous forest types. Travel by small raft or on foot provided access to sites within a few kilometres of the landing spot. Standard plots measured  $20 \times 20$  m, and cover abundance was estimated on the 10-point Domin scale (Birks 1973). The criteria for the placement of relevé plots included homogeneity of the vegetation over a minimum area of approximately  $40 \times 40$  m, uniform slope, and apparent homogeneity of the site conditions. Information recorded for each relevé included elevation, slope, slope position, and aspect.

A complete voucher collection of plants was obtained, and extensive additional collections, especially of bryophytes and lichens, were made for many relevés. Nomenclature follows Fernald (1970) for vascular species, Stotler and Crandall-Stotler (1977) for liverworts, Ireland *et al.* (1980) for mosses, and Hale and Culbertson (1970) for lichens except *Cladonia*, which follows Ahti (1961).

A phytosociological table (Table 1) was constructed using the Cornell Ecology Series program TWINSPAN, a FORTRAN program that produces hierarchical classifications by two-way analysis of indicator species (Hill 1979; Gauch 1982). The program utilizes a polythetic divisive technique, whereby the relevés are first ordinated by reciprocal averaging and are subsequently grouped into clusters based on species composition. A corresponding species classification is then based on the species distribution in the various groups of stands. The resulting arranged data matrix is similar to that produced by the standard methods of Braun-Blanquet (Gauch 1982). For analysis and classification by TWINSPAN the original cover abundance scale

(10-point Domin) was converted to a 4-point scale to avoid overweighing dominant species (cf. Hill 1979). The full phytosociological table incorporates 88 relevés and 77 species (Table 1).

The TWINSPAN program identifies indicator species of each vegetation type, and these species along with other abundant species were used to construct a summary table (Table 2) that displays the floristic affinities of the five vegetation types. For each species in each community type, the modal value of the cover abundance is given as well as the frequency of occurrence within the relevés assigned to that community.

## Results

### Description of the full phytosociological table

From the TWINSPAN output, five major plant communities are readily identified: birch, fir – spruce – feather moss, spruce – fir, spruce – *Pleurozium*, and spruce – *Sphagnum fuscum* (Table 1). The communities are distinguished on the basis of differential or characteristic species. The divisions based on floristic criteria also correspond to physiognomic differences in the vegetation.

From left to right in the table the communities are ordinated along a gradient of decreasing quality of site conditions and decreasing productivity, as judged on the basis of tree growth and vitality of the understory. There is a corresponding trend of decreasing richness in the vascular flora and increasing prominence of oligotrophic species, especially lichens, bryophytes, and ericaceous shrubs. Among the tree species, birch is dominant in the left-hand side of the table and decreases in frequency and abundance to the right; fir is most prominent in the fir – spruce – feather moss community and similarly decreases to the right; black spruce is important in all communities but increases in abundance to the right; larch is common only in the spruce – *Sphagnum fuscum* assemblage; white spruce and aspen are represented in the fir – spruce – feather moss and birch communities, respectively.

### Species groups

Species that display similar distributions within the communities are arranged in groups. The first three species groups (groups 1–3, Table 1) consist predominantly of vascular deciduous species. Group 1 includes preferential species of the birch community. Many of the species, including *Calamagrostis canadensis*, *Petasites palmatus*, *Dryopteris spinulosa*, *D. disjuncta*, *Viburnum edule*, and *Salix bebbiana* are also found in wet, nonforested sites, for example, the narrow fringe bordering watercourses and lake shores. The presence of these species and two trees of restricted occurrence (*Populus tremuloides* and *Prunus pensylvanica*) indicates the favorable site conditions found in the deciduous community.

Group 2 consists of uncommon species that are primarily restricted to the birch and fir – spruce – feather moss assemblages. Group 3 includes species frequently found in the birch, fir – spruce – feather moss, and spruce – fir communities. Among these species *Trientalis borealis*, *Betula papyrifera*, *Alnus crispa* and, to a lesser extent, *Vaccinium myrtilloides* are found most frequently and at greatest abundance in birch forests. Preferential species of the fir – spruce – feather moss assemblage comprise group 4. *Habenaria obtusata*, *Listera cordata*, and *Moneses uniflora* are primarily restricted to rich, moist, or acid woods. *Picea glauca* is rare in southeastern Labrador and occurs most frequently in association with this assemblage.

A large group of wide-ranging upland species forms group 5.

*Icmadophila ericetorum*, *Equisetum syl-*

*vaticum*, and *Coptis groenlandicum* exhibit little preference among the communities, whereas other species, either by frequency of occurrence or abundance, serve to characterize particular communities. *Ptilium crista-castrensis*, *Sphagnum girgensohnii*, and *Hylocomium splendens* occur most frequently and at highest cover values in the fir – spruce – feather moss community. Fir is most abundant, and three lichen species (*Nephroma arcticum*, *Peltigera scabrosa*, and *P. aphosa*) are most frequent, in the three upland conifer assemblages.

