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A Study Of The Effects Of Beaver Activity On Bog
Vegetation In An Area Of The Mer Bleue Bog
Near Ottawa, Canada And An Analysis Of Some Of
The Factors That Control Bog Plant Distribution
And Abundance

by

STEPHEN JOSEPH ADAMOWICZ, B.Sc., B. Ed.

A thesis submitted to the Faculty of
Graduate Studies and Research in
partial fulfillment of the requirements
for the degree of Master of Science

Department of Biology

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Ottawa, Ontario

April, 1980

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Abstract

The vegetation in the Mer Bleue bog near Ottawa, Canada has been disturbed by beaver activity beginning in about 1958. Transect data of plant distribution and abundance and selected environmental variables suggest that major changes in the vegetation are associated with a change in nutrient availability, pH, and water level. Calcium and pH appear to be the most important controlling factors. Threshold values of 5.0 for pH and 2.7 ppm for calcium are identified where major changes in the vegetation occur. Beaver activity is associated with extensive swamping and an alteration in the nutrient regime in the study area where non-bog species, primarily Typha latifolia, are beginning to flourish. Failure to manage beaver in the Mer Bleue will result in the loss of much of the bog vegetation.

The diversity states of the vegetation assemblages in the study area generally correspond to the predictions made by an hypothesis of species diversity proposed by Huston (1979).

A paradox is discussed concerning the obvious uniqueness and recognizability of many bog community types and the fact that bog species are largely distributed individualistically along environmental gradients.

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INTRODUCTION

A primary goal of ecology is to explain the patterns in the distribution and abundance of species in communities (Pielou 1975). One approach that may be used to determine the causes of these patterns involves the inspection of a community while it is undergoing disturbance. It is a fundamental assumption that changes in species distribution and abundance are in response to the disturbance.

A disturbed community is one that is being subjected to some disruptive influence that alters its structure or composition. The response of the community to disturbance reveals details of the variables or conditions that determine its composition and structure and that promote its persistence. The environmental variables whose values are changed as a result of the disturbance can be measured. These variables may be considered to be the factors controlling the adjustment in species distribution and abundance.

It is another fundamental assumption that the response to disturbance helps to identify the agents controlling the structure and composition of the community under normal or undisturbed conditions.

The degree of insight into causal relationships under disturbed and undisturbed conditions depends on

the thoroughness of enumeration and measurement of the disturbance variables. After the variables have been identified, basic techniques of analysis may be employed to characterize the results of disturbance. Changes in distribution and abundance may then be related to the changes in environmental variables.

The strength of what may be called the disturbance experiment is its formulation in reality and its consequent ability to predict changes in the disturbed community or similar communities. When the rate of change can be determined and related to the magnitude of disturbance, the predictions made from the consideration of the results of disturbance will increase in accuracy. The ability to predict changes in community structure and composition when that community is subjected to a particular disturbance is the essential foundation of community or system management.

The Mer Bleue is a large bog (6,300 acres) located about fifteen kilometers east of Ottawa. Considerable interest has been expressed in maintaining and preserving the bog (Baldwin and Mosquin 1969; Reed 1974; and others). Naturalists and scientists have a long-standing interest in the Mer Bleue (Terasmae and Mott 1964; Dore 1967; Camfield 1969; Hobson 1970; Small 1972a, 1972b, 1972c, 1974; Haber 1974; and others).

The invasion of the Mer Bleue by beaver has resulted in a large scale disturbance experiment.

Although beaver have been associated with bog development in New England (Kaye 1962) and the Hudson Bay lowlands (Sjörs 1959, p. 16), they are generally restricted to areas with deciduous trees for winter food and with suitable damsites (Heinselman 1970). Beaver have flourished in the Mer Bleue because of the deciduous trees along the bog's margins and the presence of a system of ditches excavated as a work project in 1938 (Reed 1974) or earlier as land reclamation (Ashley 1979).

Beaver damming has produced easily observed changes in the vegetation in the areas around impoundment sites. An example of such change occurs above several dam sites where dead trees, in most cases typical bog species, are found among stands of cattails that are growing amid bog vegetation. These sites contain many species that are indicators of nutrient-rich conditions (Jeglum 1971). Some of these indicator species, particularly Typha latifolia, Anchistea virginica, and a number of herbs, do not occur at undisturbed sites. It may be hypothesized that the beaver ponds are in some way involved in an increase of nutrients at these disturbed sites thereby altering the structure and composition of the bog community.

A number of reports exist in the literature that might help determine whether the vegetation changes associated with beaver activity are related to changes in the nutrient regime. The importance of various

inorganic substances have been investigated and key nutrients have been identified for bog vegetation by: Heinselman 1963, 1970; Heilman 1968; Jeglum 1971, 1972b, 1974; Clymo 1973; Small 1975; Vitt and Slack 1975; Stanek 1977; Stanek et al. 1977; Tilton 1977, 1978; and others. Other studies have been done investigating the interaction and relative importance of nutrient status and water flow as controlling factors in the distribution and abundance of bog plant species (Watt and Heinselman 1965; Sparling 1966; Armstrong and Boatman 1967; Dai 1971; and Verry 1975). These studies provide further information that might be used to clarify how beaver damming affects bog vegetation.

Not only do nutrient-demanding species occur in the bog mat along the beaver ponds, but there also appears to be an elimination of Sphagnum species at these sites. Studies on the effects of changing nutrient and moisture conditions on Sphagnum success and distribution have been done (Clymo 1963; Spearing 1972; and Clymo 1973; and Vitt and Slack 1975). These investigations might add considerably to an analysis of the vegetation changes that seem to be associated with beaver disturbance.

Areas of immediate beaver disturbance provide the opportunity to investigate the specific effects of changes in environmental variables on bog plant species in order to help define in detail the factors controlling species distribution and abundance. Also, the beaver

ponds vary in size and occur in many places along the margins of the bog resulting in an increase in the range or degree of disturbance. This range of disturbance allows for a more sensitive investigation that can, if the ages of the disturbed sites are known, include a temporal evaluation of the effects of beaver damming.

Each beaver dam can be dated from the historically complete series of aerial photographs of the bog, dating from 1945. The dating of the construction of the beaver dams provides the historical information necessary to properly evaluate the effects of beaver disturbance on the vegetation of the Mer Bleue. It is also possible, because the time of disturbance can be established, to determine the rate of change in the vegetation's composition and structure. Furthermore, large-scale vegetation changes are visible on the aerial photographs and provide for a more thorough analysis of the effects of beaver damming on the entire bog system.

The vegetation associated with beaver disturbed sites may be compared to typical bog communities that are described in the literature so that the effects of disturbance can be more adequately evaluated and the factors that control plant distribution and abundance can be more precisely determined. There exists an adequate literature on North American peatlands that describes bog, fen-marsh, and swamp plant associations in detail. Some of these studies are: Dansereau and

Segadas-Vianna 1952; Segadas-Vianna 1955; Sjörs 1961; Heinselman 1963, 1970; Jeglum 1971, 1972a, 1972b; Pollett and Bridgewater 1973; Stanek 1977; and Stanek et al. 1977. Most of these studies, and several others (Watt and Heinselman 1965; Armstrong and Boatman 1967; Clymo 1973; Dai et al. 1974; Jeglum 1974, 1975; Schwintzer and Williams 1974; Stanek 1977b; and Tilton 1978), investigated the environmental factors that characterize each bog plant association or community and that influence and control bog plant species presence and success.

Field data may also be considered within the framework of a theoretical model so that greater insight into community structure and composition may be possible and other relationships may become apparent as a consequence of the analysis. One such theoretical model that can be used to further elucidate the dynamic relationships between plant assemblages in the Mer Bleue, particularly as a consequence of beaver disturbance, is that of community succession. Succession may also be referred to as community development. There are two processes by which bogs may form, terrestrialization and paludification. The terrestrialization of limnic systems may result in a describable succession of vegetation communities that goes from an aquatic community to a facsimile of the regional climax community (Dansereau and Segadas-Vianna 1952; Hammond 1968; Camfield 1969; Swan and Gill 1970; Vitt and Slack 1975; and Griffin 1977). The rate of the

seral development is determined primarily by sedimentation rates.

The paludification of terrestrial systems allows a mire community to develop which persists as long as the water table is near the surface. The maintenance of mires as a result of paludification is primarily determined by drainage impediments. As erosion occurs or as peat accumulates the mire vegetation may be exposed to drying conditions in which case terrestriation may occur where the community will be a dry peatland, not an upland forest, that may readily undergo alteration or "regression" if disturbed (Dahl 1952; Gorham 1957; Sjörs 1959, 1961; Heinselman 1963, 1970; Malmer 1975; and Walter 1977).

Dahl (1952) describes bog succession in southern Norway (Rondane Mountains). He states that in Finland mires have expanded recently at the expense of dry land and that this paludification process is probably active in many mountain areas of Scandinavia. Dahl writes "succession in mires may be progressive; from eutrophic (nutrient-rich) communities requiring a high water table to oligotrophic (nutrient-poor) communities requiring a low water table. It may also be regressive or cyclic." Dahl suggests that the level of the bog surface rises by accumulation of peat and that this process continues until equilibrium is reached between production of organic materials by the plants and oxidation of organic materials.

He concludes that the final stage of mire succession is still a mire and that he does not know any example of the development of a mire to climax communities of dry land successions unless the mire is drained. The equilibrium stage is apparently reached at a certain thickness of peat which is determined by climate and particularly by precipitation.

In the Rondane Mountains of southern Norway the mires, according to Dahl, never develop beyond the fen stage and some fen indicators are always found, at least in the hollows. This may also be true of all sub-alpine and alpine mires in Scandinavia. The maintenance of the mire as climax is not solely determined, however, by alpine or sub-alpine conditions. Heinselman (1975) has observed the same condition in great expanses of peatland that occur in the circumpolar boreal forest, much of which is relatively flat.

Heinselman says that on wet sites in the boreal forests recycling of nutrients may be incomplete and sustained net accumulation of plant remains then begins the direct paludification of forest land. Normally, on most sites there is a gradual accumulation of raw humus on the forest floor until some disturbance destroys the old stand, initiating humus decomposition. As a result the forest will regenerate. Once paludification begins, the ionic balance and cation content of peatland waters (as controlled by water sources and water table slopes)

become decisive factors influencing vegetation and peat-land evolution.

If the water reaching the mire or bog percolates through mineral soil the concentration of available nutrients will be higher and a fen-type mire will develop. If the waters are highly deficient in mineral salts (causing a low metal-ion saturation of the peat, low pH, and mineral deficiencies for plants) the mire site will develop into the characteristic raised ombrotrophic bog that is poor in species. As long as drainage is impeded and the substrate remains saturated, the mire or bog vegetation will persist (Malmer 1975; Heinselman 1975).

Horn (1976), in a recent review of succession theory, comments that the classic example of obligatory succession often cited is the convergence of communities on sandy or boggy soil. Accumulation of organic matter from appropriately adapted plant species supposedly increases the water retention of the sandy soil or increases the depth and drainage of peat, in either case modifying the soil in favour of plant species with intermediate tolerance of aridity and dampness. He says that despite the logic of this textbook example, a careful look at communities that are described to support it shows that differences between communities are due largely to secular changes in the level of the water table. A major role of successional plants remains to be demonstrated

critically, Horn says, beyond a change in composition of only two species. He does cite, however, the clear and well-documented example of the effect of nodulated alders on the fertility of mineral soil that is exposed after glacial retreat. Other early successional plant species also have this effect and in addition insulate the soil, allowing permafrost to form in arctic and sub-arctic areas, which in turn prevents drainage and allows the development of tundra tussocks of Sphagnum mosses and sedge.

The role of mosses in bog community development should be emphasized in that they control pH, nutrient availability, and the nature and rate of peat deposition (Clymo 1963, 1973; Spearing 1972; Clymo and Reddaway 1974; Gjessing 1976; Boatman and Tomlinson 1977; Radforth 1977; Stanek 1977; Coulson and Butterfield 1978; and many others).

It may be concluded that bog community development occurs primarily as a consequence of changes in the environment that are essentially exogenous and that community development occurs in a predictable way if the environmental changes are known. A single climax community does not inevitably develop and an upland community will rarely replace a peatland vegetation community.

The application of these conclusions to a study of the factors that control bog plant distribution and

abundance is that literature descriptions of vegetation associations may be viewed as representing a real developmental series to which plant assemblages identified in the Mer Bleue may be compared in order to better define the effects of disturbance on community structure and composition and to strengthen predictions of possible future development of those plant assemblages. The developmental series described may be multidirectional and not inexorably linked to endogenous (autochthonous, autogenic) changes, but the communities with similar environments and an overlap in resident species may be considered to be related successionally. The more dissimilar the environment and community composition, the more distantly related any two communities would be.

As a consequence of these considerations, the objectives of this study are:

- 1) to describe and characterize the effects of beaver damming on vegetation structure and composition, nutrient regime, pH, and water level in a section of the Mer Bleue containing a single drainage system;
- 2) to describe the correspondence of the study areas' plant assemblages and environmental factors to bog plant associations and their characteristic environmental factors that are described in the literature;
- 3) to evaluate the relationship of the plant assemblages in the study area in terms of a developmental sequence with particular reference to disturbed sites;

- 4) to use the results of the analysis of disturbance to further define the factors that control bog species distribution and abundance;
- 5) and to investigate the nature of the influence of beaver damming on bog vegetation.

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As a result of field observation and preliminary investigation, an hypothesis is proposed concerning objective 5. The hypothesis is as follows: beaver dams function as nutrient traps, coupling adjacent ecosystems and influencing bog vegetation by increasing nutrient availability and changing hydrologic characteristics in the peat substrate. Two testable sub-hypotheses are:

- 1) the values of environmental variables that are related to plant nutrition increase as a gradient from the bog to the beaver impoundments; and 2) vegetation associated with beaver dams is indicative of nutrient-rich conditions.

METHODS

I. Time of Field Investigation and Sample Analysis

The inspection of the aerial photographs was begun in the spring of 1977 and was essentially finished in the fall of 1978. The field work was carried out during the summer of 1977. The laboratory analysis of the water samples was completed by the spring of 1978.

II. Study Area

In order to limit the scope of the field investigation, a single region of the Mer Bleue was selected that was readily accessible and small enough to be adequately sampled yet large enough to encompass an entire drainage system. The area that was chosen is found within the southwestern basin of the Mer Bleue. The study area is roughly rectangular, being bordered on the west by a Betula populifolia and Populus tremuloides woodland and on the east by an imaginary line running directly from the end of the sand island adjacent to Borthwick Ridge south to the bog margin. This area is roughly 3 km x 0.5 km.

It is possible to get to the dam sites and bog surface by walking from the end of the Borthwick Ridge Road on trails that run both west and east. Because the western two-thirds of the drainage system along the

northern edge of the study area is flooded by beaver dams, the dams themselves are the only easily walked route onto the bog in this area. The beaver ponds in the eastern one-third of the study area are not extensive enough to deny ready access to the bog proper.

III. Aerial Photograph Inspection

Aerial photograph inspection of peatlands is a standard technique in field investigations (Heinselman 1963, 1970; and others). Patterns in the distribution of major vegetation types are readily visible on the photographs. Drainage patterns are also usually detectable due to differences in colouration and reflectivity of wet and dry peats and the meso-topography of the bog surface. As well as being a source of information about vegetation structure and drainage patterns, the aerial photographs of the Mer Bleue contain historical information required to determine the date of beaver dam construction and to assess any changes in the vegetation and drainage at each dam site.

The aerial photographs used for this report are part of the National Airphoto Library of Canada (Department of Energy, Mines, and Resources in Ottawa). Dated topographic maps are furnished by the library that have marked on them the survey transects that were flown by the photographic plane. A series code is marked along

the transects that corresponds to a collection of aerial photographs. The transects that were flown over or near the Mer Bleue were recorded and the numerical code for the corresponding aerial photographs were noted. After inspecting all photographs of Mer Bleue, those judged to be of use were purchased and later assembled into mosaics. Each mosaic is composed of photographs that were taken on a single calendar date but were often made from several parallel transects.

Observations were made from aerial photographs and mosaics and outline maps in Results are reductions of overlays traced from these.

IV. Vegetation Sampling

The vegetation was sampled in 1-m² quadrats taken at 5 m intervals along line transects. Percent cover, estimated in 5% increments, and presence were recorded for each species within each quadrat. Average height within each quadrat was recorded for the shrub species.

During a preliminary survey of the study area in June, 1977, five sites were selected for transect sampling. Two of the sites are controls and occur on portions of the drainage system where there is little direct beaver disturbance. Three of the sites are beaver-disturbed sites and are located along the same drainage

ditch or series of ditches and canals that are found along most of the northern border of the study area.

At the control sites, four 100 m transects were taken approximately 25 m apart at the easternmost site and approximately 50 m apart at the westernmost site. These transects were taken perpendicular to the mineral margins of the sites into the bog vegetation. Two transects of varying length, to accommodate the proportions of the site, were taken above and below each of the three selected beaver dams.

Six transects of approximately 50 m each were taken within the center of the study area and ran parallel with the study area's east-west borders. These central transects were laid out about midway across the study area and positioned with respect to the ends of the transects above and below each dam at the three beaver disturbed sites. Two transects were taken at each of the three central sites.

The positions of the study sites and transects are shown in the Result section.

Transect sampling was chosen because of the flexibility of the method. One of the objectives of this study is to investigate patterns of vegetation distribution that are associated with beaver disturbance. Transect data best provide for a pattern analysis, where changes in plant distribution and abundance can be related to environmental factors. Also, transect data

can yield summation values that may be used to characterize the vegetation cover, and environment, of a region.

A minimum sample area of 20 m² was used to characterize the plant assemblages at each of the various study sites. The vegetation type at most of the sites is similar to an assemblage described by Segadas-Vianna (1956) as a Chamaedaphne community. This community was found to be adequately sampled with spaced quadrats of 15 m² total surface area or less. Therefore, the value of 20 m² may be considered adequate, especially since the surface area of the sites was either quite small or generally homogenous in species distribution. Site inspection over a three year period reinforced the view that the sample size was adequate to accurately represent the vegetation cover.

V. Sampling and Measurement of Environmental Variables

The most important environmental factors influencing bog plant community differentiation have been found to be pH, nutrients (particularly phosphorus and calcium), and water level (Dahl 1956; Gorham 1957; Sjörs 1959a, 1959b, 1961; Heinselman 1963, 1970; Heilman 1968; Jeglum 1971, 1972, 1974; Pollett and Bridgewater 1973; Vitt and Slack 1975; Stanek and Jeglum 1977; and others). Therefore, the following variables were selected for measurement: pH; phosphorus; potassium; calcium;

magnesium; sodium; and depth to water from the surface. Nitrogen as nitrate was also selected for measurement because of the well-known nitrogen requirement of plants.

The samples used to measure the environmental variables were collected along the same transects used to sample the vegetation located in the study area as described above. Water, or peat if water could not be obtained, was collected within 1 m of the vegetation quadrat at 5 m intervals along the transects. A broken shovel was used to chop through the Sphagnum substrate, which was interlaced with vascular plant roots, and to punch a hole into the underlying peat. The hole was then further excavated by hand to a maximum depth of about 60 cm.

Sampling was done after the entire series of holes along the transect had been dug. This allowed the holes to fill with water. Water was collected in 250 ml polyethylene bottles that were cleaned and prepared according to standard procedures. Depth to water was then measured in cm.

Preservatives were not used because of the low pH of the samples and the fact that all samples were frozen within hours after collection. The samples were also kept refrigerated after thawing during the analysis period. The samples were collected during the summer of 1977 and analyzed during the winter of 1977-1978.

Where water could not be collected, peat from several areas within the excavated hole was lightly packed into 250 ml sample bottles. Water and peat samples were brought back to the laboratory and tested for pH within six hours of collection with a standard electrode apparatus. Enough distilled water was added to the peat samples to make a slurry with moderate stirring. pH readings were taken by direct insertion of the electrode into the peat slurry or the water sample. For both types of sample, the electrode was agitated during the reading. Wet and dry peat samples were regularly measured during the summer to determine if there were any differences in pH readings. The differences were so slight that no adjustment or correction for the two sample types was considered necessary.

An attempt to measure nitrate concentration was made but abandoned because the nitrate-meter would not produce consistent or reproducible results.

During the winter of 1977-1978, the samples were thawed and filtered through fiberglass wool and standardized for measurement. Water from the peat slurries was considered to be equivalent to the water that was collected from the bottom of the excavations along the transects. Usually, the water samples were rich in peat materials and would approach the consistency of the peat slurries that were produced in the laboratory.

Phosphorus concentration was determined colorimetrically using the ammonium molybdenate-ascorbic acid colour reaction (Olsen and Dean 1965). Potassium concentration was determined by flame emission spectrophotometry and calcium, magnesium, and sodium concentrations were determined by atomic absorption spectrophotometry (McKeague 1976). The actual ppm concentrations of the nutrients were estimated from peak heights on print-out sheets that were produced by the spectrophotometric recorder.

The values of the environmental variables measured above and below each beaver dam and at the control sites were analyzed graphically and statistically. Twenty samples were used to characterize each study site. As mentioned above, all of the samples used to characterize the study sites or for the pattern analysis corresponded to the vegetation quadrats.

VI. Statistical Tests and Numerical Analysis

The calculation of the Quotient of Similarity between plant assemblage pairs from the study area followed Southwood (1975, p. 333). The abundance-rank figures constructed for the vegetation at each of the study sites were patterned after Whittaker (1972). The formulae used for the calculation of the Simpson indices of dominance and diversity were taken from Pielou (1975).

pp. 8-9). All of the statistical tests followed Zar (1974).

Following are the statistical tests used, the application of the test, and the reference pages from Zar: t-tests of sample means used to verify site designations, pp. 105-107; regression lines used to generalize the patterns observed in the transect data, pp. 199-203; correlation analysis of selected biotic and abiotic factors used to clarify the degree of association between these selected factors, pp. 236-238; and the mean square successive difference test used to test for gradients in the transect data, pp. 305-306.

All of the statistical tests were used to analyze environmental data except for the correlation analysis, which included the height values of Chamaedaphne calyculata.

RESULTS - INTRODUCTION

All figures and photographs that are referred to in the Results section are sequestered in numerical series at the end of the section beginning on page 90. All tables follow the page where they are first mentioned. It is hoped that this arrangement will provide for the clearest presentation of the data and avoid unnecessary dissection of the text.

RESULTS

I. Aerial Photograph InspectionA. Mer Bleue Drainage System

The drainage system of the Mer Bleue as shown on Figures 1 and 2 has increased in extent since 1945. The last major excavation project occurred in 1938 (Ashley 1979) so that the development of drainage ditches in the northwest and southwest regions of the bog must be attributed to other factors. All of these drainage ditches become more pronounced after beaver invaded the bog, about 1957. The extension of these ditches and their maintenance may be attributed to beaver activity. This is certainly true of the southeast lobe of the Mer Bleue where beaver are actively constructing and maintaining canals in areas where drainage ditches were not dug.

The question marks on Figure 2 represent areas on the 1945 aerial photograph where the drainage ditch could not be clearly identified. Most probably, they had become congested with vegetation and obscured by overhanging shrubs and trees. The irregular features in the central portion of the bog are sandy ridges or islands and are not bordered by man-made drainage ditches.

B. Location of Beaver Dams in the Mer Bleue

Figures 3-5 show the drainage system of 1977 and the positions of beaver dams that were evident on the 1958, 1965, and 1975 aerial photographs. Those sites that could not be unquestionably identified as beaver dams but display features associated with easily identified dam sites are shown with a question mark.

Beaver invasion of the Mer Bleue began in 1958 or a little earlier. Four dams are visible on the 1958 aerial photograph. These dams are widespread so that it would seem that beaver invasion involved more than one colonizing pair. Beaver activity has been concentrated around the western and southeastern sections, with a steadily increasing expansion into unoccupied areas. The study area was one of the last sections of the Mer Bleue to be occupied, except for the very western section near Anderson Road where beaver may have been active since 1956 or 1957.

Many smaller dams are not visible on the small-scale aerial photographs. Only one of the four dam sites shown on the southern border of the sandy ridge just east of the major ridge bordering the study area (Borthwick Ridge) is visible on the 1975 small-scale photograph. The other three are shown because they can be seen on large-scale aerial photographs and because they were investigated in the field. Other regions of the Mer Bleue were not examined in such detail so that

the number of dams shown on Figure 3 is probably less than the actual number present in the Mer Bleue in 1975.

C. Number of Beaver Dams in the Mer Bleue Over Time

Figure 6 shows the exponential-like increase in the number of beaver dams that are visible on the aerial photographs. The vertical bars are maximum-minimum lines. This figure indicates that the expansion of the beaver population in the Mer Bleue may continue for some time, assuming that the number of dams reflects the number of beaver. The relationship may be valid up to a point but, as will be seen in the study area, beaver may manage a water system so that a single lodge, or two, will be associated with several dams.

D. General Patterns in Beaver Dam Development and Vegetation Change in the Study Area

1. Current Status (1977) of Study Area and Location of the Study Regions and Study Sites.

The vegetation in the study area is presently very patchy. Study sites A1, B1, and C1 are relatively wet areas while site D1 is dry. Site A1 is covered by sparsely growing ericaceous shrubs, cotton-grass and a solid carpet of Sphagnum moss. Site C1, from the transition with site B1 to the area just south of region 7, is covered with Larix laricina and an understory of

ericaceous shrubs. Site D1 is characterized by a mixture of ericaceous shrubs and an open aspect, as well as by well developed hummocks. The region of Larix laricina abundance is shown as the patterned feature on Figure 7 south of regions 2 to 7. The margin sites are characterized by fen-type vegetation at regions 1, 2, 3, and 4, and by marsh-type vegetation at regions 6, 7, 8, 9, 10, and 11. Region 12 is characterized by tall shrubs. Detailed descriptions of the vegetation assemblages are given in part II of the Results. 7

The location of beaver dams and the extent of the ponds associated with the dams are shown on Figure 7. In 1977 there were eight beaver dams with ponds in the study area. In 1977 the dam at region 5 was opened by beaver and the pond was allowed to drain. Currently (1979), the dam has been closed so that a pond is again developing at region 5. The dam at region 3 was closed in 1977, opened in 1978, and partially closed in 1979. The pond level has fluctuated accordingly.

The beaver dams and ponds are largest at regions 7, 8, 9, 10, and 11. The dams at region 7 and 8 were also allowed to lose water over the summer of 1977. The implications of this dam manipulation by the beaver will be discussed in part IV of the Results.

The study sites are shown on Figure 7 as A1, A2, B1, B2, C1, C2, D1, D2, and D3. The sites designated by a letter and the number 1 are central heath sites. The

sites designated by a letter and the number 2 or 3 are margin sites. Study sites B2, C2, and D2 have been disturbed by beaver activity. All the site designations refer to a vegetation assemblage found at certain of the study regions as shown on Figure 7.

The entire western portion of the study area is covered with Typha marsh that grades into a wooded bog between regions 9 and 11 that contains Betula populifolia, Acer rubrum, Populus tremuloides, Salix spp., and Alnus rugosa. This area was not investigated in detail. Nor was the southern margin of the study area investigated in detail from an area even with region 7 to the area even with region 1.

2. History of the Study Area.

The series of Figures 7-10 represent the onset and development of beaver damming in the study area. The dates of construction of each beaver dam are shown on Figure 7. The dashed lines in Figures 8-10 represent the old system of drainage ditches. By 1977 these ditches had been obscured by beaver activity.

The first beaver dam in the study area was constructed at region 5 in 1968. The study area was essentially devoid of trees except for scattered Larix laricina in the eastern end within the area defined by the dashed line. Larix laricina individuals were distinguished on the air photos from Picea mariana when the

larch had dropped their leaves. Larix laricina individuals were distinguished from broad-leaved trees by the conical shape of larch shadows on the aerial photographs. All of the information shown on Figures 8-10 was not derived solely from the aerial photograph of that date but from inspections of many photographs that overlapped in scale and season.

The margin vegetation was much less extensive in 1968 with much of the vegetation being composed of deciduous broad-leaved trees and shrubs. The areas with marsh or fen vegetation generally show up as very light spots in late summer or early fall air photos. There is little evidence on the 1968 air photos of the fen vegetation presently found along the southern edge of the sandy "island" in the northeast of the study area. Vegetation along the edge of region 7 was marsh-like and forest-like. It is likely that this region was very wet in 1968 and marsh-like vegetation (primarily Typha) was growing below a fairly open canopy of broad-leaved trees and tall shrubs. This view is reinforced by the presence of dead trees in the Typha marshes that have developed above each dam site at regions 7 and 8.

From 1970-1971, the transformation of the study area by beaver damming was rapid. The dates established for the dam sites show that the initial invasion point at region 5 was followed by dam construction toward the west along the northern edge of the study area. Beginning

in 1972, the construction of dams began in the eastern area along the northern edge. This was accompanied by dam construction along the northern and southern edges of the western end of the study area. It would seem that beaver developed a system of dams at region 5, 7, and 8 and subsequently expanded the system in both directions. This may be indicative of pressure on the population to expand into available habitat or a response by the beaver to manage water levels in their ponds and canals. This will be pursued in part IV of the Results.

Two beaver lodges occur at region 4, one at region 7 and there is evidence of one at region 8. Others may exist in the study area but were not seen. There may be two distinct family groups working in the study area. One group would be working the eastern end from region 2 to 4. The other group could be working the western end from region 5 to region 10. Region 11 may be part of the western system or may represent a third group of beavers beginning the invasion of the southern edge of the study area.

However, a canal is maintained below the dam at region 4 and the entire northern edge of the study area is a single system of canals and ponds. It is possible that the entire system is being controlled, although this is highly speculative. Certainly the area west of region 5, including region 5, is being managed as is the area east of region 5.

The drainage pattern in the study area involves the flow of water from north of region 5 and from the northeast around the eastern end of the sandy "island". The pattern of Larix laricina distribution may reflect the hydrologic changes that have been evident in the study area since 1968 and perhaps began as early as 1956-1958. The occurrence of Larix laricina in the study area is associated with the development of a Typha marsh in the very western section of the study area east of Anderson Road. The pattern of Larix laricina development coincides with the increasing activity of beaver and the size of the pond at region 7. The impression of profound hydrologic changes in the study area associated with beaver damming is strong and is shown on the series of Figures 7-10.

Larix laricina is positively associated with nutrient-rich conditions (Jeglum 1971) and areas of pronounced water movement in the substrate (Dai 1971).

II. Vegetation: Description and Characterization

A. Study Regions, Study Sites, and Transect Location

1. Descriptions and Photographs.

a. Region 1

Region 1 is shown on photographs 1-5. Photographs 1, 2, and 3 were taken from the west of region 1 and

exemplify the fen-like nature of the edge vegetation where Alnus rugosa occurs in scattered pockets and where the edge is characterized by tall shrubs. This is best shown on photograph 3. The sample area is visible in the right background of photograph 3 and in the foreground of photographs 4 and 5. The well-defined edge of the Carex rostrata zone is quite visible in photographs 4 and 5. The Carex rostrata zone defines site A2 while site A1 begins to the right of this zone and extends into the bog. Note the very open aspect of site A1 and the flat topography.

The vegetation at sites A1 and A2 is supported by a continuous mat of Sphagnum species, primarily S. rubellum and S. magellanicum at site A1 and S. rubellum, S. magellanicum, S. papillosum, and S. fallax at site A2. The Carex rostrata sward becomes very dense right at the margin of site A2 and thins toward the open bog. The ericaceous cover of site A1 (primarily Chamaedaphne calyculata, Ledum groenlandicum, and Gaylussacia baccata) is short and finger-like.

This region is quite wet but standing water is found only along the margin of site A2.

Four transects were taken in region 1, two in July and two in August of 1977. The transects were 100 meters long and were spaced about 20 meters apart. They ran from the margin of site A2 toward the open bog, or from the left to the right of photographs 4 and 5,

b. Region 2

Region 2 is a beaver dam site constructed in about 1972. It is located between region 1 and region 3. No detailed information was collected for region 2.

c. Region 3

There are six photographs representing region 3. Photographs 1-5 were taken in 1978 and photograph 6 was taken in 1979. Photograph 1, 2, and 5 were taken from the west. The first and second photographs show the area below the dam site, marked by the Salix and Alnus growth in photograph 1, 3, and 5. The fresh excavations in the drainage canal are clearly visible on photograph 2. Site B2 is located above the dam and can be seen on photographs 3, 4, and 5. Site B1 lies beyond and to the right in photograph 1.

The fourth photograph shows the area just above the dam, designated site B2, and is characterized by fen and open water species (Juncus, Scirpus, Carex, Eleocharis, and Calla). Chamaedaphne calyculata is also very robust above the dam and is visible on photographs 3 and 5 as the dark, shrubby growth. The water level was much higher in this pond during the summer of 1977. The dam was opened in 1978, as seen in photograph 3, and the pond was drained. In 1979, the dam was partially closed.

The vegetation of site B1, represented by photograph 6, is characterized by Sphagnum hummocks and

hollows occupied by Chamaedaphne calyculata, Eriophorum spp., Vaccinium species, and Ledum groenlandicum, among others. Scattered Larix laricina also can be seen on photographs 1 and 6. All the shrubs at site B1 show more bushy lateral growth than those at site A1.

The position of the transects at region 3 are shown on Figure 11 as is the general vegetation distribution. The data from portions of these transects as well as two more positioned about two hundred meters south of the dam at region 3 were used to characterize site B1 (section II B 1 of the Results).

d. Region 4

Seven photographs represent region 4. The first three photographs show the beaver pond, dam, and surrounding vegetation. The last four photographs show the vegetation that is partially visible in the background of the first three photographs and essentially represent site C1. The first three photographs were taken, looking southeast to southwest and the last four were taken at intervals while walking westward from site B1 toward the Typha marsh south of regions 6 and 7.

The area immediately above the dam, from which the photograph 1 was taken represents site C2. This area is characterized by a mixture of fen and bog species such as Carex rostrata, Carex oligosperma, other Carex spp., Typha latifolia, Anchistea virginica, Iris versicolor,

Chamaedaphne calyculata, and Sphagnum spp. (S. magellanicum, S. rubellum, S. papillosum, S. fallax). Dead or dying Larix laricina and Betula populifolia can be seen in this area.

Photograph 2 shows the vegetation growing on the dam itself. Notice the Galium sp., Typha sp., graminoids, and Alnus rugosa, with the Larix stand visible in the background. Photograph 3 shows the Typha bed just below the dam and the park-like nature of the Larix laricina stand.

Photographs 4 and 5 show the hummock-hollow character of the understory at site C1. The Sphagnum mat is primarily S. rubellum and S. magellanicum, which supports Ledum groenlandicum, Chamaedaphne calyculata, Vaccinium spp., Eriophorum spp., and scattered old and young Betula populifolia, the largest of which are dead or dying. Scirpus acutis and Carex oligosperma also occur at site C1.

Photographs 6 and 7 show the increasing abundance of Typha as the marsh below regions 6 and 7 is approached. The understory vegetation changes dramatically as fen sedges, herbs, and mosses replace almost all of the more typical bog species until a solid sward of Typha prevails. The grass-like growth in photograph 7 may be in the genus Rhynchospora. Note also the Spiraea sp. The moss cover is almost pure Polytrichum strictum.

Figure 12 shows the location of the transects. The basic vegetation distributions are also shown on Figure 12. Note also two beaver lodges at region 4.

Photographs 1, 2, and 3 were taken in 1978 while photographs 4, 5, 6, and 7 were taken during the summer of 1979. The low water level shown in the pond at region 4 coincides with generally low water levels in the ponds at regions 7 and 8 relative to water levels in 1977 and 1979. Recall that the dam at region 3 was opened in 1978. The dam at region 5 was also allowed to drain water from the canal just above the dam. This may be interpreted as intentional water management by the beaver where water from regions 1, 2, and 3 was used to keep the entrances to the lodges at region 4 flooded and where water from region 5 was used to maintain water levels in the pond at region 8. The dam at region 7 also was allowed to drain pond water during the summer of 1977. There is a lodge in the pond at region 7 and it would seem that the resident beaver would have had little trouble maintaining water levels around the lodge. The water loss from the pond at region 7 may be incidental or it may reflect beaver behaviour that results in overall water management. The behaviour of the beaver in the eastern portion of the study area is unquestionably involved in system-level water management.

During the high water period of the fall of 1978, the dam at region 8 also was allowed to drain.

The data from portions of the transects shown on Figure 12 as well as two others about two hundred meters south of the dam at region 4 were used to characterize site C1 (section II B 1 of Results).

e. Region 5

Region 5 was not investigated in detail. The pond was drained during the summer of 1977. This was followed by an invasion of the exposed substrate by Typha spp., Polygonum sp., herbs, and sedges. The dam was tightened in 1978 and this area was reflooded. Most of the herbs disappeared, but many of the fen and marsh species persisted except in the deeper parts.

f. Region 6

It is uncertain whether region 6 constitutes a real dam site. There appears to be a great deal of beaver activity in the area and earlier aerial photographs indicate some dam-like features. A distinct dam site is not evident in this area now. The whole of region 6 is highly swamped, characterized by Typha and dead or dying broad-leaved trees and the shrubs Alnus rugosa and Salix spp.

g. Region 7

The dam at region 7 dates from 1969. Detailed vegetation and environmental data were taken in this region during June, 1977. The area was not sampled during July and August and the site was abandoned as a primary

study site in favour of region 8. The marginal vegetation at region 7, above and below the dam, is very similar to region 8.

The most notable feature about region 7 is the extensive Typha marsh that begins at the margin of the region just above the dam and extends into the area just south of region 6.

h. Region 8

Region 8 is represented by nine photographs. The dam was constructed in 1971 and has caused major changes in the vegetation. Figure 13 should be consulted as the features on the photographs are described.

Photographs 1 and 2 were taken from the end of the dam reaching into the bog and facing northeast and east respectively. The beaver dam is on the very left of photograph 1. The whole area has developed into a Typha marsh. Dead trees show on both photographs. The area immediately to the west of photographs 1 and 2 is shown on photographs 3, 4, and 5. The third and fourth photographs show a highly disturbed area with many of the Populus tremuloides and Acer rubrum harvested by beaver. There is evidence that this area has regenerated from previous beaver logging in that many of the Populus stumps are old (note fungus encrusted stump in right foreground of photograph 3). There is much new growth and many of the larger individuals are being harvested. The understory is composed of Calamagrostis communis,

Table 3

Species Richness and Quotients of Similarity:

a. For Field Layer

<u>Site</u>	<u>Richness</u>	<u>Site</u>	<u>Richness</u>	<u>Similarity</u>
A1	8	A2	14	.64
B1	15	B2	13	.50
C1	17	C2	24	.53
D1	10	D2	17	.63
D1	10	D3	20	.56
A1	8	B1	15	.52
A1	8	C1	17	.48
A1	8	D1	10	.56
B1	15	C1	17	.63
B1	15	D1	10	.56
C1	17	D1	10	.59

b. For All Strata

<u>Site</u>	<u>Richness</u>	<u>Site</u>	<u>Richness</u>	<u>Similarity</u>
A1	11	A2	20	.64
B1	22	B2	20	.52
C1	26	C2	32	.52
D1	14	D2	24	.63
D1	14	D3	26	.65
A1	11	B1	22	.55
A1	11	C1	26	.49
A1	11	D1	14	.64
B1	22	C1	26	.71
B1	22	D1	14	.61
C1	26	D1	14	.55

position of the beaver dam.

Photograph 9 shows the edge vegetation due west of the dam site. The trees are Larix laricina and Betula populifolia. The shrubs to the left of the Typha are Chamaedaphne calyculata, Gaylussacia baccata, and Kalmia angustifolia, with scattered clumps of Vaccinium spp. Growing amid the Typha bed are Spiraea spp., Vaccinium spp., and other tall shrubs.

The abrupt edge of the Typha bed should be noted. The area above the dam grades from a pure Typha marsh along the water's edge to an open bog that is vegetatively homogeneous across to the transition belt along the southern boundary of the study area. As the Typha becomes more abundant above the dam at region 8, Sphagnum hummocks and their associated ericaceous shrubs become less so. Between about twenty meters from the water's edge and about forty meters from the water's edge, the vegetation is made up of extremely tall and stringy Chamaedaphne shrubs and loose hummocks of Sphagnum rubellum and S. magellanicum.

i. Regions 9, 10 and 11

Regions 9 and 11 were marked by the construction of dams in 1973. The dam at region 10 was constructed in 1974. These sites were not investigated in detail.

j. Region 12

This region is shown on photographs 1, 2, 3, 4, and 5 and encompasses the open bog and the transition area to the Alnus rugosa swamp that occurs along most of the southern border of the study area.

Photograph 1 was taken near region 8 and faces south, showing the open bog of site D1 and the transition zone of site D3 to the left middleground. Site D1 is extremely homogeneous and is almost entirely Chamaedaphne calyculata, Gaylussacia baccata, and Kalmia angustifolia growing in hummocks of Sphagnum rubellum, S. magellanicum, and S. nemoreum. Scattered patches of Vaccinium spp. also occur.

The transition zone from the open bog to the Alnus rugosa swamp constitutes site D3 and is shown on photographs 3 and 4, which were taken facing the southeast, and 5 and 6, which were taken facing due south. Photographs 3 and 5 show in more detail the vegetation, composed of ericaceous shrubs, scattered Alnus and Typha, and tall shrubs such as Aronia melanocarpa, Nemopanthus mucronata, and Viburnum cassinoides. All the shrubs are taller just at the transition zone.

Four transects were taken at region 12, two in July and two in August. The transects were positioned about fifty meters apart and ran directly into the open bog from the edge of the Alnus swamp toward region 8.

Transects taken at site D1 were perpendicular to the transects from region 8 and 12 about half way between the two regions in the open bog. Data from portions of the transects from region 8 and 12 were used to characterize site D1 (part II B 1 of the Results).

2., Field Maps of Beaver-disturbed Regions.

Field maps of region 3, 4, and 8 are shown on Figures 11, 12, and 13, respectively. Major vegetation zones are shown on each figure as well as the position and date of each transect line. Each transect is numbered. Six transects were taken at each beaver-disturbed region, two above and two below the dam and two in the central heath. The transects taken in the central heath were positioned about two hundred meters into the bog, in line with the dam and perpendicular to the mineral margins of the study area. The transect data is in Appendix A where the transect numbers correspond to the designations on Figures 11, 12, and 13.

The species found in each of the zones are listed after the matching symbol in the legend facing each Figure.

The most striking feature of the three field maps is that the Typha marsh undergoes progressive enlargement from region 3 to region 8 in the area above the beaver dam. The dam at region 3 is about a year older than the dam at region 4 so that the expansion of the Typha marsh

must be linked to factors other than duration of disturbance.

Field inspection of regions 3 and 4 during the summer of 1979 showed that the Typha marsh is expanding rapidly in both regions.

B. Plant Assemblage Description and Characterization of Study Sites

1. Demarcation of Plant Assemblages.

In order to describe the demarcation of the plant assemblages in the study area, the following will be consulted: Figure 6; sections II A 1 and II A 2 of the Results; Appendix A; and Appendix C. Appendix A transect data is the primary reference and was used to determine the boundaries of the plant assemblages. Appendix C shows percent cover data that were selected from Appendix A and used for the site descriptions and characterization. Because of the correspondence of vegetation and environmental data, the same sample points were used to characterize the environments of the plant assemblages. These data are in Appendix D. The entire set of environmental data from the transects were combined for corresponding points along related transects and are shown on Figures 19-26.

Twenty sample points were used to characterize each site.

a. Sites A1-A2

The boundary between sites A1 and A2 is well defined by the limits of Carex rostrata growth. The sections on all four transects taken at region 1 from zero to forty-five meters were used to describe site A2. The section from fifty to one-hundred meters was used to describe site A1. Site A1 is physiognomically and vegetatively unchanged from the boundary of the Carex rostrata sward to the very southeast of the study area. It was considered unnecessary to collect further data two-hundred meters from the mineral margin of the site as was done for regions 3, 4, 8, and 12.

b. Sites B1 and B2

Only the transect data from above the dam were used to characterize site B2. The twenty sample points were taken from the first forty-five meters of both transects that were taken in this area. The vegetation typical of the central heath began about one-hundred meters from the beginning of the transects above the dam. This happened because the direction of the transects caused much of the two transects to fall on the very wet, spongy and open Chamaedaphne-fen sedge assemblage.

Both of the transects from the central heath were used to characterize site B1 along with the last sections of the transects taken below the dam. The transects below the dam angled directly into the central heath vegetation characterized by scattered individuals of

Larix laricina and Betula populifolia and ericaceous shrubs such as Chamaedaphne calyculata, Ledum groenlandicum, Kalmia angustifolia, and Gaylussacia baccata. None of the last three shrubs mentioned were important in the area above the dam described as site B2.

c. Sites C1 and C2

The same considerations apply to the differentiation of sites C1 and C2 as applied to sites B1 and B2. The first forty-five meters of the two transects taken above the dam were used to describe site C2. The two transects taken in the central heath as well as the sections beyond thirty meters of the two transects taken below the dam were used to describe site C1. The demarcation point for the two transects taken below the dam with respect to site designation involved the distribution of ericaceous shrubs, as at sites B1 and B2. The shrubs Ledum groenlandicum, Kalmia angustifolia, and Vaccinium spp. only occurred and became abundant about the twenty to twenty-five meter mark.

d. Sites D1 and D2

Site D2 may be readily defined as the area between the beaver pond above the dam and the outer boundary of the Typha bed toward the central heath or open bog. The first ninety meters of the two transects taken in this area adequately represent site D2. Site D2 grades from a pure Typha marsh to a mixture of Typha and bog species.

Site D1 is described by the data from the central transects and the very ends of all four transects taken in region 8. The transition zones are very obvious and there is little chance of confusing vegetation types in this area. Site D1 is extremely homogeneous from the boundaries of the Typha bed and tall shrub zone of region 8 to the narrow transition zone of site D3 that grades to the Alnus rugosa swamp. The last four sample points from the transects taken at region 12 also were used to describe site D1.

e. Site D3

Four transects were taken at this region. The distributions of the tall shrubs Nemopanthus mucronata, Viburnum cassinoides, Aronia melanocarpa, and Ilex verticillata were used to define site D3. All of these shrubs occurred within the first ninety meters of the transects and were virtually absent in the central heath. The area of greatest abundance of these shrubs, as well as where species such as Typha spp., Alnus rugosa, Acer rubrum, Solidago sp., and Spiraea sp. occurred, was within the first forty meters of each transect so that twenty sample points from this area were used to describe site D3.

2. Species' Presence and Abundance in Each Site.

a. Study Sites A1, B1, C1, D1, and D3.

The species found in the central heath study sites and site D3 are shown on Table 1A. The distribution and abundance of the plant species seems to represent a shift in species composition from a wet, nutrient-poor site dominated by Sphagnum spp., Chamaedaphne calyculata, and Eriophorum spp. to a relatively dry, nutrient rich site dominated by nutrient-demanding species such as Nemopanthus mucronata and Viburnum cassinoides. Although this, in general terms, fairly well represents the site relationships as reflected by the environmental data (see sections II B 5 and III D of Results), the actual relationships are more complex. Site relationships are thoroughly examined in part I of the Discussion.

b. Study Sites A2, B2, C2, and D2.

Species present at these sites are shown in Table 1B. The species that occur at site A2 and the three beaver-disturbed sites may also be arranged to form a series where moisture-loving fen-type plants such as Smilacina trifolia, Carex limosa, C. prairea, and Carex rostrata are gradually replaced by less water-tolerant or more nutrient-demanding species such as Nemopanthus mucronata, Typha latifolia, Aronia melanocarpa, and Calamagrostis canadensis. This shift in the environment represented by the change in species composition is supported by the data presented on Figures 14-18 and

Table 1A

Species Present at Sites A1, B1, C1, D1, and D3 With Mean % Cover Values of Non-Tree Vascular Plants ($\pm 5\%$, $n = 20\%$).*

Species	Study Sites				
	A1	B1	C1	D1	D3
<u>Eriophorum chamissonis</u>	13.00	+			
<u>Eriophorum tenellum</u>	2.50		+		
<u>Sphagnum rubellum</u>	+	+	+	+	+
<u>Polytrichum strictum</u>	+	+	+	+	+
<u>Sphagnum magellanicum</u>	+	+	+	+	+
<u>Vaccinium oxycoccos</u>	+	+	+	+	+
<u>Kalmia polifolia</u>	+		+		+
<u>Kalmia angustifolia</u>	.75	.50	7.25	10.50	6.25
<u>Chamaedaphne calyculata</u>	30.75	36.75	17.25	35.00	32.00
<u>Ledum groenlandicum</u>	8.25	1.75	26.50	1.50	5.00
<u>Gaylussacia baccata</u>	1.50	.50	1.50	32.50	13.75
<u>Eriophorum opacum</u>		+	1.25		
<u>Carex trisperma</u>		.25			
<u>Vaccinium sp.</u>		3.00	.50	+	+
<u>Tridenum virginicum</u>		+			
<u>Spinea tomentosa</u>		+			
<u>Scirpus acutis</u>		+	+		
<u>Eriophorum sp.</u>		17.25	.2.75	+	.25
<u>Galium sp.</u>		+			
<u>Andromeda polifolia</u>		+	+	+	.25
<u>Larix laricina</u>		+	+		
<u>Typha latifolia</u>		+	+		+
<u>Eriophorum virginicum</u>		+	4.50		.50
<u>Betula populifolia</u>		+	+		
<u>Alnus rugosa</u>		+	+		4.50
<u>Sphagnum nemoreum</u>			+	+	+
<u>Populus tremuloides</u>			+		
<u>Smilacina trifolium</u>			+		
<u>Scirpus atrovirens</u>			+		
<u>Scirpus sp.</u>			+		

Table 1A (Cont'd)

Species	Study Sites				
	Al	B1	C1	D1	D3
<u>Sphagnum fallax</u>			+		
<u>Anchistea</u> (Woodwardia) <u>virginica</u>			+		
<u>Nemopanthus mucronata</u>				.50	4.00
<u>Gaylussacia dumosa</u>				+	+
<u>Carex practicola</u>				+	
<u>Acer rubrum</u>					+
<u>Ilex verticillata</u>					+
<u>Sarracenia purpurea</u>					+
<u>Solidago</u> sp.					+
<u>Carex oligosperma</u>					+
<u>Viburnum cassinoides</u>					1.50
<u>Spiraea</u> sp.					1.50
<u>Aronia melanocarpa</u>					7.00

*Original data and calculation of means in Appendix C.

Table 1B

Species Present at Sites A2, B2, C2, and D2 With Mean % Cover Values of Non-Tree Vascular Plants ($\pm 5\%$, $n = 20$).

Species	Study Sites			
	A2	B2	C2	D2
<u>Smilacina trifolium</u>	+			
<u>Carex limosa</u>	+			
<u>Cladium mariscoides</u>	.50			
<u>Carex prairea</u>	1.50			
<u>Eriophorum chamissonis</u>	+	+		
<u>Tridentium virginicum</u>	+			
<u>Carex rostrata</u>	11.25	+		
<u>Eriophorum tenellum</u>	6.25	+	+	
<u>Carex oligosperma</u>	+	+	+	
<u>Sphagnum fallax</u>	+	+	+	
<u>Chamaedaphne calyculata</u>	24.00	58.25	47.00	22.00
<u>Kalmia polifolia</u>	+			+
<u>Ledum groenlandicum</u>	+	.50	1.25	+
<u>Vaccinium oxycoccos</u>	+		+	+
<u>Spiraea sp.</u>	+			+
<u>Kalmia angustifolia</u>	+	+		6.25
<u>Sphagnum papillosum</u>	+	+	+	+
<u>Sphagnum magellanicum</u>	+	+	+	+
<u>Sphagnum rubellum</u>	+	+	+	+
<u>Polytrichum strictum</u>	+	+	+	+
<u>Eriophorum opacum</u>		3.00	+	
<u>Larix laricina</u>		+		
<u>Carex sp.</u>		.75	4.75	
<u>Nemopanthus mucronata</u>		+		6.50
<u>Eriophorum sp.</u>		7.50	1.00	
<u>Juncus effuses</u>		+		+
<u>Scirpus atrovirens</u>		+		
<u>Gaylussacia baccata</u>		+		9.50
<u>Vaccinium sp.</u>		+	+	8.25
<u>Sphagnum nemoreum</u>		+	+	+

Table 1B (Cont'd)

Species	Study Sites			
	A2	B2	C2	D2
<u>Typha latifolia</u>		+	+	13.25
<u>Solidago sp.</u>			+	
<u>Eriophorum virginicum</u>			2.50	
<u>Eupatorium perfoliatum</u>			+	
<u>Scirpus acutis</u>			3.50	
<u>Ludwigia palustris</u>			+	
<u>Scirpus sp.</u>			1.00	
<u>Bidens sp.</u>			+	
<u>Betula populifolia</u>			+	
<u>Alnus rugosa</u>			+	
<u>Picea mariana</u>			+	
<u>Galium sp.</u>			+	
<u>Mentha sp.</u>			+	
<u>Iris versicolor</u>			+	
<u>Carex practicola</u>			+	
<u>Carex miliaris</u>			+	
<u>Eleocharis obtusa</u>			+	
<u>Anchistea (Woodwardia) virginica</u>			+	
<u>Gaylussacia dumosa</u>				+
<u>Andromeda polifolia</u>				+
<u>Aronia melanocarpa</u>				4.50
<u>Typha angustifolia</u>				+
<u>Calamagrostis canadensis</u>				7.50
<u>Myrica anomala</u>				+

32-37.

An obvious feature of Table 1B is the initial increase in species numbers at site B2 and C2 followed by the reduction in species numbers at site D2. The cause of this may be related to the increasing abundance of Typha latifolia at site D3. It seems that little else can grow in a Typha marsh besides Typha spp. This is especially evident in the transect data (Appendix A).

The relationships between the sites as well as species presence and absence is thoroughly explored in the parts I, II, and III of the Discussion where the environmental data are related to the vegetation data and information from the literature.

3. Simpson's Indices of Dominance and Diversity.

As part of the characterization of the study sites, Simpson's Dominance and Diversity Indices were calculated for each site. The Index values are given in Table 2. Except for sites D2 and D3, each margin site has a greater dominance value than the central heath site. And again except for sites D2 and D3, each margin site has a lower diversity value than the central heath sites.

The increase in dominance along the series of disturbed sites is broadly related to the increasing success of Chamaedaphne calyculata at sites B2 and C2. The drop in dominance as related to the central heath site at site D2 is due primarily to replacement of

Table 2

Simpson's Dominance and Diversity Indices for the Field Layer of Each Study Site.

<u>Site</u>	<u>Dominance (λ)</u>	<u>Diversity (d)</u>
A1	.370	.691
A2	.393	.675
B1	.461	.630
B2	.696	.499
C1	.287	.751
C2	.606	.546
D1	.372	.690
D2	.161	.851
D3	.231	.793

Chamaedaphne calyculata by Typha spp. The dominance value at site D3 is related to the transition nature of the zone where tall, nutrient-demanding shrubs replace the ericaceous shrubs.

Dominance and diversity are related in the calculation of Simpson's Indices so that an explanation of the dominance values in the various sites used only be reversed to explain the diversity states. However, the reduction in diversity at sites A2, B2, and C2 relative to the central heath sites reflects a general decrease in codominance rather than a reduction of species numbers. In every case the margin or disturbed site contains more species. It may be argued that changing conditions allow overlap in the distribution of species that would not normally occur together. Or, more simply, in these areas species from both fen-like and bog-like assemblages may be found so that species number is elevated (an ecotone). The reduction in codominance at sites A2, B2, and C2 reflects differential success of only one or two species in these areas.

• Because sites B2, C2, and D2 are disturbed sites the explanation of differences in dominance and diversity values with respect to the central heath sites may be based more on site development or evolution than on simple ecotonal features. Dynamic responses on the part of plant species to changing conditions at these sites would more readily explain the dominance and diversity

values and species numbers along the entire series of sites. This is especially noticeable when the transect data (Appendix A) are inspected.

At site A2, Carex rostrata becomes increasingly abundant toward the mineral margin until nearly a solid sward of C. rostrata occupies a narrow zone next to the margin that also supports various herbs, semi-bog species, and fen species. At sites B2 and C2, Chamaedaphne calyculata becomes increasingly abundant until nearly pure clumps dominate the areas above the dams. At site C2 the dominance of Chamaedaphne calyculata is being replaced by Typha spp. Within the entire area of site C2, there occur many fen species and minerophilic species such as Iris versicolor.

At site D2 the Typha bed is very dense near the beaver pond and thins progressively toward the open bog. Few herbs have invaded this disrupted transition shrub zone of the bog so that the high diversity value is due to the presence of bog and transition shrub species.

The patterns in the diversity values of the study sites are discussed thoroughly in part I of the General Discussion.

4. Species Richness and Quotients of Similarity.

The number of species present at each site, or species richness, and the Quotients of Similarity for related study site pairs are shown on Table 3. These

Table 3

Species Richness and Quotients of Similarity:

a. For Field Layer

<u>Site</u>	<u>Richness</u>	<u>Site</u>	<u>Richness</u>	<u>Similarity</u>
A1	8	A2	14	.64
B1	15	B2	13	.50
C1	17	C2	24	.53
D1	10	D2	17	.63
D1	10	D3	20	.56
A1	8	B1	15	.52
A1	8	C1	17	.48
A1	8	D1	10	.56
B1	15	C1	17	.63
B1	15	D1	10	.56
C1	17	D1	10	.59

b. For All Strata

<u>Site</u>	<u>Richness</u>	<u>Site</u>	<u>Richness</u>	<u>Similarity</u>
A1	11	A2	20	.64
B1	22	B2	20	.52
C1	26	C2	32	.52
D1	14	D2	24	.63
D1	14	D3	26	.65
A1	11	B1	22	.55
A1	11	C1	26	.49
A1	11	D1	14	.64
B1	22	C1	26	.71
B1	22	D1	14	.61
C1	26	D1	14	.55

values are shown for the field layer and for total species recorded. There is a remarkably similar sharing of species between all of the central heath sites. A minor exception occurs between sites B1 and C1, which have Quotients of Similarity of .63 and .71 for the field layer and all species, respectively. The lowest resemblance occurs between the two wettest heath sites, A1 and C1, with values of .48 and .49.

The values for the similarity between the central heath and margin sites are similar to the values for the central heath series.

5. Percent Cover and Species Rank for the Study Area Plant Assemblages.

Figures 14-18 represent the % cover and species rank for each study site and also show the environmental (shown as 1) and the diversity-dominance-similarity characteristics (shown as 2) of each site. This series of figures best represents all of the major characteristics of each site and constitutes a primary reference for this report. Figures 14-18 will be referred to very often during the course of the Discussion and General Discussion.

The primary emphasis for this section of the Results refers to the % cover-rank graphs, however the representation of the values of the environmental variables requires a brief explanation. The polygonic figures represent data presented on Figures 32-37 and in

Appendix D. In addition, the polygonic figures show the total % cover of the field layer and the mean depth to water for each site as recorded over July and August of 1977.

A major trend shown by the polygonic figures is the decrease in phosphorus concentration accompanied by an increase in pH at all related sites except A1-A2. Another trend is in the increase of calcium from the central heath to the margin sites. Potassium increases from the central heath sites to the margin sites at regions 1, 3, and 4 and decreases from the central heath sites to the margin sites at regions 8 and 12. The overall trend is for nutrient availability to increase as a gradient from sites A1 to D1, although C1 is higher in calcium than site D1, and from sites A2 to D2, again except for calcium, which is highest at site C2. These relationships are more thoroughly described in part III of the Results.

The depth to water at each site should also be noted. Each margin or disturbed site is wetter than the related central heath site. The wettest central heath sites are A1 and C1. The driest site is D1.

The pH is also an extremely important factor and much discussion will be given pH values and their relationship to nutrient availability in part III of the Discussion. Each margin or disturbed site has a higher pH than the related central heath site. The general trend is for pH

to increase from the east to the west of the study area. Site C2 has the highest pH and site A1 has the lowest pH.

The % cover-rank graphs, labelled as 3, represent the adjustments in presence and abundance implied by the arrangement of % cover data in Tables 1A and 1B, although central heath and margin sites are shown on the same figure. The abbreviations of the species' names are as described in Appendix C. Percent cover is given on the vertical axis in logarithmic increments according to convention (Whittaker 1973; Pielou 1975). Species' rank is plotted against the horizontal axis, which is arithmetic. These figures are used to represent characteristics of the plant assemblages and imply nothing about resource partitioning (*sensu* MacArthur). May (1977) recommends the use of % cover-rank or abundance-rank curves as the most useful site index because it shows species number, relative abundance, and in the case of Figures 14-18, species type. However, not all of the species present at the various sites are represented on the figures. Only the species that occurred with an abundance of 5% or greater in at least one of the twenty sample points used to characterize the site are shown. None of the species that were recorded only as present are included in the % cover-rank graphs.

The most important species at site A2 are almost all different than the important species at site A1. This is not represented by the quotients of similarity which

are .64 for the field layer (SV) and .64 for the total number of species (SVV). There is little difference in the dominance and diversity values for the two sites. This is reflected in the similar shapes of the % cover-rank curves for both sites.

Site B2 on Figure 15 has higher dominance and lower diversity than site A1. This is explained by the very high abundance of Chamaedaphne calyculata, which must be growing here under nearly ideal conditions. The other species at site B2 reflect the shift to fen-like conditions in that Carex rostrata, C. oligosperma, and C. trisperma are of importance. The graph represents the status of site B2 in 1977. Field inspection of this site during the summer of 1979 showed that the trend proposed earlier of Typha invasion and rapid takeover in the disturbed sites is accurate. Typha is much more abundant presently in the area immediately above the beaver dam.

The development of the disturbed plant assemblages into communities of high dominance and low diversity is shown by the % cover-rank graphs for sites C1 and C2. Site C2 is characterized by a high abundance of a single species, Chamaedaphne calyculata. Several fen species occur here, namely Carex oligosperma, Scirpus acutis, and Eriophorum spp. As for site B2, Typha is rapidly colonizing and dominating this site as shown by recent field inspection. In 1977, site C2 had only a few

scattered Typha, mixed with Iris versicolor and Anchistea virginica, growing on the exposed peat muck excavated by the beaver in the area just above the beaver dam. A few Typha were also growing right through what appeared to be a disintegrating Sphagnum mat in this same area. Presently, the same area is dominated by a tall, closed sward of Typha latifolia approximately ten meters on a side.

The last beaver disturbed site, site D2, is shown on Figure 17 and, as compared to site D1, shows much more codominance and a higher diversity value. This is an apparent anomaly in that the site has developed into a pure Typha marsh along the borders of the pond. What appears to be happening is that the species from the transition zone, such as Nemopanthus mucronata and Aronia melanocarpa, are persisting in the area where the Typha bed grades into the open bog. This is reflected in the reduced abundance of all three of the ericaceous shrubs that form a nearly closed dwarf shrub stratum at site D1. Only Chamaedaphne calyculata maintains a high abundance into the Typha bed. This would be expected in view of the growth response of Chamaedaphne at sites B2 and C2. However, even Chamaedaphne is replaced by Typha toward the pond's margin.

Site D3 represents an undisturbed transitional zone that is mirrored by its low dominance and high diversity values. This appears to be a true ecotone or

edge effect where species from distinct plant assemblages overlap in their distributions according to the physiological tolerances of individual species.

The series of central heath sites generally are characterized by % cover-rank curves that show little codominance. Site C1, however, definitely displays a flattened curve and a concomitant high diversity value. Also, Chamaedaphne calyculata and Gaylussacia baccata are nearly codominants at site D1 where all other species, except perhaps Kalmia angustifolia, occur very sparsely.

The relationships between the diversity states of the study sites and the causes of the diversity values at these sites is discussed in part I of the General Discussion.

III. Environmental Variables: Description, Characterization, and Analysis

A. Graphical Representation of Combined Transect Data for All Margin Sites

The transect measurements made during July, 1977 were repeated in August, 1977. These two sets of transect data were combined as sample point averages and are shown on Figures 19-26. The values of all environmental variables are presented along with the average height of Chamaedaphne calyculata. C. calyculata is the most abundant species at the margin sites, except for the area near the beaver pond at site D2, and appears to

respond to flooding very positively. This ericaceous shrub displays not only a general increase in abundance at the margin sites but also responds with increased vertical growth (see Appendix B) and a darker, more luxuriant growth. The height of this important species is therefore included with the basic transect data to provide for a kind of bioassay of the effects of changes in the values of the environmental variables along the transects.

Because phosphorus and potassium are two of the most limiting nutrients for bog species (Watt and Heinzelman 1965; Heilman 1968; and Heinzelman 1970) they are separated from the other nutrients and shown on the primary figures marked a. The values of calcium, magnesium, and sodium cations are shown on the figures marked b.

The set of data represented by Figures 19-26 will be used: to investigate the factors that control bog plant distribution as each sample point represents the environment of each corresponding sample point for the vegetation data (Appendix A); to characterize the environment of the plant assemblage at each study site; and to provide the basic data for the test of the hypothesis that beaver dams function as nutrient traps in the coupling of adjacent ecosystems.

The asterisk (*) marked on various environmental variables on Figures 19-26 indicate a gradient in values

at the 95% confidence level. The gradient analysis is given in Appendix D. Chamaedaphne calyculata height and depth to water values were not tested.

In region 1 the concentrations of potassium and phosphorus increase from the open bog to a point about twenty-five meters from the mineral margin where they then begin to decrease. Both potassium and phosphorus increase slightly just at the mineral edge of site A2. Potassium and phosphorus increase as a gradient. Other cations remain about the same along the transect except for calcium, which increases as a gradient. The site becomes progressively drier toward the open bog. The pH seems fairly constant, but toward the mineral margin it does increase as a gradient. The height of Chamaedaphne calyculata begins to increase at the thirty-five meter mark and reaches a height of about thirty-five centimeters in the area of densest Carex rostrata growth. The rapid drop in the values of potassium and phosphorus may be associated with the increased growth of C. calyculata and Carex rostrata.

Region 3, above the beaver dam (Figure 20a, b), shows many of the characteristics of region 1 but in an exaggerated sense. The only variable to test for a gradient is pH, however potassium and calcium generally increase and both potassium and phosphorus rapidly decrease toward the beaver pond from the twenty meter mark. This is the same area where Chamaedaphne calyculata

increases dramatically in height and where the pH approaches 5.0. The site is also characterized by increasing wetness toward the beaver pond. This is true for site C2 as well and would seem obvious. However, site D2 is very wet only near the pond itself, becoming quite dry just a few meters from the water's edge.

The environmental data from the transects taken below the beaver dams are interesting and tend to show the same patterns as found above the dams. The area below the dam at region 3 (Figure 21a, b) in many ways mirrors the data from above the dam. Potassium and phosphorus increase and then sharply decline, although phosphorus declines steadily from the fifty meter mark. As the pH approaches 5.0, the height of C. calyculata increases remarkably. The area is wet just below the dam. The cation concentrations fluctuate a bit along the transect however, calcium steadily increases as a gradient and sodium steadily decreases as a gradient toward the beaver dam.

Region 4 above the dam (Figure 22a, b), designated as site C2, again is similar to regions 1 and 3. The patterns described above are even more pronounced at site C2 than at site B2. This will also be seen at site D2 where the patterns are the same but much exaggerated.

At site C2 the height of C. calyculata is related to the pH, increasing where the pH approaches or exceeds 5.0. The site is progressively wetter. Phosphorus and

4.3 ppm.

These features are also evident below the dam, even to the point of finding Carex oligosperma and Typha latifolia in an area where the calcium concentration is around 4.0 ppm.

At region 8 above the beaver dam (site D2), three vegetation zones can be distinguished which might be related to the calcium concentration. The first zone occurs from zero to thirty-five meters along the transect, the second from thirty-five to eighty meters, and the third zone from eighty to one hundred meters.

The first zone is characterized by abundant Typha latifolia and a calcium concentration of between 3.0 and 5.5 ppm. The second zone is characterized by progressive thinning of the Typha stand accompanied by increased abundance of Vaccinium species, Aronia melanocarpa, Nemopanthus mucronata, as well as other bog species. The second zone contains calcium cation concentrations from about 1.7 to 2.3 ppm. The third, or last, zone is characterized by bog species such as Chamaedaphne calyculata, Kalmia angustifolia, Gaylussacia baccata, and Ledum groenlandicum. The calcium cation concentration is around 1.7 ppm in the third zone.

The third zone, or the tail of the transect, actually represents the vegetation as found throughout the central heath site D1. The mean calcium concentration at site D1 is 2.4 ppm and is higher than at the tail of the transect. The reason for this is unknown although

The differences in vegetation cover at the various margin sites must be due to some dynamic aspect of beaver disturbance. Since the chief feature that distinguishes the beaver disturbed sites is the invasion and overwhelming success of Typha latifolia, it may be concluded that the combination of increasing pH at the margin sites and the exposed peat substrate that is kept flooded by the beaver pond results in a habitat ideal for the development of a Typha marsh.

Calcium cation concentration strongly influences bog plant distribution and abundance (Sjörs 1959, 1961; Heinselman 1963, 1970; Clymo 1973; Vitt and Slack 1975; Stanek and Jeglum 1977; Wildi 1978; and others). A detailed analysis of calcium values and changes in plant growth and occurrence along the experimental transects is therefore warranted. Appendix A lists the % cover data and will be consulted so that the distributions of the various species may be related to the calcium cation concentration along the transects as shown on Figures 19b-26b.

Region 1 is characterized by Carex rostrata in a zone stretching about fifty meters from the mineral margin into the open bog. C. rostrata becomes abundant about fifteen to twenty meters from the mineral margin where the calcium cation concentration increases to 2.5 to 3.5 ppm. In the area where calcium is 2.0-2.5 ppm, most bog species, such as Ledum groenlandicum, Gaylussacia

baccata, Kalmia angustifolia, Vaccinium oxycoccos, and Eriophorum chamissonis disappear. This coincides with the fifty meter mark that is the limit of C. rostrata occurrence. Beyond the fifty meter mark, the calcium concentration drops off until the mean value in the open bog is about 2.0 ppm.

Chamaedaphne calyculata persists relatively abundantly right up to the mineral margin at region 1 and is reduced only in the areas of high C. rostrata abundance. Other fen species, such as Carex prairea and C. limosa, become abundant in the area five to twenty meters from the mineral margin where the calcium concentration fluctuates from about 2.3 to 3.5 ppm. This same pattern occurs at the other study sites.

At region 3 above the dam (site B2), the calcium concentration rises above 2.0 ppm about twenty to twenty-five meters from the beaver pond. This area coincides with the limit in the distribution of most bog species except for Chamaedaphne calyculata, Vaccinium spp., and Eriophorum opacum. In the region along the pond where the calcium concentration fluctuates between about 2.0 to 3.5 ppm, the following fen species are found: Carex rostrata, Juncus effusus, Typha latifolia, and Spiraea tomentosa. The growth of Chamaedaphne calyculata is enhanced in this area so that it almost completely dominates the vegetation. This same pattern occurs below the beaver dam at region 3. There are more herb species

below the dam than above.

Carex oligosperma is found in the area from five to fifteen meters above the pond, which is characterized by a calcium concentration of 1.7 to 2.6 ppm.

The area above the dam at region 4 (site C2) shows a marked increase in calcium concentration as compared to regions 1 and 3. The central heath (site C1) has a mean calcium cation value of 3.3 ppm that drops to just below 3.0 ppm at the tail of the transect. It rises to about 3.3 in the area sixty-five to seventy-five meters from the pond and drops to about 2.5 ppm at the sixty meter mark. From the sixty meter point along the transect to the beaver pond the calcium concentration rises to over 4.0 ppm. From the start of the transect to about fifty-five meters is the zone where fen species occur and where most bog species, except C. calyculata, Eriophorum virginicum, and E. tenellum, disappear. From zero to twenty meters the Eriophorum species disappear and at the zero meter mark, characterized by high calcium concentration and open water with excavated peats, C. calyculata is replaced by Typha latifolia, Anchistea virginica, and Iris versicolor. Other fen species occur in this fifty-five meter zone characterized by a calcium concentration of 2.5 to 4.3 ppm. These species are Scirpus acutis, Carex oligosperma, and C. miliaris. Scirpus acutis, Carex oligosperma, and Typha latifolia occur where the calcium concentration is between 3.5 and

4.3 ppm.

These features are also evident below the dam, even to the point of finding Carex oligosperma and Typha latifolia in an area where the calcium concentration is around 4.0 ppm.

At region 8 above the beaver dam (site D2), three vegetation zones can be distinguished which might be related to the calcium concentration. The first zone occurs from zero to thirty-five meters along the transect, the second from thirty-five to eighty meters, and the third zone from eighty to one hundred meters.

The first zone is characterized by abundant Typha latifolia and a calcium concentration of between 3.0 and 5.5 ppm. The second zone is characterized by progressive thinning of the Typha stand accompanied by increased abundance of Vaccinium species, Aronia melanocarpa, Nemopanthus mucronata, as well as other bog species. The second zone contains calcium cation concentrations from about 1.7 to 2.3 ppm. The third, or last, zone is characterized by bog species such as Chamaedaphne calyculata, Kalmia angustifolia, Gaylussacia baccata, and Ledum groenlandicum. The calcium cation concentration is around 1.7 ppm in the third zone.

The third zone, or the tail of the transect, actually represents the vegetation as found throughout the central heath site D1. The mean calcium concentration at site D1 is 2.4 ppm and is higher than at the tail of the transect. The reason for this is unknown although

it might be related to minerals derived from fire disturbance.

It should also be noted that Juncus effuses was found in the ninety and one hundred meter quadrats in region 8 above the dam. This seems anomalous and may be indicative of an enriched site where increased pH values result in greater phosphorus and calcium uptake.

Below the beaver dam at region 8, the vegetation is characterized by a major transition zone between a Populus tremuloides-Calamagrostis canadensis dominated community that borders an Alnus rugosa-Salix sp. swamp and the open heath designated as site D1. The transition zone is dominated by tall shrubs, primarily Nemopanthus mucronata and Aronia melanocarpa with a strong mixture of Vaccinium spp., Gaylussacia baccata, Chamaedaphne calyculata and Typha spp.

The² transition zone begins about twenty meters from the edge of the Alnus-Salix swamp and goes to sixty-five or seventy meters from the beginning of the transect into the open bog.

In this transition zone calcium concentrations range from 1.7 to 3.2 ppm. The Populus-Calamagrostis zone has 2.5 to 7.4 ppm of calcium. The southern border of the transition zone is characterized by bog species and calcium values of 2.0 to 3.2 ppm that dropped off to 2.4 ppm in the center of the raised, open bog.

The calcium cation concentrations forms a gradient along the transects taken at region 12. Calcium values from about thirty-five meters to one hundred meters range from 2.0 to 3.2 ppm, usually near 2.5 ppm. From zero meters, next to the Alnus rugosa swamp, to about thirty-five meters, calcium concentration range from 2.5 to 3.6 ppm and rise in the Alnus swamp to 7.9 ppm.

The region of elevated calcium concentration corresponds almost exactly to the transition zone to tall shrubs leading up to the Alnus swamp from the central open bog. This area is characterized by abundant tall shrubs, such as Aronia melanocarpa, and Nemopanthus mucronata, and various bog species. The area near the Alnus swamp also contains species such as Alnus rugosa, Spiraea sp., Viburnum cassinoides, Solidago sp., and Typha spp.

The correspondence of plant distribution to calcium cation concentration as described above is obviously very strong and reinforces the view and conclusions in the literature. What is of significance is the determination from the examination of the data of threshold values of invasion and subsequent success of important and characteristic species. For example, Typha latifolia can invade a flooded site where peat is exposed if the calcium concentration is in the region of 2.3 ppm and can develop into a flourishing stand when the calcium concentration approaches or exceeds 3.0 ppm. It would appear

that for a dense, luxurious Typha marsh to develop, a calcium concentration of 4.0 ppm is required.

These conclusions are in agreement with the literature that describes the chemical environment of specific peatland types that are associated with particular plant associations or assemblages (references given above). For instance, Heinselman (1970) lists fourteen ombrotrophic bogs on raised slopes that were characterized by calcium cation concentrations that range from .8 to 2.2 ppm. Transitional bogs had calcium values of 4.2 to 6.2 ppm, weakly minerotrophic swamps had calcium values of 3.2 to 8.0 ppm, and minerotrophic swamps were characterized by a calcium cation concentration ranging from 20.1 to 25.2 ppm.

It is also noteworthy that at the heads of the transects from regions 1, 3, and 4 the calcium concentration drops in proportion to the decrease in phosphorus concentration. This is shown most clearly on Figures 27-29 described in the following section. In these regions of relatively lower calcium concentrations, the levels of calcium may be low enough that the cations that are not complexed at the ion exchange sites of the peat might combine with the phosphorus being liberated from complexation with aluminum and iron as the pH increases.

Under acidic conditions the monovalent form of phosphorus ($\text{H}_2\text{PO}_4^{1-}$) is most prevalent and would form monocalcium di-hypophosphate ($\text{Ca}(\text{H}_2\text{PO}_4)_2$) (Devlon 1966).

The ratio of calcium to phosphorus in this form, of one to two, is significant in that the slopes of the regression lines for calcium and phosphorus availability at the heads of the transects as shown on Figures 26-27 reflect, roughly, this relationship.

At the western sites (regions 8 and 12 shown on Figures 30 and 31 respectively), this relationship breaks down. The reason may be due to: greater concentrations of calcium so that much of the calcium available is not taken-up by the plants; higher pH values resulting in a calcium phosphate form that has two calcium ions for every hypophosphate ion (Ca_2HPO_4); and the increased nutrient turn-over due to Typha mulch decomposition at site D2.

B. Regression Lines of Combined Transect Data

It was mentioned above that all of the margin sites exhibited a general decrease in concentration of phosphorus and potassium beginning about where Chamaedaphne calyculata increased in height and robustness. This pattern is shown more clearly on Figures 27-31 where regression slopes and y-intercepts were calculated for the serial data for each environmental variable, except pH and water level, from the head of the transect to the approximate location of increasing C. calyculata height and from the tail of the transect again to the location of increasing C. calyculata height. This division point

is marked on the figures as an arrow. Only areas above the dams are shown for the disturbed sites.

In the eastern sites (A2, B2, and C2), potassium is increasing up to the point where C. calyculata begins to increase in height and then decreases rather dramatically. Except at site C2, phosphorus does the same. Calcium tends to drop off as well but to a much lesser degree.

In the western sites (D2 and D3), phosphorus decreases steadily and rapidly toward the margins. Potassium does so at site D3 but generally is steady at site D2. This is shown on Figures 30 and 31 of region 8, above the dam, and region 12, respectively.

An obvious hypothesis is that nutrient uptake by the plants decreases the concentration of phosphorus and cations in the root zone. Except for the very wettest places, all water and peat samples were taken from the root zone. And even in the wettest places care was taken to obtain a water sample well below the surface.

In order for the plants to increase their uptake of nutrients, thus showing greater growth, there must be a mechanism that provides for the initial release of nutrients or a mechanism that makes nutrients more readily available. The relationship between pH and C. calyculata height suggests the following hypothesis: as pH increases, nutrient availability in the peat substrate increases. The increase in pH values along the transects toward the margins of the sites might be influenced by the calcium

cation concentration, shown in nearly every case to increase as a gradient away from the open bog or central heath sites. Calcium cation has been shown to be important in classifying peatland vegetation and physiognomic types (Heinselman 1970; Stanek and Jeglum 1977; Wildi 1978; and others) and to affect the pH of humic substances most probably by interacting with the cation exchange capacity of peat (Clymo 1973; Gjessing 1976; André and Pijarowski 1977; and others).

The pH value of 5.0 is proposed as a major threshold value that when approached or exceeded affects nutrient availability in peat substrates to the point of promoting plant growth and the invasion of species inimical to bog vegetation. A calcium cation concentration of 2.7 ppm, or the region between 2.5-3.0 ppm, is also proposed as a major threshold value that when approached or exceeded affects the substrate pH in a way that results in greater nutrient availability, probably by taxing the cation exchange capacity of peat thereby reducing the concentration of exchangeable hydrogen ions. The pH amelioration would then be followed by release of phosphorus from aluminum and iron complexation.

These proposals and relationships are examined in parts I and III of the Discussion.

The source of the calcium might be the mineral uplands adjacent to the bog.

Although tentative, it may be concluded that beaver dams function as nutrient traps by allowing inorganic materials such as calcium, either as salts or cations, to increase in concentration in the ponds and adjacent bog vegetation thereby raising the pH, which in turn increases nutrient availability and promotes the growth of certain bog species and allows for the invasion of other species that may replace the bog vegetation. Nutrient availability and pH are closely related in peat substrates (Lucas and Davis 1961). The mechanism by which beaver activity changes cation concentration is unknown but might be linked to the following factors: alteration of hydrologic relationships followed by passive cation concentration change as a consequence of proximity to the mineral-laden uplands; peat excavation in the ponds and canals that would be followed by increased rates of peat decomposition or exposure of sand or clay bottoms; deposition of metabolic wastes and food supplies in the ponds resulting in increased nutrient availability and stimulation of decomposer microbes; and by maintaining ponds along a drainage system that supports abundant Alnus rugosa, known (Daly 1966) as capable of supplying considerable nitrate to adjacent aquatic systems. The last mechanism mentioned could obviously be linked to the first in that availability of nitrate to the peat substrate would be a passive response dependent on site hydrology. Recall from the Methods that an attempt was made to

determine the nitrate concentrations in the samples but that the attempt was not successful.

C. Correlation Between Selected Abiotic and Biotic Factors

Correlation analysis was performed on four sets of biotic and abiotic factors in order to measure statistically the relationships pointed out in the sections above between pH and Chamaedaphne calyculata height, phosphorus and C. calyculata height, pH and calcium cation concentration, and calcium cation concentration and C. calyculata heights. Tables 4, 5, 6, and 7 present the results of the analysis. The asterisk (*) marks the test statistic that represents rejection of no correlation at the 95% confidence level. The tables also include lists of the critical values of the correlation coefficient at the 90% confidence level. The data used for the tests are given in Appendix D.

Of the twenty tests, ten were significant at $P \leq .05$ and fourteen were significant at $P \leq .10$. Of all the test statistics calculated, only two were not close to the critical value at the 90% confidence level. The most pronounced correlation occurred between pH and C. calyculata height. All test statistics between phosphorus values and C. calyculata heights were negative and two were significant.

Table 4

Correlation Between pH and Chamaedaphne calyculata Heights.

The symbol * indicates rejection of $H_0: \rho(\text{rho}) = 0$ at $P \leq .05$.

Site	n	r Statistic	Critical Values	
			0.05(2)	0.10(2)
A1-A2	16	.468	.497	.426
B1-B2, Above Dam	11	.857*	.602	.521
C1-C2, Above Dam	15	.660*	.514	.441
D1-D2, Above Dam	9	.704*	.666	.582
D1-D3	11	.905*	.602	.521

All four sets of correlations were significant at site C1-C2, above the beaver dam. Site C2 is, it seems, in the most dynamic state of beaver disturbance of all the sites in that vegetation changes are occurring rapidly, and are effectively transforming the site from a bog to a fen-marsh community. The hydrologic and vegetation changes are obvious at the site and are reflected in the relationship between high calcium cation concentration, pH, phosphorus concentration, and the height of Chamaedaphne calyculata.

The disturbance at site C2 might represent a maximum "forcing function" of beaver disturbance so that other environmental and biotic effects are obscured or overwhelmed in comparison to the immediate effects of beaver activity. Site A2 is not directly disturbed and site B2 is just beginning to show signs of disturbance. Site D2 represents a response to beaver disturbance with an almost total vegetative transformation.

In the acidic sites (A2 and B2), cation complexation, due to the cation exchange capacity of peat, may be competing for mineral input. Other materials, such as aluminum and iron, may also be more abundant and would, in turn, also compete for free cations (Devlon 1966; Gjessing 1976; and others). These relationships break down near the beaver ponds as described above.

The complex biotic interactions occurring at site D2 would tend to blur the effects of a single factor

Table 5

Correlation Between Phosphorus Concentration and
Chamaedaphne calyculata Heights.

The symbol * represents rejection of $H_0: \rho(\text{rho}) = 0$ at $P \leq .05$.

Site	n	r Statistic	Critical Values	
			0.05(2)	0.10(2)
A1+A2	16	-.273	.497	.426
B1+B2, Above Dam	11	-.495	.602	.521
C1+C2, Above Dam	15	-.514*	.514	.441
D1+D2, Above Dam	9	-.503	.666	.582
D1+D3	11	-.814*	.602	.521

Table 6

Correlation Between pH and Calcium Cation
Concentration.

The symbol * represents rejection of $H_0: \rho(\text{rho}) = 0$ at $P \leq .05$.

Site	n	r Statistic	Critical Values	
			0.05(2)	0.10(2)
A1+A2	16	.716*	.497	.426
B1+B2, Above Dam	11	.547	.602	.521
C1+C2, Above Dam	15	.583*	.514	.441
D1+D2, Above Dam	9	.579	.666	.582
D1+D3	11	.407	.602	.521

and C1-C2. This might reflect a movement of calcium-laden water from the beaver disturbed area into the central heath. Alternatively, it might reflect the presence of Alnus rugosa and Larix laricina at central heath sites B1 and C2. This is discussed further at the end of part I of the Discussion.

The values that were tested came from environmental data selected to characterize each site, which are presented in Appendix E.

IV. Note on Bryophyte Distribution and Abundance in the Study Area

During the course of data collection in my study area, moss specimens were gathered and percent cover of each species was recorded along the transects. Initial identification of four of the Sphagnum species proved to be erroneous so that the data on the non-vascular species were not included in this report. Sphagnum papillosum was confused with S. fallax and S. magellanicum was confused with S. nemoreum. However, because many specimens were regularly gathered along the transects and subsequently correctly identified, a reasonable evaluation of the distribution and abundance of Sphagnum species in my study area can be made.

Sphagnum papillosum is abundant at the wet margins of sites A2, B2, and C2. Sphagnum fallax is common at the wet margin of site A2 and occurs at sites

All four sets of correlations were significant at site C1-C2, above the beaver dam. Site C2 is, it seems, in the most dynamic state of beaver disturbance of all the sites in that vegetation changes are occurring rapidly, and are effectively transforming the site from a bog to a fen-marsh community. The hydrologic and vegetation changes are obvious at the site and are reflected in the relationship between high calcium cation concentration, pH, phosphorus concentration, and the height of Chamaedaphne calyculata.

The disturbance at site C2 might represent a maximum "forcing function" of beaver disturbance so that other environmental and biotic effects are obscured or overwhelmed in comparison to the immediate effects of beaver activity. Site A2 is not directly disturbed and site B2 is just beginning to show signs of disturbance. Site D2 represents a response to beaver disturbance with an almost total vegetative transformation.

In the acidic sites (A2 and B2), cation complexation, due to the cation exchange capacity of peat, may be competing for mineral input. Other materials, such as aluminum and iron, may also be more abundant and would, in turn, also compete for free cations (Devlon 1966; Gjessing 1976; and others). These relationships break down near the beaver ponds as described above.

The complex biotic interactions occurring at site D2 would tend to blur the effects of a single factor

or closely related complex of factors, such as pH, calcium and phosphorus concentration, and shrub height.

Because of these uncertainties and complications, the high degree of correlation between the variables tested seems remarkable but understandable in view of the tentative conclusions reached above regarding the functioning of beaver impoundments as nutrient traps in the coupling of adjacent ecosystems.

D. Graphical Representation of Mean Values of Environmental Variables for All Study Sites

This section describes the mean values in the environmental variables determined for each site and presents the data comparatively. Figures 32-37 present the mean values for pH (Fig. 32), phosphorus (Fig. 33), potassium (Fig. 34), calcium (Fig. 35), magnesium (Fig. 36), and sodium (Fig. 37). The mean value at all of the study sites are shown and the sites are arranged with respect to their relative linear position along the west-east drainage system. The central heath sites are connected with a solid line and the marginal sites are connected with a dashed line. Site D3 is shown but, to avoid confusion, is not connected to the other margin sites. The sites are connected in an attempt to determine whether there are trends in nutrient availability and pH. The same data are shown on the polygonic figures given on Figures 14-18 and described above.

The mean pH increases from the east to the west of the study area, however site C1 and D1 have nearly identical mean pH values. The pH also increases in series at the margin sites, being the lowest at site A2 and the highest at site C2. Sites D2 and D3 have the same mean pH.

The central heath sites increase in phosphorus availability from site A1 to site D1. The margin sites, except for site A2, exhibit a lower mean phosphorus concentration than the corresponding central heath sites. As proposed above, this may be due to substrate depletion of phosphorus due to increased plant growth. Increasing pH affects nutrient availability positively in peat substrates up to fairly high alkaline values when nutrient availability is again suppressed (Lucas and Davis 1961). All of the margin sites have elevated pH values compared to the respective central heath sites.

Potassium, sodium, and magnesium cations increase in concentration from the east to the west in the central heath sites of the study area. Sodium and magnesium cations increase similarly in the margin sites. Potassium generally decreases along the margin site series, with the exception of site C2 where the potassium concentration is higher than at other sites.

The calcium cation concentration is also highest at sites C1 and C2. The other study sites do not show a trend in calcium cation concentration. The calcium

values are extremely important in classifying peatland types, as mentioned above, and often indicate the limits of mineral-laden groundwater (Lucas and Davis 1961; Wildi 1978). Elevated calcium values might also be attributed to the nutrient cycling action of plants such as Alnus rugosa and Larix laricina that yield rapidly decomposing litter with high mineral contents (Watt and Heinselman 1965). Larix laricina is abundant at site C1 but has been largely removed by drowning at site C2. The source of the calcium at site C2 may also be mineral-laden groundwater from the inorganic soils on the upland sand and silt island or ridge that borders the northeastern edge of the study area and is contiguous with sites A2, B2, and C2. Although the calcium content at site C1 might be caused by nutrient cycling by way of Larix leaf decay, it is more probable that the calcium is coming from ground water flowing slowly across the site. This proposal is developed in parts I and II of the Discussion as a consequence of several lines of evidence.

The question of whether the sample means of the environmental variables from the various study sites are from the same statistical population is unimportant for this study. What is important is how these values relate to the values of these variables reported to be characteristic of specific peatland vegetation types. These comparisons are made in part I of the Discussion.

Also of considerable significance is the mean value of calcium cation concentration at site C1, which is 3.3 ppm and the only mean value for the central sites that is over the proposed threshold of 2.7 where bog vegetation may be replaced by more nutrient-demanding species.

E. t-Tests of Sample Means of Environmental Variables for Each Pair of Related Study Sites Within the Selected Study Regions

Student's t-tests between sample means of the environmental variables from each related margin-central heath site pair were performed in order to further verify the reality of the study site designations as determined by vegetation differences. The results are given in Table 8. The asterisk (*) marks the t-statistic that indicated the sample means tested are not equal at the 95% confidence level. Six variables were tested for each margin-central heath site pair: pH, phosphorus, potassium, calcium, magnesium, and sodium.

It would seem that the site designations represent areas with different environments in that all of the sites had at least three of the six variables significantly different and three of the five site pairs had four variables significantly different.

It should be noted that the calcium cation concentration was not significantly different at sites B1-B2

and C1-C2. This might reflect a movement of calcium-laden water from the beaver disturbed area into the central heath. Alternatively, it might reflect the presence of Alnus rugosa and Larix laricina at central heath sites B1 and C2. This is discussed further at the end of part I of the Discussion.

The values that were tested came from environmental data selected to characterize each site, which are presented in Appendix E.

IV. Note on Bryophyte Distribution and Abundance in the Study Area

During the course of data collection in my study area, moss specimens were gathered and percent cover of each species was recorded along the transects. Initial identification of four of the Sphagnum species proved to be erroneous so that the data on the non-vascular species were not included in this report. Sphagnum papillosum was confused with S. fallax and S. magellanicum was confused with S. nemoreum. However, because many specimens were regularly gathered along the transects and subsequently correctly identified, a reasonable evaluation of the distribution and abundance of Sphagnum species in my study area can be made.

Sphagnum papillosum is abundant at the wet margins of sites A2, B2, and C2. Sphagnum fallax is common at the wet margin of site A2 and occurs at sites

B2 and C2. Sphagnum rubellum is dominant at sites A1 and B1, becoming codominant at site C1 with Sphagnum magellanicum and codominant with S. nemoreum at site D1. Sphagnum magellanicum is found at all the central heath sites but is most abundant at site C1 and least abundant at site D1. Sphagnum rubellum and S. magellanicum dominate most of the area of sites A2, B2, and C2 and are present in loose patches at site D2.

Sphagnum pulchrum, not previously collected from the Mer Bleue (R. Ireland, personal communication), was found in the 20 m quadrat of transect 1 at site C2, region 4.

Polytrichum strictum occurs in abundance only in the transition area between the Typha marsh and the bog vegetation southeast of region 7 as well as among the branches and stems of Vaccinium shrubs at all of the central heath sites except site A1.

Figures 1 and 2: Development of drainage ditches in Mer
Bleue. Figure 1 - after 1945. Figure 2 - 1945.

DRAINAGE SYSTEM - 1977

Fig. 1

Figure 6: Increasing number of beaver dams in Mer Bleue
from 1956 to 1976. Vertical bars indicate
maximum and minimum numbers due to the uncertainty
interpretation of aerial photographs.

Figures 3-5: Beaver dams in Mer Bleue 1958 to 1975.

Figure 3 - 1975. Figure 4 - 1965. Figure 5 -
1958.

LOCATION OF BEAVER DAMS - 1975

Fig. 3

LOCATION OF BEAVER DAMS - 1965

Fig. 4

LOCATION OF BEAVER DAMS - 1958

Fig. 5

Figure 6: Increasing number of beaver dams in Mer Bleue
from 1956 to 1976. Vertical bars indicate
maximum and minimum numbers due to the uncertainty
interpretation of aerial photographs.

Fig. 6

Legend for Historical Maps of Study Area,
Figures 7-10

Mineral ridges, characterized by mixed woods and agricultural fields.

Open bog, dominated by Sphagnum species and ericaceous shrubs.

Wooded bog, dominated by Sphagnum species and ericaceous shrubs with abundant Larix laricina.

Wooded bog, dominated by Sphagnum species and ericaceous shrubs with abundant Betula populifolia.

Transition zone, containing Aronia melanocarpa and Nemopanthus mucronata in the western part of the study area and Carex rostrata in the northeastern part.

Typha latifolia marsh.

Beaver pond.

Beaver dam.

STUDY AREA - 1977

Fig. 7

STUDY AREA - 1973

Fig. 8

STUDY AREA - 1971

Fig. 9

STUDY AREA - 1968

Fig. 10 ;

Photographs - Region 1

(see text page 30)

Photograph 1

Photograph 2

Photograph 3

Photograph 4

Photograph 5

Photographs - Region 3

Photograph 1

Photograph 2

Photograph 3

Photograph 4

Photograph 5

Photograph 6

Photographs - Region 4

Photograph 1

Photograph 2

Photograph 3

Photograph 4

Photograph 5

Photograph 6

Photograph 7

Photographs - Region 8

Photograph 1

Photograph 2

Photograph 3

Photograph 4

Photograph 5

Photograph 6

Photograph 7

Photograph 8

Photograph 9

8

Photographs - Region 12

Photograph 1

Photograph 2

Photograph 3

Photograph 4

Photograph 5

Legend for Field Maps of Beaver Disturbed Regions,
Figures 11-13

Alnus rugosa thicket.

Typha latifolia marsh.

Open water.

Transect.

Open bog, dominated by Chamaedaphne calyculata and other ericaceous shrubs.

Wooded bog, dominated by ericaceous shrubs with abundant Larix laricina.

Area of enhanced Chamaedaphne calyculata growth.

Beaver dam.

Beaver lodge.

Transition woodland, dominated by Populus tremuloides.

Transition zone, dominated by ericaceous shrubs, Vaccinium species, Aronia melanocarpa, and Nemopanthus mucronata.

Mineral ridge, characterized by mixed woods and grasses.

Alnus rugosa and Salix swamp.

FIELD MAP - REGION 3

Fig. II

FIELD MAP - REGION 4

Fig. 12

Fig. 17

Figures 14-18: Graphical summaries of field measurements comparing corresponding central bog sites (designated by numeral 1) and bog margin sites (designated by numeral 2).

Part 1: pH, phosphorus concentration, cation concentrations (ppm), water level (cm below peat surface), and % cover.

Part 2: Simpson's dominance and diversity indices, species richness (number) - SV for field layer, SAA for all strata, and quotient of similarity (see Methods, p. 20).

Part 3: Percent cover - rank curves after Whittaker (1972) from Tables 1A and 1B. Abbreviations as in Appendix C.

①

③

②

Fig. 14

2.14 14

Fig. 15

③

Fig. 16

Fig 16

Fig. 17

Fig. 18

③

Figures 19-26: Graphical summaries of relationship between plant growth (represented by Chamaedaphne calyculata) and pH, water depth, phosphorus and cation concentrations for all sites studied on the bog margins. * indicates a statistically significant (.95) gradient in values along the transect.

Fig. 19a

Fig. 19b

REGION 3, ABOVE DAM

135

Fig. 20a

Fig. 20b

REGION 3, BELOW DAM

Fig. 21a

Fig. 21b

REGION 4, ABOVE DAM

Fig. 22a

Fig. 22b

REGION 4, BELOW DAM

Fig. 23a

Fig. 23b

Fig. 24a

REGION 4, ABOVE DAM

Fig. 29

REGION 8, BELOW DAM

Fig. 25a

Fig. 25b

REGION 12

Fig. 26a

Fig. 26b

Figures 27-31: Concentration changes in phosphorus and
cations along sample transects.

REGION I

Fig. 27

REGION 3, ABOVE DAM

150

Fig. 28

REGION 4, ABOVE DAM

Fig. 29

Fig. 30

Fig. 31

Figures 32-37: Mean values for each environmental
variable at all study sites oriented along the
drainage system.

Fig. 32

Fig. 33

Fig. 34

Fig. 35

Fig. 36

Fig. 37

DISCUSSION AND GENERAL DISCUSSION - INTRODUCTION

The Discussion is divided into three parts, each of which deals with the analysis of plant distribution and abundance in the study area. In part I, bog plant associations that are described in the literature are compared to the plant assemblages found in the study area. This is done in order to: 1) adopt a consistent nomenclature for the labelling of the study area plant assemblages; 2) explore the nature of bog plant associations with respect to their constancy of structure and composition; and 3) partially assess the effects of beaver damming on bog vegetation. Part II involves an examination of the comparisons made in part I within the framework of the historical information gained from the inspection of the aerial photograph record. The third part includes a detailed analysis of the plant responses to beaver disturbance and explores the hypothesis that beaver dams function as nutrient traps, therefore acting as agents of change for contiguous vegetation communities that are predicated on nutrient unavailability.

The general patterns of species distribution and abundance in the study area are discussed in the General Discussion, which is divided into three parts. In the first part, Huston's (1979) general hypothesis of species diversity is used as a paradigm for a comprehensive analysis of these general patterns in distribution and

abundance. In part II of the General Discussion, the assemblage of bog vegetation communities, their uniqueness, and their persistence are briefly discussed. The third part summarizes some of the basic aspects of the rules of bog plant community assembly and briefly describes the application of those rules to management strategies for the Mer Bleue.

In order to more easily follow the comments in the Discussion regarding study site characteristics and relationships, the reader should refer to the fold-out of Appendix F. The figure of Appendix F is the same as Figure 7 presented and described in the Results and shows the positions of the various regions and sites within my study area. A summary of each site's dominant physiognomic and floristic characteristics is given below the figure.

DISCUSSION - PART I - INTRODUCTION

The processes of peatland plant community development are complex and varied. Peatlands may develop over standing water or upon a swamped terrestrial site (Malmer 1975). The plant communities of peatlands occupy various habitats that range from dry, raised, and forested sites to nearly aquatic situations where some of the plant species may be completely submerged during wet periods (Heinselman 1963, 1970; Pollett and Bridgewater 1973; Vitt and Slack 1975; Damman 1977; Stanek 1977; Stanek et al. 1977; and others). The classification of peatland plant communities is also complex. Attempts have been made to produce a rational and coherent classification scheme for the many vegetation assemblages that are found in peatland systems (Sjörs 1959a, 1961; Jeglum 1972; Jeglum et al. 1977; all those mentioned above and others). Therefore in order to identify the plant assemblages in the study area with respect to suggested classification systems, the study site assemblages will be compared to a fairly large number of North American peatland plant communities. Recall that this will also be done in order to assess the effects of beaver damming on the vegetation in the study area. The communities chosen for comparison are found in many different habitats, varying from extensive peatlands covering many square kilometers (Heinselman 1970) to floating mats on the

edge of small ponds (Vitt and Slack 1975). Furthermore, these plant communities are located within an enormous geographic area delimited by northern Minnesota (U.S.A.), northern Saskatchewan, the Hudson Bay Lowlands, Newfoundland, southern New Brunswick, and the St. Lawrence Lowlands.

Some of the reports in the literature give detailed species lists and site characterizations. Other reports simply summarize the dominant features of the plant associations. The comparisons that follow are as detailed as the information given allows.

DISCUSSION - PART I

Vitt and Slack (1975) analyzed the vegetation of Sphagnum-dominated kettle-hole bogs in relation to environmental gradients in an extensive area of northern Michigan (U.S.A.). Of the seven community types described, five are similar to the assemblages in my study area. These are: the Acidic Lake Edge Zone, characterized by Sphagnum cuspidatum, Sphagnum papillosum, Carex limosa, and Carex paupercula; the Alkaline Lake Edge Zone, characterized by Sphagnum teres, Carex lasiocarpa, and Calliergonella cuspidata; the Open Mat Zone, characterized by Sphagnum capillaceum, Carex exilis, and Vaccinium oxycoccos; the Closed Mat Zone, characterized by Sphagnum magellanicum, Sphagnum recurvum, Ledum groenlandicum, and Picea mariana; and the Marginal Moat Zone, characterized by Ilex verticillata and Nemopanthus mucronata.

The Acidic Lake Edge Zone is similar to study sites A2, B2, and C2. This community type is found at the edge of lakes having pH between 5.0 and 7.0 and is essentially a floating mat of Sphagnum mosses that supports various species of non-vascular and vascular plants. The community displays little topographical relief and there is little shade due to poor shrub growth and a lack of trees. Sphagnum cuspidatum is found submerged or emergent and is the dominant species in the wettest areas, while Sphagnum papillosum supposedly

becomes dominant when there is less moisture. Other mosses are rare in this zone.

Site A2 closely resembles the Acidic Lake Edge Zone. The mean values for environmental variables are comparable, as shown by the following table:

	A2	Acidic Lake Edge Zone
pH	4.48	5.3
Ca++	2.57 ppm	3.5 ppm
Mg++	1.33 ppm	.6 ppm
K+	3.48 ppm	3.1 ppm
Na+	0.79 ppm	2.0 ppm

Site A2 has a similar physiognomy, being open and very wet with few trees and poor shrub growth. There are also strong floristic similarities between site A2 and the Acidic Lake Edge Zone. Site A2 and this community type share nine species from a total of twenty for site A2 and forty-two for the Acidic Lake Edge Zone (Similarity Quotient = .29). Nearly all of the species shared are important members of both communities, particularly Sphagnum papillosum and Chamaedaphne calyculata. The species shared are: Chamaedaphne calyculata, Ledum groenlandicum, Kalmia polifolia, Vaccinium oxycoccos, Smilacina trifolia, Carex oligosperma, Carex limosa, Sphagnum magellanicum, and Sphagnum papillosum.

Given the comment by Vitt and Slack regarding the distribution of Sphagnum cuspidatum and Sphagnum papillosum, the importance of Sphagnum papillosum at

site A2 may be explained by the site's very wet conditions accompanied by a lack of any permanent standing water.

Site A2 abuts the mineral margin of region I in the study area so that there is a narrow and rather ~~mushy~~ ^{lagged} area at the very edge of site A2. In the ~~wettest~~ ^{wettest} areas, Sphagnum papillosum forms a loose, quaking mat with very little vascular plant growth. This would correspond fairly well to the less moist areas of the Acidic Lake Edge Zone mentioned by Vitt and Slack.

The mineral margin of Site A2 is dominated by Carex rostrata, not by Carex limosa and Carex oligosperma as in the Acidic Lake Edge Zone. Jeglum (1971) lists Carex limosa as an indicator of oligotrophic conditions and Carex rostrata as an indicator of eutrophic conditions. Pollett and Bridgewater (1973) describe a Carex limosa variant of a Caricetum rostratae association in Newfoundland that is very similar in composition to site A2. The Carex limosa variant occurs bordering ponds or streams, which is the habitat described by Vitt and Slack for the Acidic Lake Edge Zone community. The implication of these comments is that site A2 is closely related to the ~~Acidic~~ Lake Edge Zone but is slightly more nutrient-rich, allowing it to support a few more nutrient-demanding species. A few of the more nutrient-demanding species, besides Carex rostrata, found at site A2 are the following: Tridenum virginicum, Smilacina trifolia, and Cladium mariscoides.

Although the mean pH of site A2 is lower than the value given for the Acidic Lake Edge Zone, implying that site A2 is less nutrient-rich than the Acidic Lake Edge community, site A2 is probably subject to nutrient input from the mineral margin so that nutrient availability at A2 may be greater than in a community bordering an acidic lake. It has been proposed in part IIIA of the Results that as a consequence of increasing pH there is greater nutrient availability along the margins of the various study sites so that some plant species respond positively with accelerated growth whereby the concentrations of these nutrients are locally reduced. The exact relationship between nutrient availability, pH, and species persistence and growth are complex and will be further explored in part III of the Discussion.

It should be mentioned that the mean pH reported for the Acidic Lake Edge Zone may be higher than the actual pH of the substrate around the root systems of the plants. Vitt and Slack collected water samples from natural depressions in the bog mat instead of excavating collection holes into the root zones of the bog species. Samples collected at the surface may not represent the root environment, especially when dealing with peat substrates.

Study sites B2 and C2 show a distinct similarity to the Acidic Lake Edge Zone, as mentioned above, but they also resemble the Alkaline Lake Edge Zone. The

values of the environmental variables for the study sites and both the Acidic Lake Edge Zone and the Alkaline Lake Edge Zone are shown below.

	B2	C2	Acidic Lake Edge Zone	Alkaline Lake Edge Zone
pH	4.79	5.12	5.3	6.7
Ca++	2.10 ppm	3.70 ppm	3.5 ppm	7.7 ppm
Mg++	1.49 ppm	2.40 ppm	.6 ppm	1.8 ppm
K+	3.09 ppm	3.65 ppm	3.1 ppm	3.9 ppm
Na+	0.71 ppm	1.21 ppm	2.0 ppm	3.6 ppm

The values for the study sites correspond to the values listed for the Acidic Lake Edge Zone, although there is a definite increase in all the values from site B2 to site C2. The Acidic Lake Edge Zone shares four species with site B2 (Similarity Quotient = .12) and eight species with site C2 (Similarity Quotient = .26). This is out of a total of twenty for site B2, thirty-two for site C2, and forty-two for the Acidic Lake Edge community type. The species shared by site B2 are the following: Chamaedaphne calyculata, Ledum groenlandicum, Sphagnum magellanicum, and Sphagnum papillosum. Of these, Chamaedaphne calyculata and Sphagnum papillosum achieve very high importance values in the Acidic Lake Edge Zone. The species shared by site C2 are the following, with the first four achieving high importance values in Vitt and Slack's community type: Chamaedaphne calyculata, Vaccinium oxycoccos, Sphagnum magellanicum, Sphagnum

Larix laricina is abundant at C1. Species that site C1 shares with the Closed Mat Zone are the following (Similarity Quotient = .22): Sphagnum rubellum, Sphagnum nemoreum, Sphagnum magellanicum, Andromeda glaucophylla, Eriophorum virginicum, Gaylussacia baccata, Kalmia polifolia, Larix laricina, Ledum groenlandicum, Smilacina trifolia, Vaccinium sp. (myrtilloides), and Vaccinium oxycoccos. Study site D1 shares the same species, with the exception of the following (Similarity Quotient = .19): Kalmia polifolia, Larix laricina, and Smilacina trifolia.

The composition of the Closed Mat Zone and the description by Vitt and Slack indicate that the Closed Mat community is a mature ombrotrophic bog or black spruce muskeg (Heinselman 1970; Jeglum 1972; Stanek 1977; Stanek et al. 1977; and others) tending to minerotrophy and relative dryness. Although sites C1 and D1 share many of the major shrub and Sphagnum species with the Closed Mat Zone, there are few of the numerous feather mosses and herbs at sites C1 and D1 that are characteristic of the Closed Mat community type. These species are found primarily in dry, and slightly minerotrophic, conditions (Jeglum 1971). It may be concluded that sites C1 and D1 are closely related to the Closed Mat Zone community type but also possess distinct floristic differences.

papillosum, Picea mariana, Eriophorum virginicum, and Carex oligosperma.

The Alkaline Lake Edge community type is present only around lakes with a relatively high pH and possibly where there is a drainage inflow or outflow. The mean values of the environmental factors for this community are listed above. The values for the pH, Ca⁺⁺, and Mg⁺⁺ are high with respect to the mean pH and cation concentrations given for the other communities described by Vitt and Slack. Ericaceous shrubs such as Chamaedaphne calyculata and Andromeda glaucophylla (A. polifolia in Table 1) are only a minor component of the plant community. Trees are generally absent, except for occasional islands of Alnus rugosa, Carex lasiocarpa is the dominant species. Sphagnum teres and Sphagnum subsecundum are common, with Sphagnum magellanicum, Sphagnum papillosum, and Sphagnum recurvum occasionally present in small amounts. The Alkaline Lake Edge Zone community is essentially a sedge mat.

The resemblance of study sites B2 and C2 to the Alkaline Lake Edge community type is not pronounced and is dependent primarily on a rough correspondence of physiognomy and on the presence of a number of shared species. For site B2, this involves the presence of Typha latifolia and species of Juncus and Scirpus. The similarity of site C2 to this zone is a little stronger, where site C2 shares eight species (Similarity Quotient

= .13) with the Alkaline Lake Edge community type.

Some of the shared species are indicators of eutrophic (pH 6.0-6.9) or very eutrophic (pH 7.0-7.9) conditions (Jeglum 1971). Species shared are as follows:

Chamaedaphne calyculata, Alnus rugosa, Vaccinium oxycoccus, Typha latifolia, Iris versicolor, Eriophorum virginicum, Sphagnum magellanicum, and Sphagnum papillosum. Of

these eight species, only Chamaedaphne calyculata reaches a high importance value in the Alkaline Lake Edge Zone.

Four other genera are shared, three of which may be indicators of minerotrophic conditions (Jeglum 1971).

The three genera that contain minerophilic species are Hypericum (Tridenum in Table 1), Galium, and Scirpus.

The similarity of sites B2 and C2, especially C2, to two community types may be a consequence of beaver activity. The bog vegetation at the margins of these sites could have been covered by vegetation basically similar to site A2. After beaver built dams and drainage canals, these sites would have been altered by the invasion of nutrient-demanding species such as narrow-leaved sedges and cattail. It is possible that beaver activity altered the peat environment so that nutrients became more readily available. Alternatively, an unphenomenal input of nutrients along the drainage system could have resulted in nutrients becoming concentrated in the beaver impoundments resulting in increased nutrient availability at the margin of the bog. Although

there is clear evidence, as described in the Results, of beaver dams acting as nutrient traps, how this occurs is unknown. The results of the test of the nutrient trap hypothesis are thoroughly analyzed in part III of the Discussion.

Vitt and Slack's Open Mat Zone corresponds most closely to sites A1 and B1. The Open Mat Zone is wet. The mean values of pH and cations are shown below along with the values for sites A1 and B1.

	<u>A1</u>	<u>B1</u>	<u>Open Mat Zone</u>
pH	4.42	4.57	4.9
Ca++	2.08 ppm	1.89 ppm	4.5 ppm
Mg++	1.33 ppm	1.49 ppm	.8 ppm
K+	1.73	2.04 ppm	5.0 ppm
Na+	.87	1.66 ppm	3.4 ppm

Both study sites have lower Ca++ values and higher Mg++ values than the Open Mat Zone. Adding Ca++ and Mg++ values, which is a standard procedure to evaluate total water hardness, yields 3.41 ppm for site A1 and 3.38 ppm for site B1. These values are slightly lower than the 5.3 ppm value given by Vitt and Slack. The pH of the Open Mat Zone is the lowest of the seven communities described by Vitt and Slack and near the range of values found at sites A1 and B1.

Species of the Open Mat Zone community that are shared with sites A1 and B1 are: Sphagnum rubellum, Sphagnum magellanicum, Chamaedaphne calyculata,

Gaylussacia baccata, Ledum groenlandicum, and Vaccinium oxycoccos. It also shares Kalmia polifolia with A1 (Similarity Quotient = .28) and the following with B1 (Similarity Quotient = .29): Larix laricina, Alnus rugosa, and Carex trisperma. The dominant vascular plant of the Open Mat community is Vaccinium oxycoccos, which is not abundant at any of the study sites. Physiognomically, both A1 and B1 are similar to the Open Mat Zone in that there is a lack of hummock development, which is especially pronounced at site A1, and have poor shrub growth.

Study site B1 shares many species with study site C1 (Similarity Quotient = .71). Study site C1 resembles Vitt and Slack's Closed Mat Zone. As a consequence, there is a floristic resemblance between site B1 and the Closed Mat community type. However, the greater abundance of Sphagnum rubellum, the lower importance of Ledum groenlandicum, and the greater importance of Eriophorum spp. in both the Open Mat Zone and site B1 indicate a closer relationship between B1 and the Open Mat Zone than between B1 and the Closed Mat Zone.

The Closed Mat Zone is characterized by the presence of Picea mariana and Larix laricina (as seedlings or mature trees) as well as by a tall ericaceous shrub layer of Ledum groenlandicum and Chamaedaphne calyculata. Sphagnum magellanicum is found in large amounts in this

zone. Topographic differences are often large, Vitt and Slack say, with the formation of distinct hummocks where Sphagnum nemoreum may predominate. Andromeda glaucophylla (polifolia in Table 1) is only a minor component.

Study sites C1 and D1 are similar to the Closed Mat Zone. This similarity is both floristic and environmental. The mean pH and cation concentrations for the Closed Mat Zone and sites C1 and D1 are shown below.

	<u>C1</u>	<u>D1</u>	<u>Closed Mat Zone</u>
pH	4.70	4.69	5.1
Ca ⁺⁺	3.35 ppm	2.40 ppm	2.3 ppm
Mg ⁺⁺	2.40 ppm	2.57 ppm	.6 ppm
K ⁺	2.30 ppm	3.37 ppm	4.1 ppm
Na ⁺	2.04 ppm	2.98 ppm	2.7 ppm

These values are roughly similar, although the mean values for the calcium cation at site C1 exceeds the threshold value of 2.7 ppm as described in the Results. Calcium cation values for site D1 and Vitt and Slack's community type are comparable. The concentration of calcium cation may be a limiting factor in peat bogs (Firbas 1952, Malmer 1962, Gies 1972, Wildi 1977; cited in Wildi 1978) so that the similarity of the mean values for this cation is particularly noteworthy.

Sites C1 and D1 display a floristic resemblance to the Closed Mat Zone community type. Picea mariana is absent from D1 and virtually absent from site C1.

Larix laricina is abundant at C1. Species that site C1 shares with the Closed Mat Zone are the following (Similarity Quotient = .22): Sphagnum rubellum, Sphagnum nemoreum, Sphagnum magellanicum, Andromeda glaucophylla, Eriophorum virginicum, Gaylussacia baccata, Kalmia polifolia, Larix laricina, Ledum groenlandicum, Smilacina trifolia, Vaccinium sp. (myrtilloides), and Vaccinium oxycoccos. Study site D1 shares the same species, with the exception of the following (Similarity Quotient = .19): Kalmia polifolia, Larix laricina, and Smilacina trifolia.

The composition of the Closed Mat Zone and the description by Vitt and Slack indicate that the Closed Mat community is a mature ombrotrophic bog or black spruce muskeg (Heinselman 1970; Jeglum 1972; Stanek 1977; Stanek et al. 1977; and others) tending to minerotrophy and relative dryness. Although sites C1 and D1 share many of the major shrub and Sphagnum species with the Closed Mat Zone, there are few of the numerous feather mosses and herbs at sites C1 and D1 that are characteristic of the Closed Mat community type. These species are found primarily in dry, and slightly minerotrophic, conditions (Jeglum 1971). It may be concluded that sites C1 and D1 are closely related to the Closed Mat Zone community type but also possess distinct floristic differences.

The absence of Picea mariana at both C1 and D1 may be explained by the frequent occurrence of fires in the Mer Bleue (Ashley 1979). However, the water level at Site C1, if constant, probably would have prevented widescale burning. The abundance of Larix laricina could be explained by assuming that the water level rose after a fire removed the tree cover, allowing Larix laricina to exploit the wet conditions and preventing widescale reestablishment of Picea mariana. Even though Larix laricina tolerates a wide range of soil moisture and aeration conditions (Tilton 1977), it is an indicator of wet (depth to water 39 to 20 cm) conditions whereas Picea mariana is an indicator of much drier conditions (Jeglum 1971). Larix laricina is also an indicator of eutrophic conditions (Jeglum 1971), so that the abundance of Larix laricina at site C1 may be the result of an increase in nutrient availability as well as an increase in water level. Wet areas in bogs are generally nutrient poor if the substrate water is immobile (Newbold 1960; cited in Sparling 1965). Where water is mobile, the conditions are decidedly minerotrophic (Sjörs 1961; Heinselman 1963; Sparling 1965; and others), with improved aeration (Armstrong and Boatman 1967; Jeglum 1974) and faster decomposition rates (Watt and Heinselman 1965; Walmsley 1977). This may indicate that the success of Larix laricina at site C1 is due to water slowly flowing across the surface of the site.

Another peculiarity of site C1 is the dominance of Ledum groenlandicum in the field layer. In order for Ledum groenlandicum to dominate the shrub stratum, it requires dry, slightly minerotrophic conditions .

(Dansereau and Segadas-Vianna 1952; Segadas-Vianna 1955; Sjörs 1961; Jeglum 1971, 1975; and others). The dominance of Ledum groenlandicum may be explained, again, by assuming that site C1 was drier than it is presently and that the dominance of Ledum groenlandicum is an artifact of that period. It is likely that the abundance of Ledum groenlandicum is undergoing adjustment.

The Marginal Moat Zone of Vitt and Slack is related to site D3. It is found between the bog proper and the surrounding upland forest. The dominant vascular plants are Nemopanthus mucronata, Ilex verticillata, and Viburnum cassinoides. Sphagnum magellanicum is often found if the site is dry. Chamaedaphne calyculata has the highest importance value. Other shrubs of importance are Gaylussacia baccata, Kalmia polifolia, and Ledum groenlandicum. The mean pH and cation concentrations (ppm) are given below and compared to the same factors from site D3.

	<u>.D2</u>	<u>Marginal Moat Zone</u>
pH	5.00	5.9
Ca++	2.78 ppm	.5 ppm
Mg++	3.06 ppm	.1 ppm
K+	1.55 ppm	3.0 ppm
Na+	2.96 ppm	1.5 ppm

The floristic resemblance of site D3 to the Marginal Moat Zone is very strong, sharing eleven species (Similarity Quotient = .34). All but three of the shared species are important or characteristic species for both communities. The values for the environmental variables listed for the study site and Vitt and Slack's community type are quite different, with the pH being slightly higher in the Marginal Moat Zone and all other values being higher at site D3. The nutrient load at site D3 may be influenced by an adjacent Alnus rugosa swamp that would furnish nitrate to the plants at the margin of site D3 (Daly 1966), thereby promoting growth. Increased growth would result in larger quantities of nutrients returned to the surface through leaf spoors, decomposition of dead roots, and perhaps nitrate or ammonia release from the root nodules of Alnus rugosa. Increased aeration of the exposed peats under the Alnus canopy would also likely promote nutrient availability due to aerobic decomposition.

Site D2 does not correspond to any of Vitt and Slack's community types. It may be considered to be a

highly disrupted Closed Mat Zone possibly integrated with a Marginal Moat Zone and characterized by a massive invasion and domination by Typha latifolia. Site D3 would more typically be a marsh community if it were not for the presence of scattered mats of Sphagnum rubellum and Sphagnum magellanicum.

Descriptions and analyses of vegetation associations for wetlands in central Saskatchewan are available in a series of reports by Jeglum (1971, 1972a, 1972b). Five of the nine physiognomic groups described by Jeglum are related to plant assemblages found at the study sites. These are: Emergent Fen, Sedge Fen, (Low) Shrub Fen, Tamarack Swamp, and Low Shrub Bog (Open Bog).

The Emergent Fen is characterized by relatively tall graminoid emergents found in zones or clumps along lakes, ponds, and streams. The occurrence of large sedges (Carex spp.), Jeglum says, suggests that the Emergent Fen is developing toward Sedge Fen. Monodominant stands occur in deep water whereas stands with two or three emergents tend to occur in shallow water. Bryophyte cover is generally completely lacking or low. Stands with the fewest species tend to be those with the deepest standing water. Standing water averages 25 cm deep. The pH of moist peat sampled from the Emergent Fen is 6.7.

The areas in my study area corresponding to the Emergent Fen are the margins of sites B2, C2, and D2.

The edges of the beaver canals would also be classified as Emergent Fen. Species listed for the Emergent Fen that are found growing in at least one of the three study sites are: Carex rostrata, Galium sp., Juncus sp., Scirpus acutis, and Typha latifolia.

The margins of the vegetation assemblages above each dam site all have elevated pH values compared to areas toward the bog center. The margins of these sites have a mud or muck substrate composed of decomposed peat mixed with clay and other materials. The growth characteristics and distribution patterns of the Emergent Fen community closely resembles the appearance of the margins of the impoundment sites, as mentioned above. In areas above and below the dam sites, where beaver have constructed and maintained canals, the vegetation is also similar. The vegetation along these canals is composed primarily of grasses, Scirpus spp., Carex spp., Juncus spp., Eleocharis spp., and Typha latifolia. Bog vegetation is mixed with the Emergent Fen vegetation along the beaver canals as well as at the margins of the disturbed study sites.

Chamaedaphne calyculata shows a striking growth response at these disturbed sites that is different from its response to conditions at the undisturbed margins of sites A2 and D3. Although Chamaedaphne calyculata displays enhanced growth and positive correlation of height to pH values at site D3, it does not display at

site D3 the dramatic change in height and colour that it does in the disturbed areas. At site A2, the height of Chamaedaphne calyculata is not positively correlated with pH at the 95% confidence level and a striking colour change does not occur. There is definitely a less elevated growth response at site A2 than at sites B2 and C2. The lack of correlation between the height of Chamaedaphne calyculata and pH may, however, be due to the sampling procedure. Chamaedaphne calyculata is likely rooted near the mineral substrate that is overlain by shallow peat and live Sphagnum mosses just at the margin of site A2. The roots of Chamaedaphne calyculata would therefore have access to growth nutrients from the mineral substrate. At the margin of site A2, which is very wet and soupy, the pH was measured from water sampled just beneath the surface where Sphagnum mosses were growing. The Sphagnum mosses might have kept the pH, and the nutrient availability, lower than the height of Chamaedaphne calyculata would indicate.

The disturbed sites in the study area may be undergoing vegetation adjustment in response to beaver disturbance as shown by the development of Emergent Fens along the canals and above the dam sites and by the death of Larix laricina and Betula populifolia in these places.

Study site A2 corresponds reasonably well with Jeglum's Broad-Leaved Sedge Fen. The leading dominants

of this physiognomic group are sedge (Carex) species and, less commonly, species of the grass Calamagrostis. Broad-Leaved Sedge Fen, characterized by such sedges as Carex rostrata, is associated with higher levels of nutrient availability than the Narrow-Leaved Sedge Fen. The mean pH is 6.4 and the water averages 6 cm in depth.

Site A2 shares the following species with Jeglum's Broad-Leaved Sedge Fen: Alnus rugosa, Carex rostrata, Carex limosa, Smilacina trifolia, and Sphagnum spp.

The pH at site A2 is about 4.5, which is considerably lower than the value given for the Broad-Leaved Sedge Fen. Jeglum's sites were found on peats with a high silt content or on mud substrates. The presence of mud bottoms is related, Jeglum says, to frequent flooding by nutrient-rich water. The other species listed for the Sedge Fen complex would grow well on wet, nutrient-rich sites. Their absence at site A2 is probably indicative of the site's low pH and consequent lower level of minerotrophy (Lucas and Davis 1961) as compared to the conditions in Jeglum's Sedge Fen. Site A2 is still sufficiently nutrient-rich to allow Carex rostrata to grow abundantly. Likely, the sedge species are taking up nutrients derived from the sand and clay under the peat and living Sphagnum moss cover. The abundance of Carex rostrata quickly decreases about forty meters from the mineral margin of site A2 and is not present in site

A1, which begins at fifty meters from the mineral margin of site A2. This may be interpreted as the point where nutrients carried from the mineral margin and the substrate sand and clay are no longer accessible to the plants. This area would be the demarcation between soligenous and ombrogenous conditions. The water levels at site A2 and at the Sedge Fens are comparable.

Where the vegetation of Jeglum's Low Shrub Fen occurs adjacent to Sedge Fens, there is a continuum of variation from Low Shrub Fen to Sedge Fen. Jeglum states that usually one shrub species per stand attains importance. This would be similar to the situation between sites A1 and A2 where Chamaedaphne calyculata is dominant at both sites and where the Open Bog vegetation of site A1 grades into the Sedge Fen vegetation at site A2.

There are certain features of sites B2 and C2 that indicate a relationship to Jeglum's Sedge Fen complex. The mean pH at the two sites is elevated with respect to the mean value at site A2, being 4.79 at B2 and 5.12 at C2. The mean pH value at site A2 is 4.48. These values, however, are well below the mean pH of the Sedge Fen, given as 6.4. The depth of water at the two study sites is comparable to the 6 cm listed for the Sedge Fen only at the margins of sites B2 and C2, which are floating mats located along the standing water of the beaver impoundments.

The plant assemblages along the margins of sites B2 and C2 fit the general physiognomic description of the Sedge Fen community and share a few of the important species. These species are Carex rostrata, Typha latifolia, and other Carex spp. The major portion of sites B2 and C2 are related to Jeglum's Shrub Fen complex. This would be a similar relationship as mentioned above for sites A2 and A1 where A2 resembled the Broad-Leaved Sedge Fen at its mineral margin and a Shrub Fen in the transition area to site A1, which is similar to the Open Bog community of Jeglum's.

The Low Shrub Fen consists of shrub dominant that are below breast height (less than 135 cm). Usually one shrub species per stand attains importance, the highest shrub covers occurring in the driest sites. On the average, three herb species per stand are important and dominance of Broad-Leaved Sedge Fen (Carex spp.) characterize the richest stands and dominance of Narrow-Leaved Sedge Fen (Carex spp.) characterize the poorest stands. Sphagnum species may attain importance in Chamaedaphne calyculata stands, which, Jeglum says, may be a type successional to muskeg since they possess elements of Sedge Fens, Low Shrub Fens, and Muskegs. Ground surfaces are usually fairly level. The mean pH for moist peat is 5.6. The peat is a fen peat, derived mostly from sedges. The mean depth to water is 21 cm.

Sites B2 and C2 are related floristically to the Low Shrub Fen community in that they are both dominated by Chamaedaphne calyculata and possess a number of sedge species and herbs that are minerotrophic indicators (Jeglum 1971). Mean pH values are lower for sites B2 (4.79) and C2 (5.12) than the value given for the Low Shrub Fen (5.6). This most likely is due to the Sphagnum mat present at the study sites in contrast to the sedge mat that characterizes the Low Shrub Fen. In fact, the presence of a Sphagnum mat is a principal determinant in the separation of Jeglum's peatland community types. Mean depth to water at the study sites (B2 - 18 cm, C2 - 11 cm) is very close to the value listed for the Low Shrub Fen (21 cm).

Study sites A1 and B1 are vaguely similar to the Low Shrub Fen in that they are dominated by Chamaedaphne calyculata, possess little hummock development, and are relatively wet. These sites, including C1 and D1, resemble much more strongly Jeglum's Open Bog physiognomic group. However, none of the sites bears as strong a resemblance as would be expected. Jeglum makes reference to a study of Segadas-Vianna (1955), which will be reviewed below, that concerns the status of the Chamaedaphne calyculata community in the region of central Saskatchewan. Jeglum says that the Chamaedaphne calyculata community, as described by Segadas-Vianna, is of infrequent occurrence at Candle Lake, Saskatchewan

and "is found only as narrow zones, has relatively shallow Sphagnum layers, and has fen sedges and shrubs present, which indicate the influence of mineral soil water. In eastern Canada and northeastern United States the Chamaedaphne community is more common and occupies wider zones than at Candle Lake. Segadas-Vianna (1955) recognizes three distinct phases: 'wet pioneer', characterized by such plants as Carex rostrata, Menyanthes trifoliata and Myrica gale; 'intermediate', characterized by Kalmia polifolia and Andromeda species; and 'dry', characterized by Ledum and black spruce. The stands at Candle Lake are similar to the wet pioneer phase, which is clearly minerotrophic. The intermediate and dry phases, which are chiefly ombrotrophic and underlain by deeper continuous Sphagnum peat horizons, are not present at Candle Lake."

Sites A1, B1, and D1 could fit the sequence described by Segadas-Vianna, with the transitional area of site A2 constituting the "wet pioneer" phase, most of site A1 and all of site B1 representing the "intermediate" phase, and site D1 would represent the "dry" phase. Site C1 could readily fit into this sequence because it possesses a number of the key characteristics listed by Jeglum for the Open Bog stands as well as many of the characteristics of the dry phase of the Chamaedaphne calyculata community described by Segadas-Vianna. These characteristics are: a continuous layer of ericaceous

shrubs, in central Canada the shrub layer would be dominated by Ledum groenlandicum; ground surfaces of hummocks and hollows of Sphagnum moss; and evidence of repeated fires that is reflected in a vegetation cover containing an abundance of Ledum groenlandicum, Vaccinium spp. (such as Vaccinium myrtilloides), and Polytrichum spp. (such as Polytrichum juniperum).

Site C1 does not fit the developmental series of the Chamaedaphne calyculata community described above because of: the presence of wet conditions (depth to water 39-20 cm, Jeglum 1971); an absence of Picea mariana as seedlings or trees; an abundance of Larix laricina; and the presence of other plant indicators of mineral-rich water, such as Scirpus acutis, Typha latifolia, Smilacina trifolia, Alnus rugosa, and perhaps Anchistea virginica.

The Open Bog physiognomic group is described by Jeglum as having two variants. The variant that is dominated by Chamaedaphne calyculata is found in oligotrophic, wet environments. The variant that is dominated by Ledum groenlandicum is found in very oligotrophic, relatively dry environments. Site C1 is very similar to Jeglum's Open Bog community, specifically the Ledum groenlandicum variant, but it certainly is not a very oligotrophic, dry stand. The abundance at C1 of Larix laricina suggests a relationship to Jeglum's Tamarack Swamp.

have taken place so that the plant assemblage at site Cl would be in the process of adjusting to a change in these environmental components, from a dry, relatively nutrient-poor state to wet, nutrient-rich conditions. It should be mentioned that the minerotrophic situation, particularly as measured by the calcium cation concentration, may be the consequence of both fire and swamping disturbance. The swamping is very likely the more significant disturbance of the nutrient status of site Cl.

Further corroboration of this view is provided by the resemblance of site Cl to Sjörs' Wooded Poor Fen. He writes that "some poor fen is wooded, due either to very shallow peat or to comparatively good drainage. Black spruce and tamarack are the only trees. The latter reaches a larger size here than in bogs. Shrubby thickets of willows and speckled alder occur frequently. The undervegetation is different from that of open poor fen and often resembles that of more or less wooded ombrotrophic bogs (with Ledum, Chamaedaphne, species of Vaccinium, Rubus chamaemorus, Carex paupercula, Carex trisperma, Smilacina trifolia, etc.) but it contains clearly minerotrophic species" Most of the minerotrophic species listed by Sjörs for the wooded poor fen are in the following genera: Equisetum, Carex, and Eriophorum. Although none of the minerotrophic species mentioned, except for Alnus rugosa, are found

that is essentially an open bog that is normally found on dry, oligotrophic sites further suggests that the wet condition at site C1 is a recent development and that the vegetation is adjusting to this new situation.

Water flows within the surficial, partially decomposed substrate of bogs, the lower consolidated peat being nearly impervious to water movement (Gorham and Hofstetter 1971; Radforth 1977, p. 146). A change in hydraulic relationships within the study area would cause changes in surficial water movement that could influence the development of plant assemblages by affecting both the water and nutrient regimes. Such a change would account for the unusual vegetative composition and structure of site C1.

Vegetation patterns of raised bogs in the Bay of Fundy region of Maine and New Brunswick are described by Damman (1977). Four main groups of plant communities can be recognized. These are: 1) dwarf shrub heaths; 2) Scirpus cespitosus lawns and solid Sphagnum carpets; 3) extremely nutrient-poor fens; and 4) mud bottom communities. The first three share a large group of species but possess basic physiognomic and floristic differences. The four main groups are divided into ten plant associations, six of which are similar to the plant assemblages in the study area. (Refer to Figure 38.)

Site A1 possesses several of the floristic and physiognomic characteristics of two of Damman's associations, namely the Scirpus cespitosus-Sphagnum flavicomans

Fig. 38

Water level fluctuation and distribution of plant communities in a part of Maddybamps Heath, a large convex raised bog outside the coastal belt. For communities with an irregular surface the water level extremes are shown with respect to both average hollow and hummock surface.

and the Chamaedaphne-Sphagnum rubellum communities. The first occupies wetter sites than the Scirpus-Sphagnum fuscum community, which is one of the dwarf shrub heaths and is described below. The bog surface in the Scirpus cespitosus-Sphagnum rubellum community is almost flat with few Sphagnum clumps rising more than 5.8 cm above the surface. It is distinguished from the dwarf shrub heaths by the absence of Rubus chamaemorus, Polytrichum strictum, Sphagnum fuscum, and species of the dwarf shrub heaths and by the presence of Andromeda glaucophylla and often Arethusa bulbosa. Sphagnum rubellum and Sphagnum flavicomans are the dominant Sphagnum species.

The Chamaedaphne-Sphagnum rubellum community is distinguished by the continuous carpet of Sphagnum rubellum with patches of Cladonia spp. The Cladonia lichens are described by Damman as moribund. Chamaedaphne calyculata is abundant but poorly developed and rarely over 10 cm high. Gaylussacia dumosa and Andromeda glaucophylla occur regularly and Scirpus cespitosus can be locally abundant. Rhynchospora alba and Eriophorum virginicum are found sporadically. Damman writes that "this community occupies large depressions and filled-in pools in the ombrotrophic bog centers of the inland high moors, but it can also occur along some pool margins."

Several factors indicate that site A1 is related to the Chamaedaphne-Sphagnum rubellum community. They

are similar in that they share several important species (Similarity Quotient = .33) and are basically the same structurally and physiognomically. The species that are shared are the following: Chamaedaphne calyculata, Vaccinium oxycoccos, Kalmia polifolia, Ledum groenlandicum, Sphagnum magellanicum, Sphagnum rubellum, and Polytrichum strictum. As in the Chamaedaphne-Sphagnum rubellum community, Chamaedaphne calyculata and Sphagnum rubellum are abundant at site A1 and Chamaedaphne calyculata is poorly developed, rarely exceeding 20 cm in height with little lateral growth. Polytrichum strictum occurs rarely at site A1 as in the Chamaedaphne calyculata community, where it is listed as being present in one out of nine stands of this community type. Site A1 possesses two Eriophorum species, Eriophorum chamissonis being abundant. The Chamaedaphne-Sphagnum rubellum community contains two Eriophorum species (E. virginicum and E. spissum) and a beaked rush (Rhynchospora alba), but these occur only sporadically.

Cladonia lichens were not found at site A1 while the Chamaedaphne-Sphagnum rubellum community is characterized by four Cladonia species (C. arbuscula, C. crispata, C. rangiferina, and C. mitis), all differential species. There seems to be a general absence of Cladonia lichens in the Mer Bleue as well as the entire study area (personal observation). This may be due to a general failure of Cladonia species to occur over wide areas in

the southern part of their range unlike in northern bog communities where Cladonia species may grow in such profusion that they form "lichen muskegs" and "lichen heaths" (Ritchie 1960, 1962; cited in Jeglum 1972a). Alternatively, the absence of Cladonia species from the study area may be attributed to the high incidence of fire reported for the Mer Bleue.

Site B1 bears a resemblance to Damman's Chamaedaphne-Sphagnum rubellum community. But site B1 possesses species indicative of minerotrophy and fire disturbance that are not listed for the Chamaedaphne-Sphagnum rubellum community. Because of this, site B1 shows a certain relationship to the Kalmia angustifolia-Sphagnum fuscum association, which is classified as a dwarf shrub heath (Similarity Quotient = .36). Fewer species are shared between site B1 and the Chamaedaphne-Sphagnum rubellum community (Similarity Quotient = .26), however the appearance and general structure of site B1 would indicate that site B1 is more closely related to the Chamaedaphne-Sphagnum rubellum community than to the Kalmia-Sphagnum fuscum community.

Recall that the differences between sites A1 and B1 are as follows: site B1 is drier; site B1 is characterized by a higher pH and slightly higher nutrient availability; site B1 possesses shrubs that have a greater total surface area coverage and lateral growth and that are growing in Sphagnum hummocks; and site B1

is characterized by minerophilic species, some of which are indicators of fire disturbance. These differences could be readily explained by assuming that sites A1 and B1 represent a single community type that is, or was, differentiating along a nutrient and water level gradient.

Study site C1 is also related to two of Damman's vegetation communities, although an explanation of the dual nature of the site does not appear as straightforward as for site B1. Damman's plant associations that are similar to site C1 are the Kalmia-Sphagnum fuscum community, mentioned above as being related to site B1, and the Smilacina-Sphagnum pulchrum community.

Site C1 is similar to the Smilacina-Sphagnum pulchrum community in that it possesses a high water table, minerotrophic water as reflected by the calcium concentration, and several species that are indicators of minerotrophic conditions. Site C1 is similar to the Kalmia angustifolia-Sphagnum fuscum community in general physiognomy, basic floristic composition, and the high abundance of Ledum groenlandicum.

The Smilacina-Sphagnum pulchrum community is found, in eastern bogs, on areas affected by minerotrophic water. It is distinguished by the occurrence of nutrient-demanding species, of these Eriophorum angustifolium, Smilacina trifolia, and Myrica gale are almost always present. The Sphagnum carpet contains Sphagnum pulchrum, Sphagnum papillosum, Sphagnum apiculatum, and Sphagnum

flavicomans as the most important species, with Sphagnum rubellum and Sphagnum fuscum occurring only as isolated cushions. Damman mentions that this community is most extensive in the moats of the coastal bogs.

The following species are shared by site C1 with the Smilacina-Sphagnum pulchrum community (Similarity Quotient = .39): Larix laricina, Smilacina trifolia, Eriophorum virginicum, Ledum groenlandicum, Chamaedaphne calyculata, Vaccinium oxycoccos, Kalmia polifolia, Kalmia angustifolia, Andromeda glaucophylla (polifolia), Sphagnum magellanicum, Sphagnum rubellum, and Polytrichum strictum. Larix laricina is common at site C1. The Smilacina-Sphagnum pulchrum community is the only one of Damman's communities to regularly possess Larix laricina. Larix laricina is an indicator of wet and nutrient-rich conditions even though it has wide ecological amplitude. The common occurrence of Larix laricina in a moat community such as the Smilacina-Sphagnum pulchrum community is to be expected. The presence of abundant Larix laricina at site C1, as well as other species indicative of wet, minerotrophic conditions, suggests that site C1 has the characteristics of a bog community normally restricted to a moat-like situation at the margins of a raised bog or the edge of a lake bog. Obviously, this situation does not apply to site C1.

The Kalmia angustifolia-Sphagnum fuscum community is found on relatively well-drained peat and is the most

common of the dwarf shrub heath communities identified by Damman. Kalmia angustifolia forms a 30-40 cm high dwarf shrub layer which determines the physiognomy of the vegetation. The bog surface has a clear and regular hummock-hollow topography. Other shrubs of importance are Chamaedaphne calyculata, Vaccinium oxycoccos, Kalmia polifolia, and Ledum groenlandicum. Minor shrub species are Nemopanthus mucronata and Gaylussacia baccata. Eriophorum spissum is also an important component of the shrub community. Three Sphagnum species make up the Sphagnum carpet. These are Sphagnum magellanicum, Sphagnum rubellum, and Sphagnum fuscum. This community is very similar to the shrub and moss community of site C1, except that Ledum groenlandicum is the most abundant shrub. One of Damman's stands included as a member of the Kalmia-Sphagnum fuscum community has an abundance value for Ledum groenlandicum that is nearly as high as the value given for Kalmia angustifolia, which was the most abundant shrub in all of the community stands. It may be assumed that Ledum groenlandicum regularly achieves high abundance in this community. It is noteworthy that the stand where Ledum groenlandicum is abundant is also characterized by Cladonia arbuscula, Cladonia rangiferina, and Picea mariana, where all three species have high importance values. The two latter species are indicators of dry conditions (depth to water 79 to 60 cm, Jeglum 1971). These species are not present

at site C1. It may be assumed that the stand investigated by Damman where Ledum groenlandicum is abundant is a dry site that might be referred to as a black spruce muskeg or black spruce bog forest.

Species shared by the Kalmia-Sphagnum fuscum community and site C1 are the following (Similarity Quotient = .42): Larix laricina, Betula p~~ice~~atfolia, Chamaedaphne calyculata, Vaccinium oxycoccos, Kalmia polifolia, Ledum groenlandicum, Kalmia angustifolia, Sphagnum magellanicum, Andromeda glaucophylla (polifolia), Sphagnum rubellum, Gaylussacia baccata, Sphagnum nemoreum, and Polytrichum strictum. Nearly all of the important species in both communities are the same. The similarity between site C1 and the Kalmia-Sphagnum fuscum community is striking, strongly suggesting that site C1 must possess a similar set of environmental conditions. This is not the case. The Kalmia-Sphagnum fuscum community occurs on well-drained peat in the dry parts of the bogs that Damman sampled, being replaced in the driest areas by a Gaylussacia baccata dominated community. The floristic relationship between sites C1 and D1 in the study area would appear to be the same as the relationship between the Kalmia-Sphagnum fuscum and Gaylussacia baccata communities described by Damman.

Site D1 appears to be related to Damman's Gaylussacia baccata community type. The Gaylussacia baccata community occupies the driest areas of the bogs

The presence of feather mosses (Pleurozium, etc.) and the abundance of Ledum groenlandicum shows that this community is the typical black spruce muskeg that occurs on drier sites in ombrotrophic peatlands. Sjörs describes Larix laricina as always subordinate to Picea mariana and Ledum groenlandicum as less tolerant of wet conditions than Chamaedaphne calyculata. Larix laricina certainly is not subordinate to Picea mariana at site C1 and Ledum groenlandicum is dominating the field layer in the rather wet conditions found at site C1.

I have suggested that the absence of Picea mariana at site C1 may be due to fire removal followed by swamping. I also have suggested that the dominance at C1 of Ledum groenlandicum may be an artifact of its success during the time site C1 was wooded and drier or as a consequence of fire disturbance. The fact that Ledum groenlandicum occurs in fairly dense, scattered patches at site C1 further suggests this, especially since the transect data indicates that Ledum groenlandicum occurs near areas where the depth to water is greater than in the areas near where Chamaedaphne calyculata is growing. This probably reflects the hummock-hollow topography of the site in that Ledum groenlandicum would be maintaining dominance on the dry hummocks. The patchy distribution would be the result of poor growth in the wetter areas.

If swamping has occurred at site C1 a change in nutrient and moisture-aeration regimes would certainly

significance that site D1 shares many features with both communities, especially in view of the likelihood of site D1 being a fire disturbed site.

The Rhododendron canadense-Chamaedaphne calyculata community of Damman closely resembles site D3, a margin study site that was chosen as a control for comparison to site D2. The Rhododendron-Chamaedaphne community is a wet dwarf shrub heath occupying the very slightly nutrient-enriched parts of those bogs that Damman investigated. If it occurs as a zone, this community indicates the mineral soil water limit and is most often found between the Kalmia-Sphagnum fuscum community toward the bog's center and the Rhododendron-Nemopanthus mucronata thicket at the bog's margin. Chamaedaphne calyculata completely dominates the other plant species, but other dwarf shrubs, such as Rhododendron canadense, Kalmia angustifolia, Ledum groenlandicum, Andromeda glaucophylla, and Kalmia polifolia, are often present. Eriophorum angustifolium and Rhododendron canadense are the only weakly minerotrophic vascular plants that occur regularly in this community, according to Damman. Other minerotrophic species do occur. These include Vaccinium angustifolium, Nemopanthus mucronata, Viburnum cassinoides, and Larix laricina. The moss layer is poorly developed and variable in composition, with Sphagnum teres, Sphagnum robustum, and Sphagnum cuspidatum locally abundant. The average height of the shrubs in Damman's

stands that were grouped in this community is 54 cm.

Site D3 shares the following species with the Rhododendron-Chamaedaphne community (Similarity Quotient = .35): Chamaedaphne calyculata, Vaccinium oxycoccos, Kalmia polifolia, Ledum groenlandicum, Kalmia angustifolia, Nemopanthus mucronata, Viburnum cassinoides, Sphagnum magellanicum, Sphagnum rubellum, Sphagnum nemoreum, and Polytrichum strictum. These are the more important species in the Rhododendron-Chamaedaphne community with the exception of Rhododendron canadense, which was not found at site D3. The general physiognomy, location, habitat, floristic structure and composition of site D3 is very similar to this community so that it may be assumed that site D3 is a typical marginal or transition bog community at the lower part of the bog slope.

Sites A2, B2, C2, and D2 are not similar to any of the communities that are described by Damman, although site A2 roughly resembles the mud bottom communities in general physiognomy.

The most noteworthy feature of the comparison of the study site plant assemblages with Damman's community types is the evident relationship of site C1 to two plant associations that are found growing under nearly opposite environmental conditions. The suggestion advanced earlier, in connection with a similar conclusion regarding Vitt and Slack's community types and reinforced by the comparisons with Jeglum's physiognomic groups,

that site C1 was a dry, forested site that was burned over and then subsequently swamped, would appear to be justified. The obvious agent of swamping is beaver damming, however this implies that the influence of beaver activity reaches deep into the bog rather than just along the bog margin.

In a series of reports Sjörs (1959a, 1959b, 1961) has described the bogs and fens in northeastern Manitoba, northern Ontario, and northwestern Quebec. He describes seven main types of plant communities in two main categories: ombrotrophic types, which include Wooded Bog and Open Bog; and Minerotrophic types, which include Open Poor Fen, Wooded Poor Fen, Open Rich Fen, Wooded Rich Fen, and Riparian Rich Fen. Four of these seven plant communities resemble the study sites.

Sites A1, B1, C1, and D1 are similar to the Open Bog. Site C1 also is related to the Wooded Bog and the Wooded Poor Fen. Sites B2 and C2 loosely resemble the Riparian Rich Fen. The only strong similarity is that of sites A1, B1, and D1 to the Open Bog.

The Open Bog community is characterized by a lack of trees (not completely absent) and a bottom layer of Sphagnum species overgrown by ericaceous shrubs. It shares the following species with site A1: Chamaedaphne calyculata, Ledum groenlandicum, Kalmia polifolia, Vaccinium oxycoccos, Sphagnum rubellum and Sphagnum magellanicum. In addition to the species above, site

B1 shares Andromeda polifolia and Larix laricina with Sjörs' Open Bog. Site C1 shares all those above in addition to the following: Vaccinium species (myrtilloides), Smilacina trifolia, and Eriophorum virginicum. Site D1 shares fewer species with Sjörs' Open Bog than site C1 in that Kalmia polifolia, Larix laricina, and Smilacina trifolia are not found at site D1. However, sites A1, B1, and D1 are definitely in this category.

Site C1 contains the following species that indicate a relationship to the Wooded Bog plant community: Larix laricina, Vaccinium species (myrtilloides), and Kalmia angustifolia. Sjörs writes that "among the field layer plants, the common dwarf-shrub species Vaccinium myrtilloides and the less common Kalmia angustifolia, though confined to this type as far as ombrotrophic bog vegetation is concerned, occur occasionally in seepages." This would be an indication of the minerotrophic requirements of these species. Sjörs continues by stating that the "dominance in the field layer of Wooded Bog is usually shared by Ledum groenlandicum and Chamaedaphne calyculata, the latter usually predominating in less densely wooded parts; in the more marginal parts Vaccinium myrtilloides or Vaccinium vitis-idaea subspecies minus are also sometimes dominant. In the bottom layer of wooded bog vegetation, Sphagnum is often less abundant than are other mosses, such as Pleurozium, Hylocomium and Dicranum, which also occur in other forested sites."

The presence of feather mosses (Pleurozium, etc.) and the abundance of Ledum groenlandicum shows that this community is the typical black spruce muskeg that occurs on drier sites in ombrotrophic peatlands. Sjörs describes Larix laricina as always subordinate to Picea mariana and Ledum groenlandicum as less tolerant of wet conditions than Chamaedaphne calyculata. Larix laricina certainly is not subordinate to Picea mariana at site C1 and Ledum groenlandicum is dominating the field layer in the rather wet conditions found at site C1.

I have suggested that the absence of Picea mariana at site C1 may be due to fire removal followed by swamping. I also have suggested that the dominance at C1 of Ledum groenlandicum may be an artifact of its success during the time site C1 was wooded and drier or as a consequence of fire disturbance. The fact that Ledum groenlandicum occurs in fairly dense, scattered patches at site C1 further suggests this, especially since the transect data indicates that Ledum groenlandicum occurs near areas where the depth to water is greater than in the areas near where Chamaedaphne calyculata is growing. This probably reflects the hummock-hollow topography of the site in that Ledum groenlandicum would be maintaining dominance on the dry hummocks. The patchy distribution would be the result of poor growth in the wetter areas.

If swamping has occurred at site C1 a change in nutrient and moisture-aeration regimes would certainly

have taken place so that the plant assemblage at site Cl would be in the process of adjusting to a change in these environmental components, from a dry, relatively nutrient-poor state to wet, nutrient-rich conditions. It should be mentioned that the minerotrophic situation, particularly as measured by the calcium cation concentration, may be the consequence of both fire and swamping disturbance. The swamping is very likely the more significant disturbance of the nutrient status of site Cl.

Further corroboration of this view is provided by the resemblance of site Cl to Sjörs' Wooded Poor Fen. He writes that "some poor fen is wooded, due either to very shallow peat or to comparatively good drainage. Black spruce and tamarack are the only trees. The latter reaches a larger size here than in bogs. Shrubby thickets of willows and speckled alder occur frequently. The undervegetation is different from that of open poor fen and often resembles that of more or less wooded ombrotrophic bogs (with Ledum, Chamaedaphne, species of Vaccinium, Rubus chamaemorus, Carex paupercula, Carex trisperma, Smilacina trifolia, etc.) but it contains clearly minerotrophic species" Most of the minerotrophic species listed by Sjörs for the wooded poor fen are in the following genera: Equisetum, Carex, and Eriophorum. Although none of the minerotrophic species mentioned, except for Alnus rugosa, are found

at site C1, true indicators of minerotrophy occur at site C1. These include, along with Alnus rugosa, Larix laricina, Typha latifolia, and Scirpus acutis. This list might also include Anchistea virginica, Carex oligosperma, and Smilacina trifolia. Smilacina trifolia is listed by Sjörs as being an ombrotrophic species frequently found in fen situations. Jeglum (1971) identifies it as an indicator of wet conditions.

It may be concluded that the vegetation composition of site C1 is a mixture of ombrotrophic Wooded Bog and Open Bog and minerotrophic Wooded Poor Fen and, possibly, Wooded Rich Fen.

Sites B2 and C2, in their general physiognomy, show a certain relationship to Sjörs' Riparian Rich Fen. The resemblance is due to site characteristics as much as vegetation similarity. The Riparian Rich Fens are found along very wet, clay river banks. The plant cover includes Carex species, Iris versicolor, Juncus species, Equisetum species, Eleocharis calva, Glyceria striata, and many herb species, such as Ranunculus reptans and Solidago graminifolia. Scirpus species are notably lacking. The pH values are high, ranging from 5.5 to 8.3.

Heinselman (1963, 1970) describes eight peatland types and seven vegetation communities from the Lake Agassiz Peatlands Natural Area, Minnesota (U.S.A). Peatland types are physical land types, distinct from

vegetation types, and are interesting for comparison / purposes because of the criteria used for distinguishing them. These criteria are: 1) location with respect to mineral soil margins, islands, substratum relief, and water sources; 2) topography of the peat surface; 3) water levels and water movement; 4) chemical properties of waters feeding peatlands or issuing from them; 5) botanical origin, decomposition, and thickness of peats; and 6) natural vegetation. The vegetation types were classified on the basis of floristic and physiognomic criteria. Heinzelman mentions that because peatland vegetation is often homogeneous over large areas, classification and mapping are relatively easy. Also, because the Lake Agassiz Natural Area is so large (181-Km²), vegetation types were adopted that could be mapped directly from aerial photographs. It may be that this method results in a loss of community resolution, particularly with respect to marginal or transition vegetation types.

Two of the peatland types are represented in my study area. These are the Weakly Minerotrophic Swamp and the Ombrotrophic Bog. Four of the vegetation types are related to plant assemblages in the study area. These are: Poor Swamp Forest, Larch String Bog and Fen, Sphagnum-Black Spruce-Leatherleaf Bog Forest, and Sphagnum-Leatherleaf-Kalmia-Spruce Heath.

The Sphagnum-Leatherleaf-Kalmia-Spruce Heath occurs as great expanses of nearly treeless Sphagnum heath on lower slopes of raised bogs. The terrain is wet and soggy. A low shrub layer of Chamaedaphne, Kalmia, and Vaccinium oxycoccos is typical, but a continuous blanket of Sphagnum is the most conspicuous aspect. This type is similar to sites A1, B1, C1, and D1, however it is most similar to sites A1 and B1. Plant species occurring at site A1 that are shared with this vegetation type are: Vaccinium oxycoccos, Ledum groenlandicum, Chamaedaphne calyculata, Kalmia polifolia, Eriophorum species, and Sphagnum magellanicum. Site B1 shares the above species with the heath community as well as the following: Larix laricina, Andromeda glaucophylla (polifolia), Vaccinium species (myrtilloides), and Carex species (trisperma). This is out of a total of seventeen species listed for this type (Similarity Quotient = .50).

Environmentally, sites A1 and B1 can be classified as Ombrotrophic Bog. The mean pH values at sites A1 and B1 (4.4 and 4.6, respectively) are higher than the values listed for the Lake Agassiz Sphagnum dominated sites (3.1-4.1), but is just above the upper value that is given for a Picea-Larix Bog Forest on a lower slope site. It should be mentioned that the time of sampling may influence the values recorded for environmental factors. During the month of July (1977) the pH values at A1 were

4.0-4.1 and only slightly higher at B1. The calcium cation plus magnesium cation values for sites A1 and B1 are 3.4 ppm and 3.0 ppm, respectively. The values of calcium and magnesium cations for the Ombrotrophic Bog range from 1.1 to 3.5 ppm, placing the values at A1 and B1 at the upper end of this range.

The Sphagnum-Black Spruce-Leatherleaf Bog Forest vegetation type is similar to site D1, with the exception of an absence of tree cover (Picea mariana and Larix laricina) and feather mosses. This type also bears a resemblance to site C1. Species shared by site D1 with this type are (Similarity Quotient = .54): Chamaedaphne calyculata, Andromeda glaucophylla (polifolia), Vaccinium species (myrtilloides), Vaccinium oxycoccos, Ledum groenlandicum, Eriophorum species, Polytrichum strictum, Sphagnum magellanicum, and Sphagnum species.

Species occurring in the Bog Forest type that are not found at site D1 are: Picea mariana, Larix laricina, Vaccinium vitis-idaea, Kalmia polifolia, Smilacina trifolia, Sarracenia purpurea, Dicranum rugosum, Pleurozium schreberi, Sphagnum fuscum, and Cladonia species. These species, except Larix laricina, are indicators of relatively dry (depth to water 59-40 cm) and oligotrophic (pH 3.0-3.9) conditions (Jeglum 1971). Under these conditions, Larix laricina is always subordinate to Picea mariana. Of those species shared by site D1 with Heinselman's Bog Forest, Vaccinium myrtilloides

and Ledum groenlandicum are indicators of dry environments (depth to water 79-60 cm) and Chamaedaphne calyculata, Sphagnum magellanicum, and Andromeda glaucophylla (polifolia) are indicators of oligotrophic (pH 4.0-4.9) to very oligotrophic (pH 3.0-3.9) environments (Jeglum 1971).

The present environmental status of site D1 would place it in one of the following peatland types: Raised Bog Drain, where the vegetation shows reduced growth and is open; Poor Swamp Forest; or a transitional Forested Bog where the natural vegetation is a Black Spruce-Feathermoss Forest type. This last peatland type is most similar to site D1 and can intergrade with the following peatland types: Minerotrophic Swamp; Semi-Ombrotrophic Bog; and Ombrotrophic Bog. It is also characterized by a pH of 3.2-3.8.

The composition of the community at site D1 and the slightly minerotrophic (mesotrophic) conditions found there can best be explained by assuming that the vegetation was originally a type similar to the Sphagnum-Black Spruce-Leatherleaf Bog Forest with a significant cover of Picea mariana and perhaps Larix laricina. This forested bog must have been burned off before 1909, since Nyström's map in his 1909 report on the peat bogs and peat industry in Canada does not show a heavily wooded stand at site D1. This region is currently nearly devoid of trees, with scattered individuals of Larix laricina

and Betula populifolia. There are also clumps of Vaccinium species. Vaccinium species and Betula populifolia are indicators of fire disturbance in bogs (Small 1972; and others).

Damman (1977) reports that repeated fires can eliminate trees from the bog surface, that ericaceae regenerate easily from their rhizomes and that after two or three years a normal dwarf shrub layer will have developed. He also writes that "the effect of fire on the Sphagnum carpet and tree layer is more long-lasting. Fire kills the hummock Sphagma, and they only very slowly regenerate from the hummock bases. Cladonia species, . . . , can become important after a fire."

The absence at site D1 of Cladonia lichens and feather mosses of the genera Pleurozium and Dicranum may be due to an absence of colonizing populations in the Mer Bleue since they do not appear in general descriptions of the vegetation of the Mer Bleue and were not seen in the study area. Alternatively, the absence of Cladonia lichens and feather mosses may indicate that site D1, or even the entire study area, may have been a little too wet to support species such as these. In this case, the Sphagnum carpet would be less affected by fire and either could not support xerophilic lichens and mosses or perhaps would overgrow them if they did invade the area.

(Jeglum 1974; Tilton 1978).

Waterlogged peats with little surface water flow are generally depleted of dissolved oxygen (Sparling 1966), which causes a reducing situation that inhibits the absorption of many plant nutrients (Epstein 1972, cited in Tilton 1978). An acid environment is produced that is rich in free iron and aluminum and where microbial activity is low, reducing the nitrogen and phosphorus availability in the peat (Devlin 1966; Walmsley 1977). Other toxic substances, such as manganese, can also be released in solution (Small 1975). The situation differs markedly if the water is flowing through the peat.

Greater amounts of chemical nutrients are contained in the vegetation in areas of rapid water movement than where the water movement is slow (Newbold 1960). Higher concentrations of nitrogen and phosphorus occur in black spruce foliage from trees in water tracks of bogs (Watt and Heinselman 1965). Concentrations of calcium and magnesium cations in soil water tend to be higher in fens, where water movement is typical, than in bogs (Heinselman 1970; Jeglum 1974). In fact, Veery (1975) reports that a large inflow of calcium into peatland watersheds will result in higher pH values, providing for greater nutrient availability and accounting for the presence of nutrient-demanding species in fen communities.

Sparling (1966), in a study of the relationship between water movement and water chemistry in Ontario

pH and nutrient status at site D1 would also be partially explained by the occurrence of fire and the subsequent release of nutrients to the substrate. Nutrients falling on a bog penetrate below the consolidated peats only very slowly (Gorham and Hofstetter 1971) and would remain available to the plants if the cation exchange capacity of the peat was at its limit or if the quantity of nutrients deposited was great enough to partly saturate the cation exchange capacity of the peat (the cation exchange capacity of peat will be discussed in part III of the Discussion).

Site C1, as mentioned above, may also have been an ombrotrophic forested bog that experienced fire disturbance. The high abundance of Ledum groenlandicum and Kalmia angustifolia and the presence of Vaccinium species and possibly Polytrichum strictum are indicative of this (Jeglum 1972a). The absence of Picea mariana is also significant since it is such a major component of the extensive wooded sections of the Mer Bleue. Site C1 also contains elements of Heinzelman's Poor Swamp Forest vegetation type and is environmentally related to the Weakly Minerotrophic Swamp peatland type.

The Poor Swamp Forest has Larix laricina as the usual dominant and nearly pure, open stands of stunted Larix are typical. Members of the Ericaceae form a fairly dense low shrub layer, usually dominated by Andromeda glaucophylla (polifolia) and Chamaedaphne

calyculata. Hummocks of Sphagnum mosses 0.3-0.6 m high cover much of the ground. It occurs in nearly all physiographic locations except convex ombrotrophic sites, the strongest watercourses, and margins receiving inflow.

Plant species shared by the Poor Swamp Forest with site C1 include (Similarity Quotient = .31): Larix laricina, Andromeda glaucophylla (polifolia), Vaccinium oxycoccos, Ledum groenlandicum, Chamaedaphne calyculata, Kalmia polifolia, Smilacina trifolia, Typha latifolia, Eriophorum species, Sphagnum magellanicum, Sphagnum species, and Polytrichum species. This list should also include Carex oligosperma, which was not found in the sample quadrats but it does occur at site C1 and is an important minerotrophic indicator. Several of the more important (class ≥ 1) species characteristic of the Poor Swamp Forest not shared by site C1 are: Thuja occidentalis, Picea mariana, Betula pumila, Potentilla palustris, Menyanthes trifoliata, Utricularia species, Sarracenia purpurea, Carex limosa, Thelypteris palustris, and Sphagnum fuscum.

The absence of Picea mariana at C1 has been explained by fire removal. The range of Betula pumila does not extend into Ontario from the south (Britton and Brown 1970). Sarracenia purpurea occurs very sparsely in wet areas at sites A2 and D3, making its occurrence in the wetter areas of site C1 likely even though it was not recorded along the transects or seen in the area of

site C1 that was inspected. Three Carex species are found at site C2 and in the transition area between sites C1 and C2 and, as mentioned above, Carex oligosperma was later found to be growing sparsely in certain areas of site C1.

The species absent from site C1 that are present in the Poor Swamp Forest that are most significant are Menyanthes trifolia, Sphagnum fuscum, and a number of nutrient-demanding herbs. Menyanthes trifolia and Sphagnum fuscum are two among several species, including Myrica gale, that really should have been found in the study area. These species, along with Picea mariana and the group of feather mosses, may be very sensitive to fire disturbance. The presence in the transition area between sites C1 and C2 of species such as Tridenum virginicum, Eupatorium perfoliatum, Ludwigia palustris, Bidens sp., Galium sp., and Iris versicolor, along with the similarities mentioned above, strongly suggests a relationship of site C1 to the Poor Swamp Forest. As will be noted below, the environmental similarity is even more striking.

It should be pointed out emphatically that site C1 very closely resembles, floristically, the Sphagnum-Black Spruce-Leatherleaf-Bog Forest vegetation type of Heinselman. The following species are shared by this vegetation type with site C1 (Similarity Quotient = .54): Larix laricina, Andromeda glaucophylla (polifolia),

Vaccinium species (myrtilloides), Vaccinium oxycoccos, Ledum groenlandicum, Chamaedaphne calyculata, Kalmia polifolia, Smilacina trifolia, Eriophorum species, Polytrichum species, Sphagnum magellanicum, and Sphagnum species. All of the important species of the Sphagnum-Black Spruce-Leatherleaf-Bog Forest are on this list except for Pleurozium schreberi, Sphagnum fuscum, and Picea mariana.

The pH in the Poor Swamp Forest ranges from 3.9 to 6.7. Calcium values range from 3.2 to 9.7 ppm and magnesium from .8 to 3.4 ppm. The values of these environmental variables at site C1 fall into the middle of these ranges, with a mean pH of 4.7, a mean calcium concentration of 3.35 ppm, and a mean magnesium concentration of 2.40 ppm (calcium concentration + magnesium concentration = 5.75 ppm). One of Heinzelman's sites showing weakly flowing water has the following values: pH = 4.6 and calcium plus magnesium = 5.3 ppm. Another location, at the edge of a string bog characterized by a Larix-Picea cover, had a pH of 4.6 and a combined calcium and magnesium concentration of 3.9 ppm. These values are very close to those measured for site C1.

Site C1 resembles both a Sphagnum-Black Spruce-Leatherleaf Bog Forest that has been burned and a Poor Swamp Forest typical of weakly moving minerotrophic waters. The swamping that appears to be taking place at site C1 and that may involve the movement of mineral

laden water would affect the nutrient/moisture-aeration regime of site C1 in several ways. The vegetation changes proposed as occurring at site C1 may be more thoroughly understood in view of an understanding of the relative effects of nutrient and moisture-aeration regimes on bog vegetation.

It has been found that nutrient status and moisture-aeration conditions are the primary complexes controlling growth and nutrient concentrations of peatland plant species (Sjörs 1961; Heinselman 1963, 1970; Jeglum 1971, 1972a, 1972b; Vitt and Slack 1975; Tilton 1977; and others). The nutrient regime is more important to vegetational variation than the moisture-aeration regime for most peatland species (Jeglum 1974). Calcium, phosphorus, potassium, and nitrogen are the most important nutrients. On peat soils phosphorus and potassium may be more important in limiting growth than nitrogen (Wright 1959, Heikurainan 1964, and Tamm 1965, cited in Heilman 1968). Calcium, singly or combined with the concentration of magnesium as a measurement of total hardness, appears to be the most important element in distinguishing vegetation formations (Jeglum 1974; Stanek et al. 1977). The pH is also an indicator of nutrient supply (Lucas and Davis 1961; and others). Also, peatland vascular plants grow larger where the water supply has high pH and calcium concentration (Clymo 1973).

For peatland tree species, the moisture-aeration regime is more important than the nutrient regime

(Jeglum 1974; Tilton 1978).

Waterlogged peats with little surface water flow are generally depleted of dissolved oxygen (Sparling 1966), which causes a reducing situation that inhibits the absorption of many plant nutrients (Epstein 1972, cited in Tilton 1978). An acid environment is produced that is rich in free iron and aluminum and where microbial activity is low, reducing the nitrogen and phosphorus availability in the peat (Devlin 1966; Walmsley 1977). Other toxic substances, such as manganese, can also be released in solution (Small 1975). The situation differs markedly if the water is flowing through the peat.

Greater amounts of chemical nutrients are contained in the vegetation in areas of rapid water movement than where the water movement is slow (Newbold 1960). Higher concentrations of nitrogen and phosphorus occur in black spruce foliage from trees in water tracks of bogs (Watt and Heinselman 1965). Concentrations of calcium and magnesium cations in soil water tend to be higher in fens, where water movement is typical, than in bogs (Heinselman 1970; Jeglum 1974). In fact, Veery (1975) reports that a large inflow of calcium into peatland watersheds will result in higher pH values, providing for greater nutrient availability and accounting for the presence of nutrient-demanding species in fen communities.

Sparling (1966), in a study of the relationship between water movement and water chemistry in Ontario

mires, writes that "at a flow rate of less than $0.3-0.4$ cm sec⁻¹ the diffusion of oxygen into the water would be similar to simple diffusion into a stationary water surface, and because of the respiration of roots and microorganisms in the peat, the oxygen would tend to be depleted. Above flow rates of 0.4 cm sec⁻¹ the water is agitated, and is continually replenished with oxygen from the atmosphere. Reduced states of iron and manganese were shown to be in solution at concentrations greater than 0.1 mg/l only at low rates of water flow. The pH was also shown to increase with faster rates of water movement, the increase depending on the base status of the mire. Aluminum is in solution only in situations of low water movement, where more acidic conditions are prevalent." These findings would help to explain why water movement is associated with improved growth of trees (by increasing oxygen tension at their shallow root systems) and other vascular plants (by increasing nutrient content at their roots).

A number of bog species have developed characteristics that allow them to grow and flourish in nutrient-poor, waterlogged, and acid environments. A brief discussion of some of these traits may provide insights into the rather complex relationship between species occurrence and site quality. Segadas-Vianna (1952) comments that many bog species are nodulated and are able to fix atmospheric nitrogen. This list includes

almost all the important shrubs except for Chamaedaphne calyculata. However, the roots of the shrubs in the study area were inspected many times and it was found that only Alnus rugosa had nodules that were easily identified.

It has been shown for several non-tree vascular bog species that they may selectively exclude manganese and aluminum, which at high concentrations may be toxic (Small 1972a). Small (1972b) reports that bog shrubs may have developed evergreenness as a nutrient conserving mechanism. Armstrong and Boatman (1967) report that a number of fen and bog non-tree vascular species may pass oxygen to their roots thereby oxidizing sulphide, preventing it from entering and damaging the roots. They also suggest that soluble iron salts would similarly be expected to behave as sinks for oxygen, and that a thick sheath of hydrated ferric oxide is generally found around the roots of plants growing in reduced soils. The major plant species investigated by Armstrong and Boatman were Molinia caerulea, Menyanthes trifoliata, Carex rostrata, and Eriophorum angustifolium.

The tree species that are successful in bogs have special adaptive features that promote their persistence and growth, such as extremely shallow root systems or mycorrhiziasymbionts. For example, Picea mariana has a root system that grows about six inches (15 cm) below the bog's surface (Rigg and Harrar 1931;

Heinselman 1970) and is commonly associated with fungal growth (personal observation). It is true, however, that trees are generally not as successful in dealing with waterlogging as well as field species and their presence is an indicator of either dry conditions or adequate aeration due to water movement. Jeglum (1974) reports that trees grow better in swamps than in muskeg. He shows that the better tree growth in swamp as compared with muskeg is explained by a combination of higher nutrient status and better aeration. Dai (1971) found that Larix laricina, as well as Carex oligosperma, is distributed mainly at sites characterized by water flow. Larix laricina is sensitive to extreme waterlogged conditions as many individuals were seen dead in the study area in the flooded regions directly above the beaver dams, particularly at sites B2 and C2. This is true for Betula populifolia as well, the larger specimens of which were seen dead or dying all through site C1. This may indicate a real sensitivity to wet conditions as soon as the individual tree becomes large enough to require an extensive and deep root system. This observation also may relate to the time of swamping at site C1 as the occurrence of Betula populifolia is firmly associated with dry, fire disturbed sites.

The abundant occurrence of Larix laricina at site C1, along with the elevated values of the environmental variables, particularly calcium, and the presence

of eutrophic species such as Typha latifolia, Scirpus acutis, and Carex oligosperma, suggest that the wet condition prevailing at this site involves a movement of water that is improving both the moisture-aeration and the nutrient regimes. The water movement could be continuous from the mineral margin across the center of site C1 or it could involve a hydraulic oscillation, dependent on spring and fall high water levels that would result in a regular flushing of the bog dome.

A field observation relevant to the degree of decomposition taking place at site C1 is that peat and water samples collected at site C1 did not have a noticeable odor of anaerobic decomposition (smell of hydrogen sulphide). This is also true of sites A1 and B1. At site D1, however, the samples had a definite odor of anaerobic decomposition. Aerobic decomposition may be occurring at site C1 due to increased aeration and nutrient input as a result of swamping. The consequences for peat formation are considerable and may already have altered the topography at site C1.

Peat accumulation is favoured under conditions of low nutrient availability, low evaporation-precipitation ratio, and low organic matter decomposition (Heinselman 1963; and others). Tilton (1978) writes that "edaphic factors such as site wetness, depth of water-table and water-table fluctuations, do not in themselves control growth or nutrient availability in

wetland systems. These factors, however, do influence soil aeration, which in turn affects the processes controlling nutrient cycling and primary production." Both nutrient cycling and primary production are functions of peat decomposition.

Any increase in aeration and nutrient availability that might be happening at site C1 would certainly be associated with the swamping the area may be experiencing and would accelerate aerobic peat decomposition and mineralization and reduce the rate of peat deposition. The replacement of important peat forming species would also affect the rate of peat deposition. Sphagnum rubellum typically occurs in drier sites, or dry hummocks, and Sphagnum magellanicum preferentially occurs in wetter, flushed sites, or hollows (Sjörs 1961; Jeglum 1971; Clymo 1973). Sphagnum magellanicum may also grow with Sphagnum rubellum (Sjors 1961), which is the situation at site C1. Sphagnum rubellum decays more slowly than other bog species and comes to be "over-represented" in peat (Clymo 1967; Clymo and Reddaway 1974). If swamping is occurring at site C1, it would be favouring the growth of Sphagnum magellanicum, as well as Sphagnum papillosum and Sphagnum fallax, so that peat formation would be reduced.

The overall effect of swamping at site C1 would be to slowly cut a decomposition channel through the peat, further altering the drainage relationships of the

area. The presence of water tracks in peatlands is common and is associated with reduced peat deposition, increased minerotrophy, minerophilic species, and a low lying, wet aspect (Sjörs 1961). If site C1 is developing into such a water track the community structure and composition present at the site can be expected to alter radically. If the minerotrophic conditions are weak, a Poor Swamp Forest vegetation type (as described by Heinselman) would likely develop. If eutrophic conditions prevail, a vegetation assemblage quite different would evolve. Based on the success of Typha latifolia at site D3, throughout the western end of my study area, and between regions 4 and 7 of my study area, a Typha dominated swamp could replace the bog vegetation. This is explored further in part III of the Discussion.

Pollett and Bridgewater (1973) classify the peatlands of central Newfoundland into eleven provisional associations varying in vegetation type and nutrient status from ombrotrophic bog to eutrophic fen. They give little floristic and environmental detail in this report so that a careful and itemized comparison of their associations with the study site plant assemblages is not possible. The classes are of interest, though, and two of the eleven associations are related to the assemblages in the study area.

Sites A1, B1, C1, and D1 are similar in their overall floristic composition to the Kalmio-Sphagnetum

association, distinguished by the following constant species: Ledum groenlandicum, Kalmia polifolia, Rubus chamaemorus, Vaccinium oxycoccos, Sarracenia purpurea, Andromeda polifolia, Drosera rotundifolia, and Chamaedaphne calyculata. Kalmia angustifolia and Sphagnum fuscum are the most important species.

Damman, in the report reviewed above, includes all of the plant communities that he described in the Bay of Fundy region as probably belonging to Pollett and Bridgewater's Kalmio-Sphagnetum. Damman also writes that ". . . the range of this association would cover the eastern part of Canada and the northeastern U.S.A., and is replaced by a Chamaedaphne dominated hummock association northward and from central Quebec to the interior of the continent. Geographical forms of this association . . . could be recognized to express this climatic gradient. Sub-associations based on ecological differences can then be recognized regionally." The three ombrotrophic heath communities described for the Bay of Fundy region are, Damman suggests, at the level of such sub-associations. Following the same argument, the dwarf shrub bog (after Pollett 1968, cited in Pollett and Bridgewater 1973) assemblages at sites A1, B1, D1, and even site C1, would be continental sub-associations of the Kalmio-Sphagnetum community typified by dominance of Chamaedaphne calyculata (or conversely, the Kalmio-Sphagnetum is an oceanic sub-association of a continental

Chamaedaphnetum association). The floristic differences between the study sites could be regarded as representing distinct communities, or variants, in the same sense as Danman's dwarf shrub heaths or sub-associations of Pollett and Bridgewater's Kalmio-Sphagnetum.

This type of classification of the variants of the Chamaedaphne community reflects the view of Segadas-Vianna, mentioned earlier, that the Chamaedaphne community occurs as phases along an environmental gradient. Also, that the phases represent stages in successional development, although current interpretation of peatland successional processes (Sjörs 1955; Dahl 1956; Drury 1956; Gorham 1957; Heinzelman 1963, 1970; Malmer 1975; and others) would view the phases as labile and capable of developing toward drier or wetter phases depending on the prevailing climatic humidity and temperature regimes, assuming all other influences are autochthonous. Of course, as seen at site C1, the Chamaedaphne community can be diverted from phase development into alternate assemblage configurations by external stresses.

Site A2 is similar to a marsh association of Pollett and Bridgewater's named the Myrico-Caricetum rostratae. A typical habitat is the edge of a small lake where dense swards of sedge meadow occur, composed more or less equally of Carex aquatilis and Carex rostrata. This sedge meadow has ombrotrophic hummocks associated with it, but the hummocks are small and poorly

developed. The main hummock-forming species are Sphagnum fuscum, Sphagnum rubellum, and Sphagnum papillosum.

The last descriptions to be discussed in detail will be those of Dansereau and Segadas-Vianna (1952), which refer to peat bogs throughout eastern North America.

In a major ecological study of the peat bogs of eastern North America, Dansereau and Segadas-Vianna (1952) describe fourteen bog plant associations. Eight of these associations may be related to the plant assemblages in the study area. The associations that are related to the study area vegetation assemblages are: the Caricetum rostratae, the Eriophoretum angustifolii, the Chamaedaphnetum calyculatae, the Picea ericaceum, the Kalmietum angustifoliae, the Nemopanthetum mucronatae, the Ledetum groenlandici, and the Laricetum laricinae. The Chamaedaphnetum is described in detail by Segadas-Vianna (1955).

Site A2 is similar to the Caricetum rostratae, dominated by Carex rostratae, Carex lanuginosa, and Carex lasiocarpa. The association occupies, according to Dansereau and Segadas-Vianna, "a narrow band in shallow water, usually in places where peat comes in contact with sand or some other predominantly mineral substratum and where there is quite a fluctuation in water level, to the point of emergence in the late summer." The conditions at site A2 are precisely these, although Carex lanuginosa and Carex lasiocarpa are not

present. The margins of sites B2 and C2 also show a slight resemblance to the Caricetum rostratae. Carex rostrata occurs at the margin of site B2 and Iris versicolor grows with Typha latifolia at the margin of site B2. Iris versicolor is frequently present at the inner edge of the Caricetum rostratae and will sometimes develop into a separate belt or zone.

Study site A1 shows a relationship to the Eriophoretum angustifolii and the Chamaedaphnetum calyculatae. The Eriophoretum angustifolii is a wet meadow dominated by Eriophorum virginicum, Eriophorum angustifolium, or Eriophorum spissum, has essentially continuous vegetation, and favours the growth of Sphagnum species. Dansereau and Segadas-Vianna write that it is "frequently on a floating mat, but sometimes occurs in consolidated areas where a high water level prevails throughout most of the summer." The general physiognomy of the Eriophoretum angustifolii fits the appearance of site A1, which is characterized by a wet Sphagnum carpet and is dominated by the short, erect stems of Chamaedaphne calyculata and an abundance of Eriophorum species, particularly Eriophorum chamissonis and Eriophorum tenellum. However, the sparse presence at site A1 of Ledum groenlandicum, Gaylussacia baccata, and Kalmia angustifolia, as well as Sphagnum rubellum, indicate a strong relationship to the Chamaedaphnetum calyculatae.

The Chamaedaphnetum calyculatae is the first consolidation stage of the settlement phase that is described in the successional series proposed by Dansereau and Segadas-Vianna. The previous initial wet stages, such as the Caricetum rostratae and the Eriophorum angustifoliae, are members of the pioneer phase. It would be worthwhile to quote the entire description of the Chamaedaphne calyculatae association of Dansereau and Segadas-Vianna because it closely resembles sites B1, C1, and D1, as well as site A1, and is a primary association of the bog community of eastern North America. They write that:

this association is one of the most widespread, the most extensive, and the most characteristic. The apparently wide spectrum of Chamaedaphne calyculata's tolerances also make it quite long-lived. As a matter of fact that species is probably more than any other a bog species, in that it combines the distinctions of being found in practically all boreal bogs; of being exclusively confined to the bog habitat; of usually being represented by large numbers of individuals; of withstanding for some time such diverse interferences as drainage and fire. The upper synusia (40-60 cm high as a rule) sometimes consists exclusively of Chamaedaphne which hardly ever grows more than 1.3 meter, and is usually very much smaller (30-50 cm). It is a semideciduous shrub, the tips of its branches often nipped by winter frosts. It grows in groups of several individuals, has superficial roots, fibrous and without nodules. Usually in the upper synusia there is a certain amount of Ledum groenlandicum, Kalmia polifolia, Kalmia angustifolia. A thin second synusia is sometimes formed by Vaccinium angustifolium especially following a burn. Sphagnum usually makes tremendous growth in the Chamaedaphnetum. In fact, it grows about the stem and branches of Chamaedaphne itself and forms a broad inflated cushion in which the subshrub is all but immersed. On the sides of

these emergences and in the depressions between them (difference in level: up to 50 cm), grow such plants as: Vaccinium oxycoccos, Drosera rotundifolia, and Sarracenia purpurea. The Chamaedaphnetum occurs under a number of different facies; in some cases, it bears a strong admixture of Ledum groenlandicum or Kalmia angustifolia or Eriophorum angustifolium.

The substratum always shows a strongly acid reaction and, owing to the stools of leatherleaf and the moss cushions, has an uneven relief. Water content is still very high and water-retaining capacity of the living Sphagnum is likewise considerable. The underlying peat, however, presents a firm texture favorable to shrubs (such as Aronia melanocarpa, Nemopanthus mucronata) and even trees (Picea mariana, Larix laricina). These will eventually bring about more shade than Chamaedaphne can withstand and produce a Piceetum ericaceum, where only scattered individuals or small colonies of the leatherleaf will survive.

Very frequently, however, lumbering or fire will induce a regression and the Chamaedaphnetum will form anew.

The similarity to the study area plant assemblages of the Chamaedaphnetum is obvious and will be discussed below in detail. Several statements in the above quote are of interest concerning the dynamic aspect of the Chamaedaphnetum. A detailed discussion of bog succession is outside the purview of the main text of this report and has been commented on in the Introduction. The sequence (although not the principles involved, sensu Clements) of hydrarch succession (sensu Transeau) applies, with modification, to developmental processes as currently viewed. Changes in plant assemblages are determined primarily by changes in climatic conditions (temperature, precipitation, evaporation; fog, snow cover, etc.), differences in nutrient and moisture-aeration regimes,

and disturbances of various sorts (fire, swamping, drainage, etc.). It has been mentioned above that the structure and composition of several different, yet related, wetland communities can be explained by differences in available nutrients and the aeration of the substrate. This does not imply that developmental processes are determined autogenously by virtue of the qualities of the current community but simply that as environmental conditions change, for any number of reasons, so do the structure and composition of the plant community. Also, it is possible for bog community types to shift from one to another type without there being a single climax community toward which all intermediate communities inexorably tend (Dahl 1956; Heinselman 1963, 1970; and others). Yet, because of the tremendous buffering capacity of peat (Gjessing 1976; Walmsley 1977; and others) with respect to water level, cation exchange capacity, microbial activity, and other factors, the vegetation communities of peatlands are relatively long-lived. And bog communities may represent "intermediate" phases in a community sequence in the sense that the series of vegetation types reflects a moisture, nutrient, or aeration gradient that may be temporal as well as geographical. Because the community types of Dansereau and Segadas-Vianna would represent such a series (see Figures 39 and 40), their statements regarding basic successional relationships between any two sites are probably valid even

Diagram of succession in the St. Lawrence Lowlands, where the climax is deciduous forest. The controlling ecological factors corresponding to the major phases are indicated, as is also the dominant structural unit. (Densmore and Segoda-Vienne 1952)

Fig. 39

Diagram of succession in Northern Quebec and Ontario where the Canadian or Spruce Fir forest is climax. Principal features of structure and controlling ecological factors are shown for each major phase. (Dansereau and Spegdon-Vienne 1952.)

Fig. 40

though the theoretical framework within which the statements were made is different from the current view.

The persistence of the Chamaedaphnetum over a wide range of conditions explains the floristic similarity of sites A1, B1, C1, and D1. The facies of the association that develop under conditions of wetness or dryness, or generally improving nutrient and moisture-aeration regimes, also helps to clarify the relationship between the study sites. Also, the response to disturbance of the Chamaedaphnetum as described by Dansereau and Segadas-Vianna further clarifies the complex history of the study sites.

Site B1 is very much a representative of the Chamaedaphnetum, but contains a few elements that reflect a history that may be similar to the history of site C1 as proposed above. Physiognomically, site B1 is very similar to site A1. Sphagnum forms a tight carpet and there is a low coverage of short ericaceous shrubs and Eriophorum sedges. However, there are distinct differences between the two sites. There is more hummock development at site B1 and the shrubs show more lateral growth. Also, scattered, small trees and species indicating minerotrophy suggest that there is a physicochemical difference between the two sites. There is a notable difference in the values of phosphorus and sodium determined for the two sites. All other values of the environmental factors measured, except calcium cation, were higher at site B1.

than at site A1. The mean water level was also farther below the surface at site B1. These differences indicate that site B1 has a slightly better nutrient/moisture-aeration regime than site A1 and represents a drier phase of the Chamaedaphnetum.

Vaccinium species and Betula populifolia are present at site B1 and are indicators of fire disturbance. Site B1 could have been burned over at the same time that site C1 was burned. Vaccinium shrubs and Betula populifolia trees are present in the drier phases of the Chamaedaphnetum.

Site B1 shares the following species with the Chamaedaphnetum (Similarity Quotient = .34): Betula populifolia, Larix laricina, Chamaedaphne calyculata, Ledum groenlandicum, Kalmia angustifolia, Andromeda glaucophylla (polifolia), Vaccinium oxycoccos, Vaccinium species, Eriophorum species, Carex trisperma, Sphagnum species, and Polytrichum strictum. Andromeda glaucophylla (polifolia) and Eriophorum chamissonis are indicators of oligotrophic and wet to very wet conditions (Jeglum 1971). Eriophorum chamissonis is very abundant at site B1.

Growing at site B1 are indicators of dryness and fire disturbance, oligotrophy and wetness, and minerotrophy. Because of this it may be assumed that the current environmental status of site B1 is of relatively recent origin. This is readily explained in view of the history proposed for site C1, which is floristically very similar

to site B1 (Similarity Quotient = .71).

The swamping of the eastern section of the study area must have begun long enough ago to allow for adjustments in species abundance and for invasive species to become well established. The ericaceous layer can recover from fire removal within three years (Flinn and Wein 1977), however the growth of Larix laricina at site C1 would certainly have taken much longer than three years. Wood cores were not taken at site C1 to determine the age of the trees, but the date of Larix invasion of site C1 can be determined from the aerial photographs. As reported in the Results, there are few Larix laricina individuals present in the study area on the 1958 aerial photographs. Larix is fairly common, although not as abundant as it is today, on the 1968 aerial photographs. The present abundance of Larix laricina at site C1 must be the result of approximately twenty years of invasion and growth, implying that swamping began in the area of sites B1 and C1 about twenty years ago. Fire disturbance could have taken place before this. According to information on Nystrom's 1909 map of the Mer Bleue, few fires would have burned in the study area after 1910. This is described in part II of the Discussion.

Study site D1 is related to the driest phase of the Chamaedaphnetum and also shows obvious signs of fire disturbance. It shares the following species with the Chamaedaphnetum (Similarity Quotient = .28): Chamaedaphne

calyculata, Ledum groenlandicum, Kalmia angustifolia,
Andromeda glaucophylla (polifolia), Vaccinium oxycoccos,
Vaccinium species, Eriophorum species (E. virginicum),
Sphagnum species, and Polytrichum strictum. The similarity
of site D1 to the Chamaedaphnetum seems lower than it
really is because the species list that is given by
Segadas-Vianna for the Chamaedaphnetum includes the
species present in all of the phases, from wet to dry.
Gaylussacia baccata, abundant at site D1 and present at
all the other sites except sites A2 and C2, is not
included in the Chamaedaphnetum as described by Segadas-
Vianna.

Gaylussacia baccata is dominant in drier parts
of raised bogs in the inland areas of the Bay of Fundy
region (Damman 1977). The Gaylussacia community is
absent from the coastal areas and this is attributed to
the absence of sufficiently well-drained sites in these
areas. All of the bogs investigated by Segadas-Vianna
and used to describe the Chamaedaphnetum were characterized
by poor drainage. The presence of Gaylussacia baccata
at sites A1, B1, and C1 might show that this species,
although not attaining high cover values in these sites,
is able to grow in wet and oligotrophic conditions.
Alternatively, the occurrence of this species at these
wet sites may be another indication of the change in
moisture conditions throughout the eastern section of
my study area from dry to wet. The presence of

Gaylussacia baccata at site D1 can be attributed to adequate drainage since this site is characterized by a depth to water value of 60+ cm.

The abundance of Kalmia angustifolia and the common occurrence of Vaccinium species at site D1, accompanied by the absence of Picea mariana, point to a history of fire disturbance for this site. This would reflect the relatively dry nature of the surface peat that exists at site D1. It also represents a stage in the development of the Chamaedaphnetum as proposed by Dansereau and Segadas-Vianna. The Chamaedaphnetum may develop into a Piceetum ericaceum or Aceretum rubri that when subjected to lumbering or fire can regenerate as a mature (dry) Chamaedaphnetum or the Kalmietum angustifoliae.

The Kalmietum angustifoliae, a consociation of the Chamaedaphnetum, is characterized by dominance of Kalmia angustifolia. Dansereau and Segadas-Vianna write that in the Kalmietum angustifoliae the "superficial part of the soil may dry up completely in August, whereas it is saturated and even flooded in the spring." These conditions prevail at site D1 after the snow cover melts in the spring.

The Kalmietum angustifoliae may show immense expanses of Kalmia angustifolia with only a very small quantity of Ledum groenlandicum. Pockets of Vaccinium angustifolium, which may be common, harbor abundant Rubus chamaemorus. Sarracenia purpurea and Eriophorum

species are sparse and occur in the wetter hollows. Some of the shrubby and arborescent species are always present as young individuals or isolated mature ones. These species include Nemopanthus mucronata, Larix laricina, Picea mariana, and Acer rubrum.

Dansereau and Segadas-Vianna say that the Kalmietum "is probably most successful after fire or following artificial drainage, or both."

This description fits site D1 very well, with the following exceptions: Picea mariana is completely absent, as is Rubus chamaemorus; Chamaedaphne calyculata and Gaylussacia baccata are abundant; and Betula populifolia occurs as sparsely scattered individuals. It may be concluded that site D1 represents a vegetation complex comprised of a dry phase Chamaedaphnetum with a strong admixture of the Kalmietum association. Recall that the Kalmietum is essentially a fire disturbed Chamaedaphnetum.

Site D2 and portions of region 8, on the margins of site D1, fit the description of the Nemopanthetum mucronatae of Dansereau and Segadas-Vianna. The area of region 8 that is similar to the Nemopanthetum occurs below the beaver dam along a transition zone between the open dwarf shrub heath or bog of site D1 and the Alnus-Salix swamp that is found between the beaver dams at regions 8 and 9 (see Figure 7). These transition areas at site D2 and below site D3 include the following species:

Aronia melanocarpa, Acer rubrum, Nemopanthus mucronata,
Ilex verticillata, Betula populifolia, Populus tremuloides,
and Viburnum cassinoides. An unidentified species of
Rubus was found in the transition zone below site D2.

The Nemopanthetum mucronatae can be invaded by
Betula populifolia and Acer rubrum and is in successional
sequence to the Chamaedaphnetum. The relationship
between the Chamaedaphnetum and the Nemopanthetum is a
direct one dependent on increasing dryness and nutrient
availability. The nutrient relationships between the
various sites will be discussed in part III. It was proposed
in the Results that nutrient availability is increasing at
the disturbed or transition sites even though the mean
values of some of the environmental variables are often
lower in the disturbed sites than the mean values of the
same environmental variables in the adjacent sites. The
fact that site D2 and the transition zone below site D3
are wetter than site D1 may be compensated for by
increased nutrient availability so that the Nemopanthetum
may develop. Also, site D2 and the area below site D3
are only relatively wet sites as compared to site D1,
being characterized by well-drained surface peat.

The Alnus swamp along the margin of site D3 and
below site D2 may be providing the nutrient input necessary
to support the Nemopanthetum. Increased decomposition
due to slow water flushing may also be involved. Water
could flow from the bog dome as well as parallel with

Table 9

Summary of similarity of study sites to bog plant communities described in the literature. The + sign signifies a moderate to strong resemblance.

Community	Study Sites									
	A1	A2	B1	B2	C1	C2	D1	D2	D3	
<u>Vitt and Slack:</u>										
Acidic Lake Edge Zone		+		+		+				
Alkaline Lake Edge Zone										
Open Mat Zone	+									
Closed Mat Zone					+		+			
<u>Jeglum:</u>										
Emergent Fen				+		+				
Broad-Leaved Sedge Fen		+								
Low Shrub Fen	+	+	+							
Open Bog	+		+		+		+			
Tamarack Swamp					+					
<u>Sjörs:</u>										
Riparian Rich Fen				+		+				
Open Bog	+		+				+			
Wooded Bog					+					
Wooded Poor Fen					+					
<u>Heinselman:</u>										
<u>Sphagnum-Kalmia Spruce Heath</u>	+		+				+			
<u>Sphagnum-Black spruce-</u>										
Leatherleaf Bog Forest					+					
Wooded Poor Fen					+					
Ombrotrophic Bog	+		+							
<u>Damman:</u>										
<u>Chamaedaphne-Sphagnum</u>										
rubellum	+		+							
Gaylussacia							+			
<u>Kalmia angustifolia-Sphagnum</u>										
rubellum							+			
<u>Rhododendron-Nemopanthus</u>										
thicket									+	
<u>Dansereau and Segadas-Vianna:</u>										
<u>Caricetum rostratae</u>										
<u>Nemopanthetum mucronatae</u>									+	
<u>Eriophoretum angustifoliae</u>	+									
<u>Chamaedaphnetum calyculatae</u>	+		+		+		+			
<u>Kalmietum angustifoliae</u>							+			
<u>Ledetum groenlandici</u>					+					
<u>Laricetum laricinae</u>					+					

places. The Ledetum is the final phase of the Chamaedaphnetum. A plant assemblage definitely representing this phase in the development of the Chamaedaphnetum is found outside the study area just north of region 5 in a fire scar. This assemblage may very well be precisely the type of plant assemblage that would have been found at site C1 before site C1 was swamped.

Segadas-Vianna writes of the Chamaedaphnetum that "the disintegration phase begins with the invasion of the community by taller species with higher capacity of competition, such as Aronia melanocarpa and Nemopanthus mucronata, which gradually eliminate, first the Kalmia and then the Chamaedaphne. These invaders do not restrict Ledum groenlandicum, but on the contrary they increase its cover somewhat, through the whole duration of the subsequent association, dominated by Nemopanthus. The disintegration of the community may also be caused by other species, such as Picea mariana and Larix laricina, this probably being only a question of chance." The latter situation is occurring at site C1, where Larix is invading. A general inference of the above quote is that Ledum groenlandicum is preferential to dry situations. This is supported by several authors, particularly Jeglum (1971, 1972a) who found that Ledum groenlandicum is an oligotrophic species characteristic of very moist (dry) conditions and that Ledum groenlandicum will often assume dominance in the shrub layer after a fire. This would

corroborate the proposal that site C1 was a dry, fire disturbed community before the invasion by Larix laricina.

The pure, parklike stand of Larix laricina at site C1 is typical of the Laricetum laricinae. The resemblance of site C1 to the Laricetum may be, at least for the present, superficial. Dansereau and Segadas-Vianna characterize the Laricetum as possessing a sparse tall shrub layer composed primarily of Alnus rugosa, and a sparse subshrub synusium composed of Ledum groenlandicum and Kalmia angustifolia. Also, there is generally a dense sward of Carex disperma occurring among the subshrubs. Often, Larix laricina and Carex disperma are the only two dominants, the shrubs and subshrubs being completely absent. The occurrence at site C1 of scattered Alnus rugosa, Scirpus species, and Carex oligosperma may be the first stage of the development of a wet and minerotrophic Laricetum.

Other species characteristic of the Laricetum are: Thuja occidentalis, Picea mariana, Viburnum cassinoides, Sarracenia purpurea, Vaccinium myrtilloides, Vaccinium oxycoccos, and Rubus pubescens. Sarracenia purpurea, as well as Carex disperma, are hydrophilic species. Viburnum cassinoides and Vaccinium myrtilloides are characteristic of relatively dry and minerotrophic conditions. The Laricetum seems to be able to occupy sites of various moisture regimes, where species preferring either wet or dry conditions can comprise the understory.

The Laricetum could be composed of species with varying moisture demands if its water table was constant and if hummocks and hollows were well developed, providing both wet and relatively dry sites. Alternatively, these species, including Larix laricina, may flourish where there is increased aeration or slight minerotrophy, perhaps due to faster rates of water flow through the substrate.

The preference for sites characterized by water flow of Larix laricina, as shown by Dai (reviewed above), may be the common factor that allows for Larix laricina to invade almost any bog association. This also may explain why the Laricetum is so variable and why it is only really characterized by pure stands of Larix. The suggestion by Dansereau and Segadas-Vianna that Larix laricina can invade any bog plant association where there is enough light for the germination of Larix seeds may be simplistic. This may be true in situations where Larix will occur only as scattered individuals, perhaps restricted to the wet hollows. It may not be true of nearly pure, dense stands of Larix.

SUMMARY OF PART I OF THE DISCUSSION

The margins of sites B2 and C2 are similar to Vitt and Slack's Acidic Lake Edge Zone, Jeglum's Emergent Fen, and Sjörs' Riparian Rich Fen. The closest resemblance is to the Emergent Fen. The development of fen is associated with flowing water or nutrient-rich sites.

Site A2 resembles the Acidic Lake Edge Zone of Vitt and Slack, the Broad-Leaved Sedge Fen and the Low Shrub Fen of Jeglum, and Dansereau and Segadas-Vianna's Caricetum rostratae. The site most closely resembles the Broad-Leaved Sedge Fen or the Caricetum rostratae. The major part of the site represents a normal transition community between the Sedge Fen and the Low Shrub Fen.

The region below site D2, between the Alnus-Salix swamp and the dwarf shrub heath or open bog of site D1, is related to the Nemopanthetum mucronatae of Dansereau and Segadas-Vianna. The margin of site D2 is roughly similar to Vitt and Slack's minerotrophic Alkaline Lake Edge Zone. None of the descriptions fit site D2 well, and it may be considered unrepresentative of peatland vegetation. The levels of available nutrients and pH value would put site D2 in the Fen-Marsh category (Stanek et al. 1977). It could be described simply as a Typha marsh.

The Nemopanthetum mucronatae of Dansereau and Segadas-Vianna describes the margin of site D3 extremely

well. Site D3 is also similar to Damman's Rhododendron-Nemopanthus thicket. Even though site D3 may be a transition zone grading to the Alnus rugosa swamp, it has the qualifications to be regarded as a peatland vegetation type that is representative of minerotrophic conditions.

Sites A1 and B1 resemble typical bog associations. Site A1 is similar to the Open Mat Zone of Vitt and Slack, the Low Shrub Fen and Open Bog of Jeglum, the Sphagnum-Kalmia-Spruce Heath and Ombrotrophic Bog of Heinselman, the Open Bog of Sjörs, the Chamaedaphne-Sphagnum rubellum community of Damman, and the Eriophoretum angustifoliae and Chamaedaphnetum calyculatae of Dansereau and Segadas-Vianna. The similarity of site A1 to more than one of the vegetation types described by Jeglum, Heinselman, and Dansereau and Segadas-Vianna suggests that site A1 is a transition community. Site B1 has the same relationship to the associations mentioned above for site A1 with the exception of the Eriophoretum angustifoliae. Also, site B1 is very similar floristically to site C1 and shows a relationship to a few of the associations that resemble site C1. The association that site B1 most closely resembles is the Chamaedaphnetum calyculatae of Dansereau and Segadas-Vianna.

Site D1 is the easiest site to classify, showing a strong relationship to the Closed Mat Zone of Vitt and Slack, the Open Bog of Jeglum, the Sphagnum-Leatherleaf-

Kalmia-Spruce Heath of Heinselman, the Open Bog of Sjörs, and the Chamaedaphnetum calyculatae and the Kalmietum angustifoliae of Dansereau and Segadas-Vianna. Two types of Damman's are similar to site D1, the Gaylussacia and the Kalmia angustifolia-Sphagnum rubellum communities. These communities are similar in that both generally develop in response to fires and that they occur along a moisture gradient, the Gaylussacia community occupying the driest areas.

The plant assemblage at site C1 is the most difficult to classify or show relationship to association types. It is similar to the Closed Mat Zone of Vitt and Slack, the Open Bog and Tamarack Swamp of Jeglum, Heinselman's Sphagnum-Black spruce-Leatherleaf Bog Forest and Poor Swamp Forest, and the Wooded Bog and Wooded Poor Fen of Sjörs. Site C1 seems related to three associations of Dansereau and Segadas-Vianna. These are the Chamaedaphnetum calyculatae, the Ledetum groenlandici, and the Laricetum laricinae. It can be concluded that site C1 is a mixture of community types that would normally be found on opposite ends of an environmental gradient and probably represents a transition from a dry community that was responding to fire disturbance to a wet community that is responding to swamping.

A summary of these comparisons is shown on Table 9.

Sites B2 and C2 are composed of vegetation assemblages that are typically found on the margins of

Site history and possible development. Unbarbed horizontal lines represent extent of physical distribution in study area. Barbed horizontal lines represent physical extent of disturbances. Dashed portion of line under BEAVER SWAMPING represents present area of minimal effect of beaver disturbance. Plant species represent dominant forms, abbreviations as in Appendix C. L. lar., B. pop. and P. mar. stand for *Larix laricina*, *Betula populifolia* and *Picea mariana* respectively.

Fig. 42

peatlands that are mineral-rich and wet. They may also be found on inorganic substrates that are flushed by slightly acid water. Site D2 is environmentally in the Fen-Marsh complex and likely represents a community phase that would have initially been similar to the situation at sites B2 and C2.

Site A2 is a normal transition plant assemblage that is found between wet, moderately minerotrophic lagg areas and ombrotrophic open bogs.

Site D3 is a normal transition association found between relatively minerotrophic areas and ombrotrophic open or wooded bogs.

Phases of a typical open bog community, termed the Chamaedaphnetum, are represented by sites A1, B1, and D1. Sites A1 and B1 represent the initial phase, characterized by wet, ombrotrophic conditions and the dominance of Chamaedaphne calyculata. Site D1 may be regarded as the final phase, characterized by dry, less severe ombrotrophic conditions and the loss of dominance by Chamaedaphne. This final phase is termed the Kalmia angustifoliae. Site D1 may also be referred to as a Gaylussacia baccatae community. The plant assemblage at site D1 appears to be a normal community that is found in peatlands that are dry and that are subjected to fire disturbance.

Site C1 appears to be an abnormal community responding to fire disturbance and flooding.

The relationships between the study sites is shown on Figure 41. Each site is positioned with respect to its average pH and depth to water values. The numbers near each arrow is the Quotient of Similarity Value between the respective sites. The single barbed arrows indicate a probable unidirectional relationship between the sites. The double-barbed arrows indicate that the connected sites are related successional and may develop into a community type similar to the linked site.

The dominant species are shown for each site and are abbreviated according to the list given with Appendix C.

Each of the marginal sites in the site ordination figure are deflected to the left of the parent site toward a region of high pH and greater water level. Although sites A2 and D3 show a similar shift in pH and water level as compared with the beaver disturbed sites, they are characterized by distinctly different plant assemblages. The plant assemblages at sites B2, C2, and D2, the beaver disturbed sites, are developing, or have developed, into a Typha marsh. The failure of Typha to achieve dominance at site D3 may be related to a lack of standing water, necessary for Typha seed germination. The failure of Typha to invade site A2 may be attributed to the acid environment at this site.

Model of site relationships. Numbers are percent similarity of species (as 2) between each site. Environmental classification according to Jeglum 1971.

Fig. 41

The series of central heath sites are all similar yet reflect real developmental changes along environmental, and possibly competitive, gradients. The field impression of bog community maleability is strongly reinforced by the inspection of the literature on bog community development. The double-barbed arrows in Figure 41 that are drawn between the central heath sites represent this view of developmental dynamism where community composition and structure may shift multidirectionally as the environmental infrastructure changes.

DISCUSSION - PART II

One of the central questions raised in part I of the Discussion concerns the origin of swamping in the central portion of my study area. This question can be answered with a certain degree of confidence using the results of the aerial photograph inspection. There are two features that are found associated with drainage outlets from the study area and that may be involved in the swamping. These are beaver dams and a road, Anderson Road, that runs along the entire western end of the study area.

Anderson Road transects Borthwick Creek, the drainage outlet of the study area. A road, in the same area as Anderson Road, is shown on Nystrom and Anrep's 1909 map of the Mer Bleue. It also can be seen on the 1945 photograph. The agricultural area east of Anderson Road remained relatively unchanged from 1945 to 1955. In 1958, swamping of the farm fields is well advanced. The change from the 1955 to the 1958 photograph regarding the agricultural field is dramatic. If Anderson Road is solely responsible for swamping in the study area, the development of an impediment to drainage took from 35 to 70 years.

Larix laricina is an indicator of nutrient-rich, waterlogged conditions in peatlands where the water is actively flowing through the top (20-30 cm) of the

unconsolidated peat. Larix is virtually absent in the study area from 1945 to 1955. The development of the extensive Larix cover in the study area begins at about 1958. This coincides with the flooding of the agricultural fields in the western section of the study area. 1956-1958 is most probably the time when swamping began.

Beaver did not invade the study area until 1968. At this time Larix cover was sparse but quite obvious in the same basic regions as today but in a much contracted sense. Although the present configuration of beaver dams along the drainage ditches of the study area are undoubtedly accentuating the swamping begun in 1956-1958, they may not have caused it. However, the time the agricultural area was flooded coincides with the first occurrence of beaver in the Mer Bleue, about 1958. It is certainly possible that beaver dammed the drainage culvert of the Anderson Road, or an upper portion of Borthwick Creek, in 1958 or a little before, initiating the swamping of the entire study area along the margins of the bog dome and deep into the areas of low relief. Beaver are active east of Anderson Road now and the area is nearly pure Typha marsh.

Therefore, it is proposed, with considerable reservation, that beaver damming began the swamping of the central and eastern areas of the study area initially by damming the drainage exit under Anderson Road, or an upper section of Borthwick Creek, and subsequently by

damming the drainage ditch along the margins of the bog beginning at region 5. The drainage ditches along the bog margins east of region 5 were not cut by the 1937 Works Project. The canals that occur there have been excavated and maintained by the beaver.

These conclusions, and those from part I of the Discussion, are summarized on Figure 42. The vegetation assemblages at each of the central heath sites are identified according to the dominant vascular plant species. The horizontal lines above the assemblage names indicate the geographical extent of that vegetation type in my study area with respect to the current site positions. Possible evolution of the plant community at each central heath site is shown at the bottom of the figure, the uncertainty of the development indicated by the question mark. The uncertainties are simply due to the probability of accidental flux in the environments at each site in regard to nutrient-status and moisture regime.

If site A1 continues to be unaffected by the swamping in the area, it likely will persist as an Eriophorum-dominated assemblage. If the site is subjected to swamping, Larix laricina would likely invade, accompanied by Carex and Scirpus species. If the water table drops or if the vegetation develops a domed topography resulting in slightly drier, more nutrient-rich conditions, the plant assemblage may very well develop into a robust

Chamaedaphne calyculata dominated community. The same may be said for site B1, except that currently the vegetation is similar to the Chamaedaphne-dominated plant assemblage and a rise in the water table, unaccompanied by an increase in available nutrients, would most probably result in the development of a plant community similar to site A1 that is dominated by Eriophorum spp.

The swamping at C1 will likely persist with dramatic consequences for the region. Based on the field observation concerning the onslaught of the Typha marsh east of region 7, site C1 most probably is destined to develop into a severely disrupted bog community that will be composed of a rather bizarre mixture of Larix laricina, Typha species, scattered fen graminoids, sedges, and mosses, and minerotrophic herbs.

Site D1 should persist as a Kalmia-Gaylussacia community. If Betula populifolia does not successfully invade site D1, the most likely shift in its composition will be toward the tall-shrub thicket, characterized by Aronia melanocarpa, Ilex verticillata, Nemopanthus mucronata, and Viburnum cassinoides. If Picea mariana were present as seedlings at site D1, it might be postulated that the site would develop into a black spruce muskeg.

DISCUSSION - PART III

It was proposed in the Results that the changes in height of Chamaedaphne calyculata in the area above each beaver dam was related to changes in nutrient availability in the substrate. It was shown that the height of Chamaedaphne calyculata is related to the pH values that were measured along the transects. Also, that the height of Chamaedaphne increased rapidly as the pH approached or exceeded the value of 5.0. These results are consistent with the results of an investigation into the relationship of pH to nutrient availability in peat by Lucas and Davis (1961).

I measured the concentrations of four of the twelve nutrients considered by Lucas and Davis, namely: phosphorus, potassium, calcium, and magnesium. They found that the availability of phosphorus drops when the pH is below 5.5 because of increased soluble iron and aluminum in some soils. Their results are shown on Figure 43.

Because phosphorus becomes more available in peat as the pH increases, to an optimum of 5.5, the availability of phosphorus along my experimental transects should have increased with the increasing pH. This did not occur, as described in the results. It was hypothesized that greater phosphorus availability promoted increased growth of Chamaedaphne calyculata resulting in phosphorus

Influence of reaction on availability of plant nutrients (organic soils) (widest part of bar indicates maximum availability). (Lucas and Davis 1961)

Fig. 43

depletion in the areas of greatest growth. This reduction in phosphorus availability is quite evident at every site except region 1 where pH values increased slowly to between 4.5-4.6 and where the growth response of C. calyculata is noticeable but not striking. The pH values approached and exceeded 5.0 at the other sites, which is the value proposed as a major threshold value where, according to Lucas and Davis, total nutrient availability in peat is at an optimum.

It was mentioned in the Results that potassium may be an important limiting nutrient in peat soils (Heilman 1968). The availability of potassium at the study sites follows the same pattern as phosphorus, except at region 8 (site D2) where potassium steadily increases toward the beaver pond. This may be due to increased calcium levels and is discussed below. In general, the relationships for phosphorus also apply to the potassium data. However, soil pH has less influence on potassium than on phosphorus availability (Lucas and Davis 1961).

Watt and Heinselman (1965) proposed an inverse relationship between potassium concentration in the foliage and site quality in a study of nutrient levels in Picea mariana in a northern Minnesota spruce bog. The inverse relationship and the relatively high levels of potassium on all of their study sites indicated that this element is not limiting tree growth. They write that

"the inverse relationship with site quality may be explained by growth dilution; the increase in growth due to better supply of nitrogen and phosphorus on the good sites is proportionately greater than the presumed increase in uptake of potassium."

The relationship of site quality and the percentage of potassium in leaf tissues may not be the same for Typha, Larix, and the ericaceous shrubs as for Picea mariana. The transect data generally support the view that potassium is removed from the substrate as readily as phosphorus and in roughly equal proportions regardless of site quality, except in those areas where calcium concentration is high. Lucas and Davis (1961) write that "organic soils, because of high exchange capacity, can absorb large quantities of calcium. If calcium levels in the soil are too high, then the mass-action effect and high-calcium accumulation by some plants depresses the uptake of potassium." At most of the study sites calcium levels decrease in a manner similar to phosphorus and potassium. It was mentioned in the Results that calcium may complex with phosphorus and enter the plant as calcium phosphate. Calcium does not decrease toward the beaver pond at site D2 and increases only slightly at site D3. Also, calcium and potassium values increase toward the beaver pond at site D2. If high calcium accumulation by the plants at site D2 depressed potassium uptake, the concentration of available

potassium should increase as the pH increases (up to a maximum of pH 6.0). This may explain why the potassium availability increases toward the beaver impoundment only at site D2 where calcium concentration is very high. The high calcium availability at site D2 may be due to calcium moving into the site from the beaver pond and retention through nutrient cycling by the vegetation cover.

The dominant plant occurring at site D2 in the area of high calcium availability is Typha spp. (primarily T. latifolia and some T. angustifolia). Sphagnum mosses were not found on the surface under the thickest Typha growth. The peat in this area seemed well-decomposed, which suggests that the cation exchange capacity of the peat was reduced.

Bayly and O'Neil (1972) reported that soluble calcium ions are absorbed by the tissue of Typha glauca (T. latifolia X T. angustifolia, Bayly and O'Neil 1971) and translocated to active sites of growth and that "this apparent uptake by the plant tissue is reflected by a coincident depletion in the soil substrates of the rhizosphere." Since there is not an apparent substrate depletion of calcium at site D2, it may be concluded either that the Typha spp. are not absorbing calcium or that the concentration of calcium surpasses the ability of the Typha spp. to absorb this nutrient. The latter conclusion is obviously the more probable.

Relatively high levels of sodium and calcium will leach from Typha latifolia mulch (Boyd 1970), which would partially explain the high calcium concentration at site D2. As mentioned above, calcium coming from the beaver pond might raise calcium availability in the adjacent peat substrate. The elevated calcium concentration at site D2 may be due to all of these factors.

The Typha plants at site D2 might also affect sodium concentration in the peat substrate. The decline in sodium values within the Typha stand may be attributed to passive uptake of that nutrient by Typha spp. (Bayly and O'Neil 1972). Of all the study sites, only at site D2 is the concentration of sodium markedly lower at the head of the transect as compared to the values measured along the middle of the transect. This area of depressed sodium concentration corresponds to the increasingly dense Typha growth toward the margin of the beaver pond.

Lucas and Davis (1961) say that the calcium-magnesium ratio is helpful in estimating the boundary where the bog has risen above the influence of ground water and comes under the influence of rain water. Where the bog is influenced only by rain water the calcium-magnesium ratio is less than one. This is the situation at study site D1 where the ratio is 2.40-2.57. The very noticeable doming of site D1 would further support this view.

The other central sites, A1, B1, and C1, have calcium-magnesium ratios greater than one. Sites A1, B1, and particularly C1, have been identified as sites that are being directly or indirectly subjected to swamping. The greater concentration of calcium than magnesium at these sites might indicate that the water moving through them is richer in minerals than rainwater. This supports the view that the eastern portion of my study area, specifically site C1, is being swamped with water originating at the mineral margins of the bog vegetation.

It should be recalled here that the calcium concentration at site C1 is in excess of the threshold value where major vegetation changes may begin to occur. The threshold value for pH also is approached at site C1. The invasion of site C1 by Typha latifolia is almost certainly directly related to the elevated calcium and pH values as well as to the wet conditions. The invasion of Typha spp. at the margins of the beaver disturbed sites represent the vegetation changes that may accompany an amelioration of the nutrient-poor status of wet and acid bog situations. Because of the obvious importance of Typha invasion that is taking place at the disturbed sites in conjunction with environmental changes, a discussion of the factors affecting the success of Typha spp. is warranted.

The inspection of the transect data in the Results showed that a pH of 5.0 and a calcium concentration of

about 2.7 ppm are required before Typha can invade a peat substrate. It has been mentioned that pH affects nutrient availability in organic soils. The relationships between calcium, potassium, phosphorus, and pH have been described in the Results. Nitrogen availability also is affected by pH, and the germination of Typha latifolia seeds is affected by nitrates (Morinaga 1926a, 1926b; cited in Bedish 1967), as well as light, temperature, oxygen tension (Sifton 1959; cited in Bedish 1967), and water depth (Bedish 1967).

Lucas and Davis (1961) say that nitrogen release and availability in organic soils is influenced by total nitrogen content of the soil and by microbial activity. Organic soils with a pH below 4.0 have a nitrogen content of less than 1 percent, while soils with a pH above 5.0 contain over 2 percent nitrogen which, Lucas and Davis say, halves the carbon-nitrogen ratio (from 60 to 1 to 30 to 1). They also write that if the pH falls below 5.0 there is a marked reduction in nitrate-nitrogen release (also stated in Walmsley 1977, p. 92). Liming an organic soil will increase its nitrifying capacity, however when the pH is above 5.2 there is little improvement in nitrogen availability from lime additions (Lucas and Davis 1967), implying that as much nitrate is released as is available.

The pH range of 5.0 to 5.2 determined by inspection of the transect data that corresponds to the

occurrence of abundant Typha growth is precisely the value for maximum nitrate release reported above.

As mentioned in the Results, Alnus rugosa may supply nitrogen in a usable form to adjacent aquatic systems (Daly 1966). Alnus rugosa is abundant along the drainage ditches and beaver canals in my study area. However, even though the release of usable nitrogen by Alnus rugosa into the drainage ditches may be extremely important for Typha seed germination, the critical factor would seem to be the elevation of the pH. Increasing pH frees other limiting nutrients, such as phosphorus, without which Typha could not flourish. This is evident if the chemical and vegetative characteristics of sites B2 and C2 are compared. Also, recall that Lucas and Davis mention microbial activity as important in nitrogen release. The increased decomposition of the peat at all the disturbed sites has been noted in the Results. Both factors, increased decomposition of the peat substrate and the presence of Alnus rugosa along the drainage ditches, probably affect Typha invasion and success at the disturbed sites. The encroachment of Typha on the central heath of site C1, as mentioned above, would most likely be caused by increasing calcium concentration and decomposition rates resulting from flow of water through the surface of the site.

A suitable substrate is also required for Typha seed germination, it must be very wet or covered with

shallow water to an optimum depth of about 15 cm (Bedish 1967). Typha grew in my study area directly through intact bog vegetation, including a seemingly robust Sphagnum moss mat. In places where Typha was forming a solid stand, however, the substrate was very much different. In both areas above the beaver dams and along the Typha bed encroaching upon and invading the vegetation of the central heath sites, the surface vegetation is much altered with Sphagnum mosses becoming completely eliminated in the dense Typha growth. This elimination appears to be gradual in the different sites as the degree of disturbance increases. It is probable that as the calcium and pH values increase in the peat and living Sphagnum substrate, the cation exchange capacity of the peat becomes so taxed and the environmental conditions become so stressful for the Sphagnum mosses that the substrate is transformed into a suitable habitat for a nutrient-demanding species such as Typha latifolia. The transformation of the substrate at sites B2, C2, and D2 represents this type of development where Sphagnum species are eliminated and replaced as the nutrient regime shifts from ombrotrophy to mesotrophy. At site C2 the elimination of Sphagnum species that is accompanied by the successful invasion of Typha, and other nutrient-demanding species, is most dramatic.

In order to further assess the influence of pH and nutrient changes on Sphagnum distribution and

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abundance, the pertinent literature will be discussed with reference to the experimental results.

Spearing (1972) describes the distribution of eight Sphagnum species along a moisture gradient and each species' cation exchange capacity. The species described are Sphagnum cuspidatum, S. fallax*, S. angustifolium, S. magellanicum*, S. fimbriatum, S. nemoreum*, S. rubellum*, and S. fuscum. The species marked with an asterisk were found in my study area. The order of the species corresponds to their positions along the moisture gradient, from just below to about 30 cm above the water table. The cation exchange capacity of each species increased from S. cuspidatum to S. fuscum in almost exactly the same sequence as given above. The cation exchange capacity is also closely correlated with the amount of galacturonic acid found within a species. Spearing comments that the varying amount of galacturonic acid might confer to each species a specific range of exchange ability, enabling each species to occupy a particular habitat within the bog.

Clymo (1963) reports that for the Sphagnum mosses the "variation of exchange ability is highly correlated with the height of the habitat above the free-water table and with the pH of the water round the plants." Clymo lists the following Sphagnum species as occurring in sequence along a pH gradient ranging from 5.8 to 3.5: S. cuspidatum, S. pulchrum*, S. plumulosum, S. papillosum*,

S. palustre, S. subsecundum, S. magellanicum*, and S. acutifolium (rubellum)*. The species marked with an asterisk were found in my study area.

It may be concluded that the pH of the substrate influences Sphagnum species distribution and that greater cation exchange capacity of certain species results in greater acidity at the relatively drier sites or at sites exposed only to nutrients coming from rainwater. Species with greater cation exchange capacity produce a more acidic environment that results in lower nutrient availability and lower decomposition rates. These sites, of lower nutrient availability, lower pH, and lower decomposition rates influence in turn the type of Sphagnum species that will thrive at that site and also reduces competition in that few species are capable of overgrowing the Sphagnum mat under these circumstances. This may be seen at site A1.

Sphagnum species would appear to have differentiated along a resource axis or physical gradient that involves a trade-off in a low growth rate due to low nutrient availability and increased metabolic investment in galacturonic acid for a habitat at least temporarily free of competition.

The effects of pH and nutrient concentration on Sphagnum moss growth are further described by Clymo (1973). The growth of several Sphagnum species was measured under conditions with factorial combinations of

pH (3.5-7.5) with calcium (0.05-5.0 ppm), and of water table (surface to -10 cm) with shading (0-82%). Raising the pH or the calcium concentration separately to unnaturally high levels had little effect, but raising both together was for some species fatal and for most caused much reduction in growth. Clymo lists the Sphagnum species in order of increasing susceptibility to high pH and high calcium as follows: S. subsecundum, S. squarrosum, S. plumulosum, S. recurvum, S. papillosum*, S. rubellum*, S. magellanicum*, and S. cuspidatum. As above, the species marked with an asterisk were found in my study area.

Clymo writes that the sequence mirrors the order in which the species would be placed on the basis of distribution in the field along nutrient and moisture gradients, with the exception of Sphagnum magellanicum which is, Clymo says, a species of flushed areas. Sphagnum cuspidatum, with respect to the sequence listed above by Clymo for Sphagnum species distribution along a pH gradient, appears to be out of place. The susceptibility of the species is in response to a pH plus calcium gradient, however, which Clymo showed to have an adverse synergistic effect on Sphagnum growth.

It would be worthwhile to quote Clymo's comment on the results of the pH/calcium experiment since it has direct bearing on the response of the Sphagnum species to beaver impoundment as seen in my study area. Clymo

writes:

The results of the chemical treatments are in accord . . . with expectation based on field observation. In the field, high pH is almost always associated with high Ca^{2+} concentration, and where this combination of conditions occurs Sphagnum is absent. These conditions caused some death of Sphagnum in the experiments too. S. squarrosum, which survived and grew well in these conditions, is one of the first species to appear when immersion by calcareous water of high pH becomes rarer as a fen increases in height. The ability to tolerate occasional immersion in such conditions, coupled with the ability to make acid (by cation exchange) the small amount of water left around the plants when the flood subsides could account for the natural distribution of this species. S. subsecundum, which was fairly tolerant of high pH and Ca^{2+} concentration in the experiments, is often found in slow-flowing streams and ditches. Here the ability to grow immersed in continually renewed solutions of moderate pH and Ca^{2+} concentration may be more important than that of surviving occasional short immersion in high levels . . . one may conclude that the obvious chemical factors could indeed account for the large-scale field distribution of Sphagnum species.

The elimination of Sphagnum species at the margins of the study sites and along the western edge of site C1 is most probably related to increasing pH and nutrient concentration, particularly calcium. Calcium and pH increase in value along the transect toward the pond at each disturbed site and westward along the drainage system as described in the Results. The Sphagnum species found at the pond and lagg margins in my study area are primarily S. fallax and S. papillosum. Sphagnum magellanicum and S. rubellum dominate the central sites and are displaced in the wettest lagg areas, which in

some areas constitutes a relatively narrow band along the margin of the bog or along the floating mat above the beaver ponds. Site D2 is so disrupted that the Sphagnum mosses have been completely eliminated from the pond margin.

Sphagnum papillosum was shown by Clymo (1973), as described above, to be less susceptible to high pH and calcium concentration than S. magellanicum and S. rubellum. At the very edge of the bog mat at sites B2 and C2 near the open water of the beaver ponds, Sphagnum fallax and S. papillosum are absent as well as S. magellanicum and S. rubellum. It is within these patches of exposed peat that Typha spp. show their best growth.

As a consequence of the remarks above, it may be stated fairly confidently that as the pH and calcium concentration increase in the beaver ponds, Sphagnum species are eliminated or their cation exchange capacity is overwhelmed so that species such as Typha latifolia may invade. The luxuriant growth of Chamaedaphne calyculata, as seen at the margins of sites B2 and C2, would be in response to greater nutrient availability. The success of Chamaedaphne is short-lived, as seen at the margins of sites C2 and especially D2 where Typha forms a pure stand. This elimination of Sphagnum accompanied by the invasion of Typha spp. may also be seen to the west of site C1 on the central portion of the heath in the area to the southeast of region 7. The

scattered occurrence of Typha and other nutrient-demanding species throughout site C1, along with the fact that site C1 is characterized by a calcium concentration and pH value that approaches or exceeds major threshold levels, presages the imminent development toward environmental conditions that are inimical to bog plant species. It may be that environmental conditions are so altered within the entire eastern section of my study area that the development of a Typha marsh is inevitable.

To further clarify the effects of beaver activity on bog vegetation, a brief review of two pertinent reports in the literature regarding the swamping of peatlands is given below.

Schwintzer and Williams (1974) recorded and analyzed the changes in vegetation in a small Michigan (U.S.A.) bog that occurred over a fifty-five year period, from 1917 to 1972. They use data from several older sources as well as their recent field investigations to construct an account of the changes in the vegetation communities at the bog site. They also compare those changes with the established sequence of basin-bog communities undergoing succession as described by indirect studies (i.e., bog zonation, comparing bogs with different community types, analyzing peat profiles, etc.). The communities that were described as occurring in their study bog over this period are part of the normal developmental sequence for basin-bog vegetation in northern

Michigan as outlined by Schwintzer and Williams. They write that "the vegetation changed in a successional series from the Chamaedaphne association of 1917 to the high bog-shrub association in the dry years of the 1920's to a bog forest which was well established in the late 1960's. It regressed in the early 1970's when many of the trees died and the Chamaedaphne association appeared to be re-establishing itself. The most probable cause of tree mortality was flooding caused by exceptionally high water levels due to natural weather cycles."

It is relevant to a discussion of the effects of beaver activity on bog vegetation that when flooding occurred in the bog studied by Schwintzer and Williams trees were killed and the Chamaedaphne association began to re-establish itself. It would be instructive to inspect in detail the data used in their analysis. The table of data presented by Schwintzer and Williams is partially reproduced on Table 10. Numbers for each species are frequencies of occurrence as a percentage of the total number of sample quadrates taken. The Chamaedaphne association contains the following key species: Andromeda glaucophylla, Carex trisperma, Chamaedaphne calyculata, Eriophorum virginicum, Kalmia polifolia, Vaccinium oxycoccos, and Sphagnum spp.

The 1951 and 1972 columns for the high bog-shrub association on Table 10 show that the species representing the Chamaedaphne association are increasing in frequency,

Table 10

Per cent frequencies (1-m² plots) of selected plant species found in the Chamaedaphne and high bog-shrub associations in Bryant's Bog, Cheboygan Co., Mich., U.S.A.; from 1917 to 1972 (From Schwintzer and Williams 1974).

Association Year Species	Chamaedaphne			High Bog-Shrub		
	1927	1955	1972	1927	1951	1972
	Per Cent			Per Cent		
<u>Acer rubrum</u>	1	-	27	10	38	13
<u>Andromeda glaucophylla</u>	46	64	-	13	-	-
<u>Betula papyrifera</u>	6	-	-	7	20	-
<u>Carex trisperma</u>	50	-	80	7	5	40
<u>Chamaedaphne calyculata</u>	95	100	73	83	43	47
<u>Eriophorum virginicum</u>	10	-	-	-	-	-
<u>Gaylussacia baccata</u>	35	-	40	34	78	7
<u>Kalmia polifolia</u>	48	-	33	26	2	-
<u>Nemopanthus mucronata</u>	11	-	7	67	80	40
<u>Osmunda cinnamomea</u>	-	-	-	3	10	-
<u>Picea mariana</u>	35	24	20	36	-	-
<u>Pinus strobus</u>	2	-	-	7	25	-
<u>Pyrus floribunda</u>	5	-	-	16	23	7
<u>Sarracenia purpurea</u>	31	64	13	-	-	-
<u>Sphagnum spp.</u>	98	88	100	100	60	87
<u>Trientalis borealis</u>	1	-	-	4	38	-
<u>Vaccinium angustifolium</u>	4	-	60	34	30	27
<u>V. myrtilloides</u>	23	-	33	4	75	20
<u>V. oxycoccus</u>	73	48	13	1	-	-

except for Andromeda glaucophylla and Vaccinium oxycoccos, and species representing the high-bush association, such as Acer rubrum, Gaylussacia baccata, Nemopanthus mucronata, and Vaccinium myrtilloides, are decreasing in frequency. The plant species representing the high-bush association are general indicators of minerotrophic conditions as defined by Jeglum (1971) and described in part I of the Discussion. Also, there are no plant species invading or increasing in frequency that are indicators of nutrient-rich conditions during the period of flooding in the early 1970's. The species listed on Table 10 as comprising the major part of the Chamaedaphne association are indicators of nutrient-poor and/or very wet conditions (Jeglum 1971).

The effects of high water levels on the vegetation of the bog studied by Schwintzer and Williams as described above are attributed by them to the lack of above-ground drainage in the bog. Water levels in the bog were determined completely by rainfall, indicating that the only source of nutrients was rainfall. This would explain the absence of nutrient-demanding species during conditions of high water.

It may be concluded that raising the water table does not necessarily result in minerotrophic conditions. On the contrary, where a bog site is isolated from mineral-rich waters, the effects of raising the water level most probably will result in a "regression" in the

successional sequence of basin-bog plant communities to a community characterized by oligotrophic, or nutrient-poor, conditions. The importance of water moving through a peatland and the consequences of interrupting that drainage is shown by a study of Jeglum's (1975) on a peatland in northern Ontario.

Jeglum studied the vegetation and habitat changes caused by a peatland drainageway being dammed by a road. The overall response in the treed bog plant assemblage that was flooded above the road included the drowning of trees and the development of the site into an open bog, separated into three vegetation zones as measured by a transect located parallel with the road. The treed bog below the road was divided into seven vegetation zones, also measured by a transect located parallel with the road. Jeglum describes the entire area, using historical information from aerial photographs, as initially being the same vegetation type (treed bog) that changed primarily above the road after the road was built. What is of significance for this report is that the development of open bog from treed bog was accompanied not only by an increase in the water table but also by changes in the nutrient regime of the disturbed site. Particularly noteworthy is the elevation of the pH and the reduced level of ferrous iron in the water samples from above the road as compared to the values of these variables from below the road. This is especially evident in the

central regions of both areas. An increase in pH will lower the solubility of iron and also of free phosphates that may then complex with other cations, such as calcium or magnesium, in which form the phosphate is available to plants at low to intermediate pH values.

The high water table drowned the trees in the area above the road in Jeglum's study area, but greater concentrations of nutrients resulted in nutrient-demanding plant species invading the area. The species that are described by Jeglum as occurring in the open bog along the edge of the road include the following: Alnus rugosa, Carex paupercula, Smilacina trifolia, Typha latifolia, Carex canescens, and Calla palustris. The dominant species shown as occurring along the transect taken in the treed bog below the road are indicators primarily of water level, with the exception of Alnus rugosa, and include the following: Thuja occidentalis, Abies balsamea, Chamaedaphne calyculata, Salix planifolia, Ledum groenlandicum, Carex trisperma, Glyceria striata, Gymnocarpium dryopteris, and Pleurozium schreberi.

It may be concluded that where drainageways through peatlands are blocked, the vegetation above the impediment will change as a result of a higher water table and a change in nutrient availability. The hydrologic relationships in a system and its nutrient status influence greatly the structure and composition of vegetation communities in peatlands. The changes in

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vegetation associated with road construction described by Jeglum follow a pattern similar to vegetation changes described in this report that are associated with beaver activity. Beaver dams cause a rise in the water table, eliminating some species. They also change the nutrient regime so that plant species characteristic of mineral-rich sites may invade. The result is often a plant assemblage dominated by a single species that is not necessarily a normal component of a bog community. The most aggressive non-bog species to invade the bog mat within my study area is Typha latifolia.

GENERAL DISCUSSION - PART I

It is not the purpose of this study to provide a comprehensive review of hypotheses of species diversity or to provide a field test of selected hypotheses. However, with respect to objectives 3, 4 and 5 presented in the Introduction, a discussion of plant species diversity in my study area would be appropriate. Because of the complexity of the factors that influence diversity, such as colonization, extinction, growth, resource utilization, gradual change in the environment, compensatory mortality, linear and circular competition, niche differentiation, habitat stability and heterogeneity, etc. (Pielou 1975; Krebs 1978, pp. 449-485; Connell 1978; and many others), it is helpful to use a hypothesis of species diversity as a paradigm, or model, against which field data may be analyzed. In view of this, a current hypothesis of species diversity will be used as a framework within which the diversity characteristics of the study sites will be discussed.

The hypothesis chosen as a paradigm is one proposed by Huston (1979) that clarifies an underlying pattern of variation in diversity and points out the common elements of previous hypotheses. Rather than arguing that either competition, predation, or productivity control diversity, his model demonstrates that all of these may contribute to the same basic mechanism.

Huston's general hypothesis of species diversity attempts to explain patterns of diversity using Lotka-Volterra competition equations in model communities undergoing regular disturbance. It is a non-equilibrium model with local and global application (see Pielou 1975, chps. 7 and 8) that chiefly explains diversity patterns in plant communities whose biological characteristics more generally conform to the assumptions of the Lotka-Volterra model. However, Huston comments that the diversity in the animal community usually depends on the complexity of the plant community.

The diversity (defined by Huston as species richness and evenness of abundance) values obtained for communities subjected to disturbance are, Huston says, primarily a consequence of the frequency of population reduction (disturbance) and the rate of species replacement (which Huston relates to rates of growth). Three general predictions of the model are:

- 1) Situations in which competing organisms have high population growth rates will have lower diversity (because of competitive displacement) than equivalent situations in which the organisms have low growth rates, unless some species are being eliminated by a high frequency of population reduction.
- 2) Low availability of basic nutrients (as opposed to an extreme deficiency or toxic excess) would be expected to reduce growth rates in communities of organisms requiring these nutrients and result in higher diversity than in a similar situation with high nutrient availability. Increasing the nutrient availability of any environment should tend to reduce diversity, unless

Fig. 47

Fig. 44

Generalized contour map of the dynamic equilibria between the rate of competitive displacement and the frequency (or magnitude) of population reduction, diversity is on the axis perpendicular to the page, and is represented by the contour lines, with the highest diversity within the inner ellipsoid (in the upper left corner). The dotted-line transects demonstrate the predicted changes in diversity when one parameter is held constant and the other varied (Huston 1979)

Fig. 45

Predicted relationship of diversity and frequency of population reduction; the magnitude or intensity of reduction (i.e., whether populations are reduced by .1, .5, or .9) has the same relationship to diversity.

Fig. 46

Predicted relationship of diversity and growth rates in nonequilibrium systems with a low to intermediate frequency of population reductions.

(Huston 1979)

rate of competitive displacement will be low. Further increase in growth rates will increase the rate of competitive displacement, resulting in lower diversity of dynamic equilibria at high growth rates. Finally, at high frequencies of population reduction (transect D), increasing growth rates will allow recovery from disturbances; diversity will increase as growth rates rise, then decrease at sufficiently high growth rates that the system begins to approach competitive equilibrium.

Figure 45 represents the change in diversity predicted by Huston's model when the frequency of population reduction increases, regardless of the magnitude. This would represent a transect on Figure 44 that begins between points A and B and runs directly to the bottom of the figure. Figure 46 represents the change in diversity predicted by Huston's model when the frequency of population reduction is maintained at low to intermediate levels and growth rates increase. This would represent a transect on Figure 44 that begins just below point C and runs directly to the right of the figure.

Huston suggests that since it is not always possible to measure population growth rates, any factors closely related to growth rates should show the same relationship to diversity. For plant communities these should include estimates of growth rate such as height and percent cover. Huston makes this suggestion because changes in the diversity of his model communities subjected to various growth rates and disturbance frequencies were actually caused by changes in abundance, both relative and absolute. Comparing model communities

where only growth rates were changed, the communities with larger growth rates achieved greater absolute abundances. The same was true for intermediate rates of disturbance or population reduction. However, the model clearly shows that at high growth rates and frequency of reduction, diversity will be low.

Huston also points out the relationship between nutrient availability and growth rate, as mentioned above. This view is reinforced by Clymo (1973) and Wildi (1978). Clymo relates the growth rate of Sphagnum mosses directly to the supply of inorganic ions (varied concentration and flow rate). Wildi uses the Michaelis-Menton equation (Thornby 1976, cited in Wildi 1978) for plant growth as part of a developmental simulation of peat bogs. The Michaelis-Menton equation

$$V_c = V_{\max} \frac{c}{K_S + c}$$

is used to describe the dependence of growth rate V_c on the concentration of nutrients c . $V_{\max}$ is the growth rate when c tends to infinity. The constant K_S is known as Michaelis constant which expresses the nutrient concentration at which the growth rate will reach half of its maximum value $V_{\max}$. The importance of the relationship between nutrient availability and growth rate will become apparent during the course of the discussion below.

Therefore, it will be assumed that nutrient availability, growth rate, and abundance are interrelated.

The predictions made by Huston's model that are described above can, with certain reservations, be tested by ordinating density or abundance values against measures of diversity for each plant assemblage in the study area. Discussion of the results of ordination must necessarily involve what is known of the history of each site as well as relative nutrient availability at each site. Reference will also be made to part 3 of the Discussion where the biological significance of the differences in nutrient availability between each site was described.

One of the key assumptions in Huston's hypothesis is that species replacement is a consequence of species growth rate (as growth rates increase, competitive displacement accelerates). Other factors that influence species distribution may be involved so that the effects of competitive displacement and habitat selection are difficult to distinguish. However, "mature" open bog communities are characterized by the dominance of one shrub species (Dansereau and Segadas-Vianna 1952; Segadas-Vianna 1955; Sjörs 1961, and others). The species to assume dominance is often associated with a particular characteristic of the habitat (Segadas-Vianna 1955; Damman 1977; and others). The composition of the community approaching maturity may have several co-dominants, so that the development to a "mature" open heath (probably

undergoing further development) may be accompanied by a decrease in diversity. This sequence has been shown for old field succession in oak-pine forest at Brookhaven, New York (U.S.A.) (Holt and Woodwell, unpublished data, cited in Whittaker 1972). This change in plant composition over time represents successional changes in diversity. Because of this, differences in diversity status between the plant assemblages in my study area may also be related to the successional sequence referred to in the Introduction and parts 1 and 2 of the Discussion.

It should be mentioned here that diversity is very much a conceptualization in that diversity can be identified with any of a number of indices, which implies that diversity per se does not exist (Hurlbert 1971, cited in Whittaker 1972). However, this uncertainty of definition does not reduce the usefulness of diversity as a community parameter. Of the various ways to measure diversity, Whittaker (1972) suggests that a direct diversity expression, species number or richness (S), be used as a basic measurement that could be accompanied by a suitable "slope expression" (such as Shannon-Wiener or Simpson indices) when the data permit. May (1977, p. 158) agrees, but strongly recommends that the full distribution of species' relative abundance (as in abundance-rank curves) be used rather than condensing information into a single diversity index that would be dominated by a handful of common species. Therefore a

number of measures of diversity will be used and referred to during the course of this discussion, all of which were used in the Results to compare study site characteristics. The first ordination of study site diversity and abundance values, constructed in order to analyze diversity characteristics within the framework of Huston's hypothesis, will involve a measure of diversity using the Simpson index and an estimation of growth rate calculated by multiplying the average shrub height by the total percent cover of the field layer measured at each study site. The estimate of relative growth rate for each site is given on Table 11. The results of the site ordination are shown on Figures 47 and 48. Figure 47 shows the central heath sites and Figure 48 shows the margin and disturbed sites.

Study sites B1, A1, C1, and D1 form a series that fits closely the curve predicted by Huston's model (refer to Figure 46).

The horizontal axes on Figures 47 and 48 (as well as 49 and 50) are scaled logarithmically in order to more accurately represent the change in biomass that would accompany an increase in total surface percent cover and height. Over eighty percent of bog vascular plant production is associated with subsurface components (Reader and Stewart 1971) so that a small increase in growth above the surface is accompanied by considerably greater growth below the surface. The sites with

Table 11

Index of Growth Rate by Estimating Relative
Standing Biomass.

<u>Site</u>	<u>n</u>	<u>Average Shrub Height (cm)</u>	<u>Total % Cover</u>	<u>Index (Cover X Height)</u>
A1	50	19.6 $\pm$ $\sqrt{36.84}$	56.8	1112
A2	56	27.4 $\pm$ $\sqrt{419.63}$	43.5	1192
B1	37	17.7 $\pm$ $\sqrt{39.99}$	60.0	1062
B2	30	22.1 $\pm$ $\sqrt{219.47}$	70.5	1558
C1	37	18.1 $\pm$ $\sqrt{50.47}$	61.5	1113
C2	21	29.8 $\pm$ $\sqrt{227.32}$	61.0	1818
D1	67	21.8 $\pm$ $\sqrt{32.61}$	80.3	1750
D2	38	41.3 $\pm$ $\sqrt{312.74}$	77.8	3211
D3	80	38.9 $\pm$ $\sqrt{824.80}$	77.0	2995

Fig. 47

Fig. 48

relatively greater surface percent cover and height would therefore have a very much greater below surface biomass. This can only indirectly and with difficulty be related to a similarly increasing growth rate, however recall that Huston's model makes essentially the same prediction concerning changes in diversity for sites with increasing absolute abundances as for sites with increasing growth rates. Huston's model specifically measures diversity in relation to disturbance, growth rate, and competition. It may be assumed that all of these factors directly influence abundance so that changes in plant species' abundances reflect to a large degree the interaction of these three factors, single-species epidemics and selective predation notwithstanding.

(In the discussion below the reader should also keep in mind that the bog surface is being continuously replaced as Sphagnum mosses and vascular species grow and as peat is deposited or decomposed.)

As seen on Figure 47, site B1 is positioned first on the curve predicted by Huston's model. This is surprising since there is higher nutrient availability at site B1 than at site A1, which should result in greater growth at B1 than at A1 as measured by average height and percent cover. Assuming that the diversity and growth rate estimates are correct, it may be argued that site B1 represents a relatively undisturbed site where competitive displacement has occurred with the result

that there are just a few abundant species at this site. This situation would also result in a vertical abundance-rank curve and a low diversity index value. However, a low frequency of disturbance would allow competitive displacement to occur only at high growth rates, according to Huston's model. Alternatively, again assuming that the diversity index and growth rate index values are accurate, it may be that site B1 represents a frequently disturbed site that would result in a lower diversity value. The abundance-rank curve would also be vertical because only a few species would survive frequent reduction, as predicted by the model.

Because the shrubs and sedges are so scattered at site B1 it would seem that little real competition is occurring, at least with respect to surface space and light. Although, as mentioned above, approximately eighty percent of bog field species' productivity is underground so that it is possible that competitive displacement is taking place. Site B1 has undoubtedly suffered population reductions more frequently than site A1 since fires before 1909 and swamping after 1958 have almost certainly affected site B1 more than site A1 as described in part I of the Discussion. It is possible, therefore, that the lower diversity index value and growth rate index value at site B1 have been caused by frequent disturbance. It may not be as straightforward as this, however, since site C1 has also been subjected

to these same disturbances that have resulted in site C1 being characterized by a high diversity index value, an intermediate growth rate index value, and a flatter abundance-rank curve than site B1.

Because the actual species number and the total percent cover value at site B1 are considerably higher than at site A1, the method of site ordination might be inappropriate. There is also considerably more lateral growth in the shrubs at site B1 than at site A1. Methods of ordination and the mechanics of the generation of diversity at site B1 will be further discussed below.

The diversity and growth rate indices increase in value at site A1, resulting in site A1 being positioned second along the diversity-growth rate index curve shown on Figure 47. Nutrients are less available at site A1 than at site B1, with the exception of calcium. The level of calcium at both sites is less than the threshold value as described in the Results and part III of the Discussion. The pH is lower at site A1 than at site B1. Total percent cover of the field layer is greater at site B1 than at site A1. The number of plant species in both the field layer and total number observed is also much greater at site B1 than at site A1. These site characteristics are described thoroughly in the Results.

It should be emphasized that the shrub height values at site A1 probably reflect a difference in the

growth form of the shrubs rather than greater biomass. The shrubs at site A1 grow erect, like fingers from the thick moss carpet. As mentioned above, there is little of the lateral growth that is evident at the other sites. It is possible that the difference in growth form, due most probably to extremely low growth rates, inflated the growth rate index value for site A1 resulting in site A1 being positioned after site B1 along the diversity-growth rate index curve in Figure 47. The shrubs at site A1 averaged 19.6 cm in height and 17.7 cm in height at site B1. The percent cover value at site B1 was larger than at site A1 but apparently not large enough to offset the effect of greater shrub height in the calculation of a growth rate index. Obviously, in such an indexing system a means of properly evaluating standing crop should be employed. A more significant estimate may simply involve the use of total percent cover. This will be pursued, below.

Another strong indication that site B1 might represent a peculiar situation with respect to its expected position along a diversity-growth rate index curve involves the plant species found at site B1. Nine of the species found at site B1 are indicators of eutrophic or mesotrophic conditions. The release from oligotrophy as a consequence of fire disturbance or swamping might be manifested in species readjustment accompanied by a reduction in codominance so that the

diversity index value is low and the dominance value is high as compared to site A1 even though there are more species at site B1 than at site A1. This is reflected in the abundance-rank curve for site B1.

It may be seen that the diversity index value for site A1 is greater than the index value for site B1 because the species having measurable percent cover values that were used in the calculation are more even in their relative abundances than the species at site B1. This may also be seen on the abundance-rank curves for sites A1 and B1.

The well-known diversity index of Simpson as described by Pielou (1974) was used because Huston's model measures diversity defined as a parameter consisting of both species richness and evenness of abundance. If the sites were ordinated using species number and total percent cover the pattern of site distribution would appear as in Figure 49, where site A1 precedes site B1. Note that the pattern of distribution in species numbers for each site is similar for both the field layer and for the number recorded in all strata. The positions of sites C1 and D1 are the same as in the curve using the Simpson index and the estimated growth rate index (Figure 47).

The discordance between the field observations and site characteristics and the positions of sites A1 and B1 on the diversity-growth rate index curve point

Fig. 49

out that the method of estimating growth rates and the use of the abundance values of just those species having a five percent cover value in at least one of the sample quadrats in the calculation of the Simpson index may be inappropriate. The overall results, however, so closely parallel the diversity-growth rate curve predicted by Huston's model that it may be assumed that the general correspondence is not an artifact and that it warrants a continued discussion.

Figure 48 shows the ordination of the margin sites. Except for site A2, all of the sites are highly disrupted plant assemblages that are being subjected to beaver-related disturbance. The series of four sites does not appear to conform to the theoretical curve predicted by Huston's model, however site A2 is in a sense outside of the series by virtue of its relatively undisturbed state. This same statement might be made for site C1 in that it is also outside of the central heath group of plant assemblages because it is highly disrupted. This is touched on below during the discussion of site C1.

Site A2, because of its undisturbed nature, is connected to the other sites by a dashed line. The relatively higher diversity index value at site A2 as compared to site B2 is due to the evenness of species abundances. Site A2 is a transition community where both bog and fen species are found. Field observation

and the transect data indicate that Carex rostrata becomes increasingly abundant toward the mineral margin at site A2. Areas where Carex rostrata mulch has developed, few other species are found. The implication is that a species attains dominance under a sustained improvement in growth conditions that results in competitive displacement and a reduction in diversity. This pattern may also be seen at the margins of sites C2 and D2 where Typha latifolia becomes dominant, displacing other plant species and reducing diversity toward the beaver pond. At the margin of site B2, Typha is just beginning to invade. The varying degrees of Typha dominance at sites B2, C2, and D2 almost certainly represent a developmental sequence where Typha invades and eventually completely dominates the vegetation. This has been discussed thoroughly in part III of the Discussion.

The changes in diversity at sites B2, C2, and D2 also reflect the shift in the environment that is taking place at these sites. Site B2 represents a site of moderate disturbance where threshold values in pH and calcium have not been reached so that many of the nutrient-demanding species found at site C2 do not occur at site B2. Many bog species have been eliminated or reduced in abundance in the flooded areas of sites B2 and C2. The consequence of this is that the diversity of site B2 is reduced.

Site C2 represents the next stage in the sequence where threshold values in pH and calcium are reached or exceeded so that many nutrient-demanding species can invade, including species typically not associated with bog plants. This results in an increase in diversity. The increase in the extent of the Typha marsh at site C2 from 1977 to 1979 suggests that the initial rise in diversity is short-lived. This is seen at the pond margin of site D2 where Typha is totally dominant.

The change in diversity that is associated with varying degrees of beaver disturbance represent the generation of diversity states and also correspond to the general predictions of Huston's model. Even though Huston makes the point that his model explains how diversity is maintained, it has the inherent property of predicting how diversity states might be produced.

It can be seen that initial disturbance lowers diversity. If the disturbance relieves stresses to growth, diversity will rise. If the disturbance is sustained and unimodal, the species that is the best competitor under the constant environment will displace all other species. As long as the conditions are held constant, it would be expected that the dominant species would prevail. This latter aspect is related directly to Huston's model that shows how different diversity states can be maintained.

Another ordination method that yields interesting results and shows a little more clearly how diversity might be generated is presented on Figure 50. The Simpson index value is given on the vertical axis and the total percent cover of the field layer is given on the horizontal axis. As in the other figures, the total percent cover is scaled logarithmically. The percent cover-rank (abundance-rank) curves for each central heath site are also shown on the figure. The margin sites are not represented on Figure 50.

The series of sites conform to the curve predicted by Huston's model except for site B1. The deflection in the diversity index value for site B1 points out the need for a variety of ways to evaluate diversity. For example, on Figure 49 site B1 is represented as falling on the curve predicted by Huston's model. Figure 49 used the actual species number to measure diversity.

Site relationships can be more clearly described if species number and relative abundance are represented. For this reason the abundance-rank curves for each site are shown on Figure 50. A reasonably thorough analysis of diversity patterns is possible if several measures of diversity are used and if site history is known. Figure 50 will be discussed immediately below. Sites C1 and D1 will be discussed with respect to Figures 47-50.

Site A1 is characterized by low nutrient availability and probably a low frequency of disturbance.

Fig. 50

This results in reduced growth but an intermediate diversity index value. The number of species and the percent cover values at site A1 are the lowest of all sites, indicating that nutrient stress is probably the primary cause of the intermediate diversity value. This is mirrored in the abundance-rank curve where the less abundant species are not sharply deflected downwards, explainable if it is assumed that the species are not interfering with each other but all trying to keep "on top" of the Sphagnum carpet. This relatively even distribution is expressed by the intermediate diversity index value. Also, site A1 has been shown to be an assemblage that is probably not currently subjected to nutrient stress due to the transportation of water through the surficial peat as a consequence of beaver activity. As a consequence, few species are invading or being lost. Plant indicators of fire disturbance are also rare at site A1.

Site B1 shows a marked drop in the diversity index value, as mentioned above, which is accompanied by a sharp decline in the apparent slope of the abundance-rank curve. Site B1 is composed of a vegetation assemblage that is very similar to the assemblage sampled at site C1 as the Quotient of Similarity value for the two sites is .71, the largest for all the study sites. Site C1 has been identified as an area where swamping is probably actively occurring. What might be happening is that

swamping is beginning at site B1 so that minerophilic species are invading, raising the Quotient of Similarity between sites B1 and C1, while the general growth at site B1 has not increased to the point of allowing species to move into all of the space available to them. It is possible that this increased growth would result in a more even distribution that would increase the diversity value. The total percent cover value of the field layer is greater at site C1 as compared to site B1 and the abundance-rank curve at site C1 is flatter as compared to site B1, tending to reinforce the view expressed above.

It should be mentioned that the high Quotient of Similarity between sites B1 and C1 is also due to the presence at both sites of plant species that are indicators of fire disturbance.

Alternatively, it can be argued that the reduced diversity index value at site B1 is a consequence of the reduction in growth of species sensitive to flooding, such as Ledum groenlandicum, Gaylussacia baccata, and Kalmia angustifolia, and the acceleration of growth of those species whose growth is promoted by less acid conditions and that do well in wet environments, such as Chamaedaphne calyculata. Reduction in the abundance of more xerophilic species at site B1 is certainly possible and would explain why site B1 seems to have been "dropped out" of the series predicted by Huston's model. This feature would be exactly analogous to the

reduction of diversity at site B2 as discussed above.

Given the opportunity to recover from the effects of swamping, site B1 would very likely begin to resemble site C1 where relative abundances are more even and where nutrient-demanding species are becoming well established. It also can be predicted that site C1 will suffer a reduction in diversity as adjustment is accompanied by the elimination of dry-habitat species and as increased growth result in competitive displacement. This prediction is partially verified by field observation where the large Typha stand southeast of region 7 replaces the bog vegetation west of site C1. With this in mind, Figure 50 could show Huston's theoretical curve positioned below site C1 and would represent the inflated diversity index value at this site.

Site C1 is characterized by greater nutrient availability, a higher diversity index value, and more species than sites A1 and B1. The growth rate index values differ very little between the three sites. This is also true for the total percent cover values. Huston's model predicts that where growth rates are extremely low, diversity will be low. "Nevertheless," Huston writes, "the model clearly predicts that diversity will be highest at low growth rates, and decrease monotonically as r (growth rate) values increase. This suggests that the relationship between growth rate and diversity has a 'break point' at very low growth rates where a slight

increase in growth rates will result in a rapid increase in diversity, which will then decrease as growth rates rise." The rapid change in diversity from site A1 to site C1, especially as shown on Figure 49, might represent this "break point" region predicted by Huston's model. The actual mechanics of the increase in diversity at site C1 are described below and are similar to the interactions between the environment and plant species that were described for site B1.

The last part of Huston's statement quoted above could be rephrased to say that as conditions of growth become less difficult, there will be a point where the high diversity maintained under conditions of low to moderate growth rates in response to adequate growing conditions begins to decrease rapidly due to competitive interactions. This reduction in diversity is shown at site D1 where growth conditions would seem to favour high diversity.

A point of interest concerning the high diversity index value and relatively large number of species at site C1 is that site C1 has a mean pH value very close to the threshold pH value and a calcium concentration over the threshold value as identified from the transect data and described in part III of the Discussion. Although site D1 has a mean pH value that is slightly higher than the value at site C1, the calcium availability at site D1 is much lower as compared to site C1. However,

most other nutrients are more available at site D1 than at site C1. This indicates either that high calcium levels are necessary to drive diversity up or that other factors are involved. In view of the history of site C1, it most probably is a combination of factors where the increased calcium availability promotes the growth of acidophobic and eutrophic species as a result of beaver disturbance. The increased nutrient availability that would be a concomitant of greater calcium concentration, as well as other factors related to water flowing across the peat, explains why site C1 is characterized by an increase in growth as estimated by the growth rate index or by total percent cover. This does not explain why site C1 has so many more species or why its diversity index value is so much higher than site D1. An explanation involves processes described by Huston, as mentioned above, and other factors that relate directly to the disturbance history of site C1.

The cause of the increase at site C1 in the Simpson index is attributable to both an increase in species number and in the evenness of species abundances as shown by the abundance-rank curves. The abundance-rank curve for site C1 shows a shift toward codominance in the field layer as compared to sites B1 and D1. The clustering of the species of lower percent cover at site A1 enlarges the value of the Simpson index as compared to the value for site B1 even though site B1

has one more species listed on the abundance-rank curve. This clustering is even more evident at site C1, which has the highest diversity index value of all the central study sites. Also, the increased nutrient availability, particularly calcium, allowed species such as Anchistea virginicum to invade. The additional species would further increase the index value.

It was mentioned repeatedly in part I of the Discussion that site C1 appears to be composed of overlapping plant assemblages that would normally be found at opposite environmental extremes, at least with respect to bog systems. The overlapping of assemblages would certainly affect the diversity state of site C1 as species were adjusting to the change in the environment. Dry-habitat species would become reduced in abundance as nutrient-demanding and water-tolerant species were increasing in abundance, either as a consequence of the change in the environment or through competitive displacement. Because of the relatively low total percent cover of the vascular species, readjustment of species abundance is most probably due to the change in the environment. The increase in codominance at site C1 reflects these interactions. Although this explanation might seem to deviate from the explanation presented within the framework of Huston's model, it actually does not. As mentioned above, the diversity state at site C1 can be thought of as "overshooting" the predicted value and would begin to

show a reduction in diversity as species readjustment continued. This pulse in diversity is predicted by Huston's model for sites subjected to intermediate levels of disturbance (see Figure 45). The features characterizing site C1 could readily appear at site B1 as swamping continues. Also, the diversity state at site C1 would decrease as the disturbed conditions are maintained, as growth continues to increase, and as the better competitors dominate the site as shown at the margin study sites and in the area east of region 7.

Also, within the context of Huston's hypothesis, the increase in diversity at site C1 represents the release of the growth rates of the plant species in an area where there is a good deal of room to grow before species suffer displacement due to competition.

Site D1 is characterized by a reduced diversity index value, few species, a vertical abundance-rank curve, and a high growth index value and total percent cover. Nutrient availability, particularly that of phosphorus, is highest at site D1. It has been suggested in part I of the Discussion that the relatively high level of nutrient availability at site D1 is probably due to two factors. These are increased decomposition rates in the moist, aerobic conditions at the very surface of the peat and fire related ash deposition. Because the hydrogen sulphide smell of anaerobic decomposition was noticeable in the consolidated peat (about 50 cm

below the surface) at site D1, it is likely that relatively little decomposition is taking place in the subsurface peat at site D1. This is also indicated by the extreme doming of site D1, which is very obvious by field inspection, and by the absence of Betula populifolia within most of the site. The doming would be due to peat deposition in the center and decomposition along the wetter, more nutrient-rich margins. The absence of Betula populifolia suggests that the substrate is anaerobic. In the swamped areas of site C1 mature individuals of Betula populifolia are dead or dying. This would indicate that this species is sensitive to anaerobic conditions.

The most probable source of the nutrients at site D1 is ash deposited after a fire. This is speculative, especially since nutrients could readily be coming from the decomposition of the surface peats that appear to be in aerobic conditions and is rather spongy and brownish as compared to the peat from other sites or as compared to the peat from below the surface. For whatever reason, nutrient availability at site D1 exceeds all the other sites for all nutrients that were measured except for calcium.

Site D1 also appears unchanged on the series of aerial photographs over a period of about thirty-five years. If the fires that swept the study area cleared off the surface vegetation at site D1 before 1909, as

indicated by Nystrom and Anrep's (1909) map, this area has been relatively undisturbed for at least seventy years. The significance of this in connection with Huston's model will become evident as the discussion continues.

The greater nutrient availability at site D1 is accompanied by a much higher total percent cover value in the field layer and a higher growth rate index value as compared to sites A1, B1, and C1. The value of the Simpson index at site D1 is lower than the index value at site C1 and very close to the index value at site A1. This reduction in diversity of a site characterized by high productivity and a stable environment is predicted by Huston's model. Huston writes that "diversity may be reduced either by competitive displacement (and eventually exclusion) or by a high frequency of population reduction which does not allow some competitors to recover between disturbances." It would appear that sites A1 and D1 have been the least disturbed of all the sites in the study area. These two sites have similar Simpson index values, species number, and abundance-rank curves. The low diversity at site A1 has been related to very wet, acidic conditions where nutrient availability is low to the point of extreme deficiency. Site D1 is not characterized by nutrient deficiency, nor by frequent disturbance. It is unlikely that the low diversity index value and small number of species found at site D1 are caused by

frequent population reduction or nutrient deficiency.

The high total percent cover for the field layer at site D1 suggests that these species are competing for resources. This is more evident if it is recalled that over eighty percent of the growth in bog field vascular species occurs in the subsurface components. A relatively small increase in the growth above the surface represents a substantial increase in growth below the surface. Field observations made while excavating the sample holes in the various sites reinforce this view in that the holes were much more difficult to excavate at site D1 than at the other sites and contained more and larger roots.

It is possible that a single species will come to dominate site D1. Monotypic communities are common in bog systems (see Part I of the Discussion). Because of the dry conditions at site D1, the species most likely to dominate are Gaylussacia baccata, Kalmia angustifolia, or Ledum groenlandicum. The optimum conditions for the development of a Chamaedaphne calyculata community have been described in part. III of the Discussion. Site D1 is too dry for a closed community of Chamaedaphne calyculata to develop. Pure stands of Gaylussacia baccata are not supposed to be common in continental areas (Damman 1977). Dansereau and Segadas-Vianna (1952) describe nearly pure stands of both Kalmia angustifolia and Ledum groenlandicum in the St. Lawrence Lowlands.

Heinselman (1963, 1970) describes fire disturbed stands in bogs in northern Minnesota (U.S.A.) that are dominated by Picea mariana and Ledum groenlandicum.

A single bog species may completely dominate the field layer of a bog community but it is unlikely that this would be inevitable, providing that there were regular fluctuations in the environment. It has been pointed out that in areas where the environment has been held constant and stresses to growth have been relieved, such as at the beaver disturbed study sites, a single species may come to completely exclude other species apparently adapted to the current environmental situation. This can be seen at site A2, dominated by Carex rostrata, site B2, dominated by Chamaedaphne calyculata, site C2, dominated presently (1980) by Typha latifolia, site D2, also dominated by Typha latifolia, and the area along the margin of site D2, dominated by Alnus rugosa.

Huston stresses that within his hypothesis it is not inevitable that diversity will drop to zero. He writes that "long periods of time with a low rate of competitive displacement will allow environmental fluctuations to further reduce the rate of displacement by altering competitive interactions. One species may be the best competitor under certain conditions of temperature or precipitation, while under slightly different conditions another species may assume dominance. Such reversals of competitive dominance can obviously allow coexistence,

as can frequency-dependent competitive differences."

It might be argued that the diversity state of site D1 is only partly due to competition, which stratifies the species' abundances and therefore reduces the value of the Simpson index while the actual species number is determined by habitat preferences.

The diversity increases at the margins of site D1 where the environmental conditions change as shown by the transect data presented in Appendices A and B, suggesting that more species are not found within the confines of site D1 simply because they are not capable of growing there. In this respect, the favourable environmental conditions at site D1 relative to sites A1 and B1 suggest that the number of species that could grow at site D1 would be greater than at site A1 or site B1, assuming that low nutrient availability, acidic conditions, and a high water table constitute a severe stress for most plant species. Recall that there are only three more species at site D1 than at site A1 and eight fewer at site D1 than at site B1. Furthermore, it might be expected that because of the proximity of all the study sites, species capable of growing in the environments of each site would do so.

An examination of the total species lists on Table 1 and the abundance-rank curves for the study sites clearly shows that the field-layer species that have not maintained their distributions along the length of the

entire study area are primarily the sedges. The dry conditions at site D1 would partially explain the reduced abundance of these species. Eriophorum virginicum does occur at site D1, indicating that at least one of the sedge (cotton grass) species is able to grow under relatively dry conditions.

Changes in the distribution patterns of these species obviously are related to changes in the environment, but they must also be related to the species' abilities to successfully compete for space, light, and nutrients along its entire range of peatland habitats, from marginal to optimal. This would be especially true for plant assemblages that are obviously crowded or packed with individuals from one or more species such as site D1 in my study area. Drier conditions for Eriophorum spp. may not reduce its growth rate or interfere with its general metabolism. However, the drier conditions, greater nutrient availability, and high pH at site D1 might well allow the shrubs to accelerate their growth rates or increase their productivity so that their growth habit becomes denser and taller and they develop a larger, more extensive root system. As the height and density of the shrubs increases, the narrow-leaved, shorter sedges would be severely constrained and eventually eliminated, especially if they relied on seeds for propagation. This type of replacement process has been referred to by several authors, Dansereau and

Segadas-Vianna (1952) in particular.

The effect of competition in areas of optimum growth for certain species may result in the elimination of other species even though these other species may be well within the limits of their habitat requirements.

The low diversity of site D1 might be the result of habitat exclusion related to physical characteristics of the peat. The low diversity might also be related to competitive displacement as a consequence of the greater productivity of certain species that results in the exclusion of other species with shorter growth forms and smaller photosynthetic surfaces or that rely primarily on seeds for propagation. The failure of seed propagules under a dense shrub canopy could be due to the reduced light intensities at the surface or other factors, such as failure of seedlings to become well established in the face of overwhelming competition from the established shrub species.

It may be concluded from the discussion above that the diversity patterns in my study area can at least be partially explained by applying the rationale of Huston's general hypothesis of species diversity. It should be said, though, that the use of an hypothesis as a framework for discussion does not constitute a test of that hypothesis. Huston's model does, however, provide a coherent explanation of an otherwise bewildering set of data.

GENERAL DISCUSSION - PART II

In part I of the Discussion it was found that bog plant assemblages occur consistently enough in peatlands to be identified as repeated and recognizable units by a variety of investigators. The similarities between vegetation units described in the literature and the plant assemblages in my study area are unmistakable, even though the primary point raised in part I of the Discussion was that representatives of vegetation units that normally occurred on nearly opposite ends of environmental gradients could be recognized at site C1. However, the overall field impression and the response of plant species to beaver disturbance suggest that species occur individualistically spaced along gradients in the immediate vicinity of the dams. This is not surprising since it is generally accepted (Ricklefs 1973, pp 589-604; Whittaker 1973, pp 35-46; and Krebs 1978, pp 385-406) that the classifications of plant assemblages into discrete associations representing more than accidental groupings is a highly artificial undertaking and that species are distributed as individuals according to their own genetic characteristics. Vitt and Slack (1975) specifically comment on bog plant assemblages. They write that "there are a number of species associations, a few of which have been noted between particular vascular plants and particular species of Sphagnum."

These associations are a result of similar physiological tolerances of these species pairs resulting in similar distributions within the bog. Where conditions are quite rigorous for either group, for example high pH for Sphagnum, the association may be very close. . . . On the other hand, where several factors interact in determining a species distribution in the bog, and this is the usual case, there is no reason to expect complete association. Some species pairs . . . may occur together in some areas in which both have high importance values; they have similar physiological tolerances in these areas. However, each occurs separately in other areas of the bog, indicating overlapping but not identical physiological tolerances for these species."

It is also quite evident, as mentioned above, that similar groupings of plants occur over a relatively large geographic area and extensive local regions.

If plant species exist individualistically along environmental gradients and if broad geographical areas contain definite environmental gradients, it would be expected that all possible combinations of plant assemblages would occur so that the entire series would be blurred without distinct and repeated assemblage-types existing. The effects of regional isolation, colonization, extinction, and other demographic processes should not have a dramatic effect on broad patterns of assemblage discreteness or ambiguity.

It is paradoxical that there are strong similarities in assemblage descriptions over really enormous geographical areas when bog species generally tend to be distributed individualistically along environmental gradients. A solution to this apparent problem might rest on two closely related concepts. The first deals with thresholds in key environmental variables as described in this report. A rapid and marked change in the structure and composition of a bog plant community occurs when threshold values of key environmental variables are reached or exceeded. The second concept deals with what might be termed substrate stability.

Substrate stability is related to threshold values of environmental variables in that a peat substrate has an inherent buffering capacity that, depending on the type of peat, might result in the maintenance of similar environments over relatively large areas with minor climatic gradients. These substrates might also maintain the values of the environmental variables within narrow ranges, nearly exclusive of the degree of stress impinging on the substrate and the community it supports up to the limits of the inherent buffering capacity of the peat. The structure of the peat that maintains the values of environmental variables within narrow ranges could be termed stability nodes that alter to less or more stable configurations as the result of a persistent and catastrophic stress, which would result in an

environmental shift below or above the threshold value where communities begin to change.

This would explain why assemblages are recognizable, in that the species may be responding individually to the habitat but the habitat is stratified along what would otherwise be an uninterrupted gradient so that groups of species are repeated over a layered habitat space. This is what Whittaker (1973, p. 43) refers to as "topographic, edaphic, and disturbance discontinuities in the field." It would seem that evolutionary pressures would further enhance the relationships between species in association but there would be many constraints to this happening if the habitats were constantly driven to catastrophes and if there were many stability nodes or strata.

Whittaker (1973, pp 43-44) writes, apropos of the above, that

repetition of similar species combinations in similar environments is equally to be expected whether species are individualistic or form co-adapted groups, whether communities are continuous or discontinuous. The more significant question is that of the direction of species evolution. There is, at first glance, a paradox in the evolution of species both toward co-adaption within the community and toward distributional individuality. The paradox is resolved by recognition that species evolve toward the reduction of competition by both niche difference (difference in position or role in the community as a basis of co-adaption) and habitat difference (difference in distribution, or location of population centers, along environmental gradients). The fact species differ in niche implies that they will not in general exclude one another's populations along sharp boundaries, but may form the gradually

tapered and broadly overlapping distributions observed in gradient analysis. Species do not in general evolve toward formation of discrete and clearly bounded groups . . . , but toward distributional difference and toward accommodations to one another that imply, for most species, continuously overlapping distributions.

The notion of continuous and discontinuous distributions of vegetation communities is described by Whittaker (1973, pp 35-46), as mentioned above. It is described specifically for bog vegetation by Dahl (1956) and is implied by Heinzelman (1963, 1970, 1975). The view that discontinuities in habitat will produce discontinuities in the distributions of vegetation communities has also been discussed by Whittaker (1973, pp 35-46). What is proposed regarding what has been termed stability nodes is simply an explanation of such discontinuities that is rooted in the physicochemical configurations of the habitat⁴ substrate. The buffering capacity of peat refers to characteristics such as: cation exchange capacity; hydraulic conductivity; thermal conductivity; water holding capacity; nutrient content; pore space; organic constituents; fiber content; density; etc. (Walmsley 1977). These characteristics are determined by the origin of the peat and the chemical composition of the organic materials as well as the environment of the site of peat deposition. Other secondary factors, such as decomposer organisms, would also contribute to the type of peat that develops or that is maintained in an area.

Some of the stresses on substrate stabilities of blanket bogs might be: nutrients added by fire or swamping; changes in temperature or rainfall; acid rainfall; an alteration in the precipitation/evaporation ratio; changes in deposition or decomposition rates as a consequence of shifts in local climate or the edaphic environment; etc. These stresses may drive the substrate beyond its inherent buffering capacity resulting in a threshold catastrophe that quickly alters the environmental conditions that is accompanied by a readjustment in community structure and composition.

Substrates within the plant community of differing buffering capacity might explain the phenomenon of the juxtaposition of community types such as is occurring at site C1 in my study area. The hummock-hollow configuration of bog communities, such as at sites C1 and D1, would also lend itself to this type of developmental process, producing a mottled micro-structure or multi-subset mosaic in the organization of the overlapping communities.

The buffering capacity of the substrate also might explain why boundaries between several of the plant assemblages in my study area are reasonably distinct, at least on the human scale. The reason would simply be that stresses would be dampened, preventing extensive transition gradients from occurring. For example, the limits of Carex rostrata at site A2 and Typha latifolia at site D2 are quite distinct and the surface limits to

the occurrence of these species is accompanied by a sudden drop and leveling off of the values in the environmental variables measured along the experimental transects.

The concept of substrate stability is not central to this report and is proposed only as speculative discussion and as a possible testable hypothesis of bog plant community assemblage. Other factors would certainly be involved in determining assemblage structure and composition. Some of these factors were discussed in part I of the General Discussion.

GENERAL DISCUSSION - PART III

Two aspects of ecology pertinent to a discussion of distribution and abundance patterns of plant species involve the basic rules of assembly of plant communities and their application to the management of those communities. The assembly rules influence perforce the diversity and the persistence stability of a community. In this part of the General Discussion, the few insights into rules of bog community assembly presented in this report will be briefly summarized and discussed with respect to a management rationale for the Mer Bleue.

The factors proposed or mentioned in this report that influence or control the presence and success of the various bog plant species are the following: competitive displacement; water level; nutrient availability, particularly the availability of phosphorus, calcium, and potassium; pH, which is influenced by ion concentration and the cation exchange capacity of peat and which, in turn, influences nutrient availability by affecting the solubility of aluminum, iron, and manganese; decomposition rates; the rate of water flow across the surface of the peat; and fire. All of these factors, except competitive displacement, may be combined under the category of habitat restrictions. Habitat restrictions would include the frequency of disturbance. These factors are of varying importance according to the rate of growth for

each species and its associates and the frequency and duration that any particular site is disturbed.

As total abundance increases, competitive displacement might occur. As disturbance increases in frequency or duration, up to an intermediate level, species might increase in abundance and number. Species number declines under prolonged unimodal and unidirectional stress. Those species that persist become more abundant. This effect occurs where the stress or disturbance results in greater growth, such as under improved nutrient regimes.

Because of the buffering capacity of peat, there are critical values in environmental variables that, when approached or exceeded, result in rapid and marked change in the structure and composition of bog plant communities. Of the environmental variables that influence bog plant species, pH and water level would appear to be the most critical. Nutrient availability is intimately related to pH because of the cation exchange capacity of peat and the change in nutrient solubility and complexation at varying pH values. It is probable that when nutrients, especially calcium, leak into a peat substrate they may tax the cation exchange capacity of the peat so that a point is reached where the pH rises relatively abruptly. This increase in the pH value would be accompanied by a further increase in nutrient availability as decomposition rates accelerate and as key

nutrients, such as phosphorus, become available as aluminum, iron, and perhaps manganese become insoluble. Also, calcium will complex with phosphorus at low to intermediate pH values in a form that is soluble and available to plants.

The pH might also increase if conditions favouring reduced peat deposition and reduced cation exchange activity prevail, for example when water flows across the surface of the peat. This would be followed, up to a point, by an increase in nutrient availability. The optimum pH value for nutrient availability in organic soils is in the range of 5.0-5.5. Under alkaline conditions, nutrient availability decreases. The pH value of 5.0 is a threshold value around which major changes in nutrient availability take place. A calcium value in the range of 2.5-3.0 ppm has also been shown to be a critical range where major vegetation changes may occur. A threshold value of 2.7 ppm has been proposed for calcium.

The buffering capacity of peat that results in threshold values may also explain why bog plant communities or assemblages have relatively distinct borders and occur as recognizable and repeated units over a landscape. The most dramatic effect of incremental changes in the substrate environment due to the inherent stability and buffering capacity of peat would be that coherent plant assemblages would behave dynamically and as units.

Community change would result in the juxtaposition of plant assemblages, as if one assemblage were growing up through another distinct plant assemblage.

The proposed regions or configurations of peat structure that might be inherently stable and that might permit a distinct plant assemblage to occur have been referred to above as stability nodes. The process of community change as related to the concept of nodes of substrate stability may be referred to as a dynamic mosaic of community development where coherent plant assemblages occur only within stable and repeatable habitat configurations or axes. This differs from traditional views of successional development in that the initiation and progress of change is catastrophic and potentially multidirectional rather than incremental and assumably unidirectional.

These views may be applied to a management scheme for the Mer Bleue as described below. Beaver might be used as a primary management tool to control the type of plant assemblage, site diversity, and the substrate characteristics to be found within any particular management unit of the Mer Bleue. Because of the nature of the drainage in the Mer Bleue, there are five or six distinct management units that have relatively isolated drainage systems. The study area described in this report would be one such unit.

Management decisions on the respective value of various types of plant assemblages would have to be made. Other, more general factors such as interrelationships between assemblage types and total diversity states would also have to be considered. After priorities were defined, an overall plan could be developed that would involve the removal, maintenance, or introduction of beaver into areas in order to control water level and nutrient availability. These measures would in turn control the presence and success of dominant members of the various types of plant assemblages described in part I of the Discussion. The specific effects would depend on the current status of a particular management unit and the plant assemblages that occur there.

Values of environmental variables and indices of community structure and composition could be determined or constructed for selected study sites and then monitored for changes. Environmental variables approaching threshold values would alert the manager to impending change that might be difficult to reverse. Action could be taken before such thresholds are reached, such as: removing a beaver dam; introducing beaver to an area previously denied to beaver invasion or re-invasion; or lowering the water level and direction of water flow in swamped regions by conventional means.

Other indicators of community status would need to be measured as well, such as species height, cover,

and presence. Standard indexing systems could be used or others could be developed that would yield a single index value representing the dynamic relationships between species so that the numerous sites involved could be reasonably easily compared and assessed for change. This would involve a continuous monitoring system with regular collection of data at selected sites.

Simpler management schemes could also be applied. For example, in order to reduce the extent of Typha invasion in the eastern portion of my study area, Ramsayville Marsh just east of Anderson Road could be partially drained in stages while the direction of water flow and water levels in the eastern portion of my study area were being monitored. As soon as this area was no longer being actively swamped, the drainage of the Marsh could be halted. The beaver dams at regions 7, 8, 9, and 10 would also likely have to be temporarily breached. Such a scheme would involve few personnel and little expense although it would involve careful and long-term monitoring of water levels, and water movement, nutrient availability, and vegetation status.

Failure to develop and maintain a management program for the Mer Bleue would result, in my opinion, in much of the Mer Bleue becoming a Typha Marsh or, at the very least, a mosaic of highly disrupted bog plant assemblages.

CONCLUSIONS

1. Beaver activity is evident in the Mer Bleue beginning about 1958 and in the study area beginning in 1968. Beaver disturbed sites are characterized by nutrient-demanding species and support plant assemblages that represent a temporal sequence where initial minor changes in composition may be followed by a total replacement of bog vegetation by a Typha marsh.
2. Gradients of decreasing nutrient and pH values found at both the undisturbed and beaver disturbed sites extend farther into the central bog at the beaver disturbed sites. Major changes in the structure and composition of the plant assemblages occurred where pH and calcium values reached or exceeded critical values of 5.0 for pH and 2.7 ppm for calcium. Changes in vegetation, nutrient concentrations and pH associated with beaver ponds in the bog indicate that beaver ponds function as nutrient traps.
3. Plant assemblages in the study area are similar to bog plant communities described in the literature from across eastern North America. The central bog plant assemblage that has been disturbed by beaver ponding is an unusual mixture of species that normally are found in an array of very different environments. Such changes in the vegetation are related to both swamping and increasing nutrient levels.

4. The species diversity of the plant assemblages may be explained by Huston's general hypothesis of species diversity. The correspondence of the field data to the predictions of Huston's model depends on the ordination procedures employed.

SUMMARY

The Mer Bleue is a large (6,300 acres) bog located about 15 km southwest of Ottawa, Canada. The Mer Bleue has long been a site of cultural and scientific interest. The bog is currently partly under the jurisdiction of the National Capital Commission.

Beaver are common in the Mer Bleue and in many areas have disrupted the bog vegetation. A study of the effects of beaver activity on bog vegetation was begun in 1977. It was assumed that changes in the bog vegetation in response to beaver disturbance would provide insight into factors that influence or control species distribution and abundance. Aerial photograph inspection was used in conjunction with the field investigation in order to determine the history of beaver invasion and to assess the large-scale changes in the vegetation associated with beaver disturbance. The aerial photograph record of the Mer Bleue is reasonably complete beginning in 1945.

The primary investigation was confined to the southwest portion of the Mer Bleue, bordered on the north by Borthwick Ridge.

Beaver invaded the bog in about 1958 and the study area in 1968, beginning at the eastern end of Borthwick Ridge.

Field sampling was restricted to twelve regions in the study area that represented various aspects of

disturbed and undisturbed conditions. Both vegetation and environmental data were collected along the same transects above and below selected beaver dam sites, control sites, and central heath sites. Water and peat samples were collected and analyzed for pH, phosphorus, potassium, calcium, magnesium, and sodium. The transect data were inspected and used to: evaluate the effects of beaver activity on the vegetation; characterize the various study sites; and explore the nature of beaver disturbance.

The site characterizations were compared to plant assemblage descriptions in the literature in order to further evaluate the effects of beaver activity on the plant assemblages in the study area. The comparisons of the site descriptions with the descriptions of bog plant assemblages or associations in the literature were also used to examine the basic qualities and characteristics of bog plant assemblages in general. It was found that even though there is great overlap in many community types, the bog communities do occur as repeatable and recognizable units. In many cases the bog assemblages are homogeneous over a large geographic area.

The results of the aerial photograph inspection and the analysis of the field data suggest that the beaver ponds function as nutrient traps, promoting the growth of nutrient-demanding species above the beaver dams. Changes in the values of key environmental variables

were associated with increased growth of Chamaedaphne calyculata, the most important bog species in the study area. Beaver activity was also found to be causing, or at least enhancing, the general swamping of a sizeable region in the east-central part of the study area. This swamping is resulting in the transformation of the bog vegetation in this region into a highly disrupted, nutrient-rich site.

Beaver were also found to be manipulating the water level in the ponds and canals along the entire drainage system of the study area.

The composition and structure of the vegetation in the swamped region is likely changing from a dry, fire disturbed site characterized by a high abundance of Ledum groenlandicum, scattered Vaccinium species and Betula populifolia saplings to a community characterized by Larix laricina and Typha latifolia.

It is suspected that nutrient-laden water is moving through the eastern part of the study area as a consequence of swamping and that the changes in the vegetation are related to this movement of water. The agent of change at the beaver disturbed sites and the larger swamped area is most likely an elevated calcium concentration. The calcium would likely be transported from the mineral margin across the surface of the consolidated peat. Calcium has been shown to influence pH and nutrient availability.

In agreement with the literature, the nutrient regime was found to be the primary influence on bog plant species distribution and abundance. Calcium concentration and pH seemed to be the most important environmental variables. Other environmental factors that affect bog species are water level and substrate aeration. Threshold values where major changes in species distribution and growth occur are proposed for pH and calcium. These threshold values are 5.0 for pH and 2.7 ppm for calcium.

The diversity patterns of the study sites in the study area were discussed within the framework of a current hypothesis of species diversity proposed by Huston (1979). The diversity states of the vegetation assemblages in the study area generally corresponded to the predictions made by Huston's model. The degree of correspondence, however, depended on the method of site ordination. Three processes are proposed by Huston to explain how community diversity is maintained. These are: disturbance, including predation; productivity, measured as growth rate or abundance; and competitive displacement. Nutrient availability is also mentioned by Huston as affecting community diversity.

A rigorous field test of Huston's hypothesis was not attempted.

The discussion of the field data was made considerably more coherent as a consequence of using the predictions of Huston's model.

The bog plant species seemed distributed individualistically along the experimental transects and along the length of the study area. This general distribution pattern is acknowledged by several bog ecologists. Bog plant assemblages do, however, occur as recognizable and repeated units over the landscape. Speculative discussion was offered regarding this apparent paradox.

It is proposed that the threshold values of key environmental factors as described in this report might be linked to the buffering capacity of peat. The result being that the peat maintains a stable environment only within the threshold values so that species adapted to those conditions appear to form associations. Consequently, plant assemblages behave dynamically as the substrate shifts along a stratified gradient of what might be termed stability nodes. This hypothesis also provides for an explanation of the apparent overlapping of vegetation assemblages as is occurring at site C1 in the study area. The term dynamic mosaic of species assemblage was proposed to represent the interaction of plant species, assemblage structure and composition, and the characteristics of the substrate.

All of the various topics described in this report deal with the factors that control or influence bog plant species distribution and abundance. These factors can also be seen to function as components in the rules of community assembly. Some of these factors, such as water

level, pH, nutrient availability, fire or swamping disturbance, and competitive displacement, are of varying importance depending on site history. The factors also interact to varying degree under different circumstances, some becoming important only after a general mitigation of the stresses to growth. An example would be the reduction in diversity due to competitive displacement that might be associated with site amelioration and increased growth at site D1 in my study area.

The rules of assembly of bog plant communities could be applied to system models or management schemes.

A management scheme for the Mer Bleue was briefly outlined that suggests that beaver be used as a prime management tool in controlling both the water level and nutrient concentration in selected areas of the bog. An alternate, less extravagant, scheme is also proposed for the study area.

Failure to develop and implement a management program for the Mer Bleue will almost certainly result in much of the bog vegetation being transformed into a Typha marsh or into a mosaic of bizarre and highly disrupted bog plant communities.

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APPENDIX A

Plant Species' & Cover Values Along Transects

For locations of Regions, Sites, and Transects,
see Figures 11-13 and the descriptions in
section II, A, 1 of the Results.

APPENDIX A

Date: 24 July, 1977

Locality: Region I, Sites A1, A2

Transect: 1

[illegible]

APPENDIX A

Date: 27 July, 1977

Locality: Region I, Sites A1, A2

Transect: 2

Species	Distance Along Transect in Meters															
	0	5	10	15	20	25	30	35	40	45	50	60	70	80	90	100
<u>Alnus rugosa</u>	+															
<u>Chamaedaphne calyculata</u>	30	30	30	+		30	15	30	+	5	25	25	10	+	30	35
<u>Ledum groenlandicum</u>																
<u>Kalmia angustifolia</u>																
<u>Gaylussacia baccata</u>																
<u>Aronia melanocarpa</u>	+															
<u>Spiraea alba</u>	+															
<u>Smilacina trifolia</u>																
<u>Tridentium virginicum</u>	+															
<u>Carex rostrata</u>	10	10	5	65		5	5	5	5							
<u>Carex prairea</u>		25	60	5												
<u>Eriophorum tenellum</u>	+	+	+	+		+	+	70	75	25	+	+	15	30		5
<u>Glyceria sp.</u>	+															

APPENDIX A

Date: 25 August, 1977 Locality: Region I, Sites A1, A2 Transect: 3

Species	Distance Along Transect in Meters																	
	0	5	10	15	20	20	15	25	30	35	40	45	50	60	70	80	90	100
<u>Alnus rugosa</u>	+																	
<u>Salix spp.</u>	+																	
<u>Chamaedaphne calyculata</u>	+	5	+	20	20	15	25	5	5	5	5	5	10	+	10	5	10	20
<u>Ledum groenlandicum</u>													+	10		5	10	40
<u>Kalmia angustifolia</u>																	+	+
<u>Gaylussacia baccata</u>															20		+	
<u>Vaccinium oxycoccus</u>													+			+		
<u>Kalmia polifolia</u>																+	+	
<u>Aronia melanocarpa</u>	95																	
<u>Nemopanthus mucronata</u>	+																	
<u>Ilex verticillata</u>	+																	
<u>Viburnum cassinoides</u>	+																	
<u>Smilacina trifolia</u>									+	+	+	+						+

APPENDIX A

Date: 28 August, 1977 Locality: Region III, Sites B1, B2 Transect: 4
Above Dam

Species	Distance Along Transect in Meters															Comments
	0	5	10	15	20	25	30	35	40	45	50	50	60	80	120	150
<u>Chamaedaphne calyculata</u>	50	90	50	80	60	60	60	60	90	50	50	50	90	60	80	+
<u>Ledum groenlandicum</u>																5
<u>Kalmia angustifolia</u>								+								+
<u>Gaylussacia baccata</u>																5
<u>Nemopanthus mucronata</u>																5
<u>Vaccinium spp.</u>	25		+													<u>carymbosum</u> <u>myrtilloides</u>
<u>Eriophorum virginicum</u>															+	90
<u>Carex sp.</u>																+
<u>Eriophorum spp.</u>	+	+	25	5	10	25	25	30	+	30	20	5	20	+	+	<u>opacum*</u> <u>chamissonis</u> <u>tenellum</u>

APPENDIX A

Date: 21 July, 1977 Locality: Region III, Site B1 Transect: 1
Below Dam

Species	Distance Along Transect in Meters											Comments
	0	5	10	15	20	25	30	35	40	45	50	100
<u>Larix laricina</u>						+					+	+
<u>Betula populifolia</u>						+					+	+
<u>Salix spp.</u>	+											
<u>Chamaedaphne calyculata</u>	30	75	55	40	40	40	35	35	40	40	40	70
<u>Ledum groenlandicum</u>						5			+			15
<u>Kalmia angustifolia</u>						+			5			+
<u>Gaylussacia baccata</u>												10
<u>Andromeda polifolia</u>												+
<u>Scirpus acutis</u>						+						
<u>Juncus effuses</u>												
<u>Glyceria sp.</u>												
<u>Eriophorum spp.</u>		+	5	15	+	5	10	15	5	+	+	5
												<u>chamissonis</u>
												<u>opacum</u>
												<u>tenellum</u>

APPENDIX A

Date: 24 July, 1977Locality: Region III, Site B1Transect: 3

Species	Distance Along Transect in Meters				
	<u>0</u>	<u>10</u>	<u>20</u>	<u>30</u>	<u>40</u>
<u>Larix laricina</u>					+
<u>Chamaedaphne calyculata</u>	45	60	50	35	5
<u>Ledum groenlandicum</u>	10				+
<u>Scirpus acutis</u>			+	+	+
<u>Carex trisperma</u>		5			
<u>Eriophorum chamissonis</u>	+	5	+	15	25
					20

APPENDIX A

Date: 28 August, 1977 Locality: Region III, Site B1 Transect: 6

Species	Distance Along Transect in Meters					Comments
	0	10	20	30	40	50
<u>Alnus rugosa</u>				+		
<u>Larix laricina</u>		+		+	+	+
<u>Betula populifolia</u>				+		
<u>Chamaedaphne calyculata</u>	10	30	80	55	+	+
<u>Ledum groenlandicum</u>		+				
<u>Kalmia angustifolia</u>					+	
<u>Gaylussacia baccata</u>						+
<u>Vaccinium oxycoccus</u>				+	+	+
<u>Vaccinium spp.</u>	10	50		+	+	
						<u>corymbosum</u> <u>myrtilloides</u>
<u>Eriophorum spp.</u>	60	+	+	15	60	80
						<u>chamissonis</u> <u>opacum</u> <u>tenellum</u>

APPENDIX A

Date: 12 July, 1977 Locality: Region IV, Sites C1, C2 Transect: 1
Above Dam

Species	Distance Along Transect in Meters																			Comments
	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95
<u>Larix laricina</u>					+			+			+	+	+	+	+	+	+	+	+	+
<u>Betula populifolia</u>																				
<u>Chamaedaphne calyculata</u>	5	20	45	30	30	70	95	90	35	75	70	90	60	60	40	5	90	30	30	+
<u>Ledum groenlandicum</u>									20							30	10	10		20
<u>Kalmia angustifolia</u>																			15	10
<u>Vaccinium oxycoccus</u>															5					20
<u>Vaccinium spp.</u>	+																			
<u>Typha latifolia</u>	+																			
<u>Galium sp.</u>	+																			
<u>Iris versicolor</u>	+																			
<u>Scirpus acutis</u>	5			30	5	10	5	+	5	10										+
<u>Carex oligosperma</u>																				

corymbosum
myrtilloides

5 5
OF / DE

APPENDIX A

Date: 16 July, 1977 Locality: Region IV, Site C1 Transect: 3

Species	Distance Along Transect in Meters				
	0	10	20	30	40
<u>Chamaedaphne calyculata</u>	5	5	20	10	10
<u>Ledum groenlandicum</u>	50	15	5	5	20
<u>Kalmia angustifolia</u>				5	
<u>Gaylussacia baccata</u>		10	+	5	15
<u>Andromeda polifolia</u>		+			
<u>Vaccinium oxycoccus</u>		+			
<u>Smilacina trifolia</u>					+
<u>Scirpus atrovirens</u>	+				
<u>Eriophorum opacum</u>	5	10	5	5	+

APPENDIX A

Date: 30 August, 1977 Locality: Region IV, Site C1 Transect: 6

Species	Distance Along Transect in Meters						Comments
	0	10	20	30	40	50	
<u>Larix laricina</u>	+	+	+				
<u>Betula populifolia</u>	+					+	
<u>Chamaedaphne calyculata</u>	10	10	10	30	80	50	
<u>Ledum groenlandicum</u>	25	50	50	40	+	+	
<u>Kalmia angustifolia</u>	+	10	+				
<u>Gaylussacia baccata</u>	55					40	
<u>Andromeda polifolia</u>	+					+	
<u>Vaccinium spp.</u>		+		+			<u>corymbosum</u> <u>myrtilloides</u>
<u>Smilacina trifolia</u>	+		+	+		+	
<u>Eriophorum spp.</u>	+	15	10	5	+	+	<u>opacum</u> <u>virginicum*</u> <u>tenellum</u>

<u>Typha angustifolia</u>							+
<u>Typha latifolia</u>	+	+	5	20	5	5	
<u>Rubus sp.</u>	+	+					
<u>Calamagrostis canadensis</u>	90	75	25				
<u>Carex sp.</u>					+	10	+

APPENDIX A

Date: 27 August, 1977 Locality: Region VIII, Site D1 Transect: 6
Below Dam

Species	Distance Along Transect in Meters																	Comments
	0	10	20	30	40	50	60	70	80	90	100	110	120	130	140	150		
<u>Populus tremuloides</u>	+				+	+												
<u>Betula populifolia</u>	+	+			+													
<u>Salix</u> spp.	+																	
<u>Chamaedaphne calyculata</u>		+	30	50	20	30	30	30	25	55	25	25	20	+	10	30		
<u>Ledum groenlandicum</u>					+							+						
<u>Kalmia angustifolia</u>				+		+	+			10	+	+	10	20	20	20		
<u>Gaylussacia baccata</u>	+		25	40	55	30	40	35	30	30	30	50	50	40	60	30		
<u>Andromeda polifolia</u>							+	+				\$	+	20				
<u>Vaccinium oxycoccus</u>										5								
<u>Aronia melanocarpa</u>		+	30	15	+		+											
<u>Nemopanthus mucronata</u>										10								
<u>Vaccinium</u> spp.		+		+				+										
																	<u>corymbosum</u> <u>myrtilloides</u>	

corymbosum
myrtilloides

<u>Rubus hispidus</u>	5
<u>Tridentium virginicum</u>	+
<u>Typha latifolia</u>	+
<u>Spirea sp.</u>	+
<u>Solidago uliginosa</u>	+
<u>Calamagrostis canadensis</u>	90 85
<u>Juncus sp.</u>	+
<u>Carex sp.</u>	+
<u>Eriophorum sp.</u>	+
<u>Scirpus sp.</u>	+
<u>Conioselinum sp.</u>	+
<u>Aster sp.</u>	+
<u>Apocynum sp.</u>	+
<u>Solidago sp.</u>	+

APPENDIX

Date: 26 August, 1977 Locality: Region VIII, Site D1 Transect: 5

Species	Distance Along Transect in Meters					Comments
	0	10	20	30	40	50
<u>Chamaedaphne calyculata</u>	70	45	50	40	55	30
<u>Ledum groenlandicum</u>	+				5	+
<u>Kalmia angustifolia</u>	5	+	5	+	5	20
<u>Gaylussacia baccata</u>	25	35	30	35	25	20
<u>Andromeda polifolia</u>			+			
<u>Eriophorum sp.</u>	+	+		+	+	<u>virginicum</u>

APPENDIX B

Date: 27 July, 1977 Locality: Region I, Sites A1, A2 Transect: 2

Species	Distance Along Transect in Meters															
	0	5	10	15	20	25	30	35	40	45	50	60	70	80	90	100
<u>Chamaedaphne calyculata</u>	40	40	30	45		35	15	20	15	15	15	15	15	15	15	15
<u>Ledum groenlandicum</u>													20	25	20	25
<u>Kalmia angustifolia</u>															25	20
<u>Gaylussacia baccata</u>												20	25	20	20	20

[illegible]

APPENDIX A

Date: 29 August, 1977 Locality: Region XII, Sites D1, D3 Transect: 4

Species	Distance Along Transect in Meters												Comments
	0	10	20	30	40	50	60	70	80	90	100		
<u>Alnus rugosa</u>	+		+										
<u>Acer rubrum</u>	+												
<u>Chamaedaphne calyculata</u>		50	35	30	10	40	10	15	45	45	25		
<u>Ledum groenlandicum</u>				15	10	+	20	5	10	15	+		
<u>Kalmia angustifolia</u>	+	+	5	+	10	+		20	5	5	30		
<u>Gaylussacia baccata</u>		20	20	30	10	45	25	50	10	25	30		
<u>Andromeda polifolia</u>			+										
<u>Vaccinium oxycoccus</u>					+	5	+	+	+	+	5		
<u>Kalmia polifolia</u>			+		+								
<u>Aronia melanocarpa</u>	40	20	+	+						+			
<u>Nemopanthus mucronata</u>			+	+		+	5	+	+				
<u>Spirea sp.</u>	30												
<u>Typha sp.</u>	+	+										latifolia	

+

Carex oligosperma

+ + + + + + + + + + +

Eriophorum virginicum

APPENDIX B

Plant Species' Height Values Along Transects

For locations of Regions, Sites, and Transects, see Figures 11-13 and the descriptions in section II, A, 1 of the Results. Heights are given in centimeters.

APPENDIX B

Date: 24 July, 1977 Locality: Region I, Sites A1, A2 Transect: 1

Species	Distance Along Transect in Meters															
	0	5	10	15	20	25	30	35	40	45	50	60	70	80	90	100
<u>Chamaedaphne calyculata</u>	25	40	15	20	20	15	15	15	15	15	15	20	15	15	15	20
<u>Ledum groenlandicum</u>									20	30	20	20			30	25
<u>Kalmia angustifolia</u>								30	30							
<u>Gaylussacia batcata</u>															20	20
<u>Andromeda polifolia</u>															20	
<u>Kalmia polifolia</u>									25	20			10			

APPENDIX B

Date: 27 July, 1977 Locality: Region I, Sites A1, A2 Transect: 2

Species	Distance Along Transect in Meters															
	0	5	10	15	20	25	30	35	40	45	50	60	70	80	90	100
<u>Chamaedaphne calyculata</u>	40	40	30	45		35	15	20	15	15	15	15	15	15	15	15
<u>Ledum groenlandicum</u>												20	25	20	20	25
<u>Kalmia angustifolia</u>														25		20
<u>Gaylussacia baccata</u>												20	25	20	20	20

APPENDIX B

Date: 25 August, 1977 Locality: Region I, Sites A1, A2 Transect: 4

Species	Distance Along Transect in Meters														
	0	5	10	15	20	25	30	35	40	45	50	60	70	80	90
<u>Chamaedaphne calyculata</u>	30		45	25	30	15	20	20	15	10	15	15	20	20	20
<u>Ledum groenlandicum</u>								25			35	40		15	15

APPENDIX B

Transect: 2Locality: Region III, Sites B1, B2
Above DamDate: 23 July, 1977

Species	Distance Along Transect in Meters									
	0	5	10	15	20	25	30	35	40	45
<u>Chamaedaphne calyculata</u>	65	60	15	15	15	20	15	15	15	15
<u>Ledum groenlandicum</u>					25	10	15			
<u>Kalmia angustifolia</u>									35	30
<u>Gaylussacia baccata</u>							15		30	30

APPENDIX B

Date: 28 August, 1977 Locality: Region III, Sites B1, B2
Above Dam Transect: 4

[illegible]

APPENDIX B

Date: 28 August, 1977 Locality: Region III, Site B1 Transect: 5
Below Dam

Species	Distance Along Transect in Meters												
	0	5	10	15	20	25	30	35	40	45	50	70	100
<u>Chamaedaphne calyculata</u>		15	15	10	10	10	15	15	10	10	15	20	20
<u>Ledum groenlandicum</u>						25		20		20		20	
<u>Kalmia angustifolia</u>							25				10	30	

APPENDIX B

Date: 24 July, 1977 Locality: Region III, Site B1 Transect: 3

Species	Distance Along Transect in Meters			
	<u>0</u>	<u>10</u>	<u>20</u>	<u>30</u>
<u>Chamaedaphne calyculata</u>	15	15	15	15
<u>Ledum groenlandicum</u>	20			20

APPENDIX B

Transect: 6

Locality: Region III, Site B1

Date: 28 August, 1977

Species	Distance Along Transect in Meters				
	0	10	20	30	40
<u>Chamaedaphne calyculata</u>					
<u>Ledum groenlandicum</u>					
<u>Kalmia angustifolia</u>					
<u>Gaylussacia baccata</u>					
<u>Vaccinium spp.</u>					

APPENDIX B

Date: 20 July, 1977 Locality: Region XII, Sites D1, D3 Transect: 1

Species	Distance Along Transect in Meters														
	0	5	10	15	20	25	30	35	40	50	60	70	80	90	100
<u>Chamaedaphne calyculata</u>		50	60	20	35	25	30	20	30	25	20	20	20	30	15
<u>Ledum groenlandicum</u>					40	30	35	30	30	25			30	25	25
<u>Kalmia angustifolia</u>	110	70	50	35	30	45			20	30		40	45	35	30
<u>Gaylussacia baccata</u>		55		30	40	25	25		20	25	25	20	20	20	15
<u>Andromeda polifolia</u>				10	20			40							20
<u>Aronia melanocarpa</u>	140	60	45	25			45								
<u>Nemopanthus mucronata</u>	120	75		90	40	45		40	35	40	35	35	35	30	30
<u>Vaccinium spp.</u>									90					40	

APPENDIX B

Date: 29 August, 1977 Locality: Region XII, Sites D1, D3 Transect: 3

Species	Distance Along Transect in Meters										
	0	10	20	30	40	50	60	70	80	90	100
<u>Chamaedaphne calyculata</u>	50	25	25	25	20	25	10	20	20	30	30
<u>Ledum groenlandicum</u>				25	35	20	20		30	20	30
<u>Kalmia angustifolia</u>	95	40	30	30	35	25	25	15	30	25	40
<u>Gaylussacia baccata</u>		30	25	35	20	20	20	20	20	25	30
<u>Andromeda polifolia</u>				20							
<u>Aronia melanocarpa</u>	100	30	20							25	
<u>Nemopanthus mucronata</u>	95	25		50	40	35	30	20	45	35	
<u>Vaccinium spp.</u>							40	25		35	

APPENDIX B

Date: 29 August, 1977Locality: Region XII, Sites D1, D3Transect: 4

Species	Distance Along Transect in Meters										
	0	10	20	30	40	50	60	70	80	90	100
<u>Chamaedaphne calyculata</u>		35	20	15	20	25	15	15	20	20	25
<u>Ledum groenlandicum</u>				20	30	25	20	25	20	20	15
<u>Kalmia angustifolia</u>	70	30	35	25	35	25		30	20	25	25
<u>Gaylussacia baccata</u>		35	20	20	20	20	25	20	20	20	20
<u>Andromeda polifolia</u>				15							
<u>Aronia melanocarpa</u>	140	40		20						20	
<u>Nemopanthus mucronata</u>			30	25		30	30	20	30		

APPENDIX B

Date: 27 August, 1977 Locality: Region VIII, Site C1 Transect: 6
Below Dam

Species	Distance Along Transect in Meters														
	10	20	30	40	50	60	70	80	90	100	110	120	130	140	150
<u>Chamaedaphne calyculata</u>	15	55	50	25	30	20	15	25	20	20	25	25	20	20	15
<u>Kalmia angustifolia</u>			30		30				35	35	35	40	25	25	20
<u>Gaylussacia baccata</u>	15		50	30	30	20	25	30	30	30	25	25	25	20	25
<u>Andromeda polifolia</u>						15	10				15	15	15		
<u>Aronia melanocarpa</u>	50	70	50	25		20		30							
<u>Nemopanthus mucronata</u>				85											
<u>Vaccinium spp.</u>			40				15		10						

APPENDIX B

Date: 26 August, 1977 Locality: Region VIII, Site CI Transect: 5

Species	Distance Along Transect in Meters				
	<u>0</u>	<u>10</u>	<u>20</u>	<u>30</u>	<u>40</u>
<u>Chamaedaphne calyculata</u>	10	15	15	20	15
<u>Ledum groenlandicum</u>	20				20
<u>Kalmia angustifolia</u>	25	30	15	20	25
<u>Gaylussacia baccata</u>	20	20	15	25	20
<u>Andromeda polifolia</u>			15		15

APPENDIX B

Date: 30 August, 1977 Locality: Region IV, Sites C1, C2
Above Dam Transect: 4

Species	Distance Along Transect in Meters															
	0	5	10	15	20	25	30	35	40	45	50	60	70	80	90	100
<u>Chamaedaphne calyculata</u>	30	25	30	30	35	35	20	20	10	15	10	10	10	10	15	15
<u>Ledum groenlandicum</u>									20				25	20	25	
<u>Kalmia angustifolia</u>														20	30	

APPENDIX B

Date: 16 July, 1977 Locality: Region IV, Site C1 Transect: 3

Species	Distance Along Transect in Meters			
	<u>0</u>	<u>10</u>	<u>20</u>	<u>30</u>
<u>Chamaedaphne calyculata</u>	15	✓ 15	15	15

APPENDIX B

Transect: 6Locality: Region IV, Site C1Date: 30 August, 1977

Species	Distance Along Transect in Meters				
	<u>0</u>	<u>10</u>	<u>20</u>	<u>30</u>	<u>40</u>
<u>Chamaedaphne calyculata</u>	10	10	15	15	15
<u>Ledum groenlandicum</u>	20	25	20	20	35
<u>Kalmia angustifolia</u>	20	25	15		10

APPENDIX C

Selected % Cover Data Used for Site Description and Characterization

For locations of Regions, Sites, and Transects, see Figures 12-14 and the descriptions in section II, A, 1 of the results. Only species having a cover value of 5% or more are included. Species names are abbreviated as follows:

<u>Chamaedaphne calyculata</u>	-	C. cal
<u>Ledum groenlandicum</u>	-	L. gr
<u>Kalmia angustifolia</u>	-	K. ang
<u>Gaylussacia baccata</u>	-	G. bac
<u>Eriophorum chamissonis</u>	-	E. cham
<u>Eriophorum tenellum</u>	-	E. ten
<u>Carex rostrata</u>	-	C. ros
<u>Carex prairea</u>	-	C. pra
<u>Vaccinium myrtilloides</u>	-	Vac. myr
<u>Vaccinium corymbosum</u>	-	Vac. cor
<u>Carex trisperma</u>	-	C. tri
<u>Eriophorum opacum</u>	-	E. op
<u>Eriophorum virginicum</u>	-	E. vir
<u>Carex oligosperma</u>	-	C. olig
<u>Scirpus acutis</u>	-	S. acu
<u>Vaccinium oxycoccos</u>	-	Vac. oxy
<u>Aronia melanocarpa</u>	-	A. mel
<u>Nemopanthus mucronata</u>	-	N. muc
<u>Typha latifolia</u>	-	T. lat
<u>Typha angustifolia</u>	-	T. ang
<u>Calamagrostis canadensis</u>	-	Cal. can
<u>Alnus rugosa</u>	-	A. rug
<u>Andromeda polifolia</u>	-	A. pol
<u>Viburnum cassinoides</u>	-	Vib. cass
<u>Spiraea sp.</u>	-	Spi. sp.
<u>Eriophorum sp.</u>	-	E. sp.

APPENDIX C

A1 Site Description - Vegetation & Cover

Region	Transect	Meter	C. cal	L. gr	K. ang	G. bac	E. cham	E. ten
I	1	60	70	-	-	-	5	-
		70	70	-	-	-	5	-
		80	70	-	-	-	5	-
		90	45	-	-	5	15	-
		100	55	10	-	-	-	-
I	2	60	25	-	-	-	-	-
		70	10	5	10	-	-	15
		80	-	5	-	-	-	30
		90	30	15	5	5	-	-
		100	35	15	-	-	-	5
I	3	60	5	10	-	-	10	-
		70	5	-	-	20	-	-
		80	5	5	-	-	40	-
		90	-	10	-	-	30	-
		100	20	40	-	-	-	-
I	4	60	-	5	-	-	85	-
		70	40	-	-	-	25	-
		80	45	20	-	-	5	-
		90	45	25	-	-	25	-
		100	40	-	-	-	10	-
X+			30.75	8.25	.75	1.50	13.00	2.50

APPENDIX C

A2 Site Description - Vegetation & Cover

<u>Region</u>	<u>Transect</u>	<u>Meter</u>	<u>C. cal</u>	<u>C. ros</u>	<u>C. pra</u>	<u>Cl. mar</u>	<u>E. ten</u>
I	1	5	45	5	-	-	-
		15	45	-	-	-	-
		25	20	5	-	5	-
		35	25	5	-	-	-
		45	10	5	-	5	-
I	2	5	30	10	25	-	-
		15	-	65	-	-	-
		25	30	5	5	-	-
		35	30	5	-	-	70
		45	5	-	-	-	25
I	3	5	5	50	-	-	-
		15	20	20	-	-	-
		25	15	-	-	-	-
		35	5	-	-	-	-
		45	25	-	-	-	-
I	4	5	-	5	-	-	30
		15	40	10	-	-	-
		25	20	10	-	-	-
		35	50	25	-	-	-
		45	60	-	-	-	-
X+			24.0	11.25	1.5	.5	6.25

APPENDIX C

Bl Site Description - Vegetation & Cover

| Region | Transect | Meter | C. cal | L. gr | G. bac | K. ang | Vac. spp.
(Vac. myr)
(Vac. cor) | C. tri | E. spp.
(E. cham*)
(E. op)
(E. vir) |
|--------|----------|-------|--------|-------|--------|--------|---------------------------------------|--------|--|
| III | 3 | 0 | 45 | 10 | - | - | - | - | - |
| | | 10 | 60 | - | - | - | - | 5 | 5 |
| | | 20 | 50 | - | - | - | - | - | - |
| | | 30 | 35 | - | - | - | - | - | 15 |
| | | 40 | 5 | - | - | - | - | - | 25 |
| III | 6 | 50 | - | - | - | - | - | - | 20 |
| | | 0 | 10 | - | - | - | 10 | - | 60 |
| | | 10 | 30 | - | - | - | 50 | - | - |
| | | 20 | 80 | - | - | - | - | - | - |
| | | 30 | 55 | - | - | - | - | - | 15 |
| III | 1 | 40 | - | - | - | - | - | - | 60 |
| | | 50 | - | - | - | - | - | - | 80 |
| | | 45 | 40 | - | - | 5 | - | - | 5 |
| | | 50 | 40 | - | - | - | - | - | - |
| | | 100 | 70 | 15 | 10 | - | - | - | 5 |
| III | 5 | 45 | 40 | - | - | - | - | - | - |
| | | 50 | 50 | - | - | - | - | - | 10 |
| | | 70 | 35 | 10 | - | 5 | - | - | 15 |
| | | 100 | 30 | - | - | - | - | - | 30 |
| | | 150 | 60 | - | - | - | - | - | - |
| X+ | | | 36.75 | 1.75 | .5 | .5 | 3.0 | .25 | 17.25 |

APPENDIX C

B2 Site Description - Vegetation & Cover

| Region | Transect | Meter | C. cal | L. gr | C. ros | C. sp.
(C. olig) | E. op | E. spp.
(E. op*)
(E. cham, E. ten) |
|--------|----------|-------|--------|-------|--------|---------------------|-------|--|
| III | 2 | 0 | 40 | - | 10 | - | - | - |
| | | 5 | 70 | - | - | - | - | - |
| | | 10 | 60 | - | - | - | - | - |
| | | 15 | 35 | - | - | - | 10 | - |
| | | 20 | 35 | - | - | - | 15 | - |
| | | 25 | 30 | - | - | - | 5 | - |
| | | 30 | 65 | 5 | - | - | 10 | - |
| | | 35 | 55 | - | - | - | 5 | - |
| | | 40 | 70 | - | - | - | 15 | - |
| | | 45 | 55 | - | - | - | - | - |
| | | 0 | 50 | - | - | - | - | - |
| | | 5 | 90 | - | - | - | - | - |
| III | 4 | 10 | 50 | - | - | 15 | - | 25 |
| | | 15 | 80 | - | - | - | - | 5 |
| | | 20 | 60 | - | - | - | - | 10 |
| | | 25 | 60 | 5 | - | - | - | 25 |
| | | 30 | 60 | - | - | - | - | 25 |
| | | 35 | 60 | - | - | - | - | 30 |
| | | 40 | 90 | - | - | - | - | - |
| | | 45 | 50 | - | - | - | - | 30 |
| | | | 58.25 | .5 | .5 | .75 | 3.00 | 7.5 |
| | | X+ | | | | | | |

APPENDIX C

Cl Site Description - Vegetation & Cover

| Region | Transect | Meter | C. cal | L. gr | K. ang | G. bac | Vac. spp.
(Vac. myr)
(Vac. cor) | E. spp.
(E. ten*)
(E. op)
(E. vir) | E. op | E. vir | | |
|--------|----------|-------|--------|-------|--------|--------|---------------------------------------|---|-------|--------|----|---|
| IV | 3 | 0 | 5 | 55 | - | - | - | - | 5 | - | | |
| | | 10 | 5 | 15 | - | 10 | - | - | 10 | - | | |
| | | 20 | 20 | 5 | - | - | - | - | 5 | - | | |
| | | 30 | 10 | 5 | 5 | 5 | - | - | 5 | - | | |
| | | 40 | 10 | 20 | - | 15 | - | - | - | - | - | |
| IV | 6 | 0 | 10 | 25 | 55 | - | - | - | - | - | | |
| | | 10 | 10 | 50 | - | - | - | 15 | - | - | - | |
| | | 20 | 10 | 50 | - | - | - | 10 | - | - | - | |
| | | 30 | 30 | 40 | - | - | - | 5 | - | - | - | |
| | | 40 | 80 | - | - | - | - | - | - | - | - | |
| IV | 2 | 50 | 50 | - | 40 | - | - | - | - | - | - | |
| | | 30 | 5 | 10 | 5 | - | - | 10 | - | - | - | |
| | | 35 | - | 30 | - | - | - | - | - | - | - | |
| | | 40 | 15 | 5 | 5 | - | - | 15 | - | - | - | |
| | | 45 | 5 | 50 | - | - | - | - | - | - | - | |
| IV | 5 | 35 | - | - | 20 | - | 10 | - | - | 60 | - | |
| | | 40 | 30 | 20 | - | - | - | - | - | - | - | |
| | | 45 | - | 60 | 5 | - | - | - | - | - | 10 | - |
| | | 50 | 25 | 15 | 10 | - | - | - | - | - | 20 | - |
| | | 60 | 25 | 75 | - | - | - | - | - | - | - | - |
| X+ | | | 17.25 | 26.5 | 7.25 | 1.5 | .5 | 2.75 | 1.25 | 4.5 | | |

APPENDIX C

C2 Site Description - Vegetation & Cover

| Region | Transect | Meter | C. cal | L. gr | S. acu | S. sp.
(S. acu) | E. vir | E. spp.
(E. vir*)
(E. ten)
(E. op) | C. spp.
(C. olig) |
|--------|----------|-------|--------|-------|--------|--------------------|--------|---|----------------------|
| IV | 1 | 0 | 5 | - | 5 | - | - | - | - |
| | | 5 | 20 | - | - | - | - | - | - |
| | | 10 | 45 | - | - | - | - | 15 | - |
| | | 15 | 30 | - | 30 | - | - | - | - |
| | | 20 | 30 | - | 5 | - | - | - | - |
| | | 25 | 70 | - | 10 | - | - | - | - |
| | | 30 | 95 | - | 5 | - | - | - | - |
| | | 35 | 90 | - | - | - | - | - | - |
| | | 40 | 35 | 20 | 5 | - | - | 5 | - |
| | | 45 | 75 | - | 10 | - | - | - | - |
| IV | 4 | 0 | - | - | - | - | - | - | - |
| | | 5 | - | - | - | - | - | - | 60 |
| | | 10 | 30 | - | - | - | - | - | 20 |
| | | 15 | 50 | - | - | - | - | - | 15 |
| | | 20 | 70 | - | - | - | - | - | - |
| | | 25 | 50 | - | - | 20 | 20 | - | - |
| | | 30 | 70 | - | - | - | - | - | - |
| | | 35 | 70 | - | - | - | 10 | - | - |
| | | 40 | 35 | 5 | - | - | 10 | - | - |
| | | 45 | 70 | - | - | - | 10 | - | - |
| | | | 47.0 | 1.25 | 3.5 | 1.0 | 2.5 | 1.0 | 4.75 |
| X+ | | | | | | | | | |

APPENDIX C

D1 Site Description - Vegetation & Cover

Region	Transect	Meter	C. cal	L. gr	K. ang	G. bac	Vac. oxy	N. muc
VIII	3	10	25	-	15	35	-	-
		30	65	10	5	-	-	-
		50	60	-	5	10	-	-
		70	25	-	5	40	-	-
		90	5	-	30	45	-	-
VIII	5	0	70	-	5	25	-	-
		10	45	-	-	35	-	-
		20	50	-	5	30	-	-
		30	40	-	-	35	-	-
		40	55	5	5	25	-	-
		50	30	-	20	20	-	-
XII	1	100	70	-	-	10	-	5
XII	2	100	35	5	15	35	-	5
XII	3	100	-	-	10	70	-	-
XII	4	100	25	-	30	30	5	-
VIII	1	100	30	-	5	30	-	-
VIII	4	100	30	-	15	15	-	-
VIII	2	90	-	10	-	75	-	-
VIII	6	140	10	-	20	60	-	-
		150	30	-	20	30	-	-
X+			35.0	1.5	10.5	32.5	.25	.5

APPENDIX C

D2 Site Description - Vegetation & Cover

| Region | Transect | Meter | C. cal | K. ang | G. bac | A. mel | N: muc | Vac. spp.
(Vac. myr)
(Vac. cor) | T. spp.
(T. lat*)
(T. ang) | Cal. can |
|--------|----------|-------|--------|--------|--------|--------|--------|---------------------------------------|----------------------------------|----------|
| VIII | 1 | 0 | - | - | - | - | - | - | 60 | - |
| | | 10 | - | - | - | - | - | - | 40 | - |
| | | 20 | - | - | - | - | - | - | 25 | 70 |
| | | 30 | 35 | 5 | - | - | - | 10 | 40 | - |
| | | 40 | 50 | - | - | - | - | 10 | - | - |
| | | 50 | 40 | 5 | - | - | - | 25 | - | - |
| | | 60 | 10 | - | - | - | - | 50 | - | - |
| | | 70 | 5 | - | 45 | - | 50 | - | - | - |
| | | 80 | 30 | - | 50 | - | - | - | - | - |
| | | 90 | 60 | - | 20 | - | - | - | - | - |
| | 4 | 0 | - | - | - | - | - | - | 80 | 10 |
| | | 10 | - | - | - | - | - | - | 15 | 70 |
| | | 20 | - | 20 | - | 20 | - | 30 | - | - |
| | | 30 | 75 | - | - | - | - | - | 5 | - |
| | | 40 | 50 | - | - | - | - | 40 | - | - |
| | | 50 | 10 | 40 | - | 20 | 30 | - | - | - |
| | | 60 | - | - | 20 | - | 40 | - | - | - |
| | | 70 | 5 | - | 25 | 50 | 10 | - | - | - |
| | | 80 | 40 | - | 30 | - | - | - | - | - |
| | | 90 | 30 | 55 | - | - | - | - | - | - |
| | X+ | | 22.0 | 6.25 | 9.5 | 4.5 | 6.5 | 8.25 | 13.25 | 7.5 |

APPENDIX C

D3 Site Description - Vegetation & Cover

Region	Transect	Meter	A. rug	C. cal	L. gr	K. ang	G. bac	A. pol	A. mel	N. muc	Vib. cass	Spi. sp.	E. vir	E. sp.
XII	1	0	15	-	-	-	-	-	40	40	-	-	-	-
		10	-	60	-	5	-	-	10	-	-	-	-	-
		20	-	15	-	25	25	-	-	10	-	-	-	-
		30	-	40	40	-	-	5	-	-	-	-	-	-
		40	-	35	5	20	10	-	-	5	-	-	-	-
XII	2	0	55	-	-	-	-	-	10	10	25	-	-	-
		10	-	70	-	-	-	-	-	5	5	-	-	-
		20	-	15	-	-	55	-	-	-	-	-	-	5
		30	-	70	-	-	5	-	-	-	-	-	-	-
		40	-	25	20	5	20	-	-	-	-	-	-	-
XII	3	0	20	-	-	10	-	-	20	10	-	-	-	-
		10	-	80	-	5	-	-	-	-	-	-	-	-
		20	-	50	-	20	-	-	-	-	-	-	-	-
		30	-	35	5	5	50	-	-	-	-	-	-	-
		40	-	20	15	15	30	-	-	-	-	-	-	-
XII	4	0	-	-	-	-	-	-	40	-	-	30	-	-
		10	-	50	-	-	20	-	20	-	-	-	-	-
		20	-	35	-	5	20	-	-	-	-	-	-	-
		30	-	30	15	-	30	-	-	-	-	-	-	-
		40	-	10	10	10	10	-	-	-	-	-	10	-
X+			4.5	32.0	5.5	6.25	13.75	.25	7.0	4.0	1.5	1.5	.5	.25

APPENDIX D

Gradient Analysis of Values for Environmental
Variables Measured Along Transects

The following table shows the gradient analysis of combined transect data for the following environmental variables: pH; Phosphorus; Potassium; Calcium; Magnesium; and Sodium. The symbol * indicates the rejection of H_0 : random variability at $P \leq .05$. Test statistic is the mean square successive difference test. All nutrient values are in parts per million. Tables also show depth to water in centimeters and the height of Chamaedaphne calyculata.

APPENDIX D

Region I, A1+A2, Combined Data

| Transect
Distance
in Meters | Water
Level
in cm | pH | P | K | Ca | Mg | Na | C. cal
Height
in cm |
|-----------------------------------|-------------------------|-----|------|-----|------|------|------|---------------------------|
| 0 | 1 | 4.6 | .089 | 3.3 | 2.93 | 1.48 | .89 | 32 |
| 5 | 3 | 4.5 | .056 | 3.3 | 2.91 | 1.39 | .83 | 37 |
| 10 | 3 | 4.5 | .060 | 3.0 | 2.16 | 1.07 | .77 | 29 |
| 15 | 5 | 4.4 | .079 | 3.7 | 2.18 | 1.03 | .72 | 28 |
| 20 | 9 | 4.5 | .109 | 4.0 | 2.75 | 1.27 | .79 | 23 |
| 25 | 15 | 4.6 | .168 | 4.9 | 3.43 | 1.49 | .87 | 21 |
| 30 | 19 | 4.5 | .186 | 4.9 | 2.46 | 1.26 | .82 | 19 |
| 35 | 21 | 4.5 | .121 | 3.4 | 2.24 | 1.24 | .70 | 18 |
| 40 | 25 | 4.5 | .153 | 2.5 | 2.38 | 1.36 | .76 | 14 |
| 45 | 24 | 4.4 | .091 | 2.3 | 2.10 | 1.47 | .82 | 15 |
| 50 | 33 | 4.4 | .083 | 1.7 | 2.16 | 1.70 | 1.14 | 15 |
| 60 | 24 | 4.4 | .084 | 2.5 | 2.38 | 1.39 | .94 | 15 |
| 70 | 26 | 4.4 | .109 | 2.3 | 2.08 | 1.41 | .90 | 16 |
| 80 | 26 | 4.4 | .050 | 1.4 | 2.25 | 1.36 | .86 | 16 |
| 90 | 25 | 4.5 | .080 | 1.1 | 1.81 | 1.17 | .77 | 17 |
| 100 | 24 | 4.4 | .064 | 1.5 | 1.90 | 1.33 | .86 | 16 |

C Statistic .427* .432* .825* .450* .348 .316

C 0.05, 16 = .386

APPENDIX D

Region III, B1+B2, Above Dam, Combined Data

| Transect
Distance
in Meters | Water
Level
in cm | pH | P | K | Ca | Mg | Na | C. cal
Height
in cm |
|-----------------------------------|-------------------------|-----|------|-----|------|------|-----|---------------------------|
| 0 | 0 | 5.2 | .050 | 2.7 | 2.38 | 1.10 | .60 | 55 |
| 5 | 3 | 5.2 | .020 | 4.3 | 1.85 | .87 | .63 | 48 |
| 10 | 8 | 5.0 | .090 | 3.6 | 3.55 | 1.29 | .55 | 40 |
| 15 | 18 | 4.9 | .055 | 3.5 | 2.30 | 1.17 | .68 | 13 |
| 20 | 20 | 4.8 | .187 | 6.2 | 2.73 | 1.47 | .73 | 13 |
| 25 | 20 | 4.7 | .048 | 2.2 | 2.43 | 1.41 | .64 | 15 |
| 30 | 25 | 4.6 | .068 | 3.5 | 1.75 | 1.23 | .77 | 13 |
| 35 | 25 | 4.5 | .115 | 2.6 | 1.58 | 1.13 | .81 | 13 |
| 40 | 38 | 4.6 | .098 | 2.1 | 1.35 | .94 | .80 | 18 |
| 45 | 38 | 4.5 | .085 | 2.2 | 1.53 | 1.00 | .80 | 15 |
| 50 | 30 | 4.4 | .120 | 3.0 | 1.70 | 1.02 | .84 | 13 |

C. Statistic .931* .278 .135 .270 .361 .688*

C 0.05, 11 = .452

APPENDIX D

Region III, B1-B2, Below Dam, Combined Data

| Transect
Distance
in Meters | Water
Level
in cm | pH | P | K | Ca | Mg | Na | C. cal
Height
in cm |
|-----------------------------------|-------------------------|-----|------|-----|------|------|------|---------------------------|
| 0 | 8 | 5.2 | .018 | 1.9 | 2.38 | 1.31 | .58 | 55 |
| 5 | 13 | 5.2 | .043 | 3.7 | 2.63 | 1.29 | .70 | 15 |
| 10 | 25 | 4.9 | .060 | 2.8 | 2.08 | 1.39 | .83 | 15 |
| 15 | 18 | 4.8 | .065 | 2.3 | 2.30 | 1.34 | .86 | 10 |
| 20 | 25 | 4.7 | .063 | 2.5 | 1.78 | 1.20 | .96 | 10 |
| 25 | 23 | 4.7 | .133 | 3.5 | 1.50 | 1.05 | .86 | 15 |
| 30 | 23 | 4.8 | .113 | 2.3 | 1.63 | 1.24 | 1.02 | 15 |
| 35 | 28 | 4.8 | .125 | 2.8 | 1.93 | 1.17 | .92 | 15 |
| 40 | 23 | 4.7 | .180 | 2.6 | 1.58 | 1.29 | 1.29 | 13 |
| 45 | 25 | 4.6 | .113 | 2.2 | 1.63 | 1.17 | .99 | 13 |
| 50 | 25 | 4.6 | .195 | 2.2 | 1.90 | 1.17 | .96 | 15 |

C Statistic .824* .642* .284 .569* .275 .477*

C 0.05, 11 = .452

APPENDIX D

Region IV, C1+C2, Above Dam, Combined Data

| Transect
Distance
in Meters | Water
Level
in cm | pH | P | K | Ca | Mg | Na | C. cal
Height
in cm |
|-----------------------------------|-------------------------|-----|------|-----|------|------|------|---------------------------|
| 0 | 0 | 5.6 | .008 | 3.4 | 3.70 | 2.06 | 1.02 | 33 |
| 5 | 0 | 5.3 | .040 | 3.0 | 3.53 | 1.84 | 1.01 | 45 |
| 10 | 3 | 5.4 | .043 | 1.7 | 4.25 | 1.98 | .95 | 45 |
| 15 | 3 | 5.2 | .085 | 3.0 | 4.00 | 1.98 | 1.07 | 33 |
| 20 | 13 | 5.0 | .143 | 5.9 | 3.63 | 2.26 | 1.25 | 48 |
| 25 | 10 | 5.1 | .068 | 4.5 | 4.20 | 2.28 | 1.34 | 33 |
| 30 | 18 | 4.9 | .068 | 4.4 | 4.28 | 1.96 | 1.48 | 20 |
| 35 | 20 | 5.0 | .188 | 3.4 | 2.95 | 2.39 | 1.19 | 15 |
| 40 | 28 | 4.9 | .118 | 4.1 | 3.23 | 2.30 | 1.55 | 15 |
| 45 | 18 | 4.9 | .138 | 3.2 | 3.25 | 1.78 | 1.29 | 18 |
| 50 | 30 | 5.0 | .188 | 3.4 | 2.65 | 2.60 | 1.30 | 10 |
| 60 | 28 | 4.7 | .173 | 3.0 | 2.40 | 2.21 | 1.44 | 18 |
| 70 | 20 | 4.7 | .133 | 4.2 | 3.20 | 2.14 | 1.30 | 10 |
| 80 | 35 | 4.6 | .280 | 3.9 | 3.10 | 2.17 | 1.57 | 10 |
| 90 | 30 | 4.7 | .303 | 4.9 | 2.70 | 2.14 | 1.58 | 28 |

- C Statistic .823* .694* .266 .563* .274 .591*

C 0.05, 15 = .397

APPENDIX D

Region IV, Cl+C2, Below Dam, Combined Data

| Transect
Distance
in Meters | Water
Level
in cm | pH | P | K | Ca | Mg | Na | C. cal
Height
in cm |
|-----------------------------------|-------------------------|-----|------|-----|------|------|------|---------------------------|
| 0 | 15 | 5.2 | .080 | 1.5 | 3.95 | 2.44 | 1.33 | 45 |
| 5 | 10 | 4.9 | .090 | 2.6 | 4.58 | 2.92 | 1.83 | 35 |
| 10 | 20 | 4.8 | .338 | 3.4 | 2.85 | 2.04 | 1.53 | 25 |
| 15 | 18 | 4.8 | .278 | 4.3 | 2.93 | 1.91 | 1.84 | 18 |
| 20 | 20 | 4.7 | .185 | 3.2 | 2.85 | 2.30 | 1.68 | 15 |
| 25 | 28 | 4.6 | .280 | 2.9 | 2.90 | 2.04 | 1.61 | 15 |
| 30 | 28 | 4.7 | .303 | 1.6 | 2.20 | 1.82 | 1.55 | 13 |
| 35 | 20 | 4.6 | .268 | 1.5 | 2.55 | 1.90 | 1.37 | 15 |
| 40 | 30 | 4.5 | .160 | 2.7 | 2.55 | 2.05 | 1.71 | 15 |
| 45 | 33 | 4.6 | .138 | 1.2 | 3.05 | 2.21 | 1.66 | 15 |

C Statistic .756* .306 .438 .472* .226 .303

C 0.05, 10 = .469

APPENDIX D

Region VIII, D1-D2, Above Dam, Combined Data

| Transect
Distance
in Meters | Water
Level
in cm | pH | P | K | Ca | Mg | Na | C. cal
Height
in cm |
|-----------------------------------|-------------------------|-----|-------|-----|------|------|------|---------------------------|
| 0 | 13 | 5.4 | .020 | 2.7 | 5.48 | 4.14 | 2.98 | - |
| 10 | 25 | 5.2 | .070 | 1.6 | 3.63 | 4.14 | 3.07 | 60 |
| 20 | 25 | 5.0 | .260 | 1.1 | 3.08 | 3.92 | 2.71 | - |
| 30 | 60+ | 4.9 | .523 | 1.5 | 4.25 | 5.26 | 3.51 | 63 |
| 40 | 60+ | 5.0 | .633 | 1.0 | 1.65 | 2.06 | 2.45 | 50 |
| 50 | 60+ | 4.9 | .318 | 1.0 | 1.95 | 2.24 | 2.61 | 40 |
| 60 | 60+ | 5.3 | .425 | 1.3 | 2.00 | 3.54 | 5.93 | 45 |
| 70 | 60+ | 4.7 | 1.043 | 2.8 | 2.28 | 1.76 | 1.94 | 25 |
| 80 | 60+ | 4.9 | .643 | 1.8 | 1.88 | 1.74 | 2.32 | 28 |
| 90 | 60+ | 4.8 | .578 | 1.0 | 1.65 | 1.82 | 2.05 | 20 |
| 100 | 60+ | 4.8 | .438 | 1.9 | 1.63 | 1.59 | 1.87 | 23 |

C Statistic .235 .471* .130 .589* .441 .223

C 0.05, 11 = .452

APPENDIX D

Region VIII, D1+D2, Below Dam, Combined Data

| Transect
Distance
in Meters | Water
Level
in cm | pH | P | K | Ca | Mg | Na | C. cal
Height
in cm |
|-----------------------------------|-------------------------|-----|------|-----|------|------|------|---------------------------|
| 0 | 10 | 5.5 | .278 | 2.6 | 2.70 | 4.59 | 4.74 | - |
| 10 | 28 | 5.3 | .168 | 1.5 | 5.60 | 7.34 | 6.63 | 15 |
| 20 | 55 | 5.4 | .563 | 2.5 | 2.50 | 2.07 | 2.07 | 48 |
| 30 | 60 | 5.0 | .560 | 2.2 | 3.10 | 2.83 | 1.88 | 45 |
| 40 | 53 | 5.1 | .458 | 1.7 | 3.08 | 4.54 | 4.40 | 35 |
| 50 | 60+ | 4.9 | .658 | 2.3 | 1.70 | 1.97 | 2.42 | 40 |
| 60 | 60+ | 5.0 | .090 | 3.3 | 2.80 | 4.46 | 4.77 | 15 |
| 70 | 60+ | 4.8 | .460 | 2.7 | 2.98 | 3.35 | 3.30 | 18 |
| 80 | 60+ | 5.0 | .560 | 1.4 | 2.20 | 3.11 | 4.43 | 18 |
| 90 | 60+ | 5.0 | .388 | 3.0 | 3.30 | 5.94 | 6.84 | 18 |

C Statistic .577* .274 .316 .354 .292 .001

C 0.05, 10 = .469

APPENDIX D

Region XII, D1-D2, Combined Data

| Transect
Distance
in Meters | Water
Level
in cm | pH | P | K | Ca | Mg | Na | C. cal
Height
in cm |
|-----------------------------------|-------------------------|-----|------|-----|------|------|------|---------------------------|
| 0 | 19 | 5.3 | .161 | 1.6 | 3.43 | 4.15 | 3.03 | 50 |
| 10 | 30 | 5.1 | .079 | 2.4 | 3.38 | 4.53 | 3.93 | 40 |
| 20 | 35 | 4.9 | .338 | 3.0 | 3.59 | 4.75 | 4.15 | 25 |
| 30 | 45 | 4.8 | .571 | 2.9 | 3.17 | 3.72 | 2.91 | 25 |
| 40 | 45 | 4.8 | .531 | 2.1 | 2.39 | 2.99 | 2.35 | 23 |
| 50 | 47 | 4.9 | .499 | 2.9 | 2.38 | 3.24 | 3.58 | 25 |
| 60 | 58 | 4.8 | .889 | 3.8 | 2.90 | 4.19 | 3.82 | 16 |
| 70 | 51 | 4.9 | .905 | 4.7 | 2.16 | 3.07 | 3.08 | 19 |
| 80 | 53 | 4.8 | .475 | 4.1 | 2.65 | 3.38 | 4.01 | 19 |
| 90 | 60 | 4.8 | .633 | 4.0 | 3.19 | 3.31 | 3.72 | 25 |
| 100 | 60 | 4.8 | .749 | 3.9 | 3.04 | 2.96 | 3.44 | 23 |

C Statistic .725* .608* .743* .471* .437 .047

C 0.05, 11 = .452

APPENDIX E

Selected Environmental Data Used for Site
Description and Characterization

For locations of Regions, Sites, and Transects, see Figures 12-14 and the descriptions in section II, A, 1 of the Results. Values for nutrient variables are given in parts per million. Depth to water (H_2O column) is given in centimeters.

APPENDIX E

A1 Site Description - Environmental Variables

Region	Transect	Meter	pH	P	K	Ca	Mg	Na	H ₂ O
I	1	60	4.2	.045	3.2	2.50	1.35	.90	35
		70	4.3	.200	1.1	1.90	1.28	.82	30
		80	4.3	.035	1.4	1.70	1.13	.87	30
		90	4.4	.145	1.1	1.65	1.05	.73	20
		100	4.3	.085	1.7	1.70	1.20	.74	20
I	2	60	4.2	.075	1.9	2.20	1.44	.87	20
		70	4.2	.115	.8	1.90	1.65	1.00	25
		80	4.2	.065	.6	2.00	1.13	.76	15
		90	4.2	.075	1.7	1.50	1.05	.70	25
		100	4.2	.065	2.0	1.55	1.20	.96	25
I	3	60	4.6	.095	.6	2.40	1.28	.92	20
		70	4.5	.025	1.7	3.20	1.58	.90	25
		80	4.6	.035	1.2	2.70	1.20	.79	30
		90	4.6	.065	.3	2.40	1.28	.75	25
		100	4.5	.060	1.4	2.45	1.13	.75	30
I	4	60	4.5	.120	4.1	2.40	1.50	1.08	20
		70	4.6	.095	5.4	1.30	1.11	.88	25
		80	4.6	.065	2.3	2.60	1.99	1.00	30
		90	4.7	.035	1.3	1.70	1.28	.90	30
		100	4.7	.045	.7	1.90	1.77	1.00	20
X	S.D.
S ²		4.42	.077	1.73	2.08	1.33	.87	25.0
			.19	.043	1.25	.49	.25	.25	
			.0336	.0017	1.4838	.2245	.0610	.0111	

APPENDIX E

A2 Site Description - Environmental Variables

Region	Transect	Meter	pH	P	K	Ca	Mg	Na	H ₂ O
I	1	5	4.2	.175	4.7	3.40	1.58	0.88	10
		15	4.2	.110	3.7	1.90	1.13	0.90	5
		25	4.6	.095	6.4	5.10	1.28	1.05	10
		35	4.3	.175	4.4	2.35	1.20	0.81	25
		45	4.3	.110	1.0	1.65	1.13	0.78	25
I	2	5	4.3	.045	3.1	2.90	1.50	0.90	0
		15	4.2	.120	3.7	2.45	1.05	0.91	0
		25	4.2	.460	4.6	2.70	1.58	0.91	15
		35	4.3	.050	2.2	1.70	1.05	0.68	20
		45	4.1	.130	1.5	2.00	1.44	0.94	15
I	3	5	4.7	.000	2.0	2.65	1.35	0.78	0
		15	4.5	.035	6.3	2.45	1.05	0.55	15
		25	4.6	.030	2.6	2.40	1.35	0.86	20
		35	4.6	.225	3.0	3.20	1.65	0.75	15
		45	4.6	.110	4.9	2.40	1.58	0.77	25
I	4	5	4.7	.005	3.3	2.70	1.13	0.75	0
		15	4.8	.050	1.0	1.90	0.88	0.50	0
		25	4.9	.085	5.8	3.50	1.73	0.67	15
		35	4.8	.035	3.7	1.70	1.05	0.55	25
		45	4.7	.015	1.6	2.35	1.74	0.80	30
X
S.D.
S ²			4.48	.013	3.48	2.57	1.32	.79	13.5
			.06	.010	2.62	.61	.07	.02	
			.2484	.1041	1.6603	.8035	.2630	.1425	

APPENDIX E

B1 Site Description - Environmental Variables

Region	Transect	Meter	pH	P	K	Ca	Mg	Na	H ₂ O
III	3	0	4.0	.025	2.4	1.70	1.19	1.14	25
		10	4.2	.070	1.5	1.65	1.44	2.00	45
		20	4.0	.305	1.3	1.90	1.50	1.20	30
		30	4.1	.140	0.8	1.55	1.58	1.57	45
		40	4.0	.120	0.6	1.55	1.19	1.31	40
III	4	50	4.0	-	-	-	-	-	45
		0	5.0	.175	3.8	1.90	1.58	2.50	50
		10	5.0	.160	2.8	2.30	1.99	2.75	40
		20	5.0	.265	3.5	2.30	1.81	2.50	40
		30	5.0	.195	1.4	1.90	1.43	1.43	30
III	1	40	5.0	.110	1.1	2.40	1.90	1.75	50
		50	5.0	.055	1.2	2.90	1.91	1.82	35
		45	4.4	.095	2.1	1.85	1.28	1.10	25
		50	4.4	.265	2.5	1.90	1.00	0.87	25
		100	4.3	.300	1.8	0.75	1.28	1.56	50
III	5	45	4.8	.130	2.3	1.40	1.05	0.87	25
		50	4.8	.130	1.8	1.90	1.34	1.04	25
		70	4.8	-	-	-	-	-	30
		100	4.8	-	-	-	-	-	30
		150	4.8	.730	3.8	2.30	1.79	2.85	60+
X
S.D.
S ₂			4.57	.192	2.04	1.89	1.49	1.66	37.25
			.4079	.1642	1.1811	.8198	.6140	.8532	
			.16	.026	1.33	.64	.36	.69	

APPENDIX E

B2 Site Description - Environmental Variables

Region	Transect	Meter	pH	P	K	Ca	Mg	Na	H ₂ O
III	2	0	4.9	.060	2.8	2.20	1.00	0.63	0
		5	4.9	.040	2.4	2.40	1.09	0.58	5
		10	4.7	.085	2.5	1.50	0.68	0.50	10
		15	4.6	.090	3.6	2.20	1.20	0.58	20
		20	4.4	.190	6.1	2.60	1.44	0.70	25
		25	4.3	.095	2.6	2.40	1.46	0.65	25
		30	4.2	.065	4.1	1.90	1.28	0.63	30
		35	4.1	.085	1.6	1.50	1.05	0.72	30
		40	4.1	.070	1.7	1.55	1.06	0.82	35
		45	4.1	.100	2.9	1.75	1.00	0.77	35
			5.5	.040	2.5	2.55	1.20	0.57	0
		5	5.4	.000	6.2	1.30	0.65	0.67	0
III	4	10	5.3	.095	4.7	5.60	1.90	0.59	5
		15	5.2	.020	3.3	2.40	1.13	0.77	15
		20	5.1	-	-	-	-	-	15
		25	5.1	.000	1.7	2.45	1.35	0.63	15
		30	5.0	.070	2.8	1.60	1.17	0.90	20
		35	4.9	.145	3.5	1.65	1.20	0.90	20
		40	5.0	.125	2.4	1.15	0.81	0.78	30
		45	4.9	.070	1.4	1.30	1.00	0.82	30
				.200	2.9	1.90	1.13	0.93	
		X	4.79	.082	3.09	2.10	1.14	.707	18.25
		S.D.	.45	.05	1.33	.95	.28	.124	
		S ²	.1923	.0027	1.6943	.8487	.0741	.0147	

APPENDIX E

C1 Site Description - Environmental Variables

Region	Transect	Meter	pH	P	K	Ca	Mg	Na	H ₂ O
IV	3	0	4.3	.845	7.9	4.80	3.57	3.24	35
		10	4.3	.335	3.4	3.50	2.28	1.90	35
		20	4.3	.355	2.7	3.30	2.16	2.12	35
		30	4.3	.565	2.8	2.20	1.52	1.46	35
		40	4.3	.390	5.0	2.50	2.08	2.04	30
IV	6	0	5.1	.105	1.7	2.75	2.90	3.05	40
		10	5.0	.095	1.0	3.00	2.93	2.75	30
		20	5.0	.510	2.7	2.35	2.25	2.35	40
		30	5.6	.050	0.6	1.30	2.37	1.75	35
		40	4.9	.080	1.9	2.85	2.34	2.25	30
IV	2	50	5.1	.130	1.6	2.60	2.42	2.08	35
		30	4.3	.530	2.5	1.70	1.28	1.24	25
		35	4.3	.405	2.0	1.90	1.60	1.24	25
		40	4.2	.265	3.8	2.20	1.68	1.55	30
		45	4.3	.240	1.3	2.65	1.74	1.43	30
IV	5	35	4.9	.130	1.0	3.20	2.19	1.50	15
		40	4.8	.055	1.6	2.90	2.42	1.87	30
		45	4.8	.035	1.1	3.45	2.67	1.88	35
		50	5.1	.040	0.7	4.40	4.42	2.95	35
		60	5.1	.025	0.6	3.35	3.00	2.10	35
X
S.D.
S ²			4.70	.259	2.30	3.35	2.39	2.04	32
			.41	.227	1.75	2.02	.74	.59	
			.1630	.0491	2.9235	3.8822	.5140	.3311	

APPENDIX E

C2 Site Description - Environmental Variables

Region	Transect	Meter	pH	P	K	Ca	Mg	Na	H ₂ O
IV	1	0	5.4	.005	3.0	3.60	1.65	1.13	0
		5	5.0	.065	4.0	3.45	1.74	1.12	0
		10	5.1	.070	2.0	4.30	2.17	1.07	5
		15	4.9	.035	2.1	4.70	2.15	1.20	5
		20	4.8	.140	8.9	4.40	2.77	1.35	10
		25	5.0	.025	6.8	5.40	2.66	1.42	10
		30	4.7	.095	5.1	4.55	1.89	1.59	15
		35	4.8	.145	3.2	3.00	2.52	1.14	20
		40	4.7	.075	4.8	3.60	2.17	1.55	30
		45	4.8	.120	3.7	4.00	1.74	1.36	20
IV	4	0	5.8	.010	3.8	3.80	2.46	0.90	0
		5	5.5	.015	2.0	3.60	1.94	0.90	0
		10	5.7	.015	1.3	4.20	1.79	0.82	0
		15	5.5	.135	3.8	3.30	1.81	0.93	0
		20	5.2	.145	2.9	2.85	1.78	1.14	15
		25	5.1	.110	2.2	3.00	1.90	1.26	10
		30	5.1	.040	3.7	4.00	2.03	1.36	20
		35	5.2	.230	3.6	2.90	2.25	1.24	20
		40	5.0	.160	3.3	2.85	2.42	1.55	25
		45	5.0	.155	2.7	2.50	1.81	1.22	15
	X
S.D.
S ²		5.12	.090	3.65	3.70	2.08	1.21	11.0
			.32	.064	1.76	.75	.34	.22	
			.0973	.0038	2.9385	.5330	.1071	.0477	

APPENDIX E

D1 Site Description - Environmental Variables

Region	Transect	Meter	pH	P	K	Ca	Mg	Na	H ₂ O
VIII	3	10	4.3	.820	6.2	1.75	2.12	2.83	60+
		30	4.3	.870	2.6	1.80	1.50	3.37	60+
		50	4.3	1.680	6.2	2.35	2.43	2.69	60+
		70	4.3	.880	4.4	3.10	2.50	2.34	60+
		90	4.3	.870	4.1	2.35	2.49	2.55	60+
VIII	5	0	4.8	.345	3.7	3.50	3.03	3.48	60+
		10	4.5	.175	2.6	2.30	2.08	2.17	60+
		20	4.8	.655	3.3	2.50	2.77	3.05	60+
		30	5.0	.565	3.4	2.30	2.70	2.52	60+
		40	4.9	.510	2.6	1.80	1.89	2.29	60+
XII	1	50	4.8	.755	2.5	2.30	2.25	2.18	60+
		100	4.6	.740	3.5	1.50	1.14	2.16	60+
		100	4.5	1.120	3.4	3.85	4.97	4.33	60+
		100	5.1	.580	4.7	4.20	3.09	4.56	60+
		100	5.0	.555	3.9	2.60	2.34	2.69	60+
VIII	1	100	4.6	.810	1.7	1.55	1.39	1.65	60+
		100	4.9	.065	2.0	1.70	1.78	2.08	60+
		2	4.9	.740	4.1	3.70	7.30	8.80	60+
		140	5.1	.360	0.9	1.55	1.65	2.03	60+
		150	4.8	.335	1.5	1.25	1.56	1.77	60+

X
S.D.
S_i

4.69	.672	3.37	2.40	2.57	2.98	60+
.29	.355	1.40	1.86	1.38	1.57	
.0779	.1194	1.8563	2.7014	1.8045	2.3493	

APPENDIX E

D2 Site Description - Environmental Variables

Region	Transect	Meter	pH	P	K	Ca	Mg	Na	H ₂ O
VIII	1	0	5.6	.005	4.3	5.15	3.78	2.75	0
		10	5.1	.080	2.5	3.30	3.23	2.64	15
		20	5.0	.200	1.5	3.45	5.15	3.24	50
		30	5.0	.135	1.3	4.15	6.98	4.50	50
		40	4.9	.525	1.1	1.05	1.52	2.30	60+
		50	4.9	.335	0.5	1.50	1.65	1.56	60+
		60	5.2	.335	2.0	1.90	3.98	6.35	60+
		70	4.6	.660	4.8	2.75	1.69	1.72	60+
		80	4.8	.720	2.3	2.10	2.17	2.75	60+
		90	4.7	.740	0.9	1.60	1.58	1.92	60+
VIII	4	0	5.2	.035	1.0	5.80	4.49	3.20	60+
		10	5.2	.060	0.7	3.95	5.05	3.50	60+
		20	5.0	.320	0.7	2.70	2.68	2.17	60+
		30	4.8	.910	1.6	4.35	3.53	2.52	60+
		40	5.1	.740	0.8	2.25	2.59	2.60	60+
		50	4.8	.300	1.4	2.40	2.82	3.66	60+
		60	5.4	.515	0.6	2.10	3.09	5.50	60+
		70	4.8	.425	0.7	1.80	1.82	2.16	60+
		80	5.0	.566	1.2	1.65	1.30	1.88	60+
		90	4.9	.415	1.1	1.70	2.05	2.17	60+
X	S.D.
S ₂		5.00	.401	1.55	2.78	3.06	2.96	51.25
			.24	.268	1.17	1.31	1.50	1.25	
			.0550	.0680	1.2935	1.6363	2.1326	1.4908	

APPENDIX E

D3 Site Description - Environmental Variables

Region	Transsect	Meter	pH	P	K	Ca	Mg	Na	H ₂ O
XII	1	0	5.1	.050	0.8	1.30	1.20	1.48	10
		10	4.8	.010	1.7	4.40	3.28	3.30	20
		20	4.6	.755	4.8	4.85	5.30	3.48	15
		30	4.5	.042	1.5	5.40	5.67	3.11	20
		40	4.5	.020	0.8	3.40	3.53	2.17	25
XII	2	0	5.0	.005	1.4	4.55	3.89	3.00	15
		10	4.7	.080	2.2	2.70	3.53	3.14	40
		20	4.5	.140	2.4	3.90	5.54	4.80	40
		30	4.6	.450	3.0	2.40	2.87	2.67	40
		40	4.6	.220	2.7	2.60	3.18	2.60	30
XII	3	0	5.5	.525	2.7	4.35	5.33	3.39	15
		10	5.2	.060	1.8	3.10	4.34	3.86	25
		20	5.1	.160	2.6	3.50	5.13	3.92	30
		30	5.2	.220	3.2	2.35	1.81	4.28	60+
		40	5.1	.425	1.4	1.80	2.97	1.90	60+
XII	4	0	5.7	.065	1.6	3.50	6.17	4.24	35+
		10	5.5	.165	3.8	3.30	6.98	5.43	35+
		20	5.3	.295	2.3	2.10	3.03	4.40	60+
		30	5.2	1.220	4.2	1.70	2.62	2.96	60+
		40	5.2	1.460	3.4	1.75	2.27	2.74	60+
X	S.D.
S ²		5.00	.318	2.42	3.15	3.93	3.34	34.75
			.37	.404	1.09	1.17	1.55	.99	
			.1315	.1549	1.1323	1.2964	2.2983	.9279	

APPENDIX F

Readers Reference Figure Showing Study Regions
and Study Sites with Brief Physiognomic,
Environmental, and Floristic Descriptions of
Each Study Site.

Sites	A1	B1	C1	D1
Veg. Cover	C. calyculata
E. cnamissonis
L. groenlandicum	C. calyculata
E. chamissonis
Vaccinium spp.	L. laricina
L. groenlandicum
C. calyculata	C. calyculata
G. baccata
K. angustifolia
Physiogn.	Open, flat, sparse	Open, hummocks	Parklike, hummocks	Open, hummocks
Nutrients	Poor	Poor	Moderate	Moderate
Moisture	Very wet	Wet	Wet	Dry
	A2	B2	C2	D2
Veg. Cover	C. calyculata
C. rostrata
E. teneillum	C. calyculata
E. opacum
C. oligosperma	C. calyculata
C. oligosperma
S. acutis	C. calyculata
T. latifolia
N. mucronata
Physiogn.	Open, fen	Open, fen	Open, fen	Marsh
Nutrients	Moderate	Moderate	Moderate to rich	Moderate
Moisture	Very wet	Very wet	Very wet	Moist
				D3
Veg. Cover				C. calyculata
A. melanocarpa
N. mucronata
Physiogn.				Tall shrub
Nutrients				Moderate to rich
Moisture				Wet

END

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FIN