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RAISED BOGS ON THE CAPE BRETON PLATEAU

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An ecological study of five raised bogs on the Cape Breton Plateau was undertaken with the following objectives: to obtain qualitative and quantitative data on the vegetation and environment, and from these data to describe the plant associations and their ecological relationships. Single plots from each community were selectively chosen and the vegetation was analyzed using the phytosociological methods of the Zürich-Montpellier School. Environmental analysis involved the collection of data pertaining to edaphic and climatic factors. Based on the detailed study of 46 plots, seven associations are recognised. These include the aquatic *Nuphar variegatum*, the semi-aquatic *Eriophorum angustifolium* and *Rhynchospora alba* - *Drosera intermedia*, the bog meadow *Scirpus cespitosus* - *Sphagnum* spp. and *Scirpus cespitosus* - *Dicranum leioneuron*, and the drier *Picea mariana* - *Cladonia rangiferina* and *Picea mariana* - *Rhododendron canadense* Associations. The most commonly represented associations are the *Picea* - *Cladonia* and the *Scirpus* - *Sphagnum* while those of limited occurrence include the *Eriophorum* and the *Picea* - *Rhododendron*. Chemical analysis of the bog soils reveals a high degree of similarity between associations, with the peat having greater cation concentrations than the mineral substratum. This is because the bogs receive their entire nutrient and water supply from precipitation. The proximity of the study area to the sea causes an increase in the chlorides of magnesium and sodium in rain water resulting in a cation imbalance in the peat. The mineral substratum, because of its acidity and impermeability, creates favorable sites for raised bog development. Climatic data reveal that the Cape Breton Plateau has cooler summertime temperatures than the nearby lowland coastal areas. Minimum temperatures on the Plateau are low enough to become critical for plant growth as they approach freezing even during July and August. This ensures a slower rate of decomposition in the peat deposits. Precipitation on the Plateau appears to be adequate for raised bog development with amounts slightly exceeding those recorded at Ingonish Beach and almost double the amount at Cheticamp. Four dynamic processes occur in the raised bogs: development, cyclic succession, erosion, and regeneration. The associations are discussed in relation to these successional sequences. Examination of the ecological amplitudes of bog species reveals an increase in the complexity of the flora of the associations, proceeding from hydric to mesic habitats. The majority of the bog species are found in the drier associations. It is concluded that the raised bogs on the Plateau are dynamic self-sustaining units which will continue to grow through plant succession as long as the present edaphic and climatic conditions remain constant.

Une étude écologique de 5 tourbières surélevées situées sur le Plateau du Cap Breton fut entreprise avec les objectives suivantes: obtenir des données qualitatives et quantitatives sur la végétation et l'environment et, à partir de ces données de decrire les associations végétales et leurs relations écologiques. Des parcelles de terrain de chacun des communautés furent sélectionnées. La végétation a été analysée a l'aide des méthodes phytosociologiques de l'Ecole de Zürich-Montpellier. L'analyse de l'environment consistait à recueillir des données sur les facteurs édaphiques et climatique. Sept associations peuvent être distinguiées et à partir de l'étude détaillée de 46 lots. Celles-ci incluent l'association aquatique a *Nuphar variegatum*, semi - aquatiques à *Eriophorum angustifolium* et *Rhynchospora alba* - *Drosera intermedia*, les associations de prairie marécaguese a *Scirpus cespitosus* - *Sphagnum* spp. et *Scirpus cespitosus* - *Dicranum leioneuron*, et les associations de terrains plus secs a *Picea mariana* - *Cladonia rangiferina* et *Picea mariana* - *Rhododendron*

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canadense. Les associations les plus communes sont celle à *Picea* - *Cladonia* et celle à *Scirpus* - *Sphagnum* alors que les associations a *Eriophorum* et à *Picea* - *Rhododendron* sont peu représentées. Les analyses chimiques du sol des tourbieres ont revele l'existence d'une grande similitude entre les associations, les concentrations en cations étant plus élevées dans la tourbe que dans le sous-sol mineral. Ceci fuit être attribué au fait que les tourbieres recoivent leur approvisionnement en sels nutritifs et en eau des précipitations atmosphériques. La proximité du site etudié de la mer amene une augmentation des chlorures de magnesium et de sodium dans les eaux de pluie ce qui entraine un diséquilibre cationique dans la tourbe. Le sous-sol minerale, à course de son acidité et de son imperméabilite crée des sites favorables au developpment des tourbieres surélevées. Les données climatiques révèlent que les températures d'été du Plateau du Cap Breton sont plus fraiches que celles des terres basses cotières avoisinantes. Les températures minimum sur le plateau, en approchant le point de congélation pendant les mois de juillet et août sont suffisamment bases pour devenir critique pour la croissance des plants. Ceci assure une vitesse de décomposition plus lentes des dépot dans la tourbe. Les précipitations sur la plateau semblent adéquates pour le devéloppment d'une tourbiere surélevée. Elles excèdent faiblement celles d'Ingonish Beach et sont deux fois plus importantes que celles de Cheticamp. Quatre processus dynamiques se produisant dans les tourbières surélevées: développment, succession cyclique, érosion et régénération. Les associations sont discuteés en relation avec ces successions. Un examen des amplitudes écologiques des especes des tourbières révèle qui la complexite de la flore de ces associations augmente des habitats hydriques vers les habitats mésiques. La majorité des especes végétales des tourbières se trouvent dans les associations les plus riches. Il est conclu que les tourbières surélevées du Plateau sont des unites dynamiques autosuffisantes qui continueront leur croissance par les successions végétales aussi longtemps que les conditions édaphiques et climatiques actuelles resteront constantes.

Introduction

An ecological study of raised bogs from the interior of the Cape Breton Plateau was undertaken during 1970-71 with the following objectives: (1) to obtain qualitative and quantitative data on the natural vegetation, (2) to classify and describe the major associations found on the bogs, (3) to analyze the physical environment with emphasis on climatic and edaphic factors, and (4) to describe the ecological and successional relationships of the bog associations.

The study area, located inside the Cape Breton Highlands National Park, is situated between longitudes 46°41′ and 46°44′N and latitudes 60°37′ and 60°43′W, and at elevations ranging from 488 to 518 m above Mean Sea Level (Fig 1).

A review of the literature revealed that little ecological work had been done previously on the bogs of the Cape Breton plateau. Nichols (1918) divided the vegetation of Northern Cape Breton into two climax formations, the Deciduous Forest Formation of the lowland areas and the Northeastern Evergreen Coniferous Forest Formation of the Plateau. He considered the bogs on the Plateau to be an upward extension of the latter formation. Nichols did the only ecological study of the raised bogs in this region, recognizing three association-complexes, namely, a bog meadow, wet bog, and dry bog stage. He also described the successional relations between these stages, and speculated on how the bogs may have originated.

Any literature survey of important contributions to bog vegetation and ecology in eastern North America should include local studies by Ganong (1897), Nichols (1919), and Damman (1977) in New Brunswick and Maine; Pollett (1972), Pollett and Bridgewater (1973), and Wells (1980) in Newfoundland; Gauthier and Grandtner (1975), and Gauthier (1980) in Québec; and Allington (1961) in Labrador-Ungava. In central North America, important local studies are those of Sjörs (1963), and Jeglum et al. (1974) in Ontario; Gates (1942) in Michigan; and Conway (1949), Janssen (1967), and Heinselman (1963, 1970) in Minnesota.

Early bog vegetation/ecology studies on a broader regional basis in North America include contributions by Transeau (1903), Rigg (1940, 1951), Dansereau and Segadas-Vianna (1952), and Osvald (1970). More recent works in this regard are studies by Fabiszewski (1975), Comeau (1977), and Damman (1979).

Some recent phytosociological studies have incorporated the techniques of the Zürich-Montpellier School as developed by Braun-Blanquet (1964) and used in this paper. These include the works of Pollett (1972), Pollett and Bridgewater (1973), Fabiszewski (1975), Gauthier and Grandtner (1975), Comeau (1977), Damman (1977), Gauthier (1980), Wells (1980), and Glaser et al. (1981).

Recent studies dealing with bog chemistry include contributions by Gorham (1967), Small (1972a), Damman (1978), and Waughman and Bellamy (1980).

Terminology

The term "bog" is one of several used in the English language to describe a waterlogged habitat. Ecologists recognize two classes of bog or peatland: minerotrophic types, dependent on an influx of terrestrial, nutrient-enriched water, and ombrotrophic (ombrogenous) types, dependent on atmospheric precipitation for water and nutrient supply (Gorham 1957a; Ratcliffe 1964).

Included within ombrogenous types are blanket and raised bogs. Blanket bogs, as the name implies, completely cover the ground in an unbroken mantle of peat. They usually occur on gently contoured land where precipitation is high. Raised bogs, occurring in cool, wet climatic regions, can be distinguished from blanket bogs by their characteristic convex surface, sloping from the center towards the edge (Ratcliffe 1964). Raised bogs become established once peat accumulation raises the surface above the influence of mineral soil water (Gorham 1957a; Ratcliffe 1964).

Description of the Study Area

Physiography

The Cape Breton Plateau rises steeply on its sides to heights of 300 m and more where it then levels off to form a broad flat tableland dissected by steep gorges. In the study area, the topography is gently undulating, consisting of low rounded hills and ridges surrounded by broad flat valleys. The area serves as the watershed for the Cheticamp, Mackenzie, and North Aspy Rivers as well as the Big Southwest, and Black Brooks.

Geology and Soils

The Cape Breton Plateau is underlain by resistant igneous and metamorphic rocks. Those in the study area belong to the George River Group of Precambrian time. This group is made up of undivided schist and gneiss intruded by granitic rocks (Roland 1982).

The soils of the Cape Breton Plateau are stony, and shallow, commonly occupying poorly drained sites. The parent material, from which these soils derive, is a stony sandy loam till, forming a thin layer over the bedrock. The thin glacial till covering the Plateau was deposited by ice approximately 10,000 years ago (Newman 1971). The impermeable nature of the bedrock covered by this till has led to the extensive development of peat bogs which are dependent on atmospheric precipitation for their water supply.

Climate

The climate of the Cape Breton region is influenced by two important factors: first, the region's proximity to the sea giving the area a wet maritime climate, and secondly, the Maritime Provinces lie in the direct path of storm systems leaving the North American Continent. Warm moist air from the south is constantly mixing with cold air flowing in from the northwest, and as a result, the Northern Cape Breton region can be characterized as having a wet, cool-temperate climate.

Table I Temperature and precipitation normals for Cheticamp and Ingonish Beach, Cape Breton.⁺

Meteorological Station	Mean Annual Temp (°C)	No. Months with Mean Temp above 0°C	Mean Annual Temp (°C) Max	Mean Annual Temp (°C) Min	Mean Annual Rainfall (mm)	Mean Annual Snowfall (cm)	Total Mean Annual Precipitation (mm)
Cheticamp 46°39'N, 60°57'W Elevation 11 m	6.0	8	9.8	2.1	947.3	406.7	1362.7
Ingonish Beach 46°39'N, 60°24'W Elevation 5 m	6.2	8	10.6	1.9	1287.2	343.7	1630.7

⁺Normals for Cheticamp are based on the period 1956-1980 and for Ingonish Beach from 1951-1980. (Data obtained from Atmospheric Environment Service, Environment Canada.)

The only long term climatic data available for the area are from coastal meteorological stations located at Cheticamp and Ingonish Beach. Climatic summaries for these two stations are presented in Table I. Detailed weather information for the Cape Breton Plateau, recorded during the Summer of 1970, is included under Observation and Interpretation.

Vegetation

The Plateau is covered mainly by coniferous forest, wet peatlands, and dry barrens. There are two types of forest present, namely, *Abies balsamea* which occurs on well drained slopes and ridges, and *Picea mariana* which occurs in poorly drained sites and usually surrounds the bogs.

In the study area the bogs are mainly the raised type and are located where drainage is impeded. They vary in shape, some having a pronounced convex surface while others are generally flat with only slight elevations near their centers. They sometimes cover extensive areas and are broken up only by small streams and drainage gullies.

Dry barrens occupy the higher ridges where rock outcrops are common. Here, ericaceous plants make up a substantial part of the vegetation cover.

Methods

Initially, 17 raised and blanket bogs in the central part of Cape Breton Highlands National Park were located using aerial photographs and topographic maps. A reconnaissance of these was done in June 1970 and observations made on the composition and structure of the vegetation. From the reconnaissance, five bogs (designated by the capital letters A to E) were selected for detailed study (Fig 1) and a tentative list of plant associations based on dominance and physiognomy was prepared.

Nomenclature

Plant nomenclature generally corresponds with Fernald (1950) for the vascular flora, Crum et al. (1965) for the mosses, Schuster (1953) for the liverworts, and Hale and Culberson (1966) for the lichens.

Vegetational Sampling

The methods used are taken from Beil (1969). The communities to be sampled were located using the following selection standards: (1) a community had to be homogeneous in composition and structure; (2) it had to be large enough to permit a sample plot of a given size to be included; (3) a community had to occur commonly throughout the study area. A single plot method was used in sampling all communities.

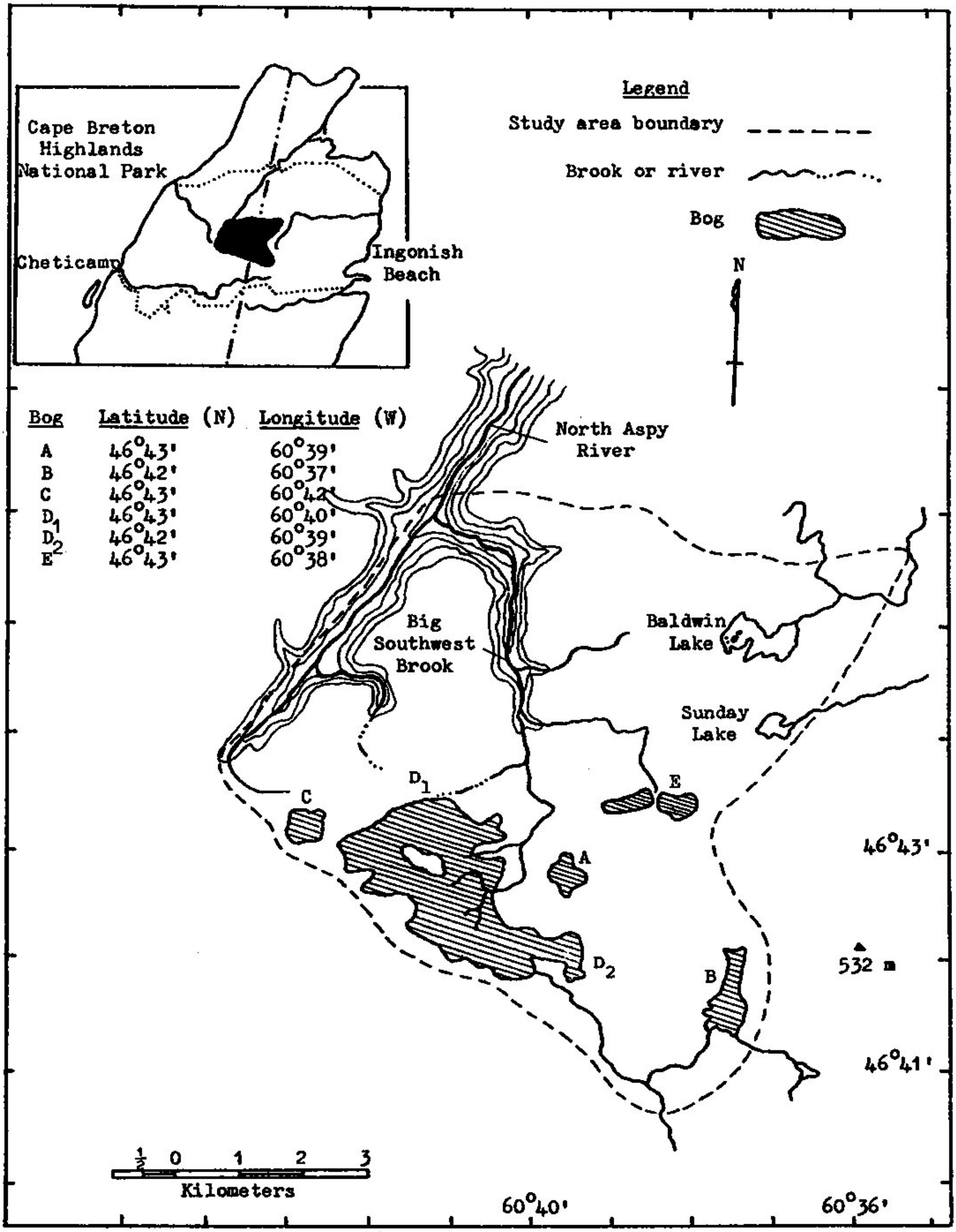

Fig 1. Map of the Sunday Lake, Baldwin Lake, Big Southwest Brook Study Area.

Communities were sampled with either 4 x 4 m (16 sq m) or 10 x 10 m (100 sq m) plots depending on the extent of the vegetation type. With the aid of a compass and metallic tape the plots were subjectively placed in the communities. This procedure permitted an accurate description of the associations to be made using as few sample plots as possible.

The phytosociological methods of the Zürich-Montpellier School were used in analyzing the vegetation (Becking 1957). Percentage cover was determined for the different vegetation layers. The parameters designated for these layers are given in the Appendix.

Species were listed according to strata, with the eleven-point Domin-Krajina scale (Krajina 1933) used to determine species significance for each. Estimates of sociability were also made for each species using an eleven-point Domin-Krajina scale (Becking 1957). These scales are presented in the Appendix. Unfamiliar species were given a descriptive name and collected for later identification.

Qualitative and quantitative data were collected for the following factors; slope gradient, exposure, latitude, longitude, elevation, landform type, pattern of topography, evidence of disturbance, degree of erosion, and percentage of ground surface covered by humus, litter, and decaying wood. Forty-six plots were analyzed.

Vegetation Synthesis and Classification

The methods are derived from Beil (1969). Based on floristic similarity, the sample plots were synthesized into associations. Constancy and average species significance were determined for each species. Constancy expresses how frequently a species will occur in an association provided all plots are of the same dimension. It was calculated by taking the number of plots in which a species occurred and expressing this as a percentage of the total number of plots. A five-class scale was used to express constancy percentages (see Appendix). Average species significance gives an indication of a species' importance in an association. It was determined by adding up the species significance values and dividing the total by the number of plots sampled in each association.

Dwarf Tree Analysis

The term "dwarf tree" was adopted to describe species of the B_1 and B_2 layers that under more favorable environmental conditions would attain normal tree size. These included *Picea mariana, Larix laricina, Ablies balsamea,* and *Sorbus decora.*

In all plots the heights of dwarf trees were measured and the presence or absence of a dead top noted. Tree age was determined by felling representative individuals, removing a section of the stem near ground level and counting the growth rings.

Loose wood fragments, uncovered while digging peat pits, were collected. The wood was thoroughly dried, sectioned, and identified to family.

Soil Sampling and Analysis

The range of peat depth in each plot was determined using a Davis peat sampler. Peat pits were dug in 40 of the 46 plots and the profiles were described by layers distinguished on the basis of color and texture. Whenever possible the peat was excavated down to the underlying mineral substratum. Only a surface sample, to a depth of approximately 30 cm, was taken from the bottom of the ponds. The profile descriptions included: layer depth and thickness, type of boundary, layer color and structure, amount of moisture, root distribution, and presence of buried wood fragments.

A total of 214 samples (195 peat and 19 mineral soil) were collected; of these 151 were selected for analysis. These included one complete profile of samples from every association, except the aquatic one, plus samples from the alternate layers of the remaining peat pits.

The peat and soil samples were thoroughly dried, crushed, screened through a 2 mm sieve, and the fraction at less than 2 mm size was collected for chemical and textural analyses.

Textural analyses on the mineral soils was determined by the hydrometer method (Bouyoucos 1951) using a mechanical stirrer to agitate the soil suspension. The textural classification follows that of the United States Department of Agriculture (sand = 2.00 to 0.05 mm; silt = 0.05 to 0.002 mm; clay = less than 0.002 mm).

Chemical analyses were made on the fraction of less than 2 mm size for the peat and soil samples. Determinations of total nitrogen, total phosphorus, and organic matter were done at the Nova Scotia Agricultural College. The determinations of pH and exchangeable potassium, sodium, magnesium, and calcium were carried out in the Biology and Geology departments, Acadia University.

Total nitrogen and phosphorus determinations entailed a digestion in sulfuric acid and hydrogen peroxide followed by analysis on a Technicon Auto-analyzer. The nitrogen was expressed as a percentage and phosphorus as parts per million. Analysis of the samples for percent organic matter involved a "loss on ignition" determination by difference in weight upon ashing in a furnace. Percentages of organic carbon were estimated from percentages of organic matter found in the samples, by dividing each value for the organic matter (O.M.) by 1.7, as suggested by Buckman and Brady (1969). Then, from the estimated carbon (C) values and the appropriate nitrogen (N) values, the carbon-nitrogen (C/N) ratios were calculated.

To extract the exchangeable cations (potassium, sodium, magnesium, and calcium), the samples were soaked in 1 N ammonium acetate solution with the pH adjusted to 7, and then filtered. The concentrations of the cations were then determined from the filtrates using an atomic absorption spectrophotometer, with atomic absorption for calcium and magnesium, and flame emission for potassium and sodium. The results were expressed in meq/100 g of soil.

Peat and soil pH were determined with a pH meter on samples soaked in distilled water for a minimum of 24 hours.

Climatic Data

A central weather station was established in Bog A (46°43'N, 60°39'W). It consisted of a Stevenson screen situated on the ground, housing a thermograph and a maximum-minimum thermometer; a precipitation gauge; and a totalizing anemometer with cups positioned 2 m above the ground.

A continuous record of temperature, precipitation and total miles of wind was obtained for the period of June 14 to August 30. Spot readings of relative humidity, wind velocity and wind direction were taken. Observations were also made on the number of days of sunshine, overcast skies, and a combination of both.

Observation and Interpretation

Descriptions of the Associations

The descriptions of the bog associations are arranged according to a moisture gradient, proceeding from the wettest to the driest. The following moisture classes are used: hydric—the water level is always above the surface; hygric—the water level is at or near the surface with the upper peat layers being continually wet; mesic—the water level is well below the surface with the surface layers being moderately well drained.

Nuphar variegatum Association (Fig 2)

This Association is common in the ponds scattered on the bogs. These ponds are generally small, thus restricting the size of the communities. The water depths vary between 60 and 120 cm. The underlying peat has an average depth of 1.78 m. The

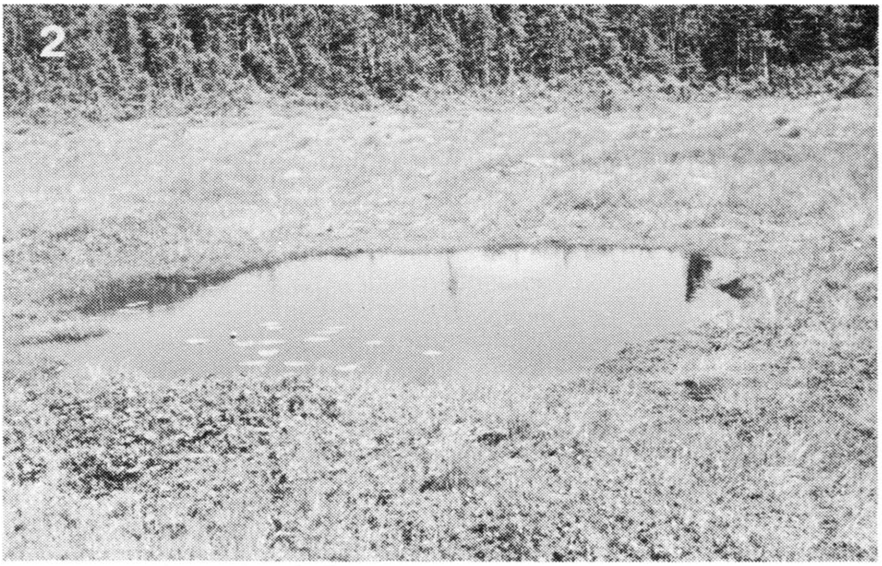

Fig 2. The species-poor *Nuphar variegatum* Association in a bog pond.

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Fig 3. The *Eriophorum* Association (white bristles of inflorescence) along the edge of a drainage area.

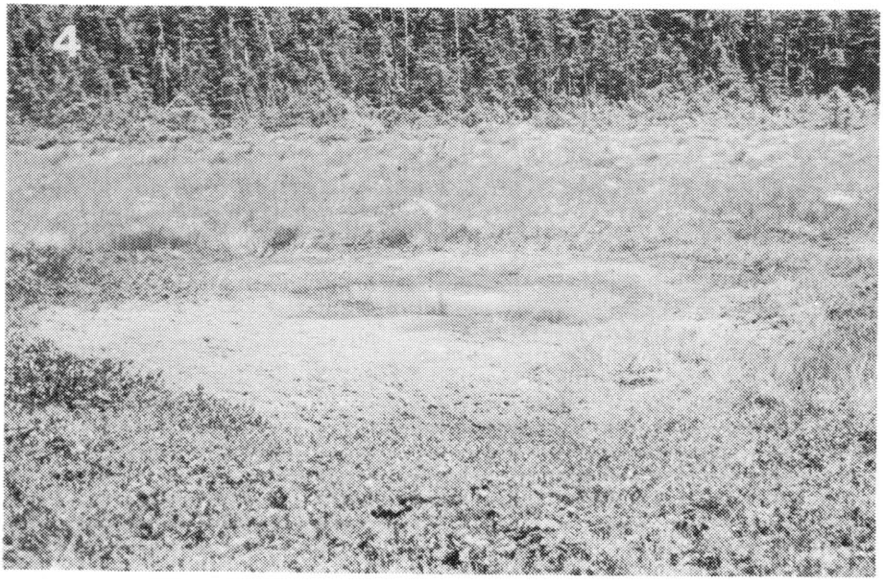


Fig 4. An early development stage of the *Rhynchospora* - *Drosera* Association with remnants of a pond.

Fig 5. Extensive development of the hygric *Scirpus* - *Sphagnum* Association surrounding bog ponds.

Fig 6. The sub-hygric *Scirpus - Dicranum* Association at the bog's outer edge.

Fig 7. The mesic *Picea - Cladonia* Association (foreground).

water level in the ponds is controlled by precipitation and evaporation with little drainage or runoff occurring. The Association is rated as hydric.

The vegetation structure of the *Nuphar variegatum* Association is simple, consisting of a poorly developed C layer with a cover ranging from 5 to 15%. Except for algae, there is no apparent D layer. The Association is characterized by the presence of *Nuphar variegatum*, a constant dominant with an average species significance of 3.8. The large floating leaves are attached by long petioles to thick rhizomes on the mucky bottoms of the ponds. The only other species found is *Eriocaulon septangulare* having an average species significance of 1.5 . It is considered characteristic because of its exclusiveness to this Association. *Eriocaulon*, when abundantly present, seems to play an important role in stabilizing the loose peat at the bottom of the ponds, due to its numerous basal leaves and dense root system. In one of the plots the basal leaves are estimated to cover from 50 to 60% of the surface of the underlying peat.

Table II *Eriophorum angustifolium* Association (5 plots).

Species (total: 19)	Constancy	Av. Species Significance
C Layer		
Eriophorum angustifolium	V	6.8
Rhynchospora alba	V	2.4
Drosera intermedia	IV	1.6
Utricularia cornuta	III	2.0
Drosera rotundifolia	II	0.6
Nuphar variegatum	II	0.4
Kalmia polifolia	II	0.2
Utricularia geminiscapa	II	0.2
D Layer		
Sphagnum cuspidatum	IV	4.6
Sphagnum papillosum	III	2.2
Gymnocolea inflata	III	1.2
Cladopodiella fluitans	II	3.2

Sporadics (with Species Significance values):

C Layer—Carex aquatilis (4), C. exilis (1), Vaccinium macrocarpon (1), V. oxycoccos (+)

D Layer—Sphagnum pulchrum (1), S. recurvum (7), Sphenolobus minutus (*)

*only presence recorded

Eriophorum angustifolium Association (Table II)

The *Eriophorum angustifolium* Association (Fig 3) is not common and is restricted to the edges of shallow ponds in the expanded portions of gullies which dissect the bogs. The surface topography is flat, the exposure neutral, and the surface of the peat completely covered with humus and litter. The edge of the Association bordering the pond is submerged, thus some sedimentation of organic matter is occurring. There is no evidence of erosion, and both runoff and drainage are controlled by the water level of the adjacent pond. The average peat depth is 1.08 m, due to the shallowness of the organic deposits in the depressional areas. The Association is considered to be semi-aquatic and is rated as sub-hydric. Following periods of prolonged rainfall it becomes completely inundated, with the water reaching depths of 25 cm.

Structurally, the Association includes moderately developed C and D vegetation layers. The C layer has a cover ranging from 33 to 60% while the D layer has a cover range of 20 to 99%. The C layer is dominated by *Eriophorum angustifolium*, the characteristic species of the Association, growing best when partially submerged; only those individuals bordering the ponds flowered. *Utricularia geminiscapa* and

Carex aquatilis are exclusive to this Association. The former has a low average species significance while the latter was found in only one plot. Both are good indicators of the semi-aquatic habitat conditions. *Rhynchospora alba* and *Drosera intermedia* are constant non-dominants which occur only in the drier portions of the Association, where the peat surface is usually exposed. *Nuphar variegatum* always shows poor development, attaining importance only in the *Nuphar variegatum* Association. Other plants characteristic of drier areas but occurring here in a stunted form with a low species significance include: *Kalmia polifolia, Carex exilis, Vaccinium macrocarpon* and *V. oxycoccos. Utricularia cornuta* plays an important role in consolidating the surface of the peat through extensive rhizome development.

Sphagnum cuspidatum, dominating the D layer, is a good indicator of the subhydric nature of the Association as it usually grows under immersed conditions. It was absent from only one plot where *S. recurvum*, a sporadic, dominated the community with a species significance of 7. *S. papillosum* is present, forming fairly firm cushions which are the initial stages of hummock development. Three liverworts are found in this Association: *Gymnocolea inflata*, usually entangled with *Sphagnum, Cladopodiella fluitans,* which is abundant in two plots, and *Sphenolobus minutus*, found intermingled with *Cladopodiella.*

Rhynchospora alba - Drosera intermedia Association (Table III)

The *Rhynchospora alba - Drosera intermedia* Association (Fig 4) occurs commonly, but never in extensive communities. The size of the largest one studied was less than 200 sq. m. Nichols (1918) used the term "muck mat" to refer to these areas, an appropriate term, as the roots and rhizomes of the plants are so tightly interwoven in the mucky peat that a vegetation mat is formed. The surface topography is extremely flat and the exposure neutral. Humus and litter cover 100% of the peat surface. There is no evidence of erosion or runoff taking place. Drainage is impeded because of the total saturation of the underlying peat. Precipitation collecting on the surface is removed by evaporation and sub-surface drainage. The average peat depth is 2.19 m, ranging from a minimum of 1.8 to a maximum of 2.4 m. Traces of this Association are also found in depressions on shallow peat between the *Eriophorum angustifolium* Association (when it is present) and the *Nuphar*

Table III *Rhynchospora alba - Drosera intermedia* Association (6 plots).

Species (total: 19)	Constancy	Av. Species Significance
C Layer		
Rhynchospora alba	V	6.6
Drosera intermedia	V	2.6
Utricularia cornuta	V	1.5
Eriophorum angustifolium	V	1.1
Vaccinium macrocarpon	V	1.1
Andromeda glaucophylla	V	0.8
Kalmia polifolia	II	0.3
Vaccinium oxycoccus	II	0.3
Chamaedaphne calyculata	II	0.3
Drosera rotundifolia	II	0.3
Sarracenia purpurea	II	0.1
D Layer		
Cladopodiella fluitans	V	8.6
Sphagnum pulchrum	V	3.6
Sphagnum cuspidatum	IV	3.6

Sporadics (with Species Significance values):

C Layer—Calamagrostis pickeringii (2), Carex exilis (+), Picea mariana (+)

D Layer—Drepanocladus revolvens (4), Orthocaulis gracilis (3) *variegatum* Association. The Association can be considered sub-hydric to hygric as, after heavy rains, standing water collects on the surface to a depth of several centimeters.

Structurally, the vegetation of this Association is composed of a moderately developed C layer with a cover range of 28 to 60% and a well developed D layer with a coverage ranging from 60 to 100%. *Rhynchospora alba*, a characteristic species, dominates the C layer where it is commonly found in clumps with a sociability ranging from 1 to 3. *Drosera intermedia*, a subdominant, attains its highest average species significance in this Association. *Utricularia cornuta* and *Vaccinium macrocarpon* help to bind the fabric of the muck mat into a firm crust through their roots and trailing rhizomes. *Eriophorum angustifolium* has a low average species significance here, having its best development in associations formed in deep depressional areas. *Kalmia polifolia, Chamaedaphne calyculata, Andromeda glaucophylla,* and *Sarracenia purpurea* grow here in stunted form. They are all characteristic of more mesic habitats. *Vaccinium oxycoccos* and *Drosera rotundifolia* are present with low species significance and constancy. Both species are more abundant in drier associations where they grow entangled with the cushion-forming *Sphagnum*.

The dominant bryophyte of the D layer is *Cladopodiella fluitans*, a characteristic species and an important constituent of the vegetation mat. *Sphagnum cuspidatum* and *S. pulchrum* are the only *Sphagnum* present. The liverworts *Drepanocladus revolvens* and *Orthocaulis gracilis* occur as sporadics.

Scirpus cespitosus - Sphagnum spp. Association (Table IV)

This Association (Fig 5) is common on the raised bogs and can be described as a "wet" bog meadow. Conditions are favourable for the growth of cushion-forming *Sphagnum*. The surface topography is flat and the slope gradient varies from 0 to 2 degrees. The peat surface is totally covered in humus and litter. There is no evi-

Table IV *Scirpus cespitosus - Sphagnum* spp. Association (6 plots).

Species (total: 30)	Constancy	Av. Species Significance
C Layer		
Scirpus cespitosus	V	4.3
Chamaedaphne calyculata	V	3.5
Andromeda glaucophylla	V	3.1
Kalmia polifolia	V	2.6
Vaccinium oxycoccos	V	2.5
Drosera rotundifolia	V	2.1
Carex exilis	V	1.6
Sarracenia purpurea	V	0.6
Eriophorum angustifolium	IV	1.0
Eriophorum spissum	III	0.5
Kalmia angustifolia	II	0.3
Ledum groenlandicum	II	0.3
D Layer (Bryophytes)		
Sphagnum tenellum	V	4.8
Sphagnum capillaceum var. tenellum	V	3.3
Sphagnum magellancium	V	3.3
Dicranum leioneuron	V	3.1
Orthocaulis gracilis	V	2.3
Sphagnum papillosum	IV	1.6
Sphagnum fuscum	IV	1.3
Gymnocolea inflata	IV	0.6
Sphagnum pulchrum	III	0.6
D Layer (Lichens)		
Cladonia sp. (alpestris?)	V	1.1
Cladonia pleurota	III	0.6
Ochrolechia frigida	II	0.5
Cetraria islandica	II	0.3
Cetraria islandica ssp. crispa	II	0.3
Cladonia rangiferina	II	0.3

Sporadics (with Species Significance values):

C Layer—Vaccinium macrocarpon (2)

D Layer—Dicranum undulatum (2), Ptilidium ciliare (1) dence of surface erosion, and runoff is retarded by the abundance of *Sphagnum*. The depth of the peat underlying the Association varies from 1 m in depressional areas to 2.5 m in the higher areas of a bog. The Association can best be described as hygric.

Structurally, the vegetation of the *Scirpus cespitosus - Sphagnum* spp. Association has a moderately developed C layer and a well developed D layer. The C layer has a cover varying from 25 to 35% while the D layer varies from 97 to 100%. The dominant species of the C layer is *Scirpus cespitosus* which is constantly present. It is a characteristic plant of the Association and is important in impeding the downward movement of water by consolidating the peat. The plants which attain their highest average species significance in this Association include: *Chamaedaphne calyculata, Andromeda glaucophylla, Vaccinium oxycoccos, Drosera rotundifolia,* and *Eriophorum spissum.* All are constant non-dominants with the exception of *E. spissum.* Both *V. oxycoccos* and *D. rotundifolia* are found growing with the *Sphagnum*.

Carex exilis, Kalmia angustifolia, K. polifolia, Ledum groenlandicum and *Sarracenia purpurea* which are characteristic of more mesic habitats occur here with low cover and poor vigor. *Eriophorum angustifolium* and *Vaccinium macrocarpon* are present with low species significance. These plants reach their ecological optima in more hydric habitats.

Sphagnum tenellum occurs largely in shallow depressions and is the most abundant bryophyte of the Association. *S. magellanicum* and *S. papillosum* are important cushion-forming species. Other *Sphagnum* found in the Association include: *S. capillaceum* var. *tenellum* (= *S. rubellum*), *S. fuscum,* and *S. pulchrum.* Entangled with the *Sphagnum* are the liverworts *Orthocaulis gracilis* and *Gymnocolea inflata*. The following lichens are present in the Association but with low cover and constancy: *Cladonia pleurota, C. rangiferina, Ochrolechia frigida, Cetraria islandica,* and *C. islandica* ssp. *crispa.* They are more abundant in the drier associations.

Scirpus cespitosus - Dicranum leioneuron Association (Table V)

The *Scirpus cespitosus - Dicranum leioneuron* Association (Fig 6) is confined to the outer edges of the bogs and is always found adjacent to the forest phase of the *Picea mariana - Rhododendron canadense* Association that surrounds most of the peatlands. The surface topography is flat with slope gradients varying from 0 to 2 degrees. The peat surface has a 100% cover of humus and litter. Surface runoff occurs and small erosional channels were found in two of the plots. Drainage is impeded because of the extremely compact underlying sedge peat. This peat is usually very shallow and has an average depth of 1.13 m. The Association is rated as sub-hygric.

Structurally, the vegetation consists of a moderately developed C layer with a cover ranging from 25 to 40% and a well developed D layer with a coverage of 95 to 99%. The C layer is dominated by the constant presence of *Scirpus cespitosus.* It is one of the characteristic species of the Association and is very important in consolidating the peat, making it almost impervious to percolation of water. This is an important step in initiating raised bog development.

The following plants attain their highest species significance in this Association: *Aronia prunifolia, Carex exilis, Sarracenia purpurea,* and *Calamagrostis pickeringii.* All are constant non-dominants. *Chamaedaphne calyculata, Kalmia polifolia,* and *Andromeda glaucophylla,* which have a wide tolerance for moisture conditions, occur in this Association with a high constancy. Species found here that are common in drier habitats include: *Coptis trifolia, Vaccinium boreale, Ledum groenlandicum,* and *Kalmia angustifolia.* In the damper hollows *Eriophorum angustifolium,*

Table V *Scirpus cespitosus - Dicranum leioneuron* Association (6 plots).

Species (total: 46)	Constancy	Av. Species Significance
C Layer		
Scirpus cespitosus	V	5.3
Chamaedaphne calyculata	V	3.0
Aronia prunifolia	V	2.8
Kalmia polifolia	V	2.8
Andromeda glaucophylla	V	2.5
Carex exilis	V	2.1
Solidago uliginosa	V	2.1
Vaccinium oxycoccos	V	1.8
Sarracenia purpurea	V	1.6
Calamagrostis pickeringii	V	1.5
Eriophorum angustifolium	V	1.5
Coptis trifolia	V	1.3
Vaccinium boreale	V	1.0
Maianthemum canadense	V	0.8
Ledum groenlandicum	IV	1.3
Trientalis borealis	IV	1.1
Kalmia angustifolia	III	1.1
Drosera rotundifolia	III	1.0
Empetrum nigrum	II	0.6
D Layer (Bryophytes)		
Dicranum leioneuron	V	5.5
Sphagnum capillaceum var. tenellum	V	3.0
Sphagnum tenellum	V	2.8
Orthocaulis gracilis	V	1.6
Sphagnum magellanicum	IV	2.5
Dicranum undulatum	III	1.1
Sphagnum pulchrum	III	0.5
Sphagnum fuscum	II	1.0
Pleurozium schreberi	II	0.6
Ptilidium ciliare	II	0.6
Gymnocolea inflata	II	0.5
D Layer (Lichens)		
Cladonia sp. (alpestris ?)	V	2.8
Cladonia rangiferina	V	1.6
Cetraria islandica	IV	1.1
Cladonia pleurota	IV	0.8
Cladonia uncialis	II	0.3
Ochrolechia frigida	II	0.3

Sporadics (with Species Significance values):

C Layer—Aster nemoralis (1), Eriophorum spissum (1), Rhynchospora alba (1), Schizaea pusilla (1)

D Layer—Cetraria islandica ssp. crispa (1), Cladonia alpestris (+), C. pseudorangiformis (1), Microlepidozia setacea (1), Mylia anomala (2), Sphagnum papillosum (2)

Rhynchospora alba, and *Schizaea pusilla* occur. The latter two are sporadics. *Vaccinium oxycoccos, Drosera rotundifolia,* and *Empetrum nigrum* are always found associated with the cushion-forming *Sphagnum. Maianthemum canadense* and *Trientalis borealis* occur here with low cover and are species of forest affinity.

The dominant bryophyte of the D layer is *Dicranum leioneuron* with a sociability of 1 to 3. *Sphagnum capillaceum* var. *tenellum, S. fuscum, Dicranum undulatum, Pleourozium schreberi* and *Ptilidium ciliare* when present can be considered as indicators of the drier conditions that prevail. Species occurring in the damper hollows include: *Sphagnum tenellum, S. pulchrum,* and *Microlepidozia setacea.* The liverworts *Orthocaulis gracilis* and *Gymnocolea inflata* grow entangled with the *Sphagnum. S. magellanicum* is the most important cushion-forming species present but occurs with a low average species significance. *Cladonia rangiferina, C. uncialis, C. pleurota, Cetraria islandica,* and *Ochrolechia frigida* are some of the lichens found here, all being of low species significance.

Picea mariana - Cladonia rangiferina Association (Table VI)

This Association (Fig 7) is widespread in the bogs studied. The surface topography is hummocky with the slope gradients varying from 1 to 2 degrees. The hummocks range from 30 to over 120 cm in diameter and from a few to more than 30 cm in height. This increase in elevation above the wetter portions of the bog provides drier conditions allowing the establishment of more mesophytic species. Humus and litter cover 100% of the peat surface. Erosion was observed only in one plot where some of the *Cladonia* cover in the hollows had been washed away. The greatest accumulation of peat is under this Association with an average depth of 2.28 m. The Association is considered to be mesic.

Structurally, the *Picea mariana - Cladonia rangiferina* Association consists of three vegetation layers. These include, together with their cover ranges, a poorly developed B_2 layer (27 to 33%), a moderately developed C layer (15 to 53%), and a well developed D layer (90 to 99%). *Picea mariana,* characteristic for the Association, dominates the B_2 and C layers. It occurs in clumps up to 60 cm in height and has a sociability of 2 to 6. *Larix laricina,* also a characteristic species, is a constant non-dominant. It usually grows singly and attains heights of 120 cm. The tallest individuals of *Larix* frequently have dead tops. This may be the result of exposure of this part of the plant above the protective blanket of snow during winter.

Rhododendron canadense, Ledum groenlandicum, Chamaedaphne calyculata, Kalmia angustifolia, K. polifolia and *Vaccinium angustifolium* occur in the B_2 layer but are more common in the C layer. In the B_2 layer these species frequently are found growing alongside and intermingled with the *Picea* clumps. In some cases this seems to provide these species the support needed for their upright position.

In the C layer the following species are usually found growing on the hummocks: *Empetrum nigrum, Rubus chamaemorus, Cornus canadensis, Vaccinium boreale, Coptis trifolia* and *Trientalis borealis*. They all have high constancy. The presence of *Scirpus cespitosus, Calamagrostis pickeringii, Eriophorum angustifolium, E. spissum* and *Schizaea pusilla* in the hollows and depressions reflects the moist conditions that prevail between the hummocks. *Geocaulon lividum* and *Gaultheria hispidula,* on the other hand, are present only under the *Picea* clumps where shade is maximum. Two species which are able to tolerate both exposure and shade are *Sarracenia purpurea* and *Melampyrum lineare.* In well shaded areas they lack the purplish pigmentation in their leaves.

The dominant bryophytes are *Pleurozium schreberi* and *Sphagnum fuscum,* the latter being an important constituent in the development of hummocks. Other species which can be considered indicative of the mesic site include: *Ptilidium ciliare, Dicranum polysetum, Hylocomium splendens, Rhacomitrium lanuginosum* and *Ptilium crista-castrensis.* Species found between the hummocks in the damper hollows include: *Sphagnum tenellum, S. pulchrum* and *Microlepidozia setacea.* The liverworts *Orthocaulis gracilis* and *Mylia anomala* are found entangled with the *Sphagnum.*

The lichen cover is a conspicuous aspect of the Association. *Cladonia rangiferina* is the dominant species with a sociability of 3, while *C. alpestris* is a constant subdominant. Other *Cladonia* present include: *C. pleurota, C. uncialis, C. gracilis, C. pseudorangiformis, C. arbuscula, C. crispata, C. mitis* and *C. squamosa. Cetraria islandica* occurs with a high constancy and low average species significance.

