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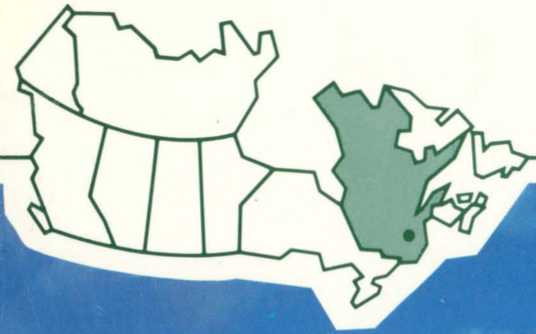
CFS spruce budworm population studies: site descriptions

Jean-Louis Lethiecq and Jacques Régnière



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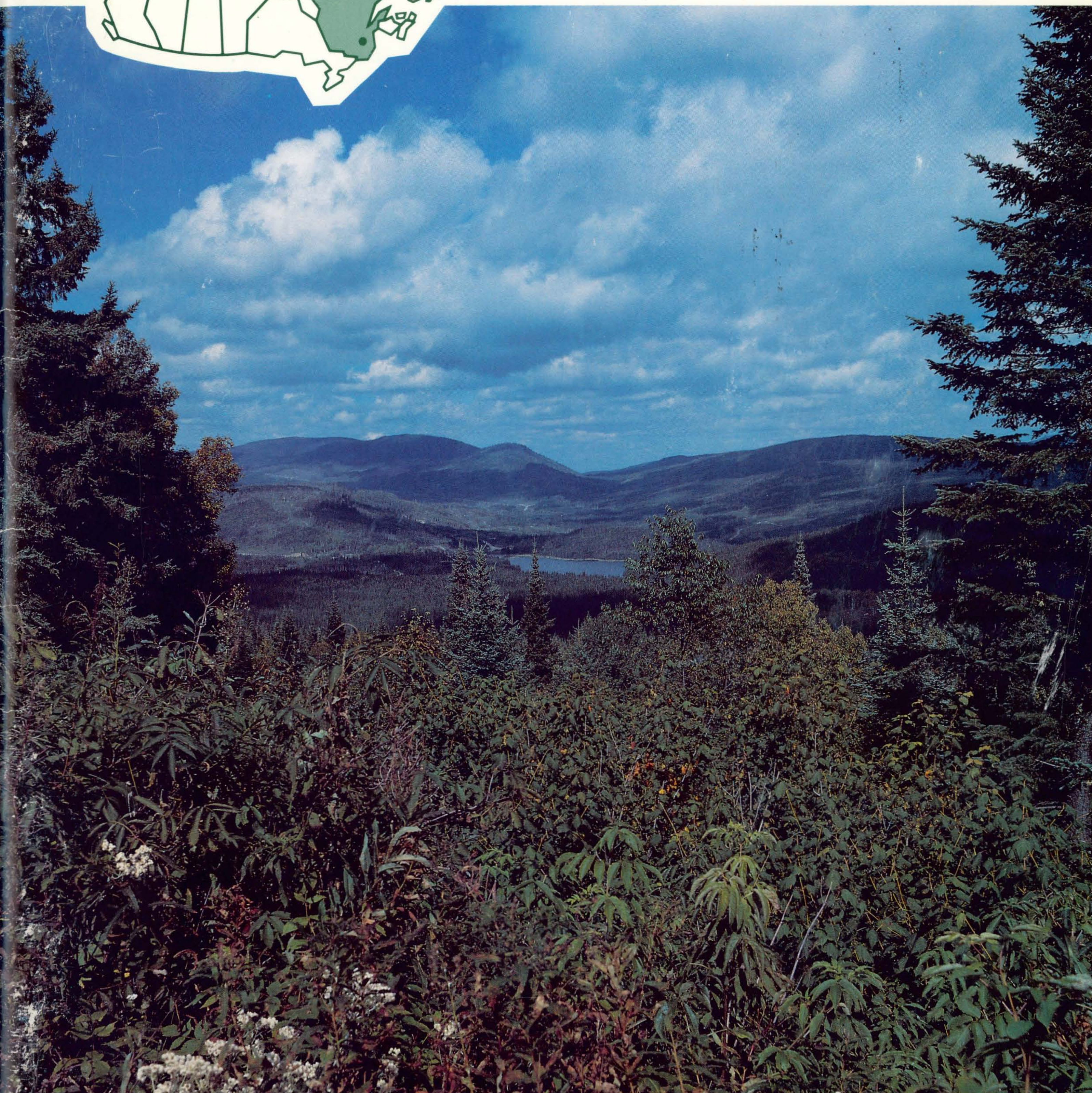

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Couverture: Milieu forestier susceptible à la tordeuse des bourgeons de l'épinette. Réserve faunique des Laurentides (photo: Claude Moffet)

Comparative description of the physical characteristics and vegetation of six sites used by the Canadian Forestry Service in the study of spruce budworm population dynamics

Jean-Louis Lethiecq and Jacques Régnière

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RÉSUMÉ

Ce document décrit l'aspect physique et la végétation de six secteurs de recherche où la dynamique des populations de tordeuses des bourgeons de l'épinette fait l'objet d'étude par le Service canadien des forêts. Les stations représentent un large éventail de conditions. L'un des secteurs, le plus méridional, est situé à l'extrémité nord-est des Appalaches au Québec. On y trouve un climat relativement doux et un peuplement hétérogène de sapins, sain et riche en espèces. Un peuplement de composition similaire se développe dans un climat plus continental et un peu plus frais, près de la rive nord-ouest du lac Supérieur. Le document traite également d'un peuplement d'épinettes blanches situé sur la rive nord-est du même lac. Ce peuplement est exposé à de fréquentes sécheresses causées par un régime de précipitations continental et un sol au drainage rapide. L'un des peuplements, constitué presque entièrement d'une dense population de sapins baumiers, occupe un site à drainage imparfait, exposé au climat maritime du sud du Nouveau-Brunswick. Une autre station a été établie dans la même région, sur un site mieux drainé. Enfin, on trouve une dernière station dans un peuplement de sapins baumiers, dans une région relativement élevée des Laurentides au Québec, sur une pente abrupte, face au nord-est, sous le rude climat qui caractérise ces régions.

ABSTRACT

The biophysic and vegetation are described for six research areas in which spruce budworm population dynamics are being studied by the Canadian Forestry Service. The sites represent a wide array of conditions. One of the most meridional areas is located at the northeastern edge of the Appalachian Mountains, in Quebec. It has a relatively mild climate, and supports a heterogeneous, healthy, balsam stand, rich in species. A structurally similar stand grows in a more continental and somewhat cooler climate near the northwestern shore of Lake Superior. A white spruce stand, growing on the northeastern shore of the lake, is also included. This stand is exposed to frequent drought stress due to a continental precipitation regime and a rapidly-drained soil. One of the research stands, an almost pure, dense population of balsam fir, is established on a imperfectly-drained site exposed to the maritime climate of southern New Brunswick. A second site was established in the same area of that province, on a site with better drainage. