PHYTOGEOGRAPHY OF THE BRYOPHYTES OF SUGAR MAPLE FORESTS IN GASPÉ PENINSULA, QUÉBEC

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BY

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Abstract

In the Gaspé Peninsula of Québec, forests dominated by sugar maple, *Acer saccharum* Marsh., occur as discrete patches within the predominant coniferous forest, and form a northern limit of the North American Deciduous Forest Biome. Extensive field studies at six of these stands revealed a bryophyte vegetation similar to that of more continuous sugar maple forests located in southernmost Québec.

The bryophyte flora of the study sites includes 96 moss and 18 liverwort species. Four North American distribution groups were defined, based on the overlapping limits of the Boreal Forest Biome and the Deciduous Forest Biome. Azonal species (widespread in both biomes) make up 32% of the flora, and grow mainly on mineral substrates. Boreal species comprise 34% of the flora, and about half of these grow on rotting wood and humus. Temperate species (25% of the flora) include a large proportion of epiphytes, and many species that are endemic to eastern North America. Ecotonal species, with just 9% of the flora, represent a heterogeneous group of bryophytes, restricted in eastern North America to the overlap zone of the two biomes. Abundance, frequency between sites, and fertility do not differ significantly between the distribution groups.

Even at the northern limit of the Deciduous Forest Biome, Gaspé sugar maple forests provide suitable habitats for many bryophyte species characteristic of the Biome; a few of these species reach their northern limit in the Gaspé. However, the bryophyte flora includes an even larger number of species of boreal affinity, or indifferent to the biomes.

Résumé

En Gaspésie, les forêts dominées par l'érable à sucre (*Acer saccharum* Marsh.) occupent une série de petites aires isolées au sein de la forêt coniférienne qui couvre la plus grande partie du territoire. Ces érablières constituent une limite septentrionale de la Forêt décidue nord-américaine. L'étude détaillée de six de ces sites a permis de constater que la végétation bryophytique y était semblable à celle d'érablières situées plus au sud au Québec.

La flore des sites étudiés comprend 96 espèces de mousses et 18 espèces d'hépatiques. Par rapport à leur répartition nord-américaine, nous avons séparé les espèces en quatre groupes fondés sur l'aire chevauchante des deux biomes concernés, soit la Forêt boréale et la Forêt décidue. Les espèces azonales (réparties sur les deux biomes) constituent 32% de la flore et croissent en majeure partie sur des substrats minéraux. Les espèces boréales comptent pour 34 % de la flore et la moitié d'entre elles croissent sur les bois pourrissants et l'humus. Les espèces tempérées (25% de la flore) comprennent une forte proportion d'épiphytes, et plusieurs espèces endémiques de l'Amérique du Nord orientale. Finalement, les espèces écotonales (9% de la flore) forment un groupe d'affinité mixte, limité en Amérique du Nord orientale à l'aire de chevauchement des deux biomes. L'abondance, la fréquence parmi les sites et la fertilité ne diffèrent pas de manière significative entre les groupes de répartition.

Malgré leur position limitrophe par rapport à la Forêt décidue, les érablières gaspésiennes procurent des habitats à bon nombre de bryophytes caractéristiques de ce biome, dont quelques-unes atteignent en Gaspésie la limite septentrionale de leur aire. Cependant, une portion encore plus grande de la flore bryophytique est d'affinité boréale ou indifférente.

Acknowledgements

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INTRODUCTION

1.1. Objectives

Forests dominated by sugar maple (*Acer saccharum* Marsh.) characterize the northern half of the eastern North American Deciduous Forest Biome. Along the northern margin of the biome, sugar maple forests are limited in area, forming small discrete patches surrounded by boreal forest. The northernmost of these outliers are located in the Gaspé Peninsula of Québec. Even at these sites, sugar maple forests harbour a great number of vascular plants characteristic of the Deciduous Forest Biome, a few of which reach the northern limit of their distribution in the Gaspé.

The bryophyte flora of these forests has never been studied in detail. While Scoggan (1950) has produced a vascular flora of the Gaspé Peninsula, the bryophyte flora of the area remains imperfectly known, at least as far as published records indicate. J. Kucyniak was preparing a moss flora of the Gaspé at the time of his death (Crum 1964-65), but the manuscript has remained unpublished. Lepage's catalogue of the bryophytes of Québec (Lepage 1944-45, 1945-46, 1960) includes many citations of Gaspé collections. Many ecological and taxonomic studies contain incidental additions to this list. According to Belland (1984), the known bryoflora of the peninsula includes 329 moss and 105 liverwort species.

Only three works mention the type of vegetation in which the bryophytes were found. Comeau (1966) discussed the bryophytes of many plant associations on Bonaventure Island, but there is no sugar maple on the island. In a study of boreal forest bryophytes across North America, La Roi and Stringer (1976) list the bryophytes of an *Abies balsamea* stand in central Gaspé. Finally, Majcen (1981) mentions a few bryophytes in his study of the forests of Forillon National Park, including 29 moss and 3 liverwort species from sugar maple stands; these are the only published bryophyte records for the Gaspé Peninsula sugar maple forests.

The purpose of this study is to describe the bryophyte vegetation and flora of the Gaspé Peninsula sugar maple forests. The vegetation will be compared with that of sugar maple forests located in more southern localities, and with that of coniferous forests located in the Gaspé Peninsula and elsewhere. Finally, a phytogeographical analysis of the bryoflora will be made, with particular reference to the northern limit of the Deciduous Forest Biome.

1.2. The area of study

The Gaspé Peninsula (or Gaspé, for short) is located at the southeastern corner of the province of Québec (Fig. 1-1). It is bordered to the north and east by the Gulf of St. Lawrence, and to the south by Chaleur Bay and New Brunswick. The western limit of the Peninsula is arbitrary, but the almost equivalent *Gaspésie* region is usually taken to include Matane, Matapédia, Bonaventure and Gaspé counties. It lies almost entirely between 64° and 68° of longitude West, and between 48° and 49°15' of latitude North. The region has an area of approximately 30,000 km^2.

The physiography of the peninsula is characterized by a series of plateaus with altitudes increasing rapidly from the St. Lawrence, and gradually from Chaleur Bay. The highest plateau level is represented by the Shickshock Mountains, which run east-west and attain altitudes of more than 1,000 metres. The plateaus are intersected in various ways by numerous valleys; these are the only sizeable areas of low altitude in the northern part of the Peninsula, since cliffs are 300 to 500 metres high along most of the northern shore. Along Chaleur Bay, a coastal plain (or a first plateau level of less than 100 metres) is almost always present.

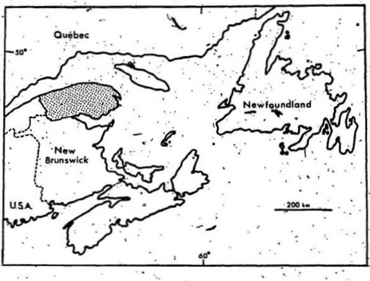

Figure 1-1: Location of the Gaspé Peninsula (stippled).

Sugar maple forests cover only a small fraction of this area, a narrow discontinuous band along the periphery of the Peninsula (Figure 1-2). Since the interior of the Peninsula has strong geological, climatic, and vegetational differences with the peripheral regions, the following sections will deal primarily with the latter area, to which sugar maple forests are restricted.

1.3. Geology

The geology of the Gaspé Peninsula has been reviewed by McGerrigle (1950) and Béland (1982). A geological map has been published by McGerrigle & Skidmore (1967).

The whole area is part of the Appalachian orogenic system, which extends from Alabama to Newfoundland. The Peninsula straddles two or three of the structural zones defined by Williams (1979): the Humber zone to the north, the Dunnage zone to the south, and possibly the Gander zone in the southeastern corner of the area (Béland 1982).

Most of the bedrock in the Gaspé is of sedimentary origin, folded and faulted along axes oriented in a NE-SW direction. The Peninsula can be divided into seven geological regions, of which three overlap the general distribution of sugar maple forests (Fig. 1-3). Region I is made of Cambrian and Ordovician sedimentary rocks of the Québec Group, mostly shales with some sandstone and quartzite. Region II includes most of the rest of the Peninsula and is made of various younger sedimentary rocks (Silurian and Devonian): limestones, conglomerates, sandstones, and siltstones; volcanic rocks are also present locally, especially in the southern part of the region. Region III consists of Carboniferous conglomerates and sandstones of the Bonaventure formation; these are the youngest rocks in the Peninsula, and lie with little or no dip over the truncated edges of earlier formations. Regions IV, V and VI are restricted to areas where sugar maple forests are not known to occur.

The Quaternary geology of the Gaspé has been reviewed by David (1982).

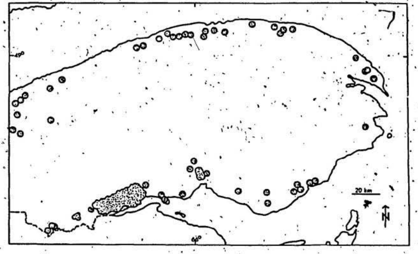

Figure 1-2: Distribution of sugar maple forests in the Gaspé Peninsula, based on Grandtner (1966b), Majcen (1981), and personal observations.

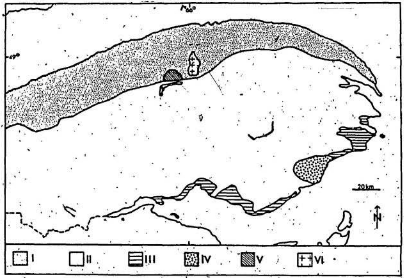

Figure 1-3: Major geological regions of the Gaspé Peninsula (adapted from Williams 1978). I: Cambrian and Ordovician sediments, mostly shales; II: Silurian and Devonian sediments (limestones, sandstones, etc.); III: Carboniferous conglomerates and sandstones; IV: Cambrian volcanics and clastic sediments (Maquereau group); V: Mt. Albert ophiolith (Ordovician); VI: McGerrigle batholith (Devonian).

Glacial deposits are locally very thick, but large parts of the Peninsula are virtually devoid of traces from the last glacial advance, except for the sporadic occurrence of large erratic boulders. These areas have probably been preserved from glacial erosion by the locally frozen base of the icecap. Recent botanical evidence (Belland 1984) suggests that some areas might have been spared by the last Wisconsinan maximum, but most of the Peninsula has certainly been glaciated. Deglaciation began at some time between 14,000 and 13,500 years B.P., and the icecap disappeared completely from the highlands at some date after 10,000 B.P.

The chronology and extent of the postglacial marine invasion has been reviewed by Dionne (1977), and Lebuis & David (1977). Marine transgression began as soon as the coastal areas became ice-free, and progressed rapidly. Along the St. Lawrence shore, it reached a maximum of 68 to 112 metres above the present sea level about 11,000 years ago. For the Chaleur Bay area, data are scarce but suggest a maximum of 30 to 76 metres above the present sea level

1.4. Climate

Climate normals are available for many stations in the area of study and adjacent New Brunswick (Anonymous 1982a, 1982b). The stations I selected for this account are all located in the general area where sugar maple forests occur. They are the stations nearest each of my study sites (see Fig. 3-1, p. 26). I also used data from Montréal (Québec) and St. John's (Newfoundland), for comparison. Climatological maps have been published in a regional atlas (Anonymous 1966), and also in Wilson (1971).

The sea has some effect on temperatures, but the climate is basically continental, with both summer and winter temperatures slightly lower than those in Montréal (Table 1-1). Summers are warm, and 4 months of the year have means above 10°C. Winters are cold, and 4 or 5 months have means below 0°C. The annual number of growing degree days (above 5°C) ranges from 1,156 in Val-d'Espoir to 1,581 in Campbellton (Anonymous 1982c).

Table 1-1: Temperature normals for selected Gaspé localities, and for Montréal and St. John's.

	July mean temperature (degrees C)	January mean temperature (degrees C)	Annual mean temperature (degrees C)
Campbellton, N.B.	19.0	-11.4	4.1
New Richmond	17.7	-11.1	3.7
Port-Daniel	17.3	-10.1	3.6
Val-d'Espoir	15.9	-11.3	2.4
Grande-Vallée	17.4	-10.5	3.4
Mont-Louis	17.4	-10.0	3.7
AVERAGE	17.3	-10.7	3.5
Montréal	21.4	-9.7	6.5
St. John's, Nfld.	15.5	-3.9	4.8

Data from Anonymous (1982a, 1982b).

Reporting on the influence of the sea on local temperatures in the Gaspé, Hufty (1968) stated that in the region, summer temperatures increase rapidly from the sea towards the interior for a few kilometres, thus reversing the effect of altitude. Further inland, this influence of the sea diminishes rapidly, and the normal altitude gradient is resumed.

Precipitation is abundant throughout the year. Amounts vary from station to station, but the average annual precipitation for my study sites is similar to that in Montréal (Table 1-2). The area receives about the same amount of snow as St. John's, but the ground usually remains covered from December to April. According to the map in Wilson (1971), potential evapotranspiration ranges from 475 mm to 525 mm. Fog is frequent on the shore, but the area receives almost as much bright sunshine as Montréal (Anonymous 1982d).

According to the available climate normals, all of peripheral Gaspé falls into the Dfb zone of the Köppen system of climate classification, as outlined in Strahler (1975). This is not surprising, since the zone corresponds to the northern part of the deciduous forest in North America. The North American map in Ackermann (1941) puts the greater part of the Peninsula in zone Dfc, which corresponds to the boreal forest, but local climatological data show that only the interior of the Peninsula should be put in this zone. Scoggan (1950) computed for the Gaspé the climatic indexes used in the Thorntwaite system and reached analogous conclusions: all of peripheral Gaspé falls within Thorntwaite's "humid microthermal climatic province", which similarly corresponds to the northern segment of the North American deciduous forest.

1.5. The Gaspé Peninsula sugar maple forests

The vegetation of the Gaspé Peninsula has been mapped in great detail by Grandtner (1966b), and summarized by Grandtner (1972). Scoggan (1950) described the vascular flora of the Gaspé Peninsula, but sugar maple forests are mentioned only incidentally. The occurrence and composition of the Gaspé sugar maple forests have been discussed by Dansereau (1944a), and in more detail, but for Forillon Park only, by Majcen (1981).

Table 1-2: Precipitation normals for selected Gaspé localities, and for Montréal and St. John's.