Epiphytic lichens found on the dwarf *Picea* and *Larix* trees include: *Cetraria aurescens, Alectoria americana, A. ochroleuca, Ramalina miniscula* and *Usnea cavernosa.*

Table VI *Picea mariana - Cladonia rangiferina* Association (6 plots).

Species (total: 68)	Constancy		Av. Species Significance	
B_2 and C Layers	*C*	*B_2*	C	*B_2*
Picea mariana	V	V	4.3	3.5
Larix laricina	V	V	1.0	1.1
Rhododendron canadense	V	III	2.1	1.1
Ledum groenlandicum	V	III	3.3	0.8
Chamaedaphne calyculata	V	III	3.0	0.8
Kalmia angustifolia	V	II	3.5	0.6
Kalmia polifolia	V	II	2.8	0.6
Vaccinium angustifolium	V	II	2.0	0.5
Scirpus cespitosus	V		3.1	
Empetrum nigrum	V		3.0	
Rubus chamaemorus	V		2.6	
Aronia prunifolia	V		2.3	
Cornus canadensis	V		1.8	
Vaccinium boreale	V		1.6	
Drosera rotundifolia	V		1.5	
Vaccinium oxycoccos	V		1.5	
Calamagrostis pickeringii	V		1.3	
Coptis trifolia	V		1.3	
Eriophorum angustifolium	V		1.1	
Solidago uliginosa	V		1.1	
Trientalis borealis	V		1.1	
Sarracenia purpurea	V		1.0	
Melampyrum lineare	IV		0.8	
Geocaulon lividum	IV		0.5	
Deschampsia flexuosa	III		0.6	
Andromedia glaucophylla	III		0.5	
Schizaea pusilla	III		0.5	
Eriophorum spissum	III		0.5	
Juniperus communis	II		0.8	
Maianthemum canadense	II		0.6	
Gaultheria hispidula	II		0.3	
D Layer (Bryophytes)				
Pleurozium schreberi	V		4.5	
Sphagnum fuscum	V		4.0	
Ptilidium ciliare	V		2.5	
Dicranum undulatum	V		1.8	
Hylocomium splendens	IV		2.1	
Orthocaulis gracilis	IV		1.3	
Sphagnum capillaceum var. tenellum	IV		1.1	
Sphagnum tenellum	IV		0.8	
Microlepidozia setacea	IV		0.6	
Rhacomitrium lanuginosum	III		1.0	
Ptilium crista-castrensis	III		0.6	
Dicranum leioneuron	II		0.6	
Cephalozia bicuspidata	II		0.5	
Sphagnum capillaceum	II		0.3	
Sphagnum pulchrum	II		0.3	
D Layer (Lichens)				
Cladonia rangiferina	V		5.6	
Cladonia alpestris	V		4.1	
Cladonia pleurota	V		1.5	
Cladonia uncialis	V		1.5	
Cetraria islandica	V		1.3	
Cladonia gracilis	V		0.8	
Cladonia sp. (alpestris ?)	IV		1.8	
Cladonia pseudorangiformis	II		0.3	
Ochrolechia frigida	II		0.3	

Sporadics (with Species Significance values):

B Layer—Aronia prunifolia (2)

C Layer—Abies balsamea (1), Amelanchier bartramiana (1), Carex exilis (1), Epigaea repens (1), Nemopanthus mucronata (1)

D Layer—Cetraria islandica ssp. crispa (1), Cladonia arbuscula (*), C. crispata (1), C. mitis (4), C. squamosa (1), Dicranum polysetum (1), Gymnocolea inflata (1), Mylia anomala (1)

*only presence recorded

Picea mariana - Rhododendron canadense Association (Table VII)

This Association is limited to the banks of the drainage gullies dissecting the bogs (Fig 8). The surface topography is irregular and the slope gradients vary from 0 to 4 degrees. Humus and litter cover between 95 and 100% of the peat surface. There is no evidence of erosion and due to the topographic position there is a slight amount of runoff occurring. The average depth of peat is 1.69 m on the banks and 1.19 m in the gullies. The driest conditions within a bog occur in this Association which is considered to be submesic.

Structurally, the *Picea mariana - Rhododendron canadense* Association consists of four strata, a poorly developed B_1 layer with a cover ranging from 1 to 40% and moderately developed B_2, C and D layers. The coverages for these layers are: B_2 (15 to 85%), C (40 to 70%), and D (7 to 85%).

Picea mariana, one of the characteristic species with a sociability of 3 to 7, dominates the shrub layer. It occurs with only minor significance in the C layer. *Abies balsamea* and *Larix laricina* occur with low constancy and cover in the B_1, B_2 and C layers. Other shrubs characteristic of the B_2 sublayer include: *Amelanchier bartramiana, Nemopanthus mucronata,* and *Viburnum cassinoides. Betula papyrifera* and *Sorbus decora* occur in the B_2 sublayer only as sporadics.

Rhododendron canadense, a characteristic species and occurring in the B_2 sublayer, is the dominant species of the C layer. Other species found in the shrub layer but becoming more common in the C layer are *Ledum groenlandicum, Kalmia angustifolia, Vaccinium angustifolium, Aronia prunifolia* and *Myrica gale.*

The C layer contains forest species which in the bogs are exclusive to this Association. Included here are: *Clintonia borealis, Carex trisperma, Taxus canadensis* and *Linnaea borealis.* The following plants attain their highest average species significance values in this Association: *Cornus canadensis, Coptis trifolia, Vaccinium boreale, Epigaea repens, Melampyrum lineare, Gaultheria hispidula, Trientalis*

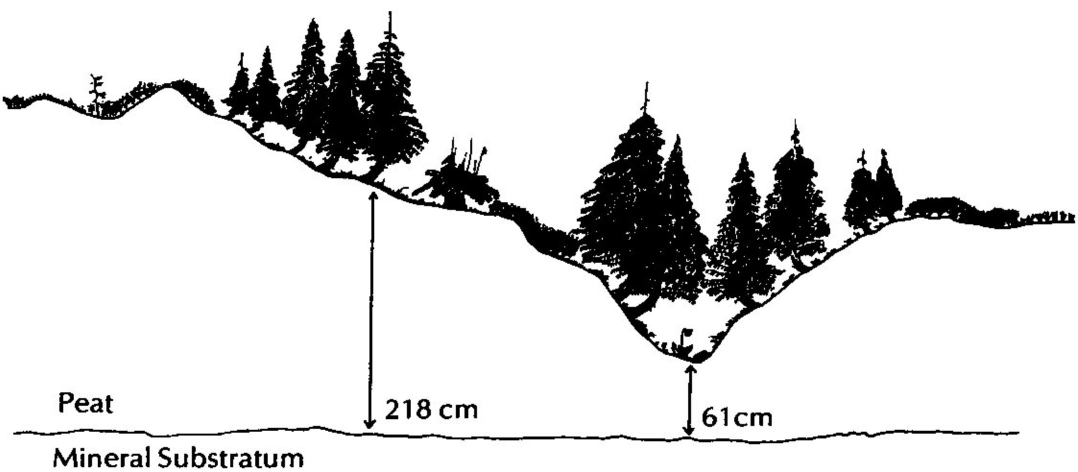


Fig 8. Profile of a drainage gully showing the *Picea mariana - Rhododendron canadense* Association.

Table VII *Picea mariana - Rhododendron canadense* Association (6 plots).

Species (total: 60)	Constancy			Av. Species Significance		
B and C Layers	C	B_2	B_1	C	B_2	B_1
Picea mariana	IV	V	V	1.1	5.8	3.3
Abies balsamea	II	III	III	0.5	0.3	0.3
Larix laricina		V	II		1.0	+.+
Amelanchier bartramiana	II	V		0.6	4.5	
Nemopanthus mucronata		V			2.3	
Rhododendron canadense	V	IV		4.1	2.8	
Ledum groenlandicum	V	IV		2.0	1.1	
Kalmia angustifolia	V	IV		1.8	0.8	
Vaccinium angustifolium	V	III		1.8	1.1	
Myrica gale	IV	III		1.3	1.1	
Aronia prunifolia	V	III		1.8	1.0	
Viburnum cassinoides		III			1.0	
Kalmia polifolia	V	III		2.0	0.6	
Taxus canadensis	III	III		0.6	0.3	
Clintonia borealis	V			3.0		
Cornus canadensis	V			2.8		
Coptis trifolia	V			1.8		
Vaccinium boreale	V			1.8		
Epigaea repens	V			1.5		
Rubus chamaemorus	V			1.5		
Melampyrum lineare	V			1.3		
Calamagrostis pickeringii	V			1.1		
Eriophorum angustifolium	V			1.1		
Gaultheria hispidula	V			1.1		
Trientalis borealis	V			1.1		
Maianthemum canadense	V			1.0		
Carex trisperma	IV			0.6		
Sarracenia purpurea	IV			0.6		
Scirpus cespitosus	IV			0.6		
Deschampsia flexuosa	III			0.5		
Linnaea borealis	III			0.5		
Andromeda glaucophylla	III			0.5		
Empetrum nigrum	III			0.5		
Carex oligosperma	II			0.3		
Geocaulon lividum	II			0.3		
Solidago uliginosa	II			0.3		
D Layer (Bryophytes)						
Pleurozium schreberi	V			4.8		
Hylocomium splendens	V			3.0		
Dicranum scoparium	V			2.8		
Ptilidium ciliare	V			2.1		
Dicranum fuscescens	V			1.3		
Sphagnum subsecundum	V			1.1		
Sphagnum palustre	IV			0.8		
Orthocaulis gracilis	II			0.6		
Leucobryum glaucum	II			0.3		
Ptilium crista-castrensis	II			0.3		
D Layer (Lichens)						
Cladonia rangiferina	V			1.3		
Cladonia gracilis	V			0.8		
Cladonia pleurota	V			0.8		
Cladonia pseudorangiformis	IV			0.5		
Cladonia squamosa	III			0.5		

Sporadics (with Species Significance values):

B_2 Layer—Betula papyrifera (1), Chamaedaphne calyculata (3), Sorbus decora (+)

C Layer—Aster nemoralis (1), Carex exilis (1), Chamaedaphne calyculata (3), Larix laricina (+), Nemopanthus mucronata (2)

D Layer—Cladonia crispata (1), C. mitis (2), Dicranum polysetum (3), D. undulatum (2)

borealis and *Maianthemum canadense*. All are constantly present and considered indicators of the drier habitat. Species occurring in areas receiving the maximum amount of light include: *Calamagrostis pickeringii, Scirpus cespitosus, Deschampsia flexuosa* and *Solidago uliginosa*. *Eriophorum angustifolium* and *Andromeda* *glaucophylla* occur here but reach their optima in wetter associations. *Rubus chamaemorus,* a characteristic species of dry bog associations, is found here with a fairly high constancy.

The dominant species of the D layer is *Pleurozium schreberi* with a sociability of 1 to 3. The following constant species are all of forest affinity: *Hylocomium splendens, Dicranum scoparium, Ptilium crista-castrensis* and *Ptilidium ciliare.* Species found on the gully bottoms where damper conditions prevail include: *Sphagnum subsecundum, S. palustre* and *Leucobryum glaucum.*

The most abundant lichen is *Cladonia rangiferina,* occurring in the exposed areas on hummocks. *C. gracilis* and *C. pseudorangiformis* are found only in well shaded areas.

Cetraria aurescens and *Alectoria americana* are the most important epiphytes on the dwarf trees.

Description of the Bog Soils

The organic deposits underlying the bog associations can be classified under two categories, sedimentary and fibrous peat (Buckman and Brady 1969). The latter category includes sedge peat, and *Sphagnum* peat, with the distinction between the two based on the higher water-holding capacity of the *Sphagnum* peat. In some bog areas deposits composed mainly of one type of fibrous peat are found while in other sections both occur in the same profile. Sedimentary peat is deposited under long standing bodies of water and occurs in the lower sections of some profiles.

The average depth of peat in the communities sampled ranged from a minimum of 108 cm in the *Eriophorum angustifolium* Association, located in depressional areas, to a maximum of 228 cm in the *Picea mariana - Cladonia rangiferina* Association. The peat overlies a mineral substratum composed largely of granitic bedrock, often bare or thinly covered with a sandy loam soil (Table VIII). This substratum is practically impervious to the downward movement of water.

The profiles studied are composed of distinct layers which differ in physical and chemical characteristics, the degree of decomposition, and the nature of the original vegetation. The boundary between each layer is clear and smooth.

Table VIII Textural Analysis - Mineral Substratum.

Association	No. of Samples	Average % Sand	Average % Silt	Average % Clay	Textural Class
Eriophorum	1	79.2	19.3	1.5	loamy sand
	2	61.8	34.7	3.5	sandy loam
Scirpus - Sphagnum	1	75.2	22.3	2.5	loamy sand
	3	61.8	36.6	1.6	sandy loam
Scirpus - Dicranum	1	81.2	16.9	1.9	loamy sand
	4	64.2	32.5	3.3	sandy loam
Picea - Cladonia	1	66.0	30.3	3.7	sandy loam
Picea - Rhododendron	1	92.1	7.9	-	sand
	3	61.2	34.5	4.3	sandy loam

Physical Characteristics

The number of layers of peat found over the mineral substratum ranged from a minimum of three to a maximum of ten. The outer edges of the bog, drainage gullies, and depressions within the bog are the areas where the minimum number of layers occur. The former represents an immature phase in bog development while the latter two are mainly erosional areas. The maximum number of layers are found in those sections of the bog where hummocks are present.

The layers vary in thickness from 4 cm to 81 cm with the average being 21 cm. There is no apparent sequence in the thickness of layers in each profile, suggesting a differential rate of bog growth. No attempt was made to describe the various colors found in a peat profile as no color chart was available. It may be noted, however, that each layer is usually distinct in color from those adjacent to it.

The structure of the peat ranges from a loose mass to a compact fibrous substance. The former is found in the surface layers of the wetter associations where it is being deposited through sedimentation. Compact peat is found throughout the profiles of the *Scirpus cespitosus - Dicranum leioneuron* Association located at the bog's edge. The peat here has been formed by the continued presence of sedges, like *Scirpus cespitosus,* which consolidate the organic matter into a dense fibrous structure that is almost impervious to the downward movement of water. Other associations on the bog overlie peat which is intermediate between these two extremes, being composed of *Sphagnum* and sedge remains. This suggests the presence of different successional stages in the bog's history.

The moisture status of the peat is dependent upon precipitation and the nature of the organic matter. The *Sphagnum* peat is always wetter than the more compact sedge peat. Lateral seepage was observed in several profiles where a layer of *Sphagnum* peat overlies a layer of sedge peat. The former allows percolation of water while the latter is impervious to drainage. Precipitation water drains to the level of the sedge peat and then moves laterally. This phenomenon, together with the high water holding capacity of the *Sphagnum,* permits the water table to be maintained near the surface.

Root distribution is concentrated in the upper peat layers, the average rooting depth being around 45 cm. The dwarf trees on the mature hummocks and in the drainage gullies have shallow, spreading root systems. This suggests edaphic conditions are more favourable for root growth near the surface where better drainage results in improved aeration of the peat.

In all associations where peat pits were dug, buried wood fragments were found. In the peat underlying the ponds solid objects were often encountered in making depth determinations. It is probable that these objects were also buried wood fragments as no other solid objects were found in the peat. The significance of the buried wood is dealt with in the Discussion.

Chemical Analysis

The chemical properties of the peat and soil samples are very similar among the associations (Table IX). All peat samples showed an acidic reaction with pH ranging from 3.9 to 5.1. In the profiles, acidity always decreased from the surface to the underlying mineral substratum. This is possibly because acidity varies with the degree of oxidation and humification that is taking place. Drier, humified peats have lower pH values (Pearsall 1938) and occur in surface layers when an equilibrium has been established between accumulation and oxidation (Daubenmire 1968). Acidity also increased in the surface layers from the wettest to the driest associations. This is possibly because in drier peat sulfides are oxidized to sulfuric acid, thus lowering the pH (Gorham 1953). The soil collected from the surface layer of the mineral substratum ranged in pH from 4.4 to 5.6, indicating the acidic nature of the parent rocks. This would have enabled the substratum to be initially colonized by plants tolerant to acidic conditions (like *Sphagnum*), thus favoring bog development.

Percent carbon remains relatively constant in all the peat samples because there is no mineral soil incorporated in the organic matter. Total nitrogen is present in very small amounts. The nitrogen content of *Sphagnum* is low (Gorham 1953; Mal-

Table IX Chemical analysis of the bog soil samples (based on averages).

Association	Layer	pH	C(%)	Total N(%)	C/N	Total P(ppm)	Exchangeable Cations K	Na	Mg	Ca
Nuphar	surface	4.4	57.68	1.84	31	237	0.37	3.12	13.28	3.56
Eriophorum	surface	4.2	57.18	1.56	36	174	0.09	1.40	10.79	5.04
	subsurface	4.7	56.33	1.63	34	390	0.08	1.25	5.83	4.92
	+substratum	4.9	3.92	0.09	43	250	0.04	0.19	0.42	0.59
Rhynchospora - Drosera	surface	4.2	57.98	1.59	36	153	0.15	1.72	13.29	3.83
Scirpus - Sphagnum	surface	4.2	58.00	1.55	37	187	0.17	1.58	9.21	2.70
	subsurface	4.4	56.80	1.43	39	316	0.09	1.59	8.69	4.18
	substratum	4.8	4.16	0.08	52	191	0.04	0.22	0.51	0.44
Scirpus - Dicranum	surface	4.2	57.38	1.20	47	260	0.56	1.69	14.73	4.14
	subsurface	4.3	56.27	1.47	38	305	0.17	1.45	9.35	2.74
	substratum	4.7	4.02	0.11	36	220	0.03	0.22	0.21	0.29
Picea - Cladonia	surface	4.2	58.12	0.91	63	137	0.42	1.89	16.14	4.57
	*subsurface	4.9	54.67	1.90	28	375	0.08	0.97	4.23	2.00
	*substratum	5.1	1.50	0.06	25	145	0.02	0.22	0.14	0.19
Picea - Rhododendron	surface	3.9	56.87	1.13	50	131	0.09	1.54	15.66	3.56
	subsurface	4.5	56.75	1.05	54	225	0.11	1.43	8.36	7.73
	substratum	4.9	2.28	0.06	38	307	0.05	0.21	0.43	0.65

+substratum = the mineral soil
*based on a single sample

mer and Sjörs 1955), and because these plants make up the bulk of the peat deposits, there will be little nitrogen available even after decomposition. The main source of nitrogen for bog vegetation comes from atmospheric precipitation (Gorham 1955; Eriksson et al. 1958-1962). The amount of nitrogen concentrated in rainwater is very small. Nitrogen, therefore, may become a severe limiting factor in raised bogs. Bog deciduous species compensate for this deficiency by reabsorbing greater amounts of nitrogen from their leaves prior to leaf fall than do non-bog plants (Small 1972b).

The carbon-nitrogen ratios are all very high, but they usually show a gradual decrease with increasing depth suggesting that some nitrogen is released in the lower layers through decomposition. The high ratios indicate that there is insufficient nitrogen available for microbial activity, and decomposition, therefore, proceeds slowly.

Phosphorus, present in low concentrations, is fairly constant within the same layers in different associations. Within the same association, however, there is always a pronounced increase in phosphorus in the sub-surface layers. This is probably due to leaching. Small amounts of phosphorus are added to the bog through atmospheric precipitation (Gorham 1957b; Sparling 1967). Available phosphorus in raised bogs is usually no greater than 16 ppm (Jasmin and Heeney 1960). Phosphorus, therefore, like nitrogen may become a limiting factor in these bogs.

Ombrogenous bogs, by definition, are removed from a nutrient-enriched water supply that has percolated through or run off the mineral soil. They are entirely dependent on atmospheric precipitation for nutrient supply, and thus enrichment of peat occurs. The peat samples contained concentrations of exchangeable cations up to 34 times as great as those of the underlying mineral substratum.

Magnesium is present in concentrations two to four times those of calcium in peat, while in the mineral substratum these cations occur in a 1:1 ratio. Magnesium is not as abundant in the lowest peat layers where the influence of precipitation decreases. Calcium, on the other hand, shows a slight increase in the lower peat layers. Next to hydrogen, calcium is the most important exchangeable cation and is taken up readily by the plants, thus reducing its availability in the upper layers. As decomposition increases with increasing depth more calcium is released from the plant remains.

Sodium is present in concentrations ranging from three to 17 times those of potassium in the peat. In the mineral substratum sodium occurs in concentrations four to 11 times as great as those of potassium. Both these cations decrease in concentration with increasing depth.

The basic cation concentrations in the peat samples differed from most soils in that both magnesium and sodium were available in large amounts. The usual order of magnitude of the major cations in soils is as follows: Ca ⁓ Mg > K > Na (Malmer and Sjörs 1955; Buckman and Brady 1969). In the analyzed peat samples these cations were available in the following order of abundance: Mg > Ca > Na > K. This change can be explained by the proximity of the Cape Breton Plateau to the sea, and the influence that the latter has in increasing the amounts of dissolved chlorides of magnesium and sodium in rain water. Sea spray, containing these chlorides, is picked up by the wind and transported inland where it becomes deposited on the bogs through precipitation. The details as to how this phenomenon takes place are described by Gorham (1957b). Large waves created by high winds develop foam patches containing numerous bubbles. These bubbles burst and create tiny droplets which are picked up by the wind and act as nuclei for the development of rain drops.

The concentrations of these chlorides in rain water vary with the distance from the sea. Sparling (1967) reports that these electrolytes have been transported over distances of up to 32 km with favorable winds. The bogs in the study area are approximately 19 km from the surrounding sea, well within the range of transport.

The cation imbalance found in the peat samples is strong evidence to suggest that sea spray is an important source of nutrients for the raised bogs of the Cape Breton Plateau. However, the overall nutritional status of the raised bogs is poor, with the low availability of nitrogen and phosphorus probably being important limiting factors. The chemistry of the peat and mineral soil samples does not show a significant difference between the bog associations so that other factors such as water level and topography probably control their distribution.

Climate

The weekly maximum temperatures for the summer of 1970 were lower on the Cape Breton Plateau than those of Cheticamp and Ingonish Beach (Fig 9). The average weekly maximum on the Plateau was 3.5°C cooler than Ingonish Beach and 1.6°C cooler than Cheticamp. The greatest difference in the maximum temperature between the Plateau and Ingonish Beach occurred during the two week period of August 16-29 when the Plateau was 5.6°C cooler, while the greatest difference between the Plateau and Cheticamp occurred during the weeks of August 2-8 and 23-29 when the former was 3.9°C cooler. The highest maximum temperature on the Plateau was recorded on July 26 at 30°C. The warmest weather for the three areas occurred during the week of July 26 to August 1.

The weekly minimum temperatures were also the lowest on the Plateau. Here the average weekly minimum temperature was 4.2°C cooler than Ingonish Beach and 2.9°C cooler than Cheticamp. The greatest difference in the minimum temperature between the Plateau and Ingonish Beach occurred during the week of June 14-20 when the Plateau was 8.8°C cooler, while the greatest difference between the Plateau and Cheticamp occurred during the week of August 2-8 when the former was 5.6°C cooler. The lowest minimum temperature on the Plateau was −0.5°C on June 14.

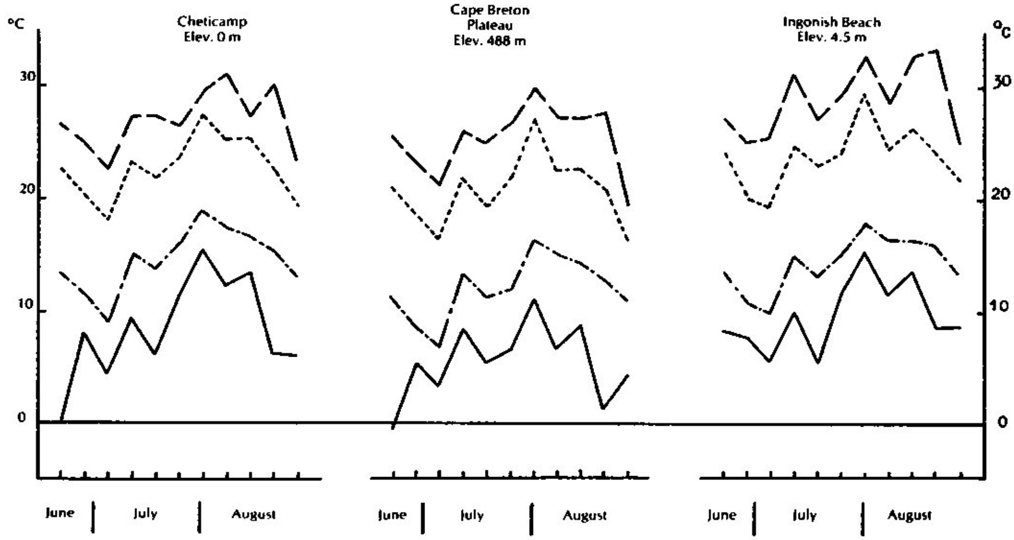
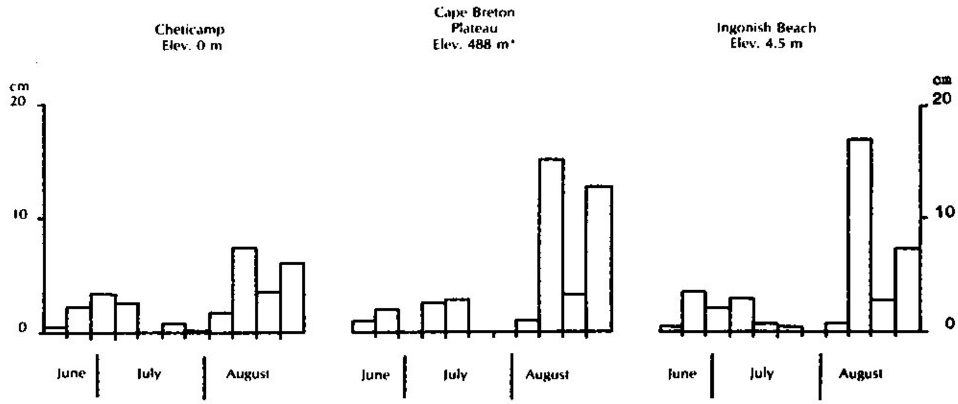


Fig 9. Weekly temperature summaries (June 14 - August 29, 1970) showing maximum (— —), mean maximum (––––), mean minimum (—–––), and minimum (———).



*The total precipitation for the week of August 24-30 on the Plateau is not shown accurately because rain which fell on August 21 was collected with the total for the last week.

Fig 10. Weekly precipitation totals (June 15 - August 30, 1970).

There is no consistent significant difference between the three areas with regard to the daily temperature ranges. Approximately 60% of the summer days on the Plateau had a greater daily temperature range than those at Cheticamp, while only 41% had a greater temperature range than those at Ingonish Beach.

The data show that the Plateau is cooler during the summer than both of the coastal areas. The minimum temperatures appear to be the most critical on the Plateau with possibly only two months of the year being frost free. This may constitute an important limiting factor in the survival and growth of some of the plant species.

During the 77 day observation period 41.12 cm of rain were recorded at the Plateau Station (Fig 10). Ingonish Beach had almost as much rain with 38.53 cm recorded. Cheticamp was the driest site receiving only 28.15 cm. These results are consistent with the long range summaries presented for the two coastal stations in Table I. As the moisture-laden clouds, moving from west to east, reach the Plateau, the storm systems rise to higher elevations where cooler air temperatures prevail. This probably results in condensation, giving the region east of Cheticamp larger amounts of rainfall.

In all three areas August was the wettest month, accounting for 79% of the total summer's precipitation on the Plateau, 72% for Ingonish Beach, and 67% for Cheticamp. The average weekly rainfall for the summer period was 3.73 cm on the Plateau. This was the highest for the three areas with Ingonish Beach having an average of 3.50 cm, and Cheticamp only 2.55 cm. The largest amount of precipitation for a one week period was recorded during August 10-16, at all three stations. The Plateau received 15.27 cm, Ingonish Beach 17.12 cm, and Cheticamp only 7.59 cm. The largest amount of rainfall over a 24 hour period occurred in all three areas on August 12. The heaviest precipitation was recorded at Ingonish Beach at 14.37 cm, while Cheticamp had the least amount at 3.96 cm. On the Plateau 8.58 cm fell over the 24 hour period, with 5.09 cm of this total amount falling between 1045 hrs and 1745 hrs. These "cloudbursts" may aid in the erosion of a bog's surface. A large amount of runoff water results from heavy rainfall. This water creates small channels which may grow to become large erosional gullies. The exposed peat in these gullies remains in a very unstable condition until a vegetation cover can be re-established.

The results from the precipitation data indicate that the Plateau was slightly wetter than Ingonish Beach during the summer months of 1970, and that both of these areas were approximately one and a half times wetter than Cheticamp.

Precipitation data for Ingonish Beach, based on a 30 year period, show the rainfall to be abundant and evenly distributed throughout the year. The present study revealed that for the summer months the Plateau approximated Ingonish Beach in total precipitation. If this similarity in the precipitation data between the two areas extends throughout the entire year, then the long range summaries available for Ingonish Beach could be used to describe the conditions on the Plateau.

Spot readings of relative humidity were made at one of the bogs from June 18 to July 11, between 0830 hrs and 1830 hrs. Based on a total of 18 readings, the average relative humidity was 62.5%, ranging from a maximum of 100% to a minimum of 18%. Readings made in the morning showed a slightly higher average relative humidity than those made in the afternoon, 65.5% compared with 59.4%. It is not uncommon to have relative humidities in the range of 100% as low-lying cloud banks often rest upon the summit of the Cape Breton Plateau. However, humidity determinations were not made when these conditions prevailed.

Wind data were recorded from June 14 to August 30. The average wind velocity during daylight hours, based on 40 readings, was 15.9 km/hr, with the maximum velocity recorded on June 19 at 28.9 km/hr. The average velocity during the mornings was 13.3 km/hr, as compared with an afternoon average of 18.9 km/hr. Wind gusts were reported up to 40.2 km/hr. The average wind velocity for the 78 day period was 12.1 km/hr based on the total kilometers of wind recorded (22631.6). Thus, there is a difference in wind velocity of 3.82 km/hr between the average for daylight hours and that for the total summer period, indicating that nocturnal wind velocities are lower than those recorded during the daytime.

Observations on wind direction showed that the wind blew mainly from the southwest and west. This is in agreement with Putnam (1940) who reported the direction of the prevailing winds in the region to be mainly from the northwest and west during the winter months, and from the southwest and west during summer.

During the period spent in the study area there were 25 days of sunshine, 23 days completely overcast during daylight hours, and 17 days partially overcast with sunny intervals. July had the most days of total sunshine (11), while August had the most completely overcast days (12).

The climatic features discussed become important when they are related to the widespread occurrence of raised bogs on the Cape Breton Plateau. Precipitation is in excess of amounts considered minimum for raised bog development, i.e., greater than 100 cm/year (Gorham 1957a). Even when it is not raining, a damp climatic condition will be maintained on the Plateau by the frequent occurrence of low-lying clouds causing high relative humidities.

Perhaps more significant is the fact that the Plateau is cooler than the coastal areas, having lower minimum temperatures. Conditions, therefore, become favorable for rapid peat accumulation on the bogs as low temperatures cause a reduction in evaporation and decomposition of the peat.

The climatic data indicate that the Plateau can be considered a distinct climatic region based on its cooler temperatures and abundant precipitation. This agrees with Putnam's (1940) classification of the area as the "Cape Breton Highlands" Climatic Region. This region corresponds to what Nichols (1918) called the "Northeastern Evergreen Coniferous Forest Formation" of the Plateau, in his vegetational study of Northern Cape Breton, and is also closely related to Loucks' (1960) "Cape Breton Plateau Ecoregion".

Discussion

There are four dynamic processes occurring in the raised bogs of the Cape Breton Plateau, namely, bog development, cyclic succession, erosion, and regeneration (Fig 11, 12).

Bog Development

The successional sequence for bog development probably begins on a gently undulating rocky substratum containing slight ridges and shallow depressions (Nichols 1918). The pioneer vegetation on the drier raised parts may consist of a thin covering of lichens and bryophytes. In the damper depressions *Sphagnum* may become established. As the layer of peat begins to accumulate, the surface vegetation of the depressions spreads laterally and coalesces, covering the slightly higher ridges.

The accumulation of organic matter produces a habitat that can support *Scirpus cespitosus*. Once this species becomes established the bog begins to develop. A layer of extremely compact sedge peat is deposited and impedes drainage. In this way the sub-hygric *Scirpus cespitosus - Dicranum leioneuron* Association is established (Fig 6). It approximates what Nichols (1918) called the "bog meadow association-type".

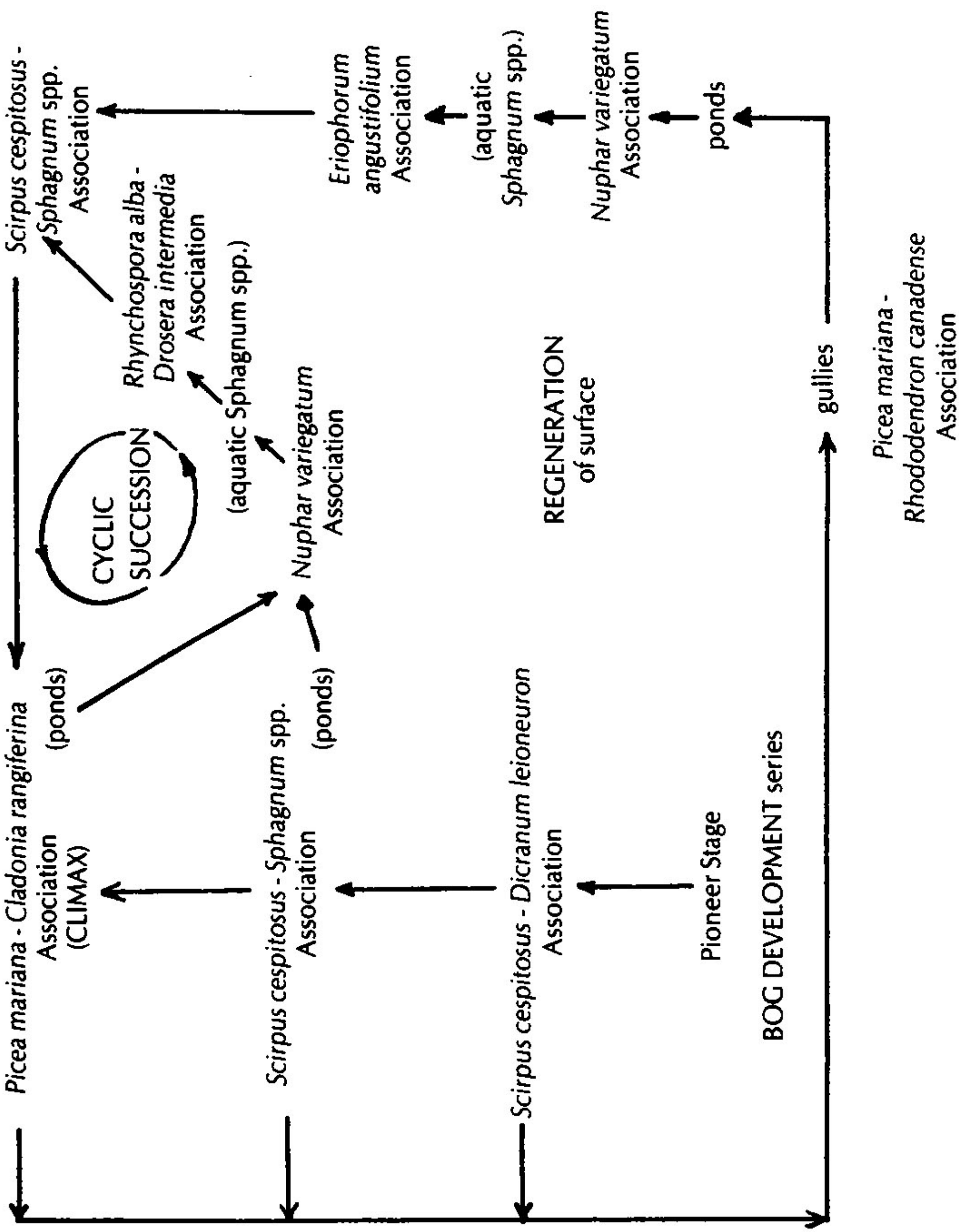


Fig 11. Successional relationships of raised bog associations.

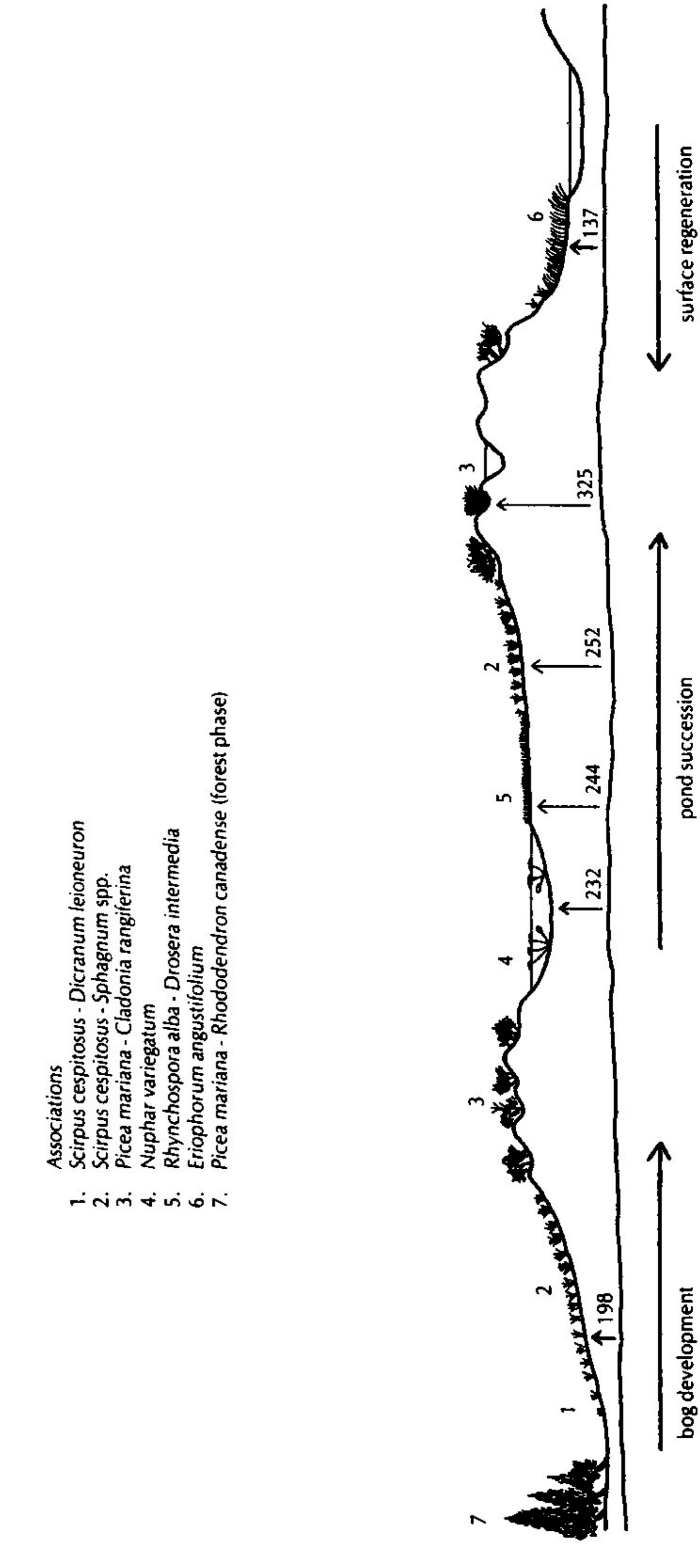


Fig 12. Topographic sequence of raised bog associations. Maximum recorded peat depths in centimeters are given under each association.

In well developed bogs the *Scirpus cespitosus - Dicranum leioneuron* Association occurs around the outer edges, sometimes covering extensive areas. This Association determines the size of a bog through its expansion into forested areas. Dwarf trees bordering a bog are subjected to severe winds which often cause small openings. Once the area is exposed to light it enables the shade intolerant *Sphagnum* and *Scirpus cespitosus* to become established. This in turn impedes the drainage causing further destruction of the forest and bog advancement. This process appears to be operative at different locations around the perimeter of bogs resulting in an irregular borderline.

The compact peat underlying the *Scirpus cespitosus - Dicranum leioneuron* Association is usually shallow (Fig 13) and has a low water holding capacity. Here, most of the precipitation is removed by runoff. As a result, surface conditions are relatively dry and a diverse vascular flora is supported. Damper conditions prevail only in the shallow depressions producing sites for the growth of *Sphagnum. S. tenellum* is one of the first plants to colonize. It is an erect slender species usually occurring in dense, loose masses and forming low lying mats. Successionally, it is soon followed by cushion-forming *S. capillaceum* var. *tenellum, S. magellanicum,* and to a lesser extent *S. pulchrum.* Once these are established the bog undergoes some important changes.

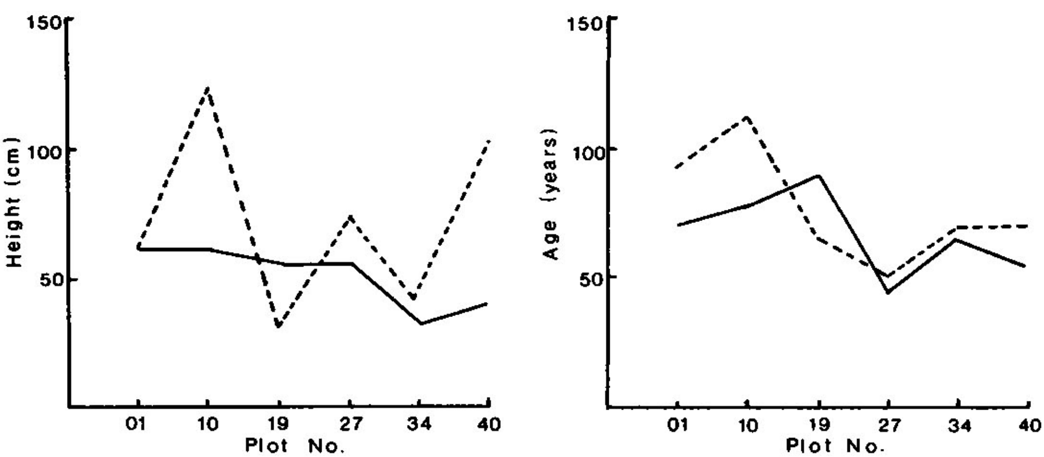


Fig 13. Height and age of dwarf *Larix laricina* (- - -) and *Picea mariana* (——) trees in the *Picea mariana - Cladonia rangiferina* Association. The data are based on one representative individual from each plot.

The new peat deposited becomes waterlogged which causes a restriction of air circulation and a depletion of the oxygen supply (Pearsall 1938; Armstrong and Boatman 1967). As a result the soil condition becomes anaerobic and dead plant remains decompose slowly. At this stage of development the peat accumulation is greatly accelerated and the *Scirpus cespitosus - Dicranum leioneuron* Association advances successionally to the hygric *Scirpus cespitosus - Sphagnum* spp. Association (Fig 5). This Association is similar to what Nichols (1918) called the "wet bog association-type". All vascular plants found in this Association are also present in the *Scirpus cespitosus - Dicranum leioneuron* Association. However, only half as many occur. This may be a result of the wetter surface conditions maintained by the abundance of cushion-forming *Sphagnum*. These species are robust, erect and rather rigid, forming dense widespread colonies. *S. magellanicum* and *S. papillosum* are the most important species, and are the most rapid peat-formers of all bog plants.

The six *Sphagnum* present in the *Scirpus cespitosus - Sphagnum* spp. Association (Table IV) have different growth rates and as a result the surface soon acquires an uneven topography of mounds and hollows. As the mounds are being built up there is a corresponding rise in the water table. Some mounds eventually coalesce and form ridges enclosing shallow depressions. The latter become filled with water and create bog ponds. The ridges are built higher by *Sphagnum*, strengthened by vascular plant remains and eventually become effective dams. With the underlying sedge peat impervious to drainage and the surrounding ridges maintaining the water table near the surface, the ponds become a permanent feature of the bog.

The bog surface is continuously raised by the growth of *Sphagnum* mounds until, eventually, it is above the water level of the ponds and is no longer influenced by seepage from them. At this stage drier surface conditions prevail and *S. capillaceum* var. *tenellum* becomes established followed by *S. fuscum*. These mesophytic species are erect, usually slender, and form very dense compact colonies. They replace the robust cushion-formers of the *Scirpus cespitosus - Sphagnum* spp. Association. As a result of this change in the bryophyte flora the bog advances to the mesic *Picea mariana - Cladonia rangiferina* Association (Fig 7). It can be regarded as the climax stage of bog development. This is equivalent to what Nichols (1918) called the "dry bog association-type".

In the earliest stages of this Association there is an increase in the number of vascular plants due to the mesophytic conditions that prevail. Dwarf trees of *Larix laricina* and *Picea mariana* become established. Age determinations and density data suggest that *Larix* is the first to colonize. Data based on representative individuals showed that this species, in every plot except one, was older than *Picea* by an average of about ten years. In one of the bogs a careful count of the dwarf trees showed a total of 54 individuals of *Larix* and only three of *Picea* per 100 sq. m.

Most of the woody plants reproduce vegetatively by layering. This is the prevalent mode of growth in the dwarf trees, especially in *Picea*. Hummocks are a distinguishing topographic feature of the *Picea mariana - Cladonia rangiferina* Association. Their growth is dependent on the combined presence of *Sphagnum* and woody vascular plants. The stems and branches of the woody species provide a framework which facilitates the upward growth of *Sphagnum* and gives a greater degree of firmness to the developing hummocks. *Picea* is the major vascular plant involved in hummock building. Once established, its upward growth corresponds with the upward growth of the hummocks. *Picea* branches are buried by *Sphagnum*, but through layering, branchtips turn upward and continue to grow above the surface. This forms characteristic *Picea* hummocks.

A common feature of these hummocks is the effect wind has on their development. Careful examination showed that at the windward end there were numerous dead branches, while on the leeward side actively growing branches occurred. Wind blowing almost continuously from the southwest causes the hummocks to become elongated in a southwest to northeast direction.

The continued upward growth of the hummocks results in further drying of the surface so that eventually *Sphagnum* is replaced by numerous lichens, especially *Cladonia rangiferina* and *C. alpestris*. Once the lichens are well established upward growth of the hummocks slows down. Evidence of the relative stability of the surface is suggested by the ages of the dwarf trees, some of which exceed 90 years.

The ponds formed in the *Scirpus cespitosus* - *Sphagnum* spp. Association are still present in the *Picea mariana* - *Cladonia rangiferina* Association. In addition new ponds are developed because of hummock growth. Older hummocks become senescent and are soon overtopped by younger actively growing ones. This results in the drainage restriction of older hummocks and surface accumulation of water. The numerous surface ponds are an important feature of the climax *Picea mariana* - *Cladonia rangiferina* Association.

The shape of the bog ponds is influenced by the topography of the bog. Flat bog surfaces lack orientation of relief features and contain ponds that have irregular or rounded shapes. On the other hand, convex bog surfaces have ridges and depressions formed at right angles to the slope. Elongated ponds, with steep downslope banks, are present in the depressions and often arranged in a step-like series. This type of alignment of ridge and depressional areas may be possibly the result of either "pressure-folding" (Pearsall 1956) or the nature of the drainage pattern affecting the bog (Boatman and Tomlinson 1973). It is possible also that the alignment may result from the tendency of the looser, saturated *Sphagnum* peat to creep over the more compact sedge peat. Often, active lateral seepage was observed at the base of the *Sphagnum* peat where it overlies the sedge peat.

Erosional forces can also change the shape of ponds, especially where the water level is almost flush with the surrounding bog. The surface of these ponds is subjected to continuous wind, blowing in a fairly constant direction. This produces small waves which scour the banks on one side of the pond resulting in expansion through erosion. Sometimes small ponds, located close together and at the same elevation, coalesce by erosion, thus creating a large single pond with a very irregular outline. In this process islands and small peninsulas are formed.

The water level in the bog ponds is controlled mainly by evaporation and precipitation. The ponds were never desiccated but the water level sometimes fluctuated markedly. Following periods of heavy and continuous rain the water level in some ponds was observed to increase as much as 15 cm.

Ponds are often found at different elevations in the same section of a bog. One of the ponds in which a plot was located, is in the middle of a series of ponds arranged in a step-like pattern. Its water level was approximately 76 cm higher than the water level in a pond only nine meters away. In another location, two ponds approximately three meters apart had a difference in water level of 106 cm. This marked change in the pond elevations demonstrates the water holding capacity of *Sphagnum* banks.

Cyclic Succession

In the ponds, a cyclic succession occurs resulting in a continued upward growth of the bog surface (Fig 11 and 12). The initial phase of the cycle involves the establishment of the *Nuphar variegatum* Association (Fig 2). The first plants to colonize are species of algae, which are found along the pond bottoms and edges. They are followed by *Nuphar variegatum* and *Eriocaulon septangulare*. These plants grow mainly in the deeper parts of the pond away from the surrounding banks. There is little change occurring in the Association until the aquatic *Sphagnum* become established. Once species like *S. cuspidatum* start to grow profusely around the edges, the filling-in process becomes greatly accelerated. Only in ponds of very small surface area was the *Sphagnum* cover complete. In the larger ponds there is greater exposure to the wind which appears to slow down the advancement of *Sphagnum* from the pond's edge. Here, shrub species have branches extending into the ponds which provide a framework supporting the aquatic *Sphagnum*. This results in the formation of vegetation mats, enabling *S. pulchrum* to become established on the surface.

These mats sometimes break loose and sink, accelerating the filling-in process. Some mats contain entrapped air enabling them to float freely or only become partly submerged. Air trapped in the peat underlying the ponds was demonstrated during depth determinations. When the sampler was removed, a steady stream of bubbles was often released.

Through the combined processes of sedimentation and the growth of vegetation mats the underlying peat is built up to the surface and eventually exposed. This exposed muck becomes the habitat in which the *Rhynchospora alba - Drosera intermedia* Association is established (Fig 4). This is equivalent to what Nichols (1918) termed the "muck mat".

Initially the surface remains semi-aquatic because of fluctuating water levels. The stabilization and consolidation of the muck is brought about by the growth and spread of a vegetation mat which provides a base upon which more mesophytic communities develop. The mat is firm, yet flexible, and when walked upon the surface quakes.

Among the first species to be established are *Cladopodiella fluitans* and *Utricularia cornuta*, the latter helping to stabilize the muck by binding together the loose peat through its extensive system of underground rhizomes. A firmer crust is produced through desiccation once the surface is continually exposed. On this crust *Drosera intermedia* is established followed by *Rhynchospora alba*. The latter species and the liverwort *Cladopodiella* eventually cover most of the mat.

The surface is not built up during this stage of succession and each community still retains the general outline of the former pond. After heavy rains the surface is inundated often to a depth of several centimeters. The only new *Sphagnum* established is *S. pulchrum*. The Association, therefore, occupies a unique position because of its paucity of *Sphagnum*. Apparently it is not wet enough to permit a greater intrusion of the aquatic *Sphagnum*, while on the other hand, it is still too wet to allow for the establishment of the cushion-forming species (Table XI).

Continuous organic matter deposition elevates the surface of the muck mat until it is no longer inundated. When this happens, the mat becomes populated by cushion-forming *Sphagnum*. The important vascular plants of the *Rhynchospora alba - Drosera intermedia* Association are replaced by *Scirpus cespitosus* and *Carex exilis*. This results in the successional advancement to the *Scirpus cespitosus - Sphagnum* spp. Association. This in turn is succeeded by the *Picea mariana - Cladonia rangiferina* Association in which new ponds may be formed thus completing the cycle.

Bog Erosion (Fig 11)

While the bogs are being continually built up through peat accumulation, wind and water erosion alter the surface. The vegetation covering a bog's surface has an important ecological function as a protective blanket, preventing the underlying peat from becoming desiccated. When this protection is removed, the surface peat will erode. Wind can loosen and remove dried out surface particles. Once this happens heavy runoff will create small erosional channels which can eventually expand to become gullies. Raised bogs, because of their slopes, are quite susceptible to gully erosion. Some gullies probably originate through subterranean channelling. Overlying peat layers are undermined and collapse creating an open gully. These gullies serve as drainage channels.

The banks of the gullies become stabilized by species like *Scirpus cespitosus* causing gully erosion to cease. Once this happens, the submesic *Picea mariana - Rhododendron canadense* Association comes into existence (Fig 8). This Association is actually an extension into the bogs, via the drainage gullies, of an Association of the same name that surrounds the bogs. The bog phase of this Association has a very important ecological function as it completely stabilizes the gully, thus preventing further erosion.

A greater degree of protection is provided to plants growing in the gullies where the slopes and bottom are situated at much lower elevations than the surrounding bog. Thus, woody species are able to grow at a faster rate and attain greater heights than their counterparts on the exposed bog. The most striking example of this is seen in the different growth habits of *Picea mariana*. In the *Picea mariana - Cladonia rangiferina* Association one of these dwarf trees had a height of 61 cm and was aged at 77 years, while a *Picea* located in a drainage gully in the same bog had a height of 229 cm and an age of 65 years. The ages of the dwarf trees in the *Picea mariana - Rhododendron canadense* Association also reflect the stable nature of this community. A dwarfed *Picea* taken from one plot was aged at 139 years while that taken from another was approximately 144 years old.

Once the *Picea mariana - Rhododendron canadense* Association is well established in the gullies, shade-intolerant species, like *Sphagnum* and *Scirpus cespitosus*, are practically eliminated. Thus without the presence of cushion-forming *Sphagnum* there is little upward growth of the surface occurring.

Water movement in most drainage gullies is only noticeable after periods of rain. In the streams water varies from a few centimeters to over 40 cm in depth and usually overlies peat. Occasionally, however, the stream has eroded to the mineral substratum. When these streams are blocked, either through sedimentation or slumping, extensive flooding results. This causes the surrounding banks to be eroded and the vegetation cover is destroyed. Flooding may remove most of the eroded peat leaving behind only a shallow pond often lying on top of the mineral substratum.

These ponds belong to the drainage gully system as they receive water from undisturbed parts of the gully. They differ from the raised surface ponds by having drainage. The water level, therefore, fluctuates and the ponds vary from almost dry to completely flooded conditions. The water level recedes quickly following heavy rains. This was demonstrated from observations carried out over a period of 48 hours. Measurements were taken 24 hours apart in a depression which is usually exposed. The initial measurement showed a water depth of 21.6 cm, the second a depth of 19.0 cm, the third 3.8 cm. This decrease of 17.8 cm in water level illustrates the rapid and continuous drainage of the depression ponds.

Bog Regeneration

The regeneration of the bog surface begins when depressional ponds gradually become filled in through the continued influx of drainage water carrying organic sediments. Eventually conditions will become favorable for the establishment of the *Nuphar variegatum* Association. As the filling in process usually proceeds from the edges towards the center of these ponds, *Nuphar variegatum* becomes confined to a deep channel that dissects the depression.

Pond filling is aided by the presence of *Sphagnum cuspidatum*. Continued deposition finally results in the exposure of organic sediments above the surface. At this point the peat depth may vary from 89 cm to 137 cm. On the newly exposed peat *Utricularia cornuta, Drosera intermedia* and occasionally *Rhynchospora alba* become established. However, none of these plants ever become dominant here as they do in the raised sections of the bog. This may be due to the large fluctuations in the water level that still occur.

The stabilization of the mucky peat is dependent on the development of the *Eriophorum angustifolium* Association (Fig 3). *Eriophorum angustifolium* thrives best when partially submerged. Species like *Sphagnum cuspidatum* and *S. papillosum* aid in slowly building up the surface until it becomes suitable for the establishment of *Scirpus cespitosus.* As a result of these changes the *Scirpus cespitosus - Sphagnum* spp. Association is formed. Through continual upbuilding it is eventually replaced by the climax *Picea mariana - Cladonia rangiferina* Association, thus completing the regeneration of the bog surface (Fig 11 and 12).

Buried Wood Fragments and Peat Depth

Strong evidence in support of the continuous cycling of associations comes from the discovery of buried coniferous wood fragments. These were found beneath most of the associations. Out of 40 peat pits, 25 contained wood fragments, located at depths ranging from 31 cm to 180 cm. The wood was usually confined to a single level in each pit. In most cases the wood was well preserved and some samples still had bark present. The fragments were of various sizes and shapes, the largest being approximately 40 cm in length and from six to eight centimeters in diameter.

This evidence indicates that the *Picea mariana - Cladonia rangiferina* and the *Picea mariana - Rhododendron canadense* Associations existed earlier in the bog's history, as coniferous species occur only in these associations. Then through cyclic succession and regeneration the associations became submerged and with time eventually developed again on the bog's surface.

The depth of peat underlying each association can be correlated with the successional sequences occurring within the bog (Fig 14). Early pioneer stages, like the *Scirpus cespitosus - Dicranum leioneuron* and the *Eriophorum angustifolium* Associations, have the shallowest peat depths. In the former, occurring at the bog's edge, the thinnest peat deposits are found in those areas where lateral bog expansion has just recently taken place. In the latter Association, occurring in depressional areas, peat depth is determined by the amount of erosion or sedimentation that has taken place. Shallow peat depths also occur in the drainage gullies that dissect the bog's surface. The depth of peat underlying the *Picea mariana - Rhododendron canadense* Association varies a great deal as illustrated in Fig 8.

In the raised sections of a bog there is usually an increase in peat depth from the wettest to the driest associations, i.e., from the *Nuphar variegatum* to the *Picea mariana - Cladonia rangiferina,* reflecting a build-up of the bog's surface. Maximum peat depths are found in the oldest sections of a bog, provided that erosion has not altered the surface. In mature raised bogs, with a convex surface, the oldest sections occur at the center. In moving from the center towards the edges both peat depth and age decrease.

Successional Variations

The successional relationships of the bog associations are varied and complex and they do not always follow exactly the patterns previously discussed. Two variations occurred in the successional sequences which require brief descriptions.

The first occurs in the successional sequence that follows the *Scirpus cespitosus - Dicranum leioneuron* Association located at the bog's edge. This Association usually is succeeded by the wetter *Scirpus cespitosus - Sphagnum* spp. Association with its robust cushion-forming *Sphagnum.* In several locations it was observed that the former Association appears to be succeeded directly by an early phase of the *Picea mariana - Cladonia rangiferina* Association, bypassing the *Scirpus cespitosus - Sphagnum* spp. Association. The successional sequence which is followed is

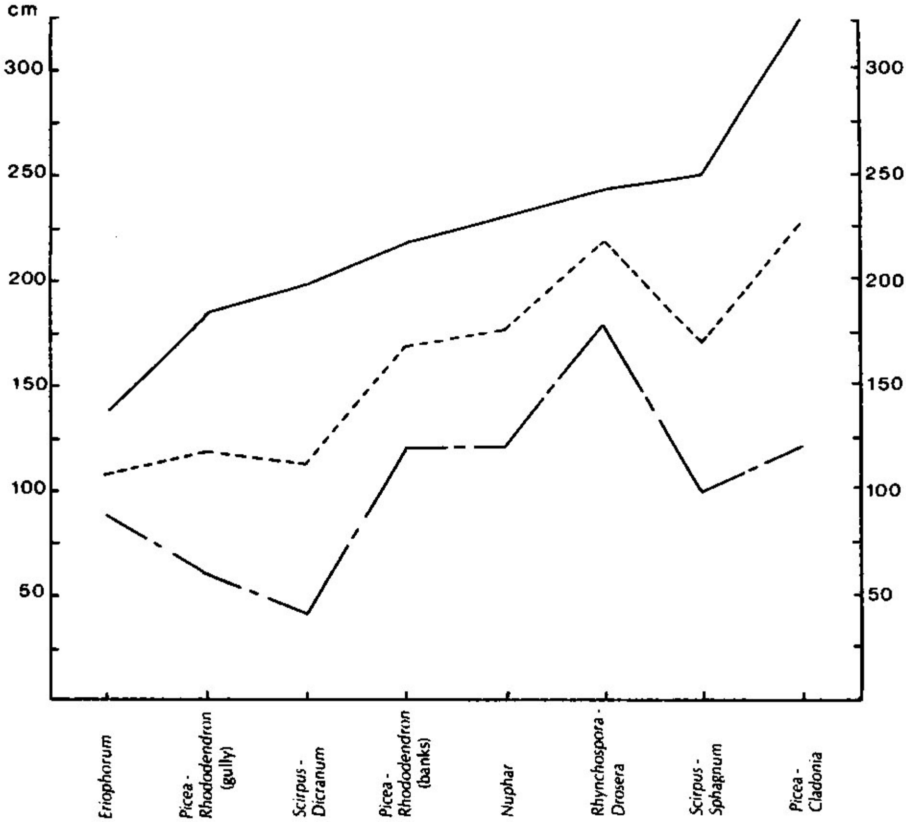


Fig 14. Peat depths for the bog associations showing maximum (——), average (- - -), and minimum (—·—).

probably dependent on the surface moisture status of the *Scirpus cespitosus - Dicranum leioneuron* Association. If the surface is too dry for the abundant growth of the hygric cushion-forming *Sphagnum,* then the mesic cushion-formers, such as *S. capillaceum* var. *tenellum* and *S. fuscum,* may become dominant and develop into small hummocks which are able to support dwarf trees and lichens.

The other variation occurs in the successional sequence that follows the *Nuphar variegatum* Association. This Association is normally succeeded by the *Rhynchospora alba - Drosera intermedia* Association in the raised bog sections, and by the *Eriophorum angustifolium* Association in the depressional areas. In some cases the filled-in pond appears to have proceeded directly to an early phase of the *Scirpus cespitosus - Sphagnum* spp. Association without going through either of the two Associations mentioned. The new Association still retains the outline of the old ponds. Here aquatic *Sphagnum,* such as *S. cuspidatum,* must have been largely responsible for filling in the pond with organic matter. As the water becomes shallow they would continue to thrive just beneath the surface while the semi-aquatic *S. pulchrum* would be established at the surface and soon dominate the emergent vegetation. This species would be able to build up the surface so that the hygric cushion-forming *Sphagnum* could become established.

Whether the regular successional processes or their variations predominate, raised bogs must be regarded as dynamic self-sustaining units whose survival is dependent on abundant atmospheric precipitation and cool temperatures. As long as these conditions remain constant the bogs will continue to grow.

Table X Ecological amplitudes of the vasular flora of raised bogs based on moisture tolerances as indicated by the average species significance values of each plant in the different associations. Sporadics are shown by the letter "S".

Species	*Nuphar*	*Eriophorum*	*Rynchospora-Drosera*	*Scirpus-Sphagnum*	*Scirpus-Dicranum*	*Picea-Cladonia*		*Picea-Rhododendron*		
	hydric ◄									► submesic
Eriocaulon septangulare	1.5	-	-	-	-	.*	-	.**	.*	-
Nuphar variegatum	3.8	0.4	-	-	-	-	-	-	-	-
Utricularia geminiscapa	-	0.2	-	-	-	-	-	-	-	-
Cares aquatilis	-	S	-	-	-	-	-	-	-	-
Utricularia cornuta	-	2.0	1.5	-	-	-	-	-	-	-
Drosera intermedia	-	1.6	2.6	-	-	-	-	-	-	-
Vaccinium macrocarpon	-	S	1.1	S	-	-	-	-	-	-
Rhynchospora alba	-	2.4	6.6	-	S	-	-	-	-	-
Drosera rotundifolia	-	0.6	0.3	2.1	1.0	-	1.5	-	-	-
Vaccinium oxycoccos	-	S	0.3	2.5	1.8	-	1.5	-	-	-
Eriophorum angustifolium	-	7.2	1.1	1.0	1.5	-	1.1	-	-	1.1
Carex exilis	-	S	S	1.6	2.1	-	S	-	-	S
Kalmia polifolia	-	0.2	0.3	2.6	2.8	0.6	2.8	-	0.6	2.0
Andromeda glaucophylla	-	-	0.8	3.1	2.5	-	0.5	-	-	0.5
Sarracenia purpurea	-	-	0.1	0.6	1.6	-	1.0	-	-	0.6
Chamaedaphne calyculata	-	-	0.3	3.5	3.0	0.8	3.0	-	S	S
Calamagrostis pickeringii	-	-	S	-	1.5	-	1.3	-	-	1.1
Eriophorum spissum	-	-	-	0.5	S	-	0.5	-	-	-
Scirpus cespitosus	-	-	-	4.3	5.3	-	3.1	-	-	0.6
Kalmia angustifolia	-	-	-	0.3	1.1	0.6	3.5	-	0.8	1.8
Ledum groenlandicum	-	-	-	0.3	1.3	0.8	3.3	-	1.1	2.0
Schizaea pusilla	-	-	-	-	S	-	0.5	-	-	-
Aster nemoralis	-	-	-	-	S	-	-	-	-	S
Solidago uliginosa	-	-	-	-	2.1	-	1.1	-	-	0.3
Empetrum nigrum	-	-	-	-	0.6	-	3.0	-	-	0.5
Aronia prunifolia	-	-	-	-	2.8	S	2.3	-	1.0	1.8
Vaccinium boreale	-	-	-	-	1.0	-	1.6	-	-	1.8
Coptis trifolia	-	-	-	-	1.3	-	1.3	-	-	1.8
Trientalis borealis	-	-	-	-	1.1	-	1.1	-	-	1.1
Maianthemum canadense	-	-	-	-	0.8	-	0.6	-	-	1.0
Juniperus communis	-	-	-	-	-	-	0.8	-	-	-
Rubus chamaemorus	-	-	-	-	-	-	2.6	-	-	1.5
Deschampsia flexuosa	-	-	-	-	-	-	0.6	-	-	0.5
Vaccinium angustifolium	-	-	-	-	-	0.5	2.0	-	1.1	1.8
Melampyrum lineare	-	-	-	-	-	-	0.8	-	-	1.3
Larix laricina	-	-	-	-	-	1.1	1.0	+ , +	1.0	S
Geocaulon lividum	-	-	-	-	-	-	0.5	-	-	0.3
Rhododendron canadense	-	-	-	-	-	1.1	2.1	-	2.8	4.1
Picea mariana	-	-	S	-	-	3.5	4.3	3.3	5.8	1.1
Gaultheria hispidula	-	-	-	-	-	-	0.3	-	-	1.1
Epigaea repens	-	-	-	-	-	-	S	-	-	1.5
Cornus canadensis	-	-	-	-	-	-	1.8	-	-	2.8
Amelanchier bartramiana	-	-	-	-	-	-	S	-	4.5	0.6
Nemopanthus mucronata	-	-	-	-	-	-	S	-	2.3	S
Abies balsamea	-	-	-	-	-	-	S	0.3	0.3	0.5
Myrica gale	-	-	-	-	-	-	-	-	1.1	1.3
Viburnum cassinoides	-	-	-	-	-	-	-	-	1.0	-
Carex oligosperma	-	-	-	-	-	-	-	-	-	0.3
Linnaea borealis	-	-	-	-	-	-	-	-	-	0.5
Taxus canadensis	-	-	-	-	-	-	-	-	0.3	0.6
Carex trisperma	-	-	-	-	-	-	-	-	-	0.6
Betula papyrifera	-	-	-	-	-	-	-	-	S	-
Sorbus decora	-	-	-	-	-	-	-	-	S	-
Clintonia borealis	-	-	-	-	-	-	-	-	-	3.0
Totals: 54	2	12	14	13	23		36			41
Relative presence (%)	4	22	26	24	43		67			76

Note: Each column represents the C layer (herb and dwarf shrub) except for those columns designated by a single asterisk (*), representing the B_2 sublayer (low shrub), and that designated by two asterisks (**) representing the B_1 sublayer (high shrub).

Ecological Amplitudes of Bog Species

The distribution of bog species appears to be dependent on moisture requirements and topographic position (Table X and XI). Bog species can be placed in two groups according to their apparent tolerance to water.

Species with Narrow Moisture Tolerances

There are very few completely aquatic species. Included here are the vascular plants, *Eriocaulon septangulare* and *Nuphar variegatum,* the only species other than algae found in the *Nuphar variegatum* Association. *Nuphar* is also found in

Table XI Ecological amplitudes of the bryophytes and lichens of raised bogs based on moisture tolerances as indicated by the average species significance values for each plant in the different associations. Sporadics are shown by the letter "S".

Species	*Nuphar*	*Eriophorum*	*Rhynchospora-Drosera*	*Scirpus-Sphagnum*	*Scirpus-Dicranum*	*Picea-Cladonia*	*Picea-Rhododendron*
	hydric ◄						► submesic
Sphenolobus minutus	-	S	-	-	-	-	-
Sphagnum recurvum	-	S	-	-	-	-	-
Sphagnum cuspidatum	-	4.6	3.6	-	-	-	-
Cladopodiella fluitans	-	3.2	8.6	-	-	-	-
Sphagnum papillosum	-	2.2	-	1.6	S	-	-
Gymnocolea inflata	-	1.2	-	0.6	0.5	S	-
Sphagnum pulchrum	-	S	3.6	0.6	0.5	0.3	-
Drepanocladus revolvens	-	-	S	-	-	-	-
Orthocaulis gracilis	-	-	S	2.3	1.6	1.3	S
Sphagnum magellanicum	-	-	-	3.3	2.5	-	-
Sphagnum tenellum	-	-	-	4.8	2.8	0.8	-
Sphagnum capillaceum var. tenellum	-		-	3.3	3.0	1.1	-
Ochrolechia frigida	-	-	-	0.5	0.3	0.3	-
Cetraria islandica ssp. crispa	-	-	-	0.3	S	S	-
Dicranum leioneuron	-	-	-	3.1	5.5	0.6	-
Cetraria islandica	-	-	-	0.3	1.1	1.3	-
Sphagnum fuscum	-	-	-	1.3	1.0	4.0	-
Cladonia pleurota	-	-	-	0.6	0.8	1.5	0.8
Cladonia rangiferina	-	-	-	0.3	1.6	5.6	1.3
Dicranum undulatum	-	-	-	S	1.1	1.8	S
Ptilidium ciliare	-	-	-	S	0.6	2.5	2.1
Cladonia uncialis	-	-	-	-	0.3	1.5	-
Mylia anomala	-	-	-	-	S	S	-
Microlepidozia setacea	-	-	-	-	S	0.6	-
Cladonia alpestris	-	-	-	-	S	4.1	-
Pleurozium schreberi	-	-	-	-	0.6	4.5	4.8
Cladonia pseudorangiformis	-	-	-	-	S	0.3	0.5
Rhacomitrium lanuginosum	-	-	-	-	-	1.0	-
Cephalozia bicuspidata	-	-	-	-	-	0.5	-
Sphagnum capillaceum	-	-	-	-	-	0.3	-
Cladonia arbuscula	-	-	-	-	-	S	-
Cladonia crispata	-	-	-	-	-	S	S
Cladonia mitis	-	-	-	-	-	S	S
Dicranum polysetum	-	-	-	-	-	S	S
Ptilium crista-castrensis	-	-	-	-	-	0.6	0.3
Cladonia gracilis	-	-	-	-	-	0.8	0.8
Hylocomium splendens	-	-	-	-	-	2.1	3.0
Cladonia squamosa	-	-	-	-	-	S	0.5
Dicranum scoparium	-	-	-	-	-	-	2.8
Dicranum fuscescens	-	-	-	-	-	-	1.3
Sphagnum subsecundum	-	-	-	-	-	-	1.1
Sphagnum palustre	-	-	-	-	-	-	0.8
Leucobryum glaucum	-	-	-	-	-	-	0.3
Totals: 43	0	7	5	16	22	31	19
Relative presence (%)	0	16	12	37	51	72	44

Note: each column represents the D layer (bryophytes and lichens).

the *Eriophorum angustifolium* Association, but it only grows in those areas that are continually submerged. The most important aquatic species in bog development is *Sphagnum cuspidatum*. It grows abundantly around the edges of ponds and accelerates the filling-in process.

Species confined to habitats that are very wet but not continally submerged include *Utricularia cornuta, Drosera intermedia, Rhynchospora alba,* and *Cladopodiella fluitans.* All of these species are important in consolidating the loose peat of the *Rhynchospora alba - Drosera intermedia* Association.

Species confined to the driest sections of a bog are numerous. Some are of forest affinity and only occur in the *Picea mariana - Rhododendron canadense* Association of the drainage gullies, none of which are very important to bog development. The most important species in the driest sections are *Picea mariana, Rhododendron canadense,* and *Cladonia alpestris.* The first two are very important in stabilizing the banks of the drainage gullies. *Picea* is also important in the hummock stage of bog development, where together with *Cladonia* they constitute a dominant part of the vegetation cover.

Species With Wide Moisture Tolerances

Species with a wider tolerance to moisture conditions but occurring only in continually exposed areas, include *Scirpus cespitosus, Sphagnum magellanicum, S. tenellum, S. capillaceum* var. *tenellum, S. fuscum, Dicranum leioneuron,* and *Cladonia rangiferina.* All of these species affect surface conditions by controlling moisture and altering the topography.

There is a steady increase in the number of species in proceeding from the wettest to the driest associations. This is possibly because in waterlogged habitats anaerobic conditions prevail, imposing severe restrictions on plant growth, whereas, in drier habitats growing conditions improve. The *Picea mariana - Rhododendron canadense* Association has the largest number of vascular plants (41) and the most complex vegetation structure. The largest number of bryophytes and lichens (31) are found in the *Picea mariana - Cladonia rangiferina* Association. There is a sharp decline in the number of bryophyte and lichen species in the former Association where maximum shade conditions occur. As a result, the latter Association contains the largest number of species, having a total of 67 (excluding epiphytes).

The bogs are ecologically complex but floristically simple. Only 60 vascular species were found. These belong to 46 genera and 27 families. The most commonly occurring families are the Ericaceae (8 genera, 12 species) and Cyperaceae (4 genera, 10 species). There were 30 bryophytes and 18 lichen species found. The most common genera among the bryophytes were *Sphagnum* (11 species) and *Dicranum* (5 species), while the most common lichen was *Cladonia* (10 species).

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APPENDIX

SCALES USED IN THE VEGETATIONAL SAMPLING AND SYNTHESIS.

Parameters designated for the vegetation layers

Layer	Sublayer	Height Range
B—Shrub		0.3 m to 3.6 m
	B_1—High Shrub	1.8 m to 3.6 m
	B_2—Low Shrub	0.3 m to 1.8 m
C—Herb/Dwarf Shrub		0.3 m
D—Bryophyte/Lichen		
E—Epiphyte		

Domin-Krajina scale for species significance (after Krajina 1933)

+	solitary	only one plant
1	seldom	cover negligible
2	very scattered	cover negligible
3	scattered	cover to 5% of the plot
4	common	cover 5% to 10%
5	often	cover 10% to 20%
6	very often	cover 20% to 30%
7	abundant	cover 30% to 50%
8	abundant	cover 50% to 75%
9	abundant	cover 75% to 95%
10	abundant	cover 95% to 100%

Domin-Krajina scale for sociability (after Krajina 1933)

+	solitary	not touching others of the same species
1	2-3 plants	bryophytes, clumps
2	a few clumps	clumps one square meter
3	groups	0.09 to 0.36 sq m
4	groups	0.36 to 0.91 sq m
5	groups	0.91 to 1.84 sq m
6	groups	1.84 to 4.62 sq m
7	groups	4.62 to 9.24 sq m
8	groups	9.24 to 46.40 sq m
9	groups	46.40 to 929.0 sq m
10	groups	over 929.0 sq m

Scale for constancy percentages

Class	Percentage
I	0- 20
II	21- 40
III	41- 60
IV	61- 80
V	81-100