Group 6 contains species that exhibit wide edaphic tolerances (*sensu* Birks 1973) and commonly occur in all five plant assemblages. Within this group *Pleurozium schreberi* and *Picea mariana* are more abundant in the conifer communities, especially those on uplands, and *Gaultheria hispida*, *Dicranum fuscescens*, and *Vaccinium vitis-idaea* are more common there. *Cornus canadensis* and *Lycopodium annotinum* are more abundant in the birch forest, whereas *Ledum groenlandicum*, *Sphagnum russowii*, and *Vaccinium angustifolium* reach peak abundance in the spruce – *Pleurozium* and spruce – *Sphagnum fuscum* assemblages.

The final group, group 7, contains numerous oligotrophic mire species (*sensu* Mueller-Dombois and Ellenberg 1974), the majority of which are preferential to the spruce – *Sphagnum fuscum* type. The group contains four species of *Sphagnum* (*S. rubellum*, *S. angustifolium*, *S. nemoreum*, and *S. fuscum*), numerous ericaceous species (*Vaccinium uliginosum*, *Chamaedaphne calyculata*, *Vaccinium oxycoccos*, and *Kalmia polifolia*), and other vascular species characteristic of weakly minerotrophic and ombrotrophic peatlands in southern Labrador (Foster and King 1984).

### Birch forest

In a region dominated by conifers the steep valley slopes that are forested with a nearly continuous canopy of paper birch (*Betula papyrifera*) create a striking pattern in the landscape (Fig. 2). In addition to the deciduous overstory, the birch forests are physiognomically distinguished by a lush and diverse understory.

The overstory is composed predominantly of birch, with scattered aspen and conifers, primarily black spruce and fir. White spruce was found in only 11.5% of the stands surveyed and is never abundant (Table 2). Tree growth is rapid, and the birch reach a maximum size of 17 m (height) and 45 cm diameter at breast height (dbh). Where present, aspen is the largest species; it may exceed 50 cm dbh and form a discontinuous super canopy 3 m or more above the surrounding birches.

The successional status of the birch forest type is indicated by a maximum age of approximately 115 years for birch and 100 years for aspen, and a near absence of these species in the smaller size classes (Foster 1983). The conifer saplings that predominate in the understory grow slowly in the shade of the deciduous canopy. Upon the death or windthrow of the taller birch the conifers rapidly occupy the resulting gap in the overstory; in the absence of widespread disturbance this process guarantees a gradual conversion of birch stands to forests dominated by fir and black spruce.

A diverse shrub understory is a distinctive feature of the birch community. Tall and medium-sized shrubs form an interrupted layer that extends from 2 to 4 m in height. The most frequent and most conspicuous species are *Alnus crispa*, *Sorbus decora*, *Salix bebbiana*, *Amelanchier bartramiana*, and *Viburnum edule* (Table 2). *Ribes glandulosum*, *Vaccinium*



FIG. 2. Distinctive landscape pattern created by a hillside stand of paper birch. Note the sharp border with the conifer forest at the bottom of the slope and the absence of birch from the exposed summit of the hill.

*myrtilloides*, and *Rubus idaeus* contribute to a low shrub layer.

The numerous herbs create a nearly continuous ground layer and contribute to the lush appearance of the stands. The most common species include *Trientalis borealis*, *Linnaea borealis*, *Solidago macrophylla*, *Dryopteris spinulosa*, *D. disjuncta*, and *Lycopodium obscurum*. Across wide stretches of the forest floor *Lycopodium annotinum* and *Cornus canadensis* frequently form extensive carpets.

Bryophytes and lichens never achieve a prominent position beneath the deciduous canopy. In older stands, however, the cryptogams increase with the conifer cover. Bryophytes are generally restricted to elevated surfaces such as windthrow mounds, tree bases, or to rotting wood where they may be associated with numerous *Cladonia* species. The importance of corticolous lichens increases with the age of the birch trees. On the fissured and rough trunks of trees 50 years or older, the prominent species are *Platismatia glauca*, *Hypogymnia physodes*, *Cetraria pinastri*, and *Parmeliopsis ambigua*.

The birch community is a successional vegetation type that develops following fire and less-extensive disturbance such as avalanche and rock slides (Foster 1983a, 1983b). In southeastern Labrador this community exhibits very specific site requirements and is located only on the most favorable habitats: protected and very moist but well-drained slopes and seepages. The majority of the stands occupy steep concave slopes and contain small streams or exhibit subsurface water flow. The strict site requirements result in distinctive forest patterns and a restricted regional distribution. The borders of the stands are very sharp, with conifer forest on the adjacent exposed hilltops, convex slopes, or level valley bottoms (Fig. 2). Within southeastern Labrador the birch vegetation type is confined to dissected terrain that has burned within the past 125 years; birch stands are absent from the broad central plateau that forms the Eagle and St. Lewis plains, both because of the paucity of suitable habitat and the low frequency of fire.

The soil within these hillslope stands is shallow because of boulders or rock ledge near the surface. The

organic profile is thin and generally consists of a mull humus formed of deciduous litter. In some locations, however, where birch has become established following a light surface fire in a moist fir-spruce forest, a layer of charcoal 1–5 cm thick and a mor humus 10 cm or more thick underlie the deciduous mull humus profile.

#### *Fir – spruce – feather moss forest*

This community is characterized by a conifer overstory with occasional birch, the general absence of a shrub layer, and a thick and continuous ground cover composed of feather mosses and *Sphagnum girgensohnii* (Table 2). Scattered herbs contribute to a rich appearance created by the deep and moist bryophyte layer. Long festoons of arboreal lichens, primarily *Ramalina thrausta*, hang from the open branches of the fir trees.

Tree growth is rapid, making this the most productive conifer forest in southeastern Labrador (Wilton 1965). Balsam fir, black spruce, and birch form a dense canopy 14–16 m in height. Individual trees are up to 35 cm dbh, although the occasional white spruce may exceed 40 cm dbh and 200 years in age. In many stands the presence of standing snags and rotting logs of birch on the forest floor testify to a greater abundance of this species in the recent past.

A shrub understory is absent and, with the exception of conifer regeneration, the forests are quite open beneath the canopy. Fir reproduces by seed and produces vigorous saplings, whereas the black spruce resulting from vegetative reproduction (layering) are generally spindly, slow growing, and strongly curved at their base (cf. Hustich 1968; Stanek 1975). The basal curvature results from the phototropic response of the shoots that takes place when adventitious roots are produced on the drooping branches that have become covered by mosses. In subsequent years the branch connection with the main trunk gradually rots and is completely severed, and the cloned individual becomes independent of the parent tree.

The ground cover is dominated by bryophytes. *Sphagnum*

1	<i>Calamagrostis canadensis</i>	.....1.....1.....1.....2.....2.....
	<i>Pectanites palmatus</i>	.....2.....2.....1.....1.....1.....
2	<i>Rubus pubescens</i>	.....2.....2.....2.....2.....2.....
	<i>Viola pallens</i>	.....2.....2.....2.....2.....2.....
	<i>Dryopteris spinulosa</i>	.....2.....2.....2.....2.....2.....
	<i>Dryopteris adajuncta</i>	.....2.....2.....2.....2.....2.....
	<i>Ribes glandulosum</i>	.....2.....2.....2.....2.....2.....
	<i>Viburnum edule</i>	.....2.....2.....2.....2.....2.....
	<i>Salix babingtona</i>	.....2.....2.....2.....2.....2.....
	<i>Solidago macrophylla</i>	.....2.....2.....2.....2.....2.....
	<i>Lycopodium obscurum</i>	.....2.....2.....2.....2.....2.....
	<i>Rubus idaeus</i>	.....2.....2.....2.....2.....2.....
	<i>Populus tremuloides</i>	.....2.....2.....2.....2.....2.....
	<i>Prunus pennsylvanica</i>	.....2.....2.....2.....2.....2.....
2	<i>Stapeptopus amplexifolius</i>	.....2.....2.....2.....2.....2.....
	<i>Clintonia borealis</i>	.....2.....2.....2.....2.....2.....
	<i>Sorbus decora</i>	.....2.....2.....2.....2.....2.....
	<i>Ameletaria bartramiana</i>	.....2.....2.....2.....2.....2.....
	<i>Matricaria canadensis</i>	.....2.....2.....2.....2.....2.....
3	<i>Trematalis borealis</i>	.....2.....2.....2.....2.....2.....
	<i>Linnaea borealis</i>	.....2.....2.....2.....2.....2.....
	<i>Betula papyrifera</i>	.....2.....2.....2.....2.....2.....
	<i>Alnus incana</i>	.....2.....2.....2.....2.....2.....
	<i>Vaccinium myrtilloides</i>	.....2.....2.....2.....2.....2.....
4	<i>Habenaria obtusata</i>	.....2.....2.....2.....2.....2.....
	<i>Listera cordata</i>	.....2.....2.....2.....2.....2.....
	<i>Picea glauca</i>	.....2.....2.....2.....2.....2.....
	<i>Homocidus uniflora</i>	.....2.....2.....2.....2.....2.....
	<i>Pyrola rotundifolia</i>	.....2.....2.....2.....2.....2.....
5	<i>Peltidium ciliare</i>	.....2.....2.....2.....2.....2.....
	<i>Abies balsamea</i>	.....2.....2.....2.....2.....2.....
	<i>Peltium ericae-castranea</i>	.....2.....2.....2.....2.....2.....
	<i>Sphagnum girgensohnii</i>	.....2.....2.....2.....2.....2.....
	<i>Rhizocarpum splendens</i>	.....2.....2.....2.....2.....2.....
	<i>Dicranum scoparium</i>	.....2.....2.....2.....2.....2.....
	<i>Imadophila ericetorum</i>	.....2.....2.....2.....2.....2.....
	<i>Equisetum sylvaticum</i>	.....2.....2.....2.....2.....2.....
	<i>Captia groenlandicum</i>	.....2.....2.....2.....2.....2.....
	<i>Nepenthes arctica</i>	.....2.....2.....2.....2.....2.....
	<i>Peltigera canabroea</i>	.....2.....2.....2.....2.....2.....
	<i>Peltigera aphthosa</i>	.....2.....2.....2.....2.....2.....
6	<i>Cornus canadensis</i>	.....2.....2.....2.....2.....2.....
	<i>Pleurostium schreberi</i>	.....2.....2.....2.....2.....2.....
	<i>Picea mariana</i>	.....2.....2.....2.....2.....2.....
	<i>Gaultheria hispida</i>	.....2.....2.....2.....2.....2.....
	<i>Dicranum fluviacens</i>	.....2.....2.....2.....2.....2.....
	<i>Cladonia rangiferina</i>	.....2.....2.....2.....2.....2.....
	<i>Leclum groenlandicum</i>	.....2.....2.....2.....2.....2.....
	<i>Sphagnum muscovi</i>	.....2.....2.....2.....2.....2.....
	<i>Polytrichum commune</i>	.....2.....2.....2.....2.....2.....
	<i>Cladonia oociferia</i>	.....2.....2.....2.....2.....2.....
	<i>Cladonia sulphurata</i>	.....2.....2.....2.....2.....2.....
	<i>Cladonia cornuta</i>	.....2.....2.....2.....2.....2.....
	<i>Deschampsia flexuosa</i>	.....2.....2.....2.....2.....2.....
	<i>Lycopodium annotinum</i>	.....2.....2.....2.....2.....2.....
	<i>Cladonia stellata</i>	.....2.....2.....2.....2.....2.....
	<i>Cladonia mitis</i>	.....2.....2.....2.....2.....2.....
	<i>Vaccinium cespitosum</i>	.....2.....2.....2.....2.....2.....
7	<i>Vaccinium vitis-idaea</i>	.....2.....2.....2.....2.....2.....
	<i>Vaccinium angustifolium</i>	.....2.....2.....2.....2.....2.....
	<i>Vaccinium uliginosum</i>	.....2.....2.....2.....2.....2.....
	<i>Chamaedaphne calyculata</i>	.....2.....2.....2.....2.....2.....
	<i>Larix laricina</i>	.....2.....2.....2.....2.....2.....
	<i>Sphagnum rubellum</i>	.....2.....2.....2.....2.....2.....
	<i>Sphagnum angustifolium</i>	.....2.....2.....2.....2.....2.....
	<i>Scirpus cespitosus</i>	.....2.....2.....2.....2.....2.....
	<i>Vaccinium oxycoccus</i>	.....2.....2.....2.....2.....2.....
	<i>Eriophorum spissum</i>	.....2.....2.....2.....2.....2.....
	<i>Sphagnum nemoreum</i>	.....2.....2.....2.....2.....2.....
	<i>Mytila anomala</i>	.....2.....2.....2.....2.....2.....
	<i>Sphagnum fuscum</i>	.....2.....2.....2.....2.....2.....
	<i>Smilacina trifolia</i>	.....2.....2.....2.....2.....2.....
	<i>Rubus chamaemorus</i>	.....2.....2.....2.....2.....2.....
	<i>Kalmia angustifolia</i>	.....2.....2.....2.....2.....2.....
	<i>Empetrum nigrum</i>	.....2.....2.....2.....2.....2.....
	<i>Dicranum undulatum</i>	.....2.....2.....2.....2.....2.....
	<i>Kalmia polifolia</i>	.....2.....2.....2.....2.....2.....

NOTE: Cover-abundance values: 1, less than 3%; 2, 3 to 10%; 3, 10 to 35%; 4, greater than 35%.



*girgensohnii*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Hylocomium splendens* form a carpet 10–25 cm thick that blankets the forest floor, including low stumps and downed logs. With the exception of *Pleurozium*, these mosses reach peak abundance in the fir – spruce – feather moss community. *Ptilidium ciliare* and *Dicranum fuscescens* are most common around the bases of trees and on rotting stumps.

Herbs common to the birch stand (groups 2 and 3) are present in the fir – spruce – feather moss forest although in low abundance. The most frequent species are *Linnaea borealis*, *Trientalis borealis*, and *Maianthemum canadense*. In addition, another group of herbs (group 4) are distinctive in this forest.

The fir – spruce – feather moss community generally occupies protected sites: sheltered locations that frequently have active water flow, good drainage, and moderate to steep soils. This forest is therefore frequently associated with birch forests in the broad valleys of the St. Augustin and Pinware rivers in the south of the study region, and the Alexis, St. Lewis, Gilbert, and Paradise rivers in the east. The fir – spruce – feather moss forest is a relatively stable vegetation type, however, and there are indications that it may develop on sites that previously contained a considerable amount of birch. Some birch may persist in old-age forests through establishment following windthrow and similar small-scale disturbances.

#### Spruce–fir forest

Black spruce trees, accompanied by fir in most stands, form a broken canopy approximately 15 m high in this community. The trees range to 20–25 dbh, are multiaged, and have a moderate cover of the arboreal lichen *Alectoria nigricans*. Birch is a prominent component of the canopy in some stands, whereas white spruce was only recorded in one relevé (Table 1). In open parts of the forests, understory conifers are abundant; layers of black spruce frequently form dense clones through vegetative reproduction around a single individual that originated from seed. Fir reproduces exclusively by seed.

With the exception of the conifer saplings and scattered shoots of alder, the understory is generally open. Alder, which resprouts prolifically following fire to form a broad and dense bush, becomes scraggly beneath a dense conifer canopy. Ericads, principally *Ledum groenlandicum*, *Vaccinium myrtilloides*, and *V. angustifolium*, constitute a discontinuous low-shrub layer.

Many of the herbs that are common enough to distinguish the fir – spruce – feather moss community (groups 2 and 3) are generally absent from the spruce–fir community. The field layer is primarily composed of such species as *Cornus canadensis*, *Gaultheria hispidula*, *Vaccinium vitis-idaea*, *Linnaea borealis*, and *Trientalis borealis*. These species occur as scattered individuals and seldom contribute more than 10% cover.

The bryophyte carpet that covers the forest floor is much less diverse than that of the fir – spruce – feather moss forest. *Pleurozium schreberi* is the dominant species followed by *Ptilium crista-castrensis*. *Hylocomium splendens*, *Sphagnum girgensohnii*, and *Polytrichum commune* require considerable moisture; when they occur in this community they occupy low depressions and seepages. *Ptilidium ciliare* is found at the base of nearly every conifer, and *Dicranum fuscescens* occupies raised mounds and decaying wood.

The abundance of fruticose lichens in many stands is an indication that more open conditions existed in the recent past. Most of the stands have burned within the past 200 years.

Lichens, which formerly covered much of the ground surface, become restricted to dry and raised microsites as the canopy closes. *Cladonia stellaris*, *C. sulphurina*, and *C. cornuta* are found on rotting stumps, downed wood, and the root crowns of trees.

#### Spruce–Pleurozium forest

Large portions of the central plateau and exposed and unproductive sites throughout the study area are occupied by a slow-growing and species-poor black spruce – *Pleurozium* forest. This community is composed of only 28 common species and is lacking in the rich vascular species (groups 1–4) that characterize the other upland forest types. The flora, in addition to being depauperate, demonstrates some affinity to the lowland spruce – *Sphagnum fuscum* community: *Empetrum nigrum*, *Dicranum undulatum*, and *Rubus chamaemorus* are frequent constituents and are occasionally accompanied by *Sphagnum fuscum*, *Smilacina trifolia*, and *Kalmia polifolia* (Table 1).

The tree canopy of the spruce–*Pleurozium* forest is uneven and discontinuous and is generally composed of narrow-crowned black spruce and scattered balsam fir that extend 8–12 m high. Tree height, however, is greatly determined by exposure; near the summit of hills and ridges the conifers decrease in stature and eventually assume a dense krummholz structure that may be only 0.5 m high. The openness of the canopy and large number of dead branches provide sites for arboreal epiphytes and *Alectoria nigricans*, *Platismatia glauca*, and *Hypogymnia physodes* densely cloak the trees.

The shrub understory is extremely discontinuous and is composed of a few ericaceous species. In open areas *Ledum groenlandicum* may form an undergrowth 0.7–1.0 m high. Low shrubs, including *Vaccinium angustifolium*, *V. vitis-idaea*, and *Kalmia polifolia*, contribute to the sparse ground cover. Common herbs are *Gaultheria hispidula*, *Cornus canadensis*, *Empetrum nigrum*, and *Rubus chamaemorus*. *Deschampsia flexuosa* grows luxuriantly and flowers prolifically under canopy openings.

The ground cover consists of a nearly continuous carpet of *Pleurozium schreberi* 5–10 cm thick. Fruticose lichens (*Cladonia rangiferina*, *C. mitis*, *C. macrophylla*, and *C. coccifera*), foliose lichens (*Nephroma arcticum*, *Peltigera scabrosa*, and *P. aphosa*), and bryophytes (*Dicranum fuscescens* and *D. scoparium*) grow among the *Pleurozium* carpet and on elevated mounds. The occasional mesic bryophytes (*Sphagnum russowii*, *S. fuscum*, *S. girgensohnii*, *Ptilium crista-castrensis*, *Polytrichum commune*, and *Hylocomium splendens*) occupy moist depressions, generally in old-age stands. The spruce–*Pleurozium* forest community is the most widespread vegetation type in southeastern Labrador and is greatly responsible for the region's reputation of poor growing conditions and low forest productivity. This community occupies a wide range of sites from poorly drained outwash plains to convex slopes and hill crests. A similar vegetation type is found across much of the rest of Labrador in unproductive habitats and, with only minor floristic changes, extends to the forest tundra.

#### Spruce – Sphagnum fuscum forest

The spruce – *Sphagnum fuscum* community develops on waterlogged sites that dominate large portions of the central plateau, and in valley bottoms and areas of restricted drainage elsewhere. This vegetation, which is physiognomically characterized by an extremely open canopy and low stature and poor



FIG. 3. Stunted larch and black spruce on the margin of a spruce – *Sphagnum fuscum* stand. Tree growth improves on areas of shallow organic soil in the background of the picture.

growth of the trees, has strong floristic affinities to mire forest communities (Fig. 3) (Foster and King 1984). Oligotrophic species (group 7) dominate, including many lichens and bryophytes, whereas species from groups 1–5 (Table 1) are generally absent. Many of the species of group 7 are also found on peat ridges on raised bogs and the mire-margin hummocks of patterned fens (Foster and King 1984).

The substratum consists of water-saturated peat that is 0.5–1.5 m thick. The ground surface is uneven because of the hummock growth form of many of the bryophytes and the presence of downed trees and scattered windthrows. The microrelief provides much variation in local environmental conditions, especially moisture and temperature.

Tree cover, which seldom exceeds 60% and is frequently much less, consists of clumps of low, poorly formed individuals. Black spruce trees generally occupy raised microsites, are up to 8–10 m high, seldom exceed 15 cm dbh, and have narrow crowns that are densely covered with *Alectoria nigricans*. Larch is generally scattered towards the open and moister parts of stands, whereas fir tends to be preferentially located near the upland borders in areas of shallow peat.

Under the open canopy the shrub and herb layers are frequently well-developed. Ericaceous shrubs (*Kalmia polifolia*, *Ledum groenlandicum*, *Chamaedaphne calyculata*, *Vaccinium uliginosum*, and *V. angustifolium*) form a layer ranging from 0.10 to 1.0 m in height. The shrubs grow well and generally flower abundantly. Among the herbs, *Equisetum sylvaticum*, *Lycopodium annotinum*, *Gaultheria hispidula*, and *Cornus canadensis* grow on raised microsites formed by carpets of *Pleurozium* or fallen logs. *Carex trisperma*, *Geocaulon lividum*, *Scirpus cespitosus*, *Rubus chamaemorus*, *Smilacina trifolia*, and *Eriophorum spissum* are found on moister spots on *Sphagnum* carpets.

The ground cover consists of a mosaic of bryophytes and lichens with fairly strict moisture preferences. *Sphagnum rubellum*, *S. angustifolium*, and *S. russowii* generally occupy the lowest moist locations; *Sphagnum fuscum* and *S. nemoreum* are

hummock builders that may form raised areas 30 cm or more high and 1 m or more across and support such species as *Mylia anomala* and *Polytrichum strictum*. *Pleurozium schreberi* occupies raised dry sites, such as windfalls, tree bases, and decayed stumps, and is often associated with the *Cladonia* lichens.

Poor drainage produces a waterlogged and cold soil that, when coupled with the acidic nature of the ground cover, results in slow rates of decomposition and the gradual accumulation of a thick organic layer. The insulating effect of the peat layer is demonstrated by the persistence of discontinuous ice lenses well into the middle of July. The unfavorable soil environment and restricted nutrient availability are undoubtedly responsible for the poor tree growth and limited productivity.

### Discussion

Early reports and even some recent phytogeographical descriptions incorrectly portray southern Labrador as a region dominated by unproductive woodlands and open nonforested barrens. For example, in the general classification of forest regions of Canada (Rowe 1972) most of southeastern Labrador is placed within the section B.31: Newfoundland–Labrador Barrens. This forest section is characterized by stunted open and patchy to sometimes continuous forest cover that alternates with moss and heath barrens and rock outcrops. Open lichen woodland is described as more common in Labrador than Newfoundland.

In contrast to many of these general descriptions, observations made during the course of the present study indicate that the upland areas of southeastern Labrador are either thickly forested or are in various stages of forest development following fire. The proportion of the land surface occupied by rock outcrops and moss and heath barrens is less than 3%; closed forest comprises approximately 70%; the remainder is lichen woodlands and peatlands (see Hare and Taylor (1956) and Wilton (1959) for other comparable estimates).

Slow tree growth, however, is a characteristic of the forests.



Factors responsible for limited productivity of upland areas include semipermanently frozen soil, short growing season, nutrient-deficient mineral substratum, and intensive root competition in the poorly aerated soils (Hustich 1965). The soil characteristics are largely a result of the extremely long fire cycle and cool maritime climate (Foster 1984). The long period that elapses between fires enables the development of a thick bryophyte cover and a deep organic humus. This insulating blanket results in decreased soil temperatures, increased levels of soil moisture, and reduced nutrient availability because of the storage of minerals in the ground vegetation and organic layers.

Changes in community characteristics that accompany the formation of a thick and continuous organic layer in older-aged stands include increased prominence of fir and arboreal lichens, increased importance of vegetative reproduction in black spruce, decreased vigor in shrub and herb growth, a reduction in floral productivity, and gradual changes in bryophyte species dominance, with *Sphagnum* species (*S. girgensohnii* and *S. russowii* especially) and mesic species (*Hylacomium splendens*, *Ptilium crista-castrensis*, and *Polytrichum commune*) being favored over *Pleurozium schreberi*. As a result of the extremely long interval between fires, most of the conifer forests across the central plateau are composed of individuals that exceed 250 years in age. Long periods between fires, along with the poor seedbed conditions following fire (cf. Foster 1983, 1984), result in a multiaged structure of the conifer forests. The absence of even-aged conifer forests and the extreme age of much of the forest vegetation are in sharp contrast to the age-structure data from black spruce forests in the central and western boreal forest, where the fire rotation (*sensu* Heinselman 1973) is much shorter (Johnson and Rowe 1977; Heinselman 1981; Viereck 1983).

The distribution of communities in the landscape appears to be largely controlled by soil conditions, including drainage and moisture, and to a lesser extent by exposure. Across the broad plateau on the St. Lewis and Eagle plains, spruce – *Sphagnum fuscum* forest covers large areas where poor drainage and a surplus of moisture produce waterlogged soils and have resulted in the accumulation of a thick organic peat. On these sites tree growth is remarkably slow and is largely restricted to black spruce and larch.

On dry and well-drained sites *Pleurozium schreberi* forms a continuous carpet in the spruce – *Pleurozium* forest. This vegetation is extremely widespread in Labrador and covers extensive portions of the St. Lewis and Eagle plains and much of the dissected terrain towards the coast, on exposed hills, coarse and shallow soils, or convex slopes.

Forest growth improves greatly on sites characterized by abundant moisture and good drainage as is apparent in the distribution of the birch and fir – spruce – feather moss communities. These are the most productive forest types in the study area (Wilton 1965) and are restricted to the banks and hills above watercourses and to moist seepage routes on concave slopes. Such sites are prevalent in the dissected terrain of the major river systems. The continual movement of water through the soil undoubtedly results in enhanced aeration and increases nutrient availability. In addition, water-flow results in an earlier spring thaw and may thereby enable a longer period of growth.

To some extent the regional distribution of the forest types may be controlled by broad-scale climatic factors. Although the data are largely interpolative because of the limited number

of meteorological stations on the plateau, the interior apparently experiences a more severe climate than the coastal area. It has been reported that as a result of its higher elevation and distance from the sea the plateau has a shorter growing season, a colder mean annual temperature, and greater precipitation (Peach 1975). These climatic conditions would be expected to favor the spruce – *Sphagnum fuscum* and spruce – *Pleurozium* forest types over the more productive communities.

The forest vegetation and its floristic composition presents an interesting comparison to other parts of Labrador and to the boreal region to the west. The floristic diversity of the forests is low, and differences among the communities are largely determined by the relative abundance and the presence or absence of a few species. Much of the region is rather monotonously covered with a species-poor black spruce – *Pleurozium* forest of low productivity.

The canopy cover is dominated by two species, black spruce and balsam fir, which together account for greater than 95% of the forest cover in the study. Black spruce is the prominent species across the study area and is an important member of all forest communities. Fir exhibits an unusually high abundance in southeastern Labrador when compared with the rest of the boreal region, and fir was found in all the community types. The importance of fir decreases markedly to the west and north; in the area from Wabush to Schefferville along the western border of the province, fir is seldom found as a mature tree (cf. Hustich 1951).

Birch forms discrete stands following fire and occurs sporadically in other forests; with larch, which is primarily a wetland species, birch accounts for the remainder of the tree cover. White spruce, which is a common and important constituent in forests throughout western Labrador and much of the boreal region, is uncommon in southeastern Labrador and is generally restricted to the most productive forests. Hustich (1965) indicates that the absence of white spruce is a characteristic feature of granitic bedrock areas of interior Labrador. The range limit of aspen lies approximately 50 km north of the study area. This species never assumes more than limited importance as a postfire successional species. Another important successional species, jack pine, although it forms extensive stands on burns just 65 km west of the provincial border, does not occur in Labrador.

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- ABBE, E. C. 1936. Botanical results of the Grenfell-Forbes northern Labrador Expedition, 1931. *Rhodora*, **38**: 102-161.
- AHTI, T. 1961. Taxonomic studies on reindeer lichens (*Cladonia*, subgenus (*Cladina*)). *Ann. Bot. Soc. Zool. Bot. Fenn. (Vanamo)*, **32**: 1-160.
- BIRKS, H. J. B. 1973. Past and present vegetation of the Isle of Skye. Cambridge University Press, Cambridge, England.
- FERNALD, M. L. 1925. Persistence of plants in unglaciated areas of Boreal America. *Am. Acad. Arts Sci.* **15**: 237.
- 1970. Gray's manual of botany. 8th ed. D. Van Nostrand Co., New York.
- FOSTER, D. R. 1983a. Phytosociology, fire history, and vegetation development of the boreal forests of southeastern Labrador, Canada. Ph.D. thesis, University of Minnesota, Minneapolis, MN.
- 1983b. The fire history of southeastern Labrador. *Can. J. Bot.* **61**: 2459-2471.
- FOSTER, D. R., and G. A. KING. 1984. Landscape features, vegetation, and developmental history of a patterned fen in southeastern Labrador, Canada. *J. Ecol.* **72**. In press.
- GAUCH, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, England.
- GREENE, B. A. 1974. An outline of the geology of Labrador. Newfoundland Department of Mines and Energy, Mining Development Division, Inf. Circ. No. 15.
- HALE, M. E., and W. L. CULBERSON. 1970. A fourth checklist of the lichens of the Continental United States and Canada. *Bryologist*, **73**: 499-533.
- HARE, F. K., and R. G. TAYLOR. 1956. The position of certain forest boundaries in southern Labrador-Ungava. *Geogr. Bull.* **8**: 51-73.
- HEINSELMAN, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quat. Res.* **3**: 329-382.
- 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. In *Fire regimes and ecosystem properties*. U.S. For. Serv. Gen. Tech. Rep. WO-26.
- HILL, M. O. 1979. TWINSPAN — a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, NY.
- HUSTICH, I. 1939. Notes on the coniferous forest and tree limit on the east coast of Newfoundland-Labrador. *Acta Geogr.* **7**: 1-77.
- 1949a. Phytogeographical regions of Labrador. *Arctic*, **2**: 36-42.
- 1949b. On the forest geography of the Labrador peninsula. A preliminary synthesis. *Acta Geogr.* **10**: 1-63.
- 1951. The lichen woodlands in Labrador and their importance as winter pastures for domesticated reindeer. *Acta Geogr.* **12**: 1-48.
- 1965. A black spruce feather moss forest in the interior of southern Quebec — Labrador Peninsula. *Acta Geogr.* **18**: 1-26.
- 1968. La forêt d'épinette noire à mousses du Québec Septentrional et du Labrador. *Nat. Can. (Que.)*, **95**: 413-421.
- IRELAND, R. R., C. D. BIRD, G. R. BRASSARD, W. B. SCHOFIELD, and D. H. VITT. 1980. Checklist of the mosses of Canada. *Natl. Mus. Nat. Sci. (Ottawa) Publ. Bot. No. 8*.
- IVES, J. D. 1978. The maximum extent of the Laurentide Ice Sheet along the east coast of North America during the last glaciation. *Arctic*, **31**: 14-53.
- JOHNSON, E. A., and J. S. ROWE. 1977. Fire and vegetation change in the western subarctic. *ALUR (Rep.) No. 75-76-61*.
- LOW, A. P. 1896. Reports on explorations in the Labrador Peninsula along the East Main, Koksoak, Hamilton, Manicougan, and portions of other rivers in 1892-93-94-95. *Geol. Surv. Can. Annu. Rep. No. 8, Part L*. pp. 1-387.
- MUELLER-DOMBOIS, D., and H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.
- PEACH, J. A. 1975. The tourism and recreation climate of Newfoundland and Labrador. Canada Department of the Environment, Atmospheric Environment Service, REC-2-75.
- ROUSSEAU, J. 1952. Les zones biologiques de la péninsule Québec-Labrador et l'hémisphère arctique. *Can. J. Bot.* **30**: 436-474.
- 1968. The vegetation of the Quebec-Labrador peninsula between 55° and 60° N. *Nat. Can. (Que.)*, **95**: 469-563.
- ROWE, J. S. 1972. Forest regions of Canada. *Can. For. Serv. Publ. No. 1300*.
- STANEK, W. 1975. The role of layering in black spruce forests on peatlands in the Clay Belt of northern Ontario. In *Black spruce symposium*. Great Lakes For. Res. Cent. Publ. No. O-P-4.
- STOTLER, R., and B. CRANDALL-STOTLER. 1977. A checklist of the liverworts and hornworts of North America. *Bryologist*, **80**: 405-428.
- TANNER, V. 1944. Outlines of the geography, life, and customs of Newfoundland-Labrador. *Acta Geogr.* Vol. 8.
- VIERECK, L. 1983. The effects of fire in black spruce ecosystems in Alaska and Northern Canada. *SCOPE Publ. No. 18*. pp. 201-220.
- WILTON, W. C. 1959. The forests of the Sandwich Bay area, Labrador. Canada Department of Northern Affairs and National Resources, Forest Bureau Mimeograph No. 59-10.
- 1965. The forests of Labrador. *Can. For. Branch Dep. Publ. No. 1066*.