	Total annual rainfall (mm)	Total annual snowfal (cm),	Total annual precipitation (mm)
Campbellton, N.B.	664	387	1050
New Richmond	736	262	1002
Port-Daniel	860	368	1229
Val-d'Espoir	917	400	1319
Grande-Vallée	593	393	987
Mont-Louis	518	320	843
AVERAGE	715	355	1072
Montréal	805	266	1071
St. John's, Nfld.	1157	359	1514

Data from Anonymous (1982a, 1982b).

Most of the Peninsula is occupied by coniferous forests, typically dominated by *Abies balsamea* (L.) Mill. Sugar maple forests are restricted to the warmer areas of the Peninsula, with an altitudinal limit of about 300 metres. They are thus entirely absent from the central part of the Peninsula (Fig. 1-2, p. 5). They are also lacking completely in areas immediately adjacent to the coast, probably because of the depressing effect of the sea on local summer temperatures (see p. 9).

Within these climatically favourable areas, sugar maple forests are further restricted to sites with moderate or good drainage, and slopes of less than 40%. Moreover, much of the land that originally supported sugar maple forests has been cleared for agriculture, and is now covered with meadows, pastures, and various successional communities.

Because of these climatic, edaphic, and anthropogenic influences, sugar maple forests occupy a somewhat continuous area only in the southwestern corner of the region. Elsewhere, they occur as a series of small discrete stands, embedded in the surrounding coniferous forest, or adjacent to areas cleared for agriculture. The stands are mostly located on hilltops in the southern portion of the Gaspé (Fig. 1-4), while in the north, they are found only in valleys (Fig. 1-5).

According to Dansereau (1944a) and Majcen (1981), the forests are clearly dominated by *Acer saccharum*, but other tree species are present, especially *Betula lutea* Michx. f., and *Abies balsamea*. *Fagus grandifolia* Ehrh., a characteristic tree of sugar maple forests in southern Québec, is present only in the southwestern part of the Peninsula. The shrubby layer is very variable in extent, but is usually dominated by *Acer spicatum* Lam., *Corylus cornuta* Marsh., and the *Acer saccharum* regeneration; *Taxus canadensis* Marsh. is locally abundant. The most common herbs are boreal species such as *Aralia nudicaulis* L., *Clintonia borealis* (Ait.) Raf. and *Dryopteris austriaca* (Jacq.) Woynar, but many species of more southern affinity are also present. In fact, many characteristic sugar maple forest species reach here the northern limit of

Figure 1-4: Sugar maple stand, near St-Jules-de-Cascapédia (site SJC).

Figure 1-5: Sugar maple stand, near Mont-St-Pierre (site MSP).

their distribution, as mapped by Rousseau (1974): *Acer pensylvanicum* L., *Acer saccharum* Marsh., *Dentaria diphylla* Michx., *Dicentra cucullaria* (L.) Bernh., *Lonicera canadensis* Bartr., and *Viola eriocarpa* Schwein. All of these species show good vigour, both in growth and reproduction. Sugar maple itself attains a good height and is present in every layer, which gives the community a strong stability. In Forillon Park at least, sugar maple forests constitute the terminal association of many successional series. In Grande-Vallée, very near the northern limit of *Acer saccharum*, areas cleared of all trees are known to have been recolonized by sugar maple (E. Minville, pers. comm. 1982).

According to Majcen (1981), the most common soil type in Forillon Park sugar maple stands is the Ferro-Humic Podzol, but various types of Brunisols are also present. These soil types are widespread in peripheral Gaspé (Anonymous 1966).

These composition and soil characteristics fit well the concept of the *Betulo-Aceretum* association[1], which Grandtner (1966a) reports for many sites across southern Québec, from northwestern New Brunswick to Algonquin Park, Ontario. The sugar maple stands in Forillon Park have been formally ascribed to this association by Majcen (1981). The association is also present in the Lac-Saint-Jean region (Gérardin 1969).

Dansereau (1944a, 1944b) has suggested that the Gaspé maple forests are remnants from an earlier and more widespread forest which would have invaded the Peninsula during a warm postglacial period and become restricted under the pressure of subsequent cooling of the climate. This hypothesis might still be applicable to all or part of the forests located around Chaleur Bay, but not in the northern part of the Peninsula. Recent palynological evidence (Labelle & Richard 1984) shows that in Mont-Saint-Pierre at least, sugar maple forests never occupied the plateaus, and appeared in the Mont-Saint-Pierre valley only about

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[1] The full name for this association is *Betulo luteae-Aceretum sacchari* Lemieux.

4,700 years B.P. They were thus absent in the area during the climatic optimum, which occurred before 5,000 years B.P. The authors suggest that the postglacial migration of *Acer saccharum* along the north coast of the Gaspé must have been slowed down by the discontinuity the favourable sites, since in that area the valleys are separated by long stretches of high coastal plateaus, and the large propagules of this tree have a relatively limited dispersal ability.

1.6. The Betulo-Aceretum climax area

The most widely used system of vegetation zonation, for southern Québec, is that of Grandtner (1966a, 1972), who uses the Braun-Blanquet (1932) approach. Each zone represents a climax area (*domaine climacique*), or, as defined by Richard (1978), an area where all mesic sites with zonal soil bear the same climatically-controlled vegetation series. The terminal association of this series, or climatic climax, gives its name to the climax area. Richard (1978) has shown that most of these zones can be correlated with simple climatological data: mea annual temperature and total annual precipitation. As a climax of mesic sites, the *Betulo-Aceretum* association gives its name to the *Betulo-Aceretum* climax area, which is the most thermophilous zone in the Gaspé. As in other parts of its range, this climax area also includes non-climacic and non-mesic associations of an edaphic, hydric, xeric, or successional nature.

To the north, or with altitude, the *Betulo-Aceretum* climax area is replaced by the various climax areas of the Boreal Forest Biome, where the climacic vegetation is dominated by conifers. Communities dominated by deciduous trees occur as far north as the tree-line (e.g. the alluvial balsam poplar stands in Comtois & Payette 1984), but these do not represent climatic climaxes. In southernmost Québec, the *Betulo-Aceretum* climax area is replaced by more thermophilous vegetation zones with climaxes also dominated by sugar maple (Fig. 1-6).

Since the area of study is located near the borders of New Brunswick and Maine, it is desirable to examine the zonation of vegetation in those areas as well.

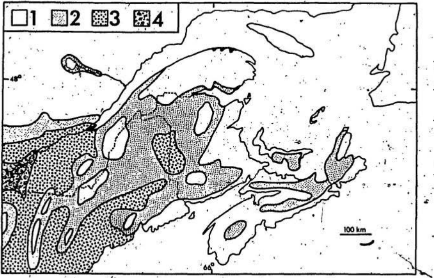

Figure 1-6: The climax areas of southern Québec, with corresponding zones in the Maritime Provinces and New England. 1: Boreal climax areas. 2: *Betulo-Aceretum* climax area (in the Maritimes, Sugar Maple - Hemlock - Pine and Sugar Maple - Yellow Birch - Fir Zones; in the U.S.A., Northern Hardwood - Spruce Forest). 3: *Aceretum sacchari* climax area (in the Maritimes, Sugar Maple - Ash Zone; in the U.S.A., Northern Hardwoods). 4: *Caryo-Aceretum* climax area (in the U.S.A., Beech - Maple Forest). Adapted from Grandtner (1966a), Loucks (1962), and Küchler (1964).

However, the climax areas are hard to follow south of the Québec border, because different systems were used to describe the distribution of vegetation. Rowe (1972) admittedly did not use the climax concept in his classification of the forests of Canada; in Québec, his units only very roughly correspond to the climax areas. Braun (1950) used the climax concept in her classification of the deciduous forests of North America, but her zones are too broad in the north: Gaspé and Maritime sugar maple forests are all within the "New England Section" of her "Hemlock - White Pine - Northern Hardwoods Region".

For the Maritime Provinces, the best available classification is probably that of Loucks (1962). His concepts are quite different from those used by Grandtner in Québec, but the description of his zones makes it possible to group them into units comparable to Grandtner's climax areas (figure 1-6). Powell (1984) pointed out that Louck's "Sugar Maple - Yellow Birch - Fir Zone" joins at the Québec border with the *Betulo-Aceretum* climax area.

For New England, vegetation zones were proposed by Westfeld *et al.* (1956), but they are too generalized towards the north to allow any comparison. More useful information is given in a map by Küchler (1964) that covers all of the conterminous United States. His vegetation zones are based on the dominant genera of natural vegetation, and very clearly join Grandtner's and Louck's zones at the Canadian border (Fig. 1-6).

A few conclusions can be drawn from Fig. 1-6:

(1) Gaspé sugar maple forests are characteristic of a vegetation zone that extends across Québec. This *Betulo-Aceretum* climax area is also an extension of similar vegetation zones south of the border.

(2) More thermophilous climax areas are restricted in Québec to the St. Lawrence lowland and piedmont areas, but Maine and New Brunswick counterparts approach to within 150 km of the Gaspé Peninsula.

(3) Conifer-dominated zones extend to the south along the coast and in the mountains.

1.7. The Deciduous Forest Biome

According to Odum (1971), biomes are the largest land community units, defined by the uniform life-form of its climatic climax vegetation. This life-form is usually taken to be that of the highest stratum of vegetation, which has a determining influence on the ecology of the whole ecosystem. In the case of the Deciduous Forest Biome and the Boreal Forest Biome, the predominance of broad-leaved deciduous trees or needle-leaved evergreen trees has a dramatic influence on the chemical nature of the litter and resulting soil type, and on the seasonality of the light regime below the canopy.

A biome usually includes many climax areas, in which the same dominating life-form is represented by different species assemblages. In Québec, the *Betulo-Aceretum* climax area is the northernmost unit of the Deciduous Forest Biome, while the *Betulo papyriferae-Abietetum* climax area[2], to which belongs most of the Gaspé Peninsula, is the southernmost unit of the Boreal Forest Biome. The limit between these two climax areas may be considered the limit between the biomes.

At a continental scale, the biome-limits are widely overlapping (Fig. 1-7). In eastern Canada at least, truly mixed forests are largely successional in nature, and do not determine climax areas. The area of biome overlap is a mosaic of the two biomes, with patches of Deciduous Forest Biome progressively smaller and fewer as one approaches the northern limit of the formation. In the United States, Küchler's (1964) "Northeastern Spruce - Fir Forest" has outliers as far south as West Virginia, and a similar "Southeastern Spruce - Fir Forest" occurs in the southern Appalachians. This concept of biome overlap is central to the geographical analysis that will be used in this study.

The Boreal Forest Biome is basically holarctic in nature, extending across both North America and Eurasia. The Deciduous Forest Biome occurs

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[2] The case of the *Betulo luteae-Abietetum* climax area is discussed in Richard (1978).

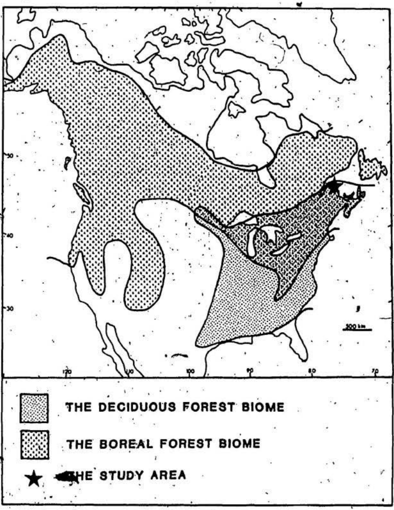

Figure 1-7: The overlapping ranges of the Boreal Forest Biome and the Deciduous Forest Biome in North America. Adapted from Dansereau (1943), Küchler (1964), and Anonymous (1973).

disjunctively in eastern North America, in Europe, in eastern Asia, and in a few smaller and floristically very distinct areas of the Southern Hemisphere. The three Northern Hemisphere segments have strong floristic similarities which point to ancient connections (Kornas 1972), but whether there ever was a holarctic Deciduous Forest Biome remains an open question; the exact sequence of connections and separations is still much debated. Based on paleobotanical evidence, Hsü (1983) suggests that there was a more or less continuous deciduous forest during the late Cretaceous and early Paleocene, with plants migrating from China across Asia to Europe and eastern North America. According to McKenna (1983), the Bering region was a wide land bridge throughout most of the Tertiary, but it was too cold to allow plant migration until the Miocene, while a temperate land bridge existed between Europe and North America at least until the Eocene. Davis (1983) suggests that the severe Quaternary climatic conditions destroyed most of the deciduous forests of Europe and, to a lesser extent, North America; present-day formations would be the result of incomplete recolonization of climatically favourable areas, from isolated refugia.

Although vegetation units and distribution patterns are independently derived, many floristic elements have been defined in terms of their correspondence with a given biome, e.g. the circumboreal element, or the eastern North American deciduous forest element. In an essay on the relation between vegetational and floristic analyses, Dansereau (1983) defined the floristic elements (*les unités floristiques*) as "...groups of taxa sharing a common history of adaptation, compatibility, and migration". The uniformity of biomes provide a perfect matrix for the development of such elements, allowing the requirements, tolerance and competitive ability of the individual species to interact over a long period of time with each other and with available resources. The ecological differences between coniferous and deciduous forests are critical in this respect. Vegetation units and floristic elements must remain separate concepts, but their interrelationships are obvious and verifiable. At the Boreal Forest Biome - Tundra Biome limit of northern Québec-Labrador, for instance, there is a marked change in the vascular flora (Morisset *et al.* 1983). Of course, as pointed out by

Dansereau (1943, 1983), many species appear to be equally adapted to the conditions in more than one biome, and have correspondingly widespread distributions.

Floristic elements cannot be discussed solely in terms of biome ecology. They have been profoundly influenced by the geographical history of the biomes, and particularly by the disruptive effect of Quaternary climates, which resulted in the disjunctive distributions of many plant species. Most floristic studies of bryophytes have been concerned with this aspect of their distribution (Crum 1972, Schuster 1983, and, in the present area of study, Belland 1984).

The present study will focus on the the ecological aspect of distribution patterns. Since deciduous forests were eliminated from Québec during the Quaternary glaciations, recolonization by this type of vegetation and its characteristic flora is a recent event, which occurred less than 5,000 years ago in the northern part of the Gaspé. Temperate vascular plants are already an important part of the flora of these northernmost sugar maple forests. This study will investigate the bryophyte portion of this flora. After an overview of the bryophyte vegetation of the study sites, the bryophyte flora will be analysed in terms of North American distribution patterns, and local status of the species.

METHODS

2.1. Field studies

The first field studies were made in the Gaspé from May to July 1982. Sugar maple stands were easy to distinguish from the surrounding vegetation types, even from a few kilometres away (see Figs. 1-4 and 1-5, pp. 12 and 13). They could thus easily be located from Highway 132, which encircles the peninsula. The study sites were selected according to the following two criteria: (1) *Acer saccharum* had to be clearly dominating the stand, present in all strata, and constituting more than 50% of the tree cover; (2) the sites had to be sufficiently far apart to give a good geographical representation of the whole area of study. All potential sites turned out to be at easy walking distance from a road, so that the selection was in no way limited by accessibility.

At each study site, notes were taken on the physical environment, the vascular flora, and the vegetation. The bryophyte vegetation was described in general terms, noting the most abundant species in each microhabitat type. The bryophyte flora was investigated in great detail; an attempt was made to collect every bryophyte species present on each substrate type, using the following classification: (1) bark of each tree species (above 0.5 metre), (2) base of each tree species, (3) rotting wood, (4) litter and humus, (5) mineral soil, and (6) rocky outcrops and boulders; wet or unusual habitats were also given special attention. Trees were climbed as high as bryophytes could be found, using a rope ladder.

The following year (May 1983), the sites were revisited, to collect any overlooked species, and to complete ecological data on the sites. Overall, three to six days were spent at each site.

2.2. Analysis

More than a thousand samples were collected in this fashion. Every species present in each sample was identified, whenever possible. For mosses, Crum & Anderson (1981), and Ireland (1982) were used, as well as special treatments of a few groups. For liverworts, the books by Schuster (1953, 1966-80) were used. The Bryophyte Herbarium of Memorial University of Newfoundland (NFLD) was used as a reference collection, and as a deposit for voucher specimens.

Based on this data, the following characteristics were assessed for each species: overall abundance, frequency among sites, fertility, and main substrate. Four abundance classes were derived from field experience, with limits based on the number of samples containing the species: rare (1 or 2 collections), occasional (3 to 8), common (10 to 19), and very common (more than 20). Frequency was taken as the number of study sites where a species was present (1 to 6). Fertility was based on the presence or absence of sporophytes. Finally, main substrate was defined as the substrate observed for more than half of the samples of a given species.

For each species, the North American distribution was mapped, using the information in Crum & Anderson (1981), Ireland (1982), Schuster (1966-80), and more than 200 taxonomic and floristic papers; the indexes of the journals *Lindbergia* and *The Bryologist* were especially useful in this respect. Special attention was given to the detailed distribution of each species in eastern Canada, using primarily Ireland & Cain (1975) for Ontario, Lepage (1944-45, 1945-46, 1960) for Quebec, Ireland (1982) for the Maritime Provinces, Brassard & Weber (1978) and Brassard & Williams (1975) for Labrador, the references in Brassard (1983) for Newfoundland; this information was sometimes supplemented by the collections at NFLD.

Distribution in Eurasia was noted as presence or absence in Europe (Ural Mountains and west), central Eurasia (between the Urals and Lake Baikal), and eastern Asia (Lake Baikal and east). The following references were used: Abramov

& Abramova (1983), Abramova *et al.* (1961), Gao (1977, 1981), Iwatsuki & Mizutani (1972), Koponen *et al.* (1978), Koponen *et al.* (1983), Nyholm (1956-69), Schuster (1966-80), Smith (1978), and many papers concerning individual species.

The maps were used to separate the species into North American distribution groups. Four latitudinal groups were used as a basis for the phytogeographical analysis and were based on the overlapping limits of the Boreal Forest Biome and the Deciduous Forest Biome: (1) Azonal species, widely distributed in both biomes; (2) Boreal species, with a wide distribution in the Boreal Forest Biome, and a southern limit corresponding roughly to that of the same biome; (3) Temperate species, with a wide range in the Deciduous Forest Biome, and a northern limit corresponding roughly to that of the same biome; and (4) Ecotonal species, restricted in eastern North America to the overlap area of the two biomes. The presence in other biomes was noted, but it was not used in this classification.

Three longitudinal groups were recognized: (1) Eastern species, with a western limit corresponding roughly to that of the Deciduous Forest Biome, or with local extensions into the central part of the continent; (2) Disjunct species, with a similar eastern distribution, in addition to a disjunct range in western North America; and (3) Transcontinental species, which extend to the Pacific Coast and have no important gap in their longitudinal distribution. Disjunction was defined as a minimum 800 km discontinuity in the known North American distribution.

Using contingency tables and a chi-square method (Milton & Tsokos 1983), I looked for any significant association between the distribution groups and the local characteristics of the species: abundance, frequency, fertility, and main substrate.

THE STUDY SITES

Six study sites were selected. All are mature sugar maple stands, and their locations are spread over the general area of the Gaspé sugar maple forests (Fig. 3-1).

Site PG (48°05'10" N, 66°34'40" W, altitude 200-250 m, area 8.4 ha) is located 2.8 km W of the community of Pointe-à-la-Garde, near the old road to L'Alverne. It occupies a small basin perched between the summits of two adjacent hills. The slope is moderate, and generally to the southeast. The stand also extends down a little gully through which the basin is drained. The bedrock is composed mostly of green conglomerates and sandstones that probably belong to the Lower Devonian La Garde formation (Bourque & Lachambre 1980). The nearest climatological station is in Campbellton, N.B.

Site SJC (48°14'50" N, 65°58'20" W, alt. 150-300 m, area 6.9 ha) is located 5 km W of St-Jules-de-Cascapédia, on the property of Mr. Jules Bernard. The stand is on a rather steep hillside , with the NE-oriented slope interrupted by a few narrow terraces (see Fig. 1-4, p. 12). The bedrock could be observed only near the bottom of the hill and consisted there of a green volcanic rock probably referable to the Silurian Black Cape formation (Bourque & Lachambre 1980). The nearest climatological station is in New Richmond.

Site AG (48°12'50" N, 64°52'40" W, alt. 165-170 m, area 6.1 ha) is located 2.2 km NNW of Anse-aux-Gascons, near a microwave antenna on Route Chapados. The stand occupies a relatively flat hilltop. I could not locate any bedrock outcrop at this site, but a detailed map in Bourque & Lachambre (1980) suggests a bedrock of calcareous rocks of the Chaleur group (Silurian). The nearest climatological station is in Port-Daniel.

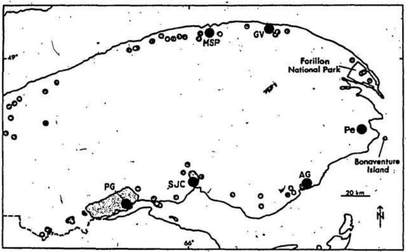

Figure 3-1: Location of the study sites (black dots) and other places mentioned in the text. PG, Pointe-à-la-Garde; SJC, St-Jules-de-Cascapédia; AG, Anse-aux-Gascons; Pe, Percé; GV, Grande-Vallée; MSP, Mont-St-Pierre. Stippling represents other sugar maple forests, as in Fig. 1-2.

Site Pe (48°33'50" N, 64°21'20" W, alt. 105-130 m, area 13.9 ha) is located just northwest of the Route à Lemieux, about 4.5 km W of Coin-du-Banc, in the municipality of Percé. As in the case of site AG, the stand occupies a relatively flat hilltop, but it also includes part of an adjacent valley. The flat-lying calcareous conglomerate bedrock can be seen at many places and is very characteristic of the Carboniferous Bonaventure formation. The nearest climatological station is in Val-d'Espoir.

Site GV (49°13'10" N, 65°11'10" W, alt. 60-80 m, area 4.6 ha) is located along Highway 132, about 4.3 km W of Grande-Vallée, on the property of Mr. Edelbert Minville. The stand grows on a NW-facing slope, at the upper end of a hanging valley. The site is protected from northerly winds by a bend in the valley. The bedrock is grey shale, probably belonging to the Middle Ordovician Cloridorme formation (Hesse 1982). There is a climatological station in Grande-Vallée.

Site MSP (49°11'10" N, 65°49'10" W, alt. 35-80 m, area 4.9 ha) is located 4.3 km south of the community of Mont-St-Pierre, along and on both sides of the road to Mt. Jacques-Cartier. The stand is on the flat bottom of a deep glacial valley (see Fig. 1-5, p. 13). The bedrock is apparently the same as at the preceding site, grey shale probably belonging to the Middle Ordovician Cloridorme formation (Hesse 1982). The nearest climatological station is in Mont-Louis.

The six sites constitute a good sampling of the topographic and geologic diversity of Gaspé sugar maple forests, since both hilltop and valley situations are represented, as well as the three geological regions where sugar maple forests are known to occur (see Fig. 1-3, p. 6).

The temperature and precipitation data in Fig. 1-1 (p. 8) and Fig. 1-2 (p. 10) are from the stations nearest each study site. They fall within the limits determined by Richard (1978) for the *Betulo-Aceretum* climax area (2.5°-4.5°

mean annual temperature, 800-1250 mm annual precipitation), except for Val-d'Espoir (near site Pe), which is slightly cooler and rainier. This may be related to local climate differences between the site and the climatological station.

The structure and composition of the stands agree very closely to the Gaspé sugar maple forests described by Dansereau (1944a) and Majcen (1981) (see pages 11-14). The tree layer is very homogeneous throughout the stands, with *Acer saccharum* making up about 90% of the cover. The rest of the layer consists mostly of *Betula lutea* (5%) and *Abies balsamea* (5%). At site PG, *Fagus grandifolia* Ehrh. is also present, with an importance comparable to that of *A. balsamea* and *B. lutea*; however, in contrast to these two species, its distribution is very irregular within the stand.

The understory is also in conformity with the descriptions of Dansereau (1944a) and Majcen (1981), with a mixture of boreal and deciduous forest species. The stands Pe, GV, and MSP had a slightly distinct facies, in that the fern *Matteucia struthiopteris* (L.) Todaro completely covered large parts of the forest floor. At the other three sites, *M. struthiopteris* was absent, or very localized. A few thermophilous species of herbaceous plants are present only at site PG: *Panax trifolius, Trillium erectum*, and *T. undulatum*. A complete list of vascular plants observed at each site is given in Appendix A. Sites PG, AG, and Pe showed little evidence of disturbance from human activity. The other sites (SJC, GV, and MSP) were used for maple syrup production, which involved the maintenance of access roads, and the selective cutting of trees.

THE BRYOPHYTE VEGETATION

The bryophyte vegetation was very uniform among the six study sites, in structure as well as in general composition. The bulk of the bryophyte vegetation was clearly concentrated on the bark of living trees, and on rotting logs and stumps. The forest floor was almost uniformly covered by a thick layer of dry leaves, which left little room for the growth of bryophytes. Erratic boulders were small and generally few, and often devoid of bryophytes. One seepy cliff and the edges of a few creeks had a rich bryophyte vegetation, but these habitats were very limited in extent. There was no bog, marsh or other body of standing water at any of the sites.

4.1. Epiphytes

Gaspé sugar maple forests have a strikingly abundant epiphyte vegetation (Figs. 4-1 and 4-2). Most trees had at least some epiphytes present, and large tree trunks were often completely covered with epiphytes to a height of about two metres. This vegetation was dominated by bryophytes, but lichens were also important.

Trunks of *Acer saccharum* had a strikingly richer epiphyte vegetation than those of the other tree species. Between 0.5 and about 3 metres, the following species were most common and made up the bulk of the bryophyte vegetation:

Leskeella nervosa
Leucodon brachypus
Neckera pennata
Orthotrichum obtusifolium
Orthotrichum sordidum
Platygyrium repens
Pylaisiella intricata
Pylaisiella polyantha
Ulota coarctata
Ulota crispa
Frullania eboracensis
Porella platyphylloidea
Ptilidium pulcherrimum
Radula complanata

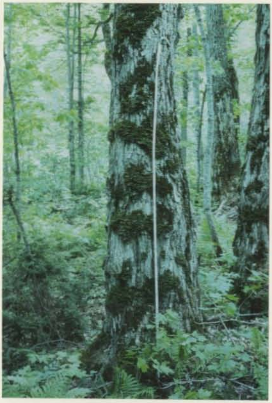

Figure 4-1: Epiphytes on *Acer saccharum* (Site MSP, 12 June 1982). The white tape measures 2.3 metres. At a 2 m height, dominating species are *N. pennata, Leucodon brachypus, Orthotrichum obtusifolium, Porella platyphylla,* and the lichen *Lobaria pulmonaria* (L.) Hoffm.; at about 1 m height, dominating species are *Neckera pennata* and *Leskeella nervosa.*

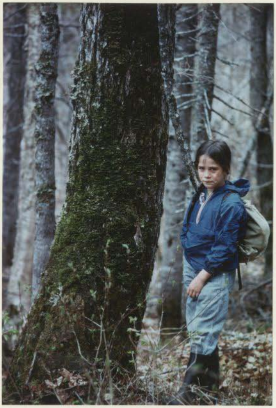

Figure 4-2: Epiphytes on *Acer saccharum* (Site Pe, 21 May 1983). The dominating species are: near top of photo, *Leucodon brachypus* and *Neckera pennata*; near centre, *N. pennata*, *Porella platyphylla*, *Leskeella nervosa* and *Amblystegium sp.*; on base of tree, *Plagiomnium cuspidatum* and *Brachythecium* cf. *salebrosum*.

Higher up on the trunks, and on the branches, the bryophyte vegetation became progressively sparser, but *Platygyrium repens*, *Ulota coarctata*, *U. crispa* and *Frullania eboracensis* were frequently found as far up as 10 metres. On *Betula lutea* trunks, the epiphyte vegetation was generally sparse, and *Frullania eboracensis* was the only common bryophyte; a few very large and old trees of *Betula lutea* had an abundant bryophyte vegetation, including most commonly *Leskeella nervosa*, *Orthotrichum sordidum*, *Ulota coarctata*, *U. crispa*, and *Frullania eboracensis*. No bryophytes were found above 0.5 m on *Abies balsamea* or *Fagus grandifolia*. Most of the species found above 0.5 m on trees were exclusive epiphytes in the study sites.

The bases of all tree species (below 0.5 m) supported a rich bryophyte vegetation, consisting of many of the species found above 0.5 metres, together with more characteristically saxicolous or terricolous species (Figs. 4-2 and 4-3). The following species were most common:

Brachythecium reflexum
Brachythecium salebrosum
Dicranum montanum
Hypnum pallescens
Leskeella nervosa
Plagiomnium cuspidatum
Platydictya subtile

4.2. Bryophytes of rotting logs and stumps

At all sites, there was an abundance of fallen trees of various size and degree of decomposition (Fig. 4-4). Recently fallen trees still had their original epiphyte vegetation, but when the bark had begun to decompose, epiphytes were replaced by more distinct assemblages of mosses and liverworts. Rotting logs of all sizes and all tree species were usually completely covered with a thick mat of mosses, with patches of lichens of the family Cladoniaceae. Liverworts were also well represented, especially on older logs retaining more humidity.

The bryophyte vegetation of rotting logs consisted mainly of the following species:

Figure 4-3: Bryophytes on base of *Acer saccharum* (Site MSP, 15 June 1982). The following species are present: *Brachythecium reflexum*, *Brachythecium sp.*, *Leskeella nervosa*, *Platydictya subtile*, and *Radula complanata*.

Figure 4-4: Bryophytes on a rotting log of *Acer saccharum* (Site MSP, 26 May 1983). The bryophyte species were not identified, but *Brachythecium reflexum* seems to be the dominant species on the photo.

Brachythecium reflexum
Callicladium haldanianum
Dicranum montanum
Herzogiella turfacea
Hypnum pallescens
Plagiothecium laetum
Tetraphis pellucida
Blepharostoma trichophyllum
Lophocolea heterophylla
Ptilidium pulcherrimum

In those stands where some selective cutting had been done, rotting stumps were also available for bryophyte colonization. On these old stumps, the vegetation was similar to that of rotting logs, but liverworts were fewer, *Tetraphis pellucida* was particularly abundant, and *Pohlia nutans* was common.

4.3. Terricolous bryophytes

At all sites, the forest floor was covered by a thick layer of dry dead leaves (Fig. 4-5) which was easily shifted around by the wind and was entirely devoid of bryophyte vegetation. A very small fraction of the forest floor area was covered by bryophyte vegetation, where the leaf litter layer was broken: on a few steep slopes, along roads maintained for maple sap harvest, on eroded stream banks, and most characteristically on scars left by the uprooted bases of fallen trees. On such sites, organic and mineral layers of soil were exposed.

Organic layers included superficial mats of twigs and leaf shreds held together by humidity, and deeper horizons of fully decomposed humus. The most frequent bryophytes were: *Brachythecium reflexum*, *B. salebrosum*, and *Plagiomnium cuspidatum*. This last species was particularly abundant at the base of large maple trees, where dead bark material accumulates and is possibly damper because of rain runoff along the trunk.

Bare mineral soil was less frequently available to bryophytes, and only one species was common on this substrate, *Polytrichastrum alpinum*.

Figure 4-5: Accumulation of dead leaves on the forest floor (Site AG). The white string was placed above leaf litter in June 1982, and the photo was taken 19 May 1983.

4.4. Saxicolous bryophytes

Erratic boulders were present at all sites, but generally small and poorly vegetated by bryophytes. Monospecific clumps of *Brachythecium reflexum*, *Fissidens cristatus*, and *Paraleucobryum longifolium* were frequent on boulders, but overall, boulders were of very marginal importance in the study sites, in terms of bryophyte vegetation.

Bedrock outcrops were rare and very limited in extent, except at Pointe-à-la-Garde, where I found a small seepy conglomerate cliff in the vicinity of a creek. It was much wetter than the erratic boulders and carried an abundant bryophyte vegetation, including *Bartramia pomiformis*, *Dichodontium pellucidum*, *Homalia trichomanoides*, *Mnium ambiguum*, *Polytrichastrum alpinum*, and *Conocephalum conicum*.

4.5. Wet habitats

Drainage was very good at all sites, and there were no bogs or standing water. This was reflected in the total absence of the genera *Aulacomnium*, *Calliergon*, *Philonotis*, and *Sphagnum*. All stands (except AG) had a few small creeks that probably dried out in the summer. In the vicinity of these, the bryophyte vegetation was generally more abundant for all substrates mentioned above. The following species were collected only in the vicinity of creeks:

Brachythecium plumosum
B. rivulare
Bryum weigelii
Cirriphyllum piliferum
Dichodontium pellucidum
Eurhynchium riparioides
Hygroamblystegium tenax
Hygrohypnum luridum
Mnium marginatum
Plagiomnium medium
Rhizomnium appalachianum
R. magnifolium
R. punctatum
Thuidium recognitum
Conocephalum conicum

Only two of these species were common: *Brachythecium rivulare*, which was usually present in the vicinity of creeks, and *Plagiomnium medium*.

4.6. Discussion

In their abundant epiphyte vegetation dominated by bryophytes, and very reduced terricolous bryophyte vegetation, Gaspé sugar maple forests are very different from the coniferous forests typical of the Boreal Forest Biome. In a study of 60 study sites across the North American taiga from Alaska to Newfoundland, La Roi & Stringer (1976) summarized the bryophyte vegetation of boreal spruce-fir forests as follows:

> "Humicolous bryophyte microcommunities are usually strongly dominated by robust pleurocarps such as *Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castensis*, with large species of *Dicranum* important associates. Corticolous and xylicolous bryophyte microcommunities near the ground are physiognomically more diverse, much richer in species, mainly successional, and consist of small mosses and liverworts such as *Tetraphis pellucida* and *Jamesoniella autumnalis*. Corticolous microcommunities on tree trunks and crowns are usually dominated by lichens, but species of *Orthotrichum*, *Ulota*, and *Ptilidium* are often minor associates."

These conclusions are consistent with the findings of Comeau (1966) and Majeen (1981) for coniferous forests in the Gaspé Peninsula.

In the Gaspé sugar maple forests, as noted earlier, terricolous mosses have an extremely limited coverage. *Pleurozium schreberi* never dominates microcommunities; it is restricted to decaying logs, and always mixed with other mosses. *Hylocomium splendens* and *Ptilium crista-castrensis* are rare, while large *Dicranum* species (*D. majus*, *D. polysetum* and *D. scoparium*) are also of marginal importance, mostly restricted to rotting wood. Climacic sugar maple forests in L'Islet Co. (Jean 1982) and in southern Québec (Grandtner 1966a) also have a very fragmentary bryophyte cover on the forest floor (maximum 5%, probably including rocks and rotting wood).

The tree base and rotting wood vegetation of the Gaspé sugar maple forests, on the other hand, is more similar to that of boreal forests. It is rich in small mosses and liverworts, and its composition is similar to that of similar habitats in Bonaventure Island balsam fir forests, as described in Comeau (1966).

However, in the Gaspé sugar maple forests, large mosses are well represented on the bases of sugar maples; on rotting maple trunks, the large pleurocarpous moss *Callicladium haldanianum* is always abundant. This species is not even reported for coniferous forests by Comeau (1966), La Roi & Stringer (1976), and Majcen (1981), while it is an important rotting log species in the southern Québec sugar maple forests studied by LeBlanc (1962), and Muhle & LeBlanc (1975).

Finally, the epiphyte vegetation of Gaspé sugar maple forests is abundant and clearly dominated by bryophytes. It seems to be almost identical to that reported by Leblanc (1960) for five sugar maple stands located in southern Québec, including one *Betulo-Aceretum* and four climacic stands of a more southern type. The dominating epiphytes are the same, but a few species that are common in the Gaspé seem to be rare or absent in southern Québec sugar maple stands: *Neckera pennata*, *Orthotrichum sordidum*, and *Pylaisiella intricata*. Also, the liverworts *Porella platyphylloidea* and *Radula complanata* ar characteristic of tree bases in southern Québec, while in my st[illegible]rea they usually grow higher up on the trunks. Differences in pollution and local humidity levels might account for these differences. In the crowns and the upper part of the trunks, the species are the same in the two areas. In southern Québec, as in the Gaspé, the epiphyte vegetation is much poorer on *Betula lutea*, and limited to the bases of *Fagus grandifolia*. *Abies balsamea* is not present in southern Québec stands.

In the preceding account, I described the bryophyte vegetation only in general terms, without having systematically assessed the abundance or coverage of each species. Comparative data from other regions is equally fragmentary. Notwithstanding these limitations, it seems obvious that the bryophyte vegetation of the Gaspé Peninsula sugar maple forests has much more similarities with that of similar forests in southernmost Québec than with that of the surrounding coniferous forests.

THE BRYOPHYTE FLORA

One hundred and fourteen bryophyte species were identified in the samples (Table 5-1). An annotated list of the species is given in Appendix B, with data on local substrate, abundance, frequency, and fertility. The 96 moss species represent 24 families and 55 genera, while the 18 liverwort species are from 14 families and 17 genera. The genera with most species in the flora are *Brachythecium* (8 species) and *Dicranum* (6 species). Many widespread genera are totally absent from the flora (*e.g., Calliergon, Sphagnum, Lophozia*) and the diverse family Pottiaceae is represented by few collections of only two species.

Although it is probable that a few uncommon species were overlooked during the field work, I believe the list is nearly complete for the sites investigated. The second field season produced new species records for individual sites, but added only five species to the general list. Only three of the species mentioned by Majcen (1981) for sugar maple stands were not found in my study sites. These are included and discussed in Appendix B.

5.1. The distribution groups

The flora does not contain any species that can be considered rare in eastern North America. The distribution groups were defined p. 24. The separation into latitudinal groups was very clear in most cases. A few species were clearly boreal in western North America, but temperate or ecotonal in the East. These will be discussed individually.

Separation into eastern, disjunct and transcontinental species was often less clear. Most eastern species extended into some parts of central North America, and sometimes those western extensions were such that differentiation was

Table 5-1: Number of bryophyte species collected at each study site.

STUDY SITE	MOSSES	LIVERWORTS	TOTAL
Pointe-à-la-Garde	55	11	66
St-Jules-de-Cascapédia	54	13	67
Anse-aux-Gascons	42	8	50
Percé	52	14	66
Grande-Vallée	54	11	65
Mont-St-Pierre	49	11	60
TOTAL FOR COMBINED SITES	96	18	114

difficult from transcontinental species. The differentiation between transcontinental and disjunct species was also difficult; it was often not clear if the minimal 800 km distribution gap was present, and every possible intermediate was observed between fully transcontinental species and *Orthotrichum sordidum*, the species with the widest disjunction.

The number of bryophytes in each distributional group is given in Table 5-2. A list of the species in each group is given in Appendix C, with a summary of their Eurasian distribution. Since this study is primarily concerned with the Deciduous Forest Biome - Boreal Forest Biome ecotone, the latitudinal groups will be used as a basis for the following analysis.

5.2. Azonal species

Azonal species, as defined earlier (p. 24), constitute the largest distribution group in this study. A few of the azonal species (*e.g.*, *Bartramia pomiformis*, Fig. 5-1) are restricted in North America to the combined areas of the Boreal Forest and Deciduous Forest Biomes, but most species have wider ranges that extend into the Arctic and/or the tropics. The species are transcontinental in North America, except for four disjunct species. The disjunction of *Plagiothecium cavifolium* is limited to a narrow gap in central Canada, and the species is widespread on both sides of the continent. The other disjunct species, *Diphyscium foliosum* (Fig. 5-2), *Pylaisiella selwynii*, and *Oxystegus tenuirostris* have a temperate distribution in eastern North America, but occur disjunctively in Greenland and/or arctic Alaska and/or boreal western North America. These distribution patterns will be discussed together with the boreal disjunct species.

All but two of the transcontinental species are also transcontinental in Eurasia; except for a few truly cosmopolitan species, these belong to the classical circumpolar element described for vascular plants by Hultén (1964). It corresponds to the almost continuous circumpolar Boreal Forest Biome, with extensions including the Deciduous Forest Biome. *Plagiomnium ciliare* is

Table 5-2: Number of bryophyte species in each distribution group.

	Eastern	Disjunct	Trans-continental	TOTAL
Azonal	-	4 (4%)	33 (29%)	37 (32%)
Boreal	-	9 (8%)	30 (26%)	39 (34%)
Temperate	11 (10%)	12 (11%)	5 (4%)	28 (25%)
Ecotonal	6 (5%)	4 (4%)	-	10 (9%)
TOTAL	17 (15%)	29 (25%)	68 (60%)	114 (100%)

Figure 5-1: Generalized distribution of *Bartramia pomiformis* in North America.

Figure 5-2: Generalized distribution of *Diphyscium foliosum* in North America. Dots represent isolated localities. Crum & Anderson (1981) also report the species from Mexico, Guatemala, and Jamaica.

endemic to North America, but it is very closely related to *P. tezukae* (Sak.) Kop. from Japan, and *P. affine* (Funck) Kop. from Europe (Koponen 1971); *P. ciliare* is also much more widespread in the Deciduous Forest Biome than in the Boreal Forest Biome, and Koponen (1971) considers it to belong to a deciduous forest element. Similarly, *Plagiochila porelloides* is known from Europe and North America only, but it is closely allied to the Asiatic *P. ovalifolia* Mitt. (Schuster 1966-80). Among the species that are disjunct in North America, two are transcontinental in Eurasia, while the others occur disjunctively in Europe and eastern Asia.

5.3. Boreal species

My definition of boreal species includes a southern limit corresponding roughly to that of the Boreal Forest Forest Biome (see p. 24). Most boreal species had this limit in the southern Appalachian Mountains. In a few cases, this limit was not located that far south, i.e. it was somewhere else along the Appalachian Mountains, between Québec and West Virginia. A few species occur disjunctively in the Ozark Mountains.

The northern limit of the boreal species is most frequently located near the tree-line, but many species are also widespread in the Arctic. A few species are somewhat restricted to the southern portion of the Boreal Forest Biome. Two species, *Plagiomnium drummondii* and *Pylaisiella polyantha*, could be included in the ecotonal group with respect to their eastern North American range, but are included here because of their extensive boreal range in the west; some ecological or historical cause might explain their apparent absence in the northeastern part of the biome, but this may simply be due to undercollection. *Herzogiella turfacea* has an unusual distribution in that this low-boreal species does not occur west of the Rocky Mountains, but has been found across the Prairies as far west as western Alberta and western Montana. It is apparently transcontinental in Eurasia.

The great majority of boreal species are transcontinental in North America

Figure 5-3: Generalized distribution of *Drepanocladus uncinatus* in North America (adapted from Janssens 1983).

(Fig. 5-3). These form a very homogeneous group of boreal and arctic-boreal bryophytes, but a few of the taxa tend to be less common in central Canada. Nine boreal species show strong disjunctions in their North American range. Five of these have a regular pattern of widespread occurrence in both eastern and western North America, and a disjunction of variable width in the central part of the continent (*e.g.*, *Hylocomium pyrenaicum*, Fig. 5-4). The other four species, *Brachythecium erythrorrhizon*, *Heterocladium dimorphum*, *Isopterygium muellerianum*, and *Orthotrichum sordidum* (Fig. 5-5), have more irregular distributions, with their eastern and/or western range restricted in various ways.

All the transcontinental species and most of the disjunct species are also transcontinental in Eurasia. These plants belong to the circumpolar element described by Hultén (1964), as with most of the azonal transcontinental species, but their distribution does not extend significantly into the Deciduous Forest. They correspond more strictly to the circumboreal element mentioned for Québec vascular plants (Rousseau 1974) and eastern Canadian lichens (Brodo & Gowan 1983). Their distribution can be correlated with that of the almost continuous circumpolar boreal forest.

The North American disjunctions can be explained in various ways. The three *Brachythecium* species may very well have been undercollected or misidentified in central Canada. This genus has a long history of taxonomic confusion and it is hard to include most species in any analysis.

Jäger (1972) has discussed continentality and oceanity in European vascular plant distributions. Various climatological factors associated with distance from the oceans can also explain the disjunct distributions of many North American plants, especially those with a wide latitudinal distribution on both sides of the continent. Humidity and precipitation differences across the continent do not restrict significantly the transcontinentality of the coniferous forest, but many individual species characteristic of the Boreal Forest Biome show variations in this respect. These climatological factors can probably explain the distribution of

Figure 5-4: Generalized distribution of *Hylocomium pyrenaicum* in North America. The black dot represents an isolated group of localities. *H. pyrenaicum* is also reported from the Aleutian Islands (Crum & Anderson 1981).

Figure 5-5: Generalized distribution of *Orthotrichum sordidum* in North America (expanded from Lewinsky 1977). Black dots represent isolated localities.

most boreal disjuncts in this study, as well as that of the azonal *Plagiothecium cavifolium*. Brodo & Gowan (1983) distinguish an oceanic element for lichens, and the species they mapped (*Bryoria bicolor* (Ehrh.) Brodo & Hawksw.) would be considered boreal and disjunct in my classification.

Orthotrichum sordidum (Fig. 5-5, p. 50) has the largest disjunction in this analysis and its distribution cannot be related to Jäger's (1972) "oceanity areas" alone, since it is also disjunct latitudinally, between the Great Lakes-St. Lawrence region and the Arctic; it is absent from true boreal latitudes, except for one locality in coastal Labrador. In the southern part of its range, *O. sordidum* is a common and obligate epiphyte, while in the Arctic it grows on rocks. The species has a similar amphizonal distribution in eastern Asia, with the same ecological difference. In European longitudes, it is only reported from Svalbard. Lewinsky (1977) explained this pattern in terms of widespread preglacial distribution and survival in refugia during the last glaciation. The arctic populations are from areas thought to have remained unglaciated. The southern populations would have reinvaded part of their former range from regions south of the glacial limit. Other species of epiphytes are known to grow on rock in the northern part of their range (Piippo 1982). The azonal disjuncts *Diphyscium foliosum* (Fig. 5-2, p. 45), *Pylaisiella selwynii*, and *Oxystegus tenuirostris* probably have similar histories.

5.4. Temperate species

My definition of temperate species includes a northern limit corresponding roughly to that of the Deciduous Forest Forest Biome (see p. 24). Seven species reach their eastern North American northern limit in the area of study:

Anacamptodon splachnoides
Anomodon rugelii
Atrichum altecristatum
Callicladium haldanianum
Drummondia prorepens
Fissidens cristatus
Porella platyphylla

The other species had a few localities north of the Gaspé, usually on the island of Newfoundland. These outlying stations were not taken to indicate a northern affinity, since they were very few, or located only slightly to the north of my area of study. In a few cases, the decision was made with hesitation, and further research might move these species to the azonal group. This is notably the case of *Platygyrium repens*, which is clearly temperate in eastern North America, but has a more boreal distribution in the western half of the continent, where it is found along major rivers as far as Alberta, and near hot springs in northern British Columbia.

The southern limit of the temperate species is most frequently in the southeastern United States, but many extend into the tropical zone.

A large portion of the temperate species have an eastern distribution (Figs. 5-6 and 5-7). A few of the species are also widespread in the American tropics, but otherwise, this group is very homogeneous, with most species distributed over the full range of the Deciduous Forest Biome, frequently with a few outlying stations in the lower boreal zone and/or extensions into the Prairies. This distribution type basically corresponds to the eastern North American Deciduous Forest Biome, and such a floristic element has been noted for vascular plants (Rousseau 1974), mosses (Crum 1966), and lichens (Brodo & Gowan 1983).

Other temperate species have a similar range, but also occur disjunctively in western North America (Fig. 5-8). This disjunction is very wide in most cases, but the range in western North America is very variable: to mention extreme examples, *Metzgeria furcata* is known from a single western locality, in Oregon, while *Jungermannia leiantha* has a broad cordilleran and coastal range in Western North America. For species with a restricted range in western North America, the western populations probably represent relicts from a Tertiary transcontinental Deciduous Forest Biome. Rousseau (1974) mentions a few vascular plants of the deciduous forest element, with disjunct localities in western North America. Disjunct species with a wider latitudinal range in the west usually

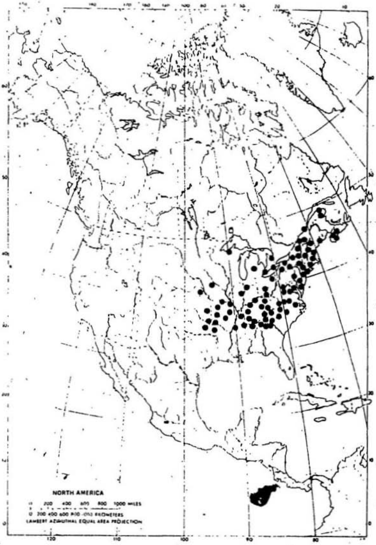

Figure 5-6: North American distribution of *Drummondia prorepens* (expanded from Vitt 1970).

Figure 5-7. North American distribution of *Anacamptodon splachnoides* (expanded from Crum 1958, and Ireland 1984).

Figure 5-8: Generalized distribution of *Callicladium haldanianum* in North America. Open squares represent state records for which there was no precise locality information.

have a narrower disjunction that can be explained by present-day climatological factors, as for the boreal disjuncts (see p. 48).

Most eastern and disjunct temperate species are endemic to North America or have disjunct ranges in Europe and/or eastern Asia. This is consistent with the present-day discontinuous range of the Deciduous Forest Biome. At least two of the North American endemics, *Drummondia prorepens* and *Leucodon brachypus*, have very close relatives in eastern Asia: *Drummondia sinensis* C. Müll. (see Vitt 1972), and *Leucodon perdependens* Okam. (see Crum & Anderson 1971).

Finally, two moss and three liverwort species have a temperate transcontinental distribution (Fig. 5-9). They are recorded from most of the United States, and across southermost Canada. This type of distribution is seldom mentioned for vascular plants, but Brodo & Gowan (1983) mention it for lichens. These species are also transcontinental in Eurasia and can be considered to belong to a circumtemperate floristic element.

5.5. Ecotonal species

Ecotonal species constitute the smallest group of taxa, and the most restricted distribution type in this study. My definition of ecotonal species includes a northern limit corresponding roughly to the northern limit of the Deciduous Forest Forest Biome, and a southern limit corresponding roughly to the southern limit of the Boreal Forest Forest Biome (see page 24). All ecotonal species have a few localities north of the Gaspé Peninsula, mostly in central Labrador or northern Ontario. These outlying stations were not taken to indicate a northern affinity, since they were very few, or located only slightly to the north of my area of study. A few species might prove to be more frequent in the Boreal zone. All ecotonal species in this study have their southern limit in the southern Appalachian Mountains, except *Platydictya subtile*, which is not known from the southeastern United States, but reaches a southern limit in Texas.

Most ecotonal eastern species (*e.g.*, *Rhizomnium appalachianum*, Fig. 5-10)

Figure 5-9: Generalized distribution of *Porella platyphylla* in North America.

Figure 5-10: Generalized distribution of *Rhizomnium appalachianum* in North America (adapted from Koponen 1973).

have a very uniform distribution pattern, including the Appalachian Mountains, the Great Lakes region, and the Gulf of St. Lawrence. The four ecotonal disjunct species have the same uniform distribution pattern in eastern North America, with a similarly restricted range in the western part of the continent, in British Columbia and adjacent territories. *Ulota coarctata* (Fig. 5-11) is known in the west from a single locality, in northern Idaho.

By their very definition, ecotonal species are subject to interpretation problems. From distribution map analysis at a continental scale, an extreme southern boreal species and a northern temperate species cannot be distinguished. A finer analysis of local habitat characteristics, especially altitude, might sort them out in part. Some of the species may be original low-boreal species that were eliminated from most of their former range during the last glaciation. Their present distribution would reflect survival south of the glacial limit, and subsequent incomplete recolonization. This may particularly apply to most ecotonal disjuncts, since these species are transcontinental in Eurasia (except *Ulota coarctata*). On the other hand, all of my ecotonal eastern species (except *Cirriphyllum piliferum*) occur disjunctively in Europe and eastern Asia, which is characteristic of the deciduous forest element. Their remarkably uniform Appalachian -- Great Lakes - St. Lawrence distribution pattern was mentioned by Rousseau (1974) for vascular plants, and Brodo & Gowan (1983) for lichens. These authors consider this pattern as a sub-element of the deciduous forest element.

5.6. Local status of species in each distribution group

For the purpose of this study, the local status of each species was defined in terms of abundance, frequency, fertility, and main substrate (see p. 23). The statistical analysis of the data is detailed in Appendix D. In the case of abundance and frequency, ecotonal species had to be removed from the analysis, but there is no significant difference between the three remaining groups. Similarly, the proportion of fertile and sterile species did not differ significantly,

Figure 5-11: Generalized distribution of *Ulota coarctata* in North America (adapted from Vitt 1970). The black dot represents an isolated locality.

for mosses of all four distribution groups. These findings indicate that on the average, temperate and boreal species are equally successful vegetatively and reproductively in the set of microhabitats provided by the study sites; neither the temperate or the boreal species can be considered to be accidental or otherwise atypical with respect to the Gaspé Peninsula sugar maple forests. However, the three species most common and widespread in the Boreal Forest Biome are ecologically restricted or rare in the study sites (see p. 38). The local status of azonal species is not surprising, given their wide distribution both north and south of the area of study. For the small ecotonal group, abundance and frequency could not be included in this analysis, but the proportion of fertile species suggests that their local status does not differ from that of the other groups.

Ten species could not be assigned to one main substrate type: *Amblystegium varium, Anomodon attenuatus, Brachythecium erythrorrhizon, B. reflexum, B. velutinum, Eurhynchium riparioides, Oncophorus wahlenbergii, Plagiothecium denticulatum, Conocephalum conicum*, and *Ptilidium pulcherrimum*. On the other hand, the single collection of *Leptobryum pyriforme* grew on an unclassifiable substrate (ash in an abandoned boiler). For the remaining 103 species (Fig. 5-12), the main substrate classes are distributed differently in the four distribution groups. The differences are significant, at least for the azonal, boreal, and temperate groups (Appendix D, p. 104). More than half of the azonal species are from rock or mineral soil, about half of the boreal species grow on dead organic substrates, and almost half of the temperate species are epiphytes.

Mineral substrates are widespread in both the Boreal Forest and the Deciduous Forest Biomes. This is reflected in the large number of azonal species with this as a main substrate.

It was noted earlier that the bryophyte vegetation of rotting wood is similar in coniferous and deciduous forests. On the other hand, the litter produced by

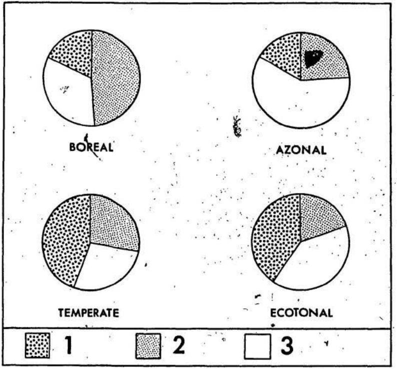

Figure 5-12: Proportion of bryophyte species of each main substrate class, for each distribution group. 1: bark of living trees; 2: dead organic substrates; 3: mineral substrates.

coniferous trees is a much better habitat for bryophytes than deciduous forest litter, as shown by the important bryophyte cover of most boreal forest floors; in sugar maple forests, boreal terricolous mosses apparently find similar conditions of acidity, humidity, and possibly stability on rotting logs or occasional exposed humus. These factors can explain the large proportion of species from dead organic substrates in the boreal group, as well as the large number of boreal bryophytes in Gaspé sugar maple forests.

Finally, not surprisingly, epiphytes predominate among temperate bryophytes. The bark of deciduous trees (except birches) is known to be more suitable for the growth of epiphytic bryophytes than the bark of the main boreal trees, *i.e.* birches and conifers (Barkman 1958).

5.7. Floristic synthesis

Grandtner (1966a, 1966b) and Majcen (1981) have shown that the Gaspé sugar maple forests belong to a vegetation type widespread across southern Québec. I have shown in the preceeding chapter that the bryophyte vegetation of my study sites is also similar to that of sugar maple forests in other parts of Québec.

Dansereau (1944a) mentioned that the vascular flora of Gaspé sugar maple forests consists of a mixture of deciduous forest and boreal forest elements. The vascular flora of my study sites (Appendix A) includes many species of both deciduous forest and circumboreal elements mentioned by Rousseau (1974) for the Québec flora.

Using Dansereau's (1983) definition (see p. 20), I would distinguish four floristic elements in the Gaspé sugar maple forest bryophyte flora, based on distribution patterns and, to a lesser extent, on the local status of the species.

The cosmopolitan element includes a few azonal transcontinental species with particularly widespread distributions in all continents, *e.g.*, *Ceratodon* *purpureus* and *Leptobryum pyriforme.* These species are rare in the study sites, and restricted to disturbed or man-made habitats.

The circumboreal element includes most of the azonal and boreal species. This element corresponds to the holarctic Boreal Forest Biome, but many species are arcto-boreal or boreo-temperate. In the study sites, it is represented by species of habitats found equally in deciduous and coniferous forests (*e.g.*, rocks and rotting wood), and species with a shift of habitat between biomes, such as boreal forest floor mosses growing locally on sugar maple rotting logs. Disjunct species with a wide latitudinal distribution can be distinguished as a boreal oceanic sub-element, while a true boreal disjunct sub-element would include the rest of the azonal and boreal disjuncts, and some of the ecotonal disjuncts, in which Quaternary glaciations have had a strong restrictive effect on distribution.

The circumtemperate element is a small group including all temperate transcontinental species, and two temperate species that are narrowly disjunct in North America and transcontinental in Eurasia. The local habitats of these species are diverse, and the element is poorly documented in the literature.

The deciduous forest element mainly includes my temperate eastern and ecotonal eastern species, as well as those temperate and ecotonal disjuncts whose western populations might be relicts from a former western North American deciduous forest. The bulk of this element consists of species with ecologies most specifically adapted to the deciduous forest, *e.g.*, epiphytes. The species can be separated into sub-elements on the basis of their presence or absence in the other sections of the Deciduous Forest Biome (*i.e.* in Europe and/or eastern Asia), but the number of identical versus vicariant species in these regions depends much on taxonomic opinion.

In conclusion, the bulk of the bryophyte flora of Gaspé Peninsula sugar maple forests belongs to the circumboreal and deciduous forest elements, as for vascular plants. The present flora is a result of recent recolonization from regions south of the glacial limit, but the floristic elements originated from ancient and prolonged coevolution in pre-Quaternary biomes. The differences in main substrate are suggestive in this respect, but more studies are needed on the ecology of deciduous forests bryophytes, especially in relation to the seasonality of the light and moisture regimes. The floristic analysis of non-mesic and non-climacic vegetation types within the climax areas could also lead to a better understanding of the dynamic relationships between flora and vegetation.

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7.

Appendix A

List of the vascular plants found at the study sites

Nomenclature follows Scoggan (1978-79). This list includes the first records of *Panax trifolius* and *Viburnum alnifolium* from the Gaspé Peninsula.

	PG	SJC	AG	Pe	GV	MSP
PTERIDOPHYTES						
Botrychium virginianum (L.) Sw.		+	+	+	+	+
Cystopteris bulbifera (L.) Bernh.				+		
Dryopteris austriaca (Jacq.) Woynar	+	+	+	+	+	+
Gymnocarpium dryopteris (L.) Newm.		+	+	+	+	+
Lycopodium lucidulum Michx.	+	+	+	+	+	+
Lycopodium obscurum L.	+	+	+	+	+	+
Matteucia struthiopteris (L.) Todaro	+			+	+	+
Osmunda claytoniana L.			+	+		
Polystichum braunii (Spenner) Fée	+	+			+	+
Thelypteris phegopteris (L.) Slosson	+	+	+	+	+	+
SPERMATOPHYTES						
Abies balsamea (L.) Mill.	+	+	+	+	+	+
Acer pensylvanicum L.	+	+	+	+	+	
Acer rubrum L.			+			
Acer saccharum Marsh.	+	+	+	+	+	+
Acer spicatum Lam.	+	+	+	+	+	+
Actaea rubra (Ait.) Willd.	+	+	+	+	+	+
Amelanchier sp.				+		
Anaphalis margaritacea (L.) Clarke			+			
Aralia nudicaulis L.	+	+	+	+	+	+
Arctium lappa L.				+	+	+
Arisaema atrorubens (Ait.) Blume		+				
Betula lutea Michx. f.	+	+	+	+	+	+
Betula papyrifera Marsh.		+	+		+	

	PG	SJC	AG	Pe	GV	MSP
Chrysosplenium americanum Schwein.	+					
Circaea alpina L.		+		+	+	+
Claytonia caroliniana Michx.		+		+		+
Clintonia borealis (Ait.) Raf.	+	+	+	+	+	+
Cornus alternifolia L. f.			+	+		+
Cornus canadensis L.				+	+	
Corylus cornuta Marsh.	+	+	+	+	+	+
Dentaria diphylla Michx.		+				+
Dicentra cucullaria (L.) Bernh.	+			+		+
Erythronium americanum Ker						+
Eupatorium rugosum Houtt.				+		+
Fagus grandifolia Ehrh.	+					
Fraxinus nigra Marsh.						+
Galium triflorum Michx.		+	+	+	+	+
Habenaria viridis (L.) R.Br.				+		
Heracleum lanatum Michx.					+	
Impatiens capensis Meerb.						+
Lonicera canadensis Bartr.		+	+	+	+	+
Maianthemum canadense Desf.	+	+	+	+		+
Medeola virginiana L.		+				
Milium effusum L.				+		+
Mitella nuda L.				+	+	+
Osmorhiza sp.			+	+		+
Oxalis montana Raf.		+	+	+	+	
Panax trifolius L.	+					
Picea glauca (Moench) Voss			+			
Prenanthes cf. *altissima* L.		+	+	+	+	
Prunus cf. *pensylvanica* L.f.				+		
Prunus virginiana L.	+					
Ranunculus abortivus L.					+	
Ribes lacustre (Pers.) Poir.				+	+	
Ribes triste Pallas				+		+
Rubus idaeus L.			+	+		+
Rubus pubescens Raf.	+	+	+	+	+	+
Sambucus racemosa L.		+		+		
Sanicula marilandica L.		+				
Smilacina racemosa (L.) Desf.		+	+	+		
Solidago macrophylla Pursh				+		+
Sorbus decora (Sarg.) Schneid.						+
Streptopus roseus Michx.	+	+	+	+	+	+
Taraxacum officinale Weber			+			+
Taxus canadensis Marsh.	+	+	+	+	+	+
Thalictrum cf. *dioicum* L.					+	

	PG	SJC	AG	Pe	GV	MSP
Thuja occidentalis L.					+	+
Trientalis borealis Raf.		+	+	+	+	+
Trillium cernuum L.		+	+	+	+	+
Trillium erectum L.	+					
Trillium undulatum Willd.	+					
Tussilago farfara L.						+
Viburnum alnifolium Marsh.		+				
Viola eriocarpa Schwein.		+				+
Viola incognita Brainerd	+					+
Viola renifolia Gray			+	+		
Viola selkirkii Pursh				+		

Appendix B

Annotated list of the bryophytes of Gaspé Peninsula sugar maple forests

The following list is based on collections at the six study sites, but other reports are also included. Altogether, the known bryophyte flora of the Gaspé sugar maple forests includes 97 moss and 20 liverwort species. *Metzgeria furcata* is reported here for the first time from the Gaspé Peninsula.

For mosses, I followed the nomenclature of Ireland (1982), except for *Brachythecium oedipodium, Fissidens bryoides, Schistidium gracile*, and the genus *Polytrichastrum*. For liverworts, I followed Stotler & Crandall-Stotler (1977).

Collection numbers 101 to 2144 are by M. Favreau, and numbers 3601 to 4304 are by M. Favreau and Z. Brabant. Collection numbers followed by an asterisk (*) represent specimens with sporophytes. Abbreviations PG, SJC, AG, Pe, GV, and MSP represent the study sites, as per Fig. 1-2 (p. 5). "Fo" indicates a report by Majcen (1981) from sugar maple stands in Forillon National Park.

In most cases, I have cited only one specimen of each species for each locality, but abundance and substrate data is based on my entire collections. The epithets "occasional", "common", and "very common" refer to the abundance classes defined on p. 23. All specimens cited are deposited in the Bryophyte Herbarium of Memorial University of Newfoundland (NFLD). A second, almost complete set of specimens is kept in my personal herbarium.

CLASS MUSCI

Amblystegium serpens (Hedw.) B.S.G. GV: *1509**; MSP: *1311**. Occasional, on bases of *Acer saccharum*, usually on damper parts of bark.

Amblystegium varium (Hedw.) Lindb. PG: *104**; Pe: *2141a*. Only two collections, from the base of an *Acer saccharum* and from conglomerate rock, with other mosses.

Anacamptodon splachnoides (Fröhl. *ex* Brid.) Brid. GV: *1427a*. Only one collection, from a knothole in the upper part of an *Acer saccharum* trunk. This is the northernmost record for this species (Fig. 5-7, p. 54).

Anomodon attenuatus (Hedw.) Hüb. PG: *3708*; Pe: *1717*; MSP: *4304a*. Occasional, in large mats over rock, rotting wood, or the base of *Acer saccharum*.

Anomodon rostratus (Hedw.) Schimp. Pe: *1715a*. Only one collection, from conglomerate rock.

Anomodon rugelii (C. Müll.) Keissl. PG: *3702a*. Only one collection, forming a large mat on the base of an *Acer saccharum*. This is the northernmost record for this species in North America. An earlier record from Rimouski Co. (Lepage 1945-46), is *A. attenuatus* (*Lepage 1768*, QFA, seen).

Atrichum altecristatum (Ren. & Card.) Irel. SJC: *721**; AG: *613**. Occasional, on mineral soil.

Bartramia pomiformis Hedw. PG: *224a**. Only one collection, from a conglomerate cliff ledge.

Brachythecium erythrorrhizon B.S.G. SJC: *[illegible]87*; AG: *541*; GV: *4115a**; MSP: *4210*; Fo. Occasional, on diverse substrates (rock, base of *Acer saccharum*, thin litter over mineral soil, rotting log).

Brachythecium oedipodium (Mitt.) Jaeg. GV: *1534a*; Fo. Only one collection, over humus near rock. My specimen corresponds clearly to *B. oedipodium* (*B. curtum* (Lindb.) Limpr.), as distinguished from *B. starkei* (Brid.) B.S.G. by Piippo (1983).

Brachythecium plumosum (Hedw.) B.S.G. SJC: *836a**. Only one collection, from a rock near a creek.

Brachythecium populeum (Hedw.) B.S.G. PG: *261*; SJC: *840**; AG: *651*; GV: *1542*; MSP: *1305**; Fo. Common, usually on rock; a few collections from rotting wood and a piece of detached bark.

Brachythecium reflexum (Starke *ex* Web. & Mohr) B.S.G. PG: *308**; SJC: *863**; AG: *648**; Pe: *1835** & *2127b*; GV: *1504* & *1512*; MSP: *1009**; Fo. Very common, on diverse substrates (base of trees, rotting wood, rocks, mineral soil, litter).

Brachythecium rivulare B.S.G. PG: *212**; SJC: *3809*; Pe: *2136*; GV: *1545*. Common, near creeks, on various substrates (rocks, mud, dead wood, scrap metal).

Brachythecium salebrosum (Web. & Mohr) B.S.G. PG: *328*; SJC: *716**; AG: *507**; Pe: *1852*; GV: *1503**; MSP: *1312**. Very common, mostly on tree bases, humus, rotting bark, and rotting wood near tree bases; isolated collections from *Betula lutea* trunks, mineral soil, and a rock near a creek.

Brachythecium starkei (Brid.) B.S.G. *s.s.* SJC: *715**; AG: *505**; MSP: *1211**. Occasional, on humus, thin litter over rock, and mineral soil.

Brachythecium velutinum (Hedw.) B.S.G. SJC: *875a**; AG: *559a**; Pe: *2100**; MSP: *1301**. Occasional, on various substrates (thin humus over rock, partly mineralized soil, birch bark on a rotting log, pebbles in mineral soil).

Brotherella recurvans (Michx.) Fleisch. PG: *401a*; SJC: *845b*. Only two collections, from rotting logs.

?*Bryhnia graminicolor* (Brid.) Grout. This species is mentioned by Majcen (1981) for a sugar maple stand in Forillon National Park. I have examined the specimen in CANM: it consists mostly of *Brachythecium erythrorrhizon*, but some stems belong to the genus *Bryhnia*. The small size of the plants, and the coarse papillae suggest *B. graminicolor*, but the ovate leaves with plane margins and twisted apices point to *B. novae-angliae*. I have not found *B. graminicolor* in my study sites.

Bryhnia novae-angliae (Sull. & Lesq. *ex* Sull.) Grout. PG: *204*; SJC: *834*; AG: *536*; Pe: *2148*; GV: *1580*. Fo: see *B. graminicolor*. Common, on mineral soil or rotting wood, usually near streams.

Bryum caespiticium Hedw. SJC: *850c*. Only one collection, from recently disturbed mineral soil.

Bryum capillare Hedw. MSP: *1325b*. Only one collection, from the mineral soil of a shaded, eroding stream bank.

Bryum weigelii Spreng. PG: *3705a*. Only one collection, from wet soil, near a creek.

Callicladium haldanianum (Grev.) Crum. PG: *245**; SJC: *712**; AG: *618*; Pe: *1704**; GV: *1502*; MSP: *1222*; Fo. Very common, mostly on rotting wood; one collection from the base of a large *Belula lutea*. The GV collection constitutes the northern limit for this species in North America, but it is known from nearly the same latitude in Newfoundland (Fig. 5-8, p. 55).

Campylium chrysophyllum (Brid.) J. Lange. Pe: *2144**; MSP: *1329*. Only two collections, from conglomerate rock, and from the eroded bank of a stream.

Campylium hispidulum (Brid.) Mitt. PG: *310a*; SJC: *849**; GV: *1507**; MSP: *1303*. Common, on rotting wood, or rock; one collection, from humus on a slope.

Ceratodon purpureus (Hedw.) Brid. SJC: *850**. Only one collection, from recently disturbed mineral soil.

Cirriphyllum piliferum (Hedw.) Grout. SJC: *835b*. Only one collection, from soil near a stream, mixed with other mosses.

Dichodontium pellucidum (Hedw.) Schimp. PG: *226a*, *228*; GV: *1546*. Occasional, on rocks near streams, usually very close to the water.

Dicranella heteromalla (Hedw.) Schimp. PG: *246**; AG: *3908**. Only two collections, from mineral soil and rotting wood adjacent to mineral soil.

Dicranum fuscescens Turn. PG: *243*; SJC: *709**; AG: *615*; Pe: *1820**; GV: *4109b**; MSP: *1008**; Fo. Common, [illegible] rotting logs.

Dicranum majus Sm. GV: *1555a*; Fo. Only one collection, from humus on a slope, near a stream.

Dicranum montanum Hedw. PG: *257**; SJC: *706**; AG: *637**; Pe: *2105**; GV: *1563*; MSP: *1025*; Fo. Very common, on rotting wood and tree bases; a few collections from trunks of *Acer saccharum*.

Dicranum polysetum Sw. Pe: *2118a*; MSP: *1027*. Occasional, on rotting *Betula lutea* logs.

Dicranum scoparium Hedw. PG: *253a*; SJC: *896a**; AG: *654**; Pe: *1708*; GV: *1574*; MSP: *1231*; Fo. Common; usually on rotting wood, but occasionally on rock or mineral soil.

Dicranum viride (Sull. & Lesq. *ex* Sull.) Lindb. PG: *836*; SJC: *3805*; AG: *560*;

Pe: *1833*; GV: *1417*; MSP: *1101*. Common, mostly as an epiphyte of *Acer saccharum*; also a few collections from bases of *Betula lutea* and *Acer rubrum*, and from rotting wood.

Diphyscium foliosum (Hedw.) Mohr. PG: *252a**. Only one collection, from soil.

Ditrichum pusillum (Hedw.) Hampe. PG: *247a**. Only one collection, from mineral soil.

Drepanocladus uncinatus (Hedw.) Warnst. PG: *220a**; SJC: *720**; AG: *3909*; Pe: *2427a**; GV: *1540*. Common, mostly on rotting wood; a few collections from tree bases, from a gravelly shore, and from seepy conglomerate.

Drummondia prorepens (Hedw.) Britt. SJC: *809*; MSP: *1104**. Occasional, on *Acer saccharum* trunks. The MSP specimen is the northernmost record for this species (Fig. 5-6, p. 53).

Eurhynchium pulchellum (Hedw.) Jenn. SJC: *891a**; GV: *4114*; MSP: *1219*. Occasional, mostly on rock or mineral soil; one collection from humus at the base of *Acer saccharum*.

Eurhynchium riparioides (Hedw.) Rich. SJC: *825a*. Only one collection, submerged in a creek.

Fissidens bryoides Hedw. *s.l.* GV: *4117a**. Only one collection, from rock.

Fissidens cristatus Wils. *ex* Mitt. SJC: *838a*; AG: *659*; Pe: *1716a*; GV: *1533*; MSP: *1230*. Common, on vertical sides of boulders; one collection from humus adjacent to a boulder. The GV specimen is the northernmost record for this species in eastern North America, but it is reported from Alaska, and Iceland.

Herzogiella turfacea (Lindb.) Iwats. PG: *242**; SJC: *853**; AG: *3906**; Pe:

*2110**; GV: *1562**; MSP: *1017**. Common, on rotting logs, particularly those of *Betula lutea*.

Heterocladium dimorphum (Brid.) B.S.G. GV: *1535*; MSP: *1322a*; Fo. Occasional, on litter or humus.

Homalia trichomanoides (Hedw.) B.S.G. PG: *227a**. Four collections from a single site, on a conglomerate cliff.

Hygroamblystegium tenax (Hedw.) Jenn. Pe: *2137a**. Only one collection, from a stream bed, with *Brachythecium rivulare*.

Hygrohypnum luridum (Hedw.) Jenn. GV: *1548**. Only one collection, from a rock on the shore of a stream.

Hylocomium pyrenaicum (Spruce) Lindb. SJC: *803*; Pe: *2119*; GV: *1554*; MSP: *4213*; Fo. Occasional, most frequently on rotting wood; also on tree bases, rocks, and litter.

Hylocomium splendens (Hedw.) B.S.G. PG: *230b*; MSP: *1326a*. Only two collections, from a rock near a stream, and from an eroded stream bank, both mixed with other mosses.

Hylocomium umbratum (Hedw.) B.S.G. SJC: *701*; Pe: *2122a*; GV: *1550*; Fo. Occasional, on rock, rotting wood, or humus.

Hypnum lindbergii Mitt. Pe: *2113a*. Only one collection, from the top of a rotting stump, among other mosses.

Hypnum pallescens (Hedw.) P. Beauv. PG: *237**; SJC: *790** & *870**; AG: *552**; Pe: *1830**; GV: *1560**; MSP: *1221**. At least one specimen (*870*) is var. *protuberans* (Brid.) Aust. Very common, mostly on rotting wood or the base of trees; a few collections from tree trunks, and rock.

Isopterygium muellerianum (Schimp.) Jaeg. & Sauerb. PG: *3719a*. Only two collections, from the same site, a seepy conglomerate rockface.

Leptobryum pyriforme (Hedw.) Wils. Pe: *2125a**. Only one collection, from the charcoal and ashes of an abandoned maple sugar boiler.

Leskeella nervosa (Brid.) Loeske PG: *327*; SJC: *865*; AG: *508*; Pe: *1802*; GV: *1559**; MSP: *1007*. Very common, on tree bases, and as an epiphyte of *Acer saccharum*; two collections from rotting wood.

Leucodon brachypus Brid. var. *andrewsianus* Crum & Anders. PG: *3703*; SJC: *720*; AG: *511*; Pe: *1849*; GV: *1406*; MSP: *1225*; Fo. Very common, as an epiphyte of *Acer saccharum*, and occasionally *Betula lutea*.

Mnium ambiguum H. Müll. PG: *223*; SJC: *833**; GV: *1544**; MSP: *1321*. Common, on diverse substrates (rock, mineral soil, humus, rotting wood, base of *Acer saccharum*), often near streams.

Mnium marginatum (With.) Brid. *ex* P. Beauv. Pe: *2141b**; GV: *1576b**. Only two collections, both near springs, on rock and on scrap metal.

Neckera pennata Hedw. PG: *3610a**; SJC: *728a**; AG: *542a**; Pe: *1851*; GV: *1414*; MSP: *1001**; Fo. Common, on bases and trunks of trees.

Oncophorus wahlenbergii Brid. PG: *349a**; MSP: *1324b**. Only two collections, from a rotting log, and from mineral soil, on an eroded bank.

Orthotrichum obtusifolium Brid. PG: *344*; AG: *3919*; Pe: *4004**; GV: *4102a*; MSP: *1011*. Common, on *Acer saccharum* trunks. I have seen another specimen, from a locality very near my stand SJC: *Belland 6818a* (NFLD), in packet with *Zygodon viridissimus*, "on maple, Cascapédia River valley, maple stand on Hwy 299, ca 10 km N of New Richmond."

Orthotrichum sordidum Sull. & Lesq. *ex* Aust. PG: 313*; SJC: 3808*; AG: 513*; Pe: 4001*; GV: 1401*; MSP: 4211*. Very common, as an epiphyte of *Acer saccharum*, and occasionally *Betula lutea*.

Orthotrichum speciosum Nees *ex* Sturm (incl. var. *elegans* (Schwaegr. *ex* Hook. & Grev.) Warnst.) AG: 3916*; Pe: 1856*; GV: 4105a*. Occasional, on *Acer saccharum* trunks.

Orthotrichum stellatum Brid. SJC: 810*; Pe: 4003a*; GV: 1343b*; MSP: 1107*. Common, on *Acer saccharum* trunks.

Oxystegus tenuirostris (Hook. & Tayl.) Steere. PG: 205a; GV: 4111; Fo. Only two collections, from rock.

Paraleucobryum longifolium (Hedw.) Loeske. PG: 231*; SJC: 702; AG: 664a*; Pe: 1836a; MSP: 1235; Fo. Common, mostly on erratic boulders; a few collections from bases of *Betula lutea* and *Fagus grandifolia*.

Plagiomnium ciliare (C. Müll.) Kop. MSP: 1325a*; Fo. Occasional, usually on mineral soil; one collection from rotting wood.

Plagiomnium cuspidatum (Hedw.) Kop. PG: 258*; SJC: 801*; AG: 534*; Pe: 1721*; GV: 1501*; MSP: 1109*; Fo. Very common, usually on humus or bases of *Acer saccharum*, sometimes on humus in cracks of bark, as high up as 2 m; a few collections from rotting wood, mineral soil, and rock.

Plagiomnium drummondii (Bruch & Schimp.) Kop. Pe: 1724a*. Only one collection, from the bark of a rotting log.

Plagiomnium medium (B.S.G.) Kop. PG: 3710*; SJC: 3811*; Pe: 2138a*; GV: 4120*. Common, near streams, usually on soil; one collection from rock, and one from dead wood.

Plagiothecium cavifolium (Brid.) Iwats. PG: *3711b**; GV: *1528**. Occasional, on rock or mineral soil, near streams.

Plagiothecium denticulatum (Hedw.) B.S.G. PG: *107**; AG: *3905**; GV: *1566b*; MSP: *1205*; Fo. Occasional, most frequently on rotting wood, and sometimes on mineral soil or bases of *Acer saccharum*.

Plagiothecium laetum B.S.G. PG: *241**; SJC: *854**; AG: *624**; Pe: *1702**; GV: *1514**; MSP: *1216**; Fo. Very common, mostly on rotting wood; a few collections from rocks.

Platydictya subtile (Hedw.) Crum. PG: *3613**; SJC: *723**; AG: *529**; Pe: *2101a**; GV: *1511**; MSP: *1024**. Common, on bases and trunks of *Acer saccharum*; a few collections from humus, rock, and the base of a *Thuja occidentalis*.

Platygyrium repens (Brid.) B.S.G. PG: *338*; SJC: *823*; AG: *516*; Pe: *1823*; GV: *1434a*; MSP: *1102*. Very common, mostly on trunks of *Acer saccharum*; a few collections from bases of *A. spicatum*, *A. rubrum*, and *Betula lutea*.

Pleurozium schreberi (Brid.) Mitt. PG: *243c*; AG: *656b*; Pe: *1706*; GV: *1524*; MSP: *1328*; Fo. Common, mostly on rotting *Abies balsamea* and *Betula lutea* logs; a few collections from unidentified rotting logs, and one from mineral soil.

Pohlia cruda (Hedw.) Lindb. PG: *226b*. Only two collections, from a conglomerate rockface.

Pohlia nutans (Hedw.) Lindb. PG: *357**; SJC: *722**; AG: *620**; Pe: *1808**; GV: *4109a**; MSP: *4206**; Fo. Common, usually on rotting wood, especially old stumps; a few collections from mineral soil.

Polytrichastrum alpinum (Hedw.) G.L. Smith. PG: *230a**; SJC: *892a*; AG: *3925*; Pe: *2139*; GV: *1539*; MSP: *1214*. Common, mostly on mineral soil; a few collections from rock, rotting wood, and humus.

Polytrichastrum longisetum (Hedw.) G.L. Smith. PG: *3701*; GV: *1527a**. Only two collections, from rotting wood.

Polytrichastrum pallidisetum (Funck) G.L. Smith. SJC: *3803*; AG: *3926*; Pe: *2123a**. Occasional, mostly on mineral soil; one collection from rotting wood. This species has not been reported previously from the Gaspé Peninsula or the Maritime Provinces, but most of the reports of *Polytrichum ohioense* Ren. & Card. (Ireland 1982; La Roi & Stringer 1976; Lepage 1944-46; Majcen 1981) probably belong here.

Polytrichum juniperinum Hedw. SJC: *892b*; AG: *616*; Pe: *2113b*; Fo. Occasional, mostly on mineral soil; one collection from rotting wood.

Ptilium crista-castrensis (Hedw.) De Not. Pe: *2117*; MSP: *1201*; Fo. Occasional, on rotting logs, usually of *Betula lutea*.

Pylaisiella intricata (Hedw.) Grout. PG: *113**; SJC: *806**; AG: *3901**; Pe: *1855**. Common, on *Acer saccharum* trunks.

Pylaisiella polyantha (Hedw.) Grout. PG: *316**; SJC: *807**; AG: *535**; Pe: *1818**; GV: *1421**; MSP: *4202a**. Very common, usually on *Acer saccharum* trunks; one collection from the trunk of a large *Betula lutea*, and one from the base of *Acer spicatum*.

Pylaisiella selwynii (Kindb.) Crum, Steere & Anders. AG: *530**; Pe: *1846a**; MSP: *4201a**. Occasional, on *Acer saccharum* trunks.

Rhizomnium appalachianum Kop. PG: *3706**. Only two collections, from wet soil and rock, both near streams.

Rhizomnium magnifolium (Horik.) Kop. GV: *1575*. Only two collections, from soil and rock, both in streams.

Rhizomnium punctatum (Hedw.) Kop. PG: *214**; SJC: *842**. Occasional, on the margin of streams, on rotting wood or mineral soil.

Schistidium gracile (Röhl.) Limpr. (*Grimmia apocarpa* Hedw. var. *gracilis* Röhl.) SJC: *826**; GV: *1570**. Only two collections, from rock.

Tetraphis pellucida Hedw. PG: *233**; SJC: *843**; AG: *623**; Pe: *1804**; GV: *1513**; MSP: *1220**; Fo. Very common, on rotting wood (especially abundant on old stumps); one collection from a rock adjacent to rotting wood.

Thuidium recognitum (Hedw.) Lindb. SJC: *835a*; Fo. Only one collection, from soil near a stream. Majcen (1981) reports the species as an epiphyte, in two Forillon National Park sugar maple stands.

Tortella tortuosa (Hedw.) Limpr. SJC: *827*; AG: *650*; Pe: *1718**. Common, on rock.

Ulota coarctata (P. Beauv.) Hamm. PG: *3604a**; SJC: *821**; AG: *3903**; Pe: *1843**; GV: *1426**; MSP: *1105**; Fo. Common, on *Acer saccharum*, mostly above a height of 5 m; one collection from the trunk of a large *Betula lutea*.

Ulota crispa (Hedw.) Brid. PG: *3604b**; SJC: *819**; AG: *518**; Pe: *1819**; GV: *1425**; MSP: *1106**; Fo. Common, on *Acer saccharum*, mostly above a height of 5 m; a few collections from *Betula lutea* trunks, and one from *Acer spicatum*.

Zygodon viridissimus (Dicks.) Brid. I have not found this species in any of my study sites, but I have seen a specimen from "Cascapédia River valley, maple stand on Hwy 299, ca 10 km N of New Richmond, on maple." *Belland 6818a* (NFLD). This locality is very close to my site SJC.

CLASS HEPATICAE

Anastrophyllum helleranum (Nees) Schuster. SJC: *711a*. Only one collection, from a rotting log of *Abies balsamea*.

Barbilophozia sp. I have not found any liverwort belonging to this genus in my study sites, but Majcen (1981) reports *B. hatcheri* (Evans) Loeske from two sugar maple stands in Forillon National Park. I was unable to see the specimens, but most of the material collected by Majcen in other forest types of the Park and labeled "*B. hatcheri*" is in my opinion *B. lycopodioides* (Wallr.) Loeske (specimens in CANM; !).

Bazzania trilobata (L.) S. Gray. Majcen (1981) reports this species from two sugar maple stands in Forillon National Park. I have not been able to see the specimens, but there is no reason to doubt the identity of such a characteristic and widespread species.

Blepharostoma trichophyllum (L.) Dumort. PG: *201*; SJC: *719a*; AG: *655b*; Pe: *2129*; GV: *1568a*; MSP: *1204a**. Common, mostly on rotting wood; a few collections from rock, one from humus, and one from mineral soil.

Cephalozia lunulifolia (Dumort.) Dumort. Pe: *1813*. Only two collections, from rotting logs.

Conocephalum conicum (L.) Lindb. PG: *218*; SJC: *3810*; GV: *1576a*. Occasional, near streams, on various substrates (rotting wood, rock, mineral soil, truck wreck)

Frullania eboracensis Gott. PG: *332**; SJC: *808**; AG: *520*; Pe: *1824**; GV: *1423**; MSP: *1033**. Very common, on the trunk of trees. The species is usually regarded as an eastern North American endemic, but it was reported from the Mongolian Republic by Abramov & Abramova (1983).

Geocalyx graveolens (Schrad.) Nees. Pe: *1705b*; GV: *1568b*. Only two collections, from rotting logs of *Betula lutea*.

Jamesoniella autumnalis (DC.) Steph. PG: *402*; SJC: *710*; AG: *632*; MSP: *1204b*. Common, on rotting wood.

Jungermannia leiantha Grolle. Pe: *2130*; GV: *1564a**; MSP: *1324a**. Occasional, usually on rotting wood; one collection from mineral soil.

Lepidozia reptans (L.) Dumort. SJC: *844*; Pe: *1803a*; GV: *1525*; Fo. Occasional, on rotting wood.

Lophocolea heterophylla (Schrad.) Dumort. PG: *321*; SJC: *876*; AG: *604*; Pe: *1711**; GV: *1557*; MSP: *1019*. Very common, usually on rotting wood; some collections from mineral soil, humus, dead bark, and an exposed root of *Acer saccharum*.

Marchantia polymorpha L. SJC: *851*; Pe: *2126a*. Only two collections, one from wet freshly disturbed mineral soil, and the other from the ashes and charcoal of an abandoned maple sugar boiler.

Metzgeria furcata (L.) Dumort. Pe: *2101b*; MSP: *1008*. Occasional: two collections from *Acer saccharum* bases, and one from the vertical side of a boulder.

Nowellia curvifolia (Dicks.) Mitt. PG: *322*; SJC: *711a*; Pe: *1705a*. Occasional, on rotting wood.

Plagiochila porelloides (Torrey ex Nees) Lindenb. PG: *205b*; SJC: *832*; Pe: *2142*; GV: *1543*; MSP: *1319*. Common, usually near streams, on various substrates (rocks, mineral soil, humus, base of trees).

Porella platyphylla (L.) Pfeiff. PG: *320**; SJC: *728b**; AG: *3923*; Pe: *1831*; GV:

1410; MSP: *1004**. Common, on trunks and bases of *Acer saccharum*; one collection from the trunk of a large *Betula lutea*. The GV collection is the northernmost record for this species in eastern North America. In western North America, this transcontinental species occurs as far north as southern Alaska (Fig. 5-9, p. 57).

Porella platyphylloidea (Schwein.) Lindb. PG: *3610b*; AG: *3902*; MSP: *4202b*. Occasional, on trunks and bases of *Acer saccharum*.

Ptilidium pulcherrimum (G.Web.) Hampe. PG: *323*; SJC: *847**; AG: *556**; Pe: *1701**; GV: *1515**; MSP: *1215*. Very common, on rotting wood, and on the trunks and/or bases of all tree species.

Radula complanata (L.) Dumort. PG: *260*; SJC: *820**; AG: *510**; Pe: *1859*; GV: *1404**; MSP: *1012**. Very common, on *Acer saccharum* trunks; one collection from a *Betula lutea* trunk, and one from the base of a *Thuja occidentalis*.

Appendix C

List of Gaspé sugar maple forest bryophytes in each distribution group, with a summary of their Eurasian distribution

The distribution groups are defined p. 24. Eurasian distribution is derived from the literature (see page 23). The following abbreviations are used: Eu, Europe; CE, central Eurasia; EA, eastern Asia. Greenland is considered part of North America, and Svalbard is considered part of Europe. Species preceded by an asterisk are endemic to North America. In each group, the species are in alphabetical order, but liverworts are listed separately after the mosses.

AZONAL SPECIES

Transcontinental:

Amblystegium serpens	Eu	CE	EA
Amblystegium varium	Eu	CE	EA
Bartramia pomiformis	Eu	CE	EA
Brachythecium plumosum	Eu	CE	EA
Brachythecium rivulare	Eu	CE	EA
Brachythecium salebrosum	Eu	CE	EA
Bryum caespiticium	Eu	CE	EA
Bryum capillare	Eu	CE	EA

Campylium chrysophyllum	Eu	CE	EA
Campylium hispidulum	Eu	CE	EA
Ceratodon purpureus	Eu	CE	EA
Dicranum montanum	Eu	CE	EA
Dicranum scoparium	Eu	CE	EA
Ditrichum pusillum	Eu	CE	EA
Eurhynchium pulchellum	Eu	CE	EA
Fissidens bryoides	Eu	CE	EA
Hypnum lindbergii	Eu	CE	EA
Hypnum pallescens	Eu	CE	EA
Leptobryum pyriforme	Eu	CE	EA
Mnium ambiguum	Eu	CE	EA
Mnium marginatum	Eu	CE	EA
**Plagiomnium ciliare*			
Plagiomnium cuspidatum	Eu	CE	EA
Plagiomnium medium	Eu	CE	EA
Pohlia nutans	Eu	CE	EA
Polytrichum juniperinum	Eu	CE	EA
Tetraphis pellucida	Eu	CE	EA
Thuidium recognitum	Eu	CE	EA
Cephalozia lunulifolia	Eu	CE	EA
Jamesoniella autumnalis	Eu	CE	EA

Marchantia polymorpha	Eu	CE	EA
Plagiochila porelloides	Eu		
Radula complanata	Eu	CE	EA

Disjunct:

Diphyscium foliosum	Eu		EA
Oxystegus tenuirostris	Eu	CE	EA
Plagiothecium cavifolium	Eu	CE	EA
Pylaisiella selwynii	Eu		EA

BOREAL SPECIES

Transcontinental:

Brachythecium reflexum	Eu	CE	EA
Brachythecium velutinum	Eu	CE	EA
Bryum weigelii	Eu	CE	EA
Dichodontium pellucidum	Eu	CE	EA
Dicranum fuscescens	Eu	CE	EA
Dicranum polysetum	Eu	CE	EA
Drepanocladus uncinatus	Eu	CE	EA
Herzogiella turfacea	Eu	CE	EA
Hygrohypnum luridum	Eu	CE	EA
Hylocomium splendens	Eu	CE	EA
Leskeella nervosa	Eu	CE	EA

Neckera pennata	Eu	CE	EA
Oncophorus wahlenbergii	Eu	CE	EA
Orthotrichum obtusifolium	Eu	CE	EA
Orthotrichum speciosum	Eu	CE	EA
Paraleucobryum longifolium	Eu	CE	EA
Plagiomnium drummondii	Eu	CE	EA
Plagiothecium denticulatum	Eu	CE	EA
Plagiothecium laetum	Eu	CE	EA
Pleurozium schreberi	Eu	CE	EA
Pohlia cruda	Eu	CE	EA
Polytrichastrum alpinum	Eu	CE	EA
Polytrichastrum longisetum	Eu	CE	EA
Ptilium crista-castrensis	Eu	CE	EA
Pylaisiella polyantha	Eu	CE	EA
Schistidium gracile	Eu	CE	EA
Tortella tortuosa	Eu	CE	EA

Blepharostoma trichophyllum	Eu	CE	EA
Lepidozia reptans	Eu	CE	EA
Ptilidium pulcherrimum	Eu	CE	EA

Disjunct:

Brachythecium erythrorrhizon	Eu	CE	EA
Brachythecium oedipodium	Eu	CE	EA

Brachythecium starkei	Eu		EA
Dicranum majus	Eu	CE	EA
Heterocladium dimorphum	Eu		
Hylocomium pyrenaicum	Eu	CE	EA
Isopterygium muellerianum	Eu	CE	EA
Orthotrichum sordidum	Eu		EA
Rhizomnium magnifolium	Eu	CE	EA

TEMPERATE SPECIES

Eastern:

Anacamptodon splachnoides	Eu	CE?	
Anomodon attenuatus	Eu	CE?	EA?
Anomodon rostratus	Eu		
Anomodon rugelii	Eu		EA
**Atrichum altecristatum*			
Brotherella recurvans			EA
**Drummondia prorepens*			
Orthotrichum stellatum	Eu		
Platygyrium repens	Eu	CE	EA

Frullania eboracensis			EA?
Nowellia curvifolia	Eu	CE	EA

Disjunct:

Bryhnia novae-angliae	Eu		EA
Callicladium haldanianum	Eu	CE	EA
Eurhynchium riparioides	Eu	CE	EA
Fissidens cristatus	Eu		EA
Homalia trichomanoides	Eu		EA
**Leucodon brachypus*			
Pylaisiella intricata			EA
Rhizomnium punctatum	Eu		

Geocalyx graveolens	Eu		EA
Jungermannia leiantha	Eu		
Metzgeria furcata	Eu		EA
Porella platyphylloidea	Eu		

Transcontinental:

Dicranella heteromalla	Eu	CE	EA
Hygroamblystegium tenax	Eu	CE	EA

Conocephalum conicum	Eu	CE	EA
Lophocolea heterophylla	Eu	CE	EA
Porella platyphylla	Eu	CE	EA

ECOTONAL SPECIES

Eastern:			
Cirriphyllum piliferum	Eu	CE	EA
Dicranum viride	Eu		EA
Platydictya subtile	Eu		EA
Polytrichastrum pallidisetum	Eu		EA
Rhizomnium appalachianum			
Ulota crispa	Eu		EA
Disjunct:			
Brachythecium populeum	Eu	CE	EA
Hylocomium umbratum	Eu	CE	EA
Ulota coarctata	Eu		
Anastrophyllum helleranum	Eu	CE	EA

Appendix D

Statistical tests

For the following contingency tables, I used the chi-square method described in Milton & Tsokos (1983), and a level of significance $\alpha = 5\%$.

D.1. Association between distribution groups and abundance

Both mosses and liverworts were used in this test, but ecotonal species had to be excluded, because their small number caused more than 20% of the expected frequencies to be less than five. The abundance classes were defined p. 23.

Null hypothesis: The proportion of rare, occasional, common, and very common bryophytes is the same in azonal, boreal, and temperate groups.

	Rare	Occ.	Common	V. C.	TOTAL
Azonal	17	6	8	6	37
Boreal	12	11	10	6	39
Temperate	9	9	5	5	28
TOTAL	38	26	23	17	104

The marginal totals are used to compute the frequencies expected under the null hypothesis:

	Rare	Occ.	Common	V. C.	TOTAL
Azonal	13.52	9.25	8.18	6.05	37
Boreal	14.25	9.75	8.63	6.38	39
Temperate	10.23	7.00	6.19	4.58	28
TOTAL	38	26	23	17	104

An "observational chi-square" value of 3.784 is obtained, which is lower than $\chi^2_{.05}(6) = 12.592$. The null hypothesis cannot be rejected, at a significance level of 5%.

D.2. Association between distribution groups and frequency

Both mosses and liverworts were used, but in order to make the expected frequencies large enough for this test, ecotonal species were excluded, and only three frequency classes were used: species found at only 1 or 2 sites, species found at 3 or 4 sites, and species found at 5 or all 6 sites.

Null hypothesis: The proportion of species found in 1 or 2 sites, in 3 or 4 sites, or in 5 or 6 sites is the same for the azonal, boreal and temperate distribution groups.

	1-2	3-4	5-6	TOTAL
Azonal	20	8	9	37
Boreal	16	8	15	39
Temperate	13	7	8	28
TOTAL	49	23	32	104

The marginal totals are used to compute the frequencies expected under the null hypothesis:

	1-2	3-4	5-6	TOTAL
Azonal	17.43	8.18	11.38	37
Boreal	18.38	8.63	12.00	39
Temperate	13.19	6.19	8.62	28
TOTAL	49	23	32	104

An "observational chi-square" value of 2.14 is obtained, which is lower than $\chi^2_{.05}(4) = 9.488$. The null hypothesis cannot be rejected, at a significance level of 5%.

D.3. Association between distribution groups and fertility

Only mosses were used in this test, since liverwort sporophytes are very short-lived. Most moss sporophytes will remain on the gametophyte year-round and would be noted during the field seasons.

Null hypothesis: The proportion of sterile and sporophyte-producing mosses is the same in all distribution groups.

	Sterile	Fertile	TOTAL
Azonal	6	26	32
Boreal	13	23	36
Temperate	8	11	19
Ecotonal	3	6	9
TOTAL	30	66	96

The marginal totals are used to compute the frequencies expected under the null hypothesis:

	Sterile	Fertile	TOTAL
Azonal	10.00	22.00	32
Boreal	11.25	24.75	36
Temperate	5.94	13.06	19
Ecotonal	2.81	6.19	9
TOTAL	30	66	96

An "observational chi-square" value of 3.78 is obtained, which is lower than $\chi^2_{.05}(3) = 7.815$. The null hypothesis cannot be rejected, at a significance level of 5%.

D.4. Association between distribution groups and main substrate

Both mosses and liverworts were used in this test, but in order to make the expected frequencies large enough for this test, ecotonal species were excluded, and main substrates were grouped in three classes: (E) bark of living trees, including tree bases; (X) dead organic substrates, *i.e.* rotting wood, humus, and litter; and (M) mineral substrates, *i.e.* rock or mineral soil. Species without a clear main substrate were excluded.

Null hypothesis: The proportion of bryophyte species growing mainly on E, X, and M substrates are the same for Azonal, Boreal, and Temperate distribution groups.

	E	X	M	TOTAL
Azonal	6	8	21	35
Boreal	6	16	11	33
Temperate	11	7	7	25
TOTAL	23	31	39	93

The marginal totals are used to compute the frequencies expected under the null hypothesis:

	E	X	M	TOTAL
Azonal	8.66	11.67	14.68	35
Boreal	8.16	11.00	13.84	33
Temperate	6.18	8.33	10.48	25
TOTAL	23	31	39	93

An "observational chi-square" value of 13.25 is obtained, which is higher than $\chi^2_{.05}(4) \doteq 9.488$. The null hypothesis is rejected, with a significance level of 5%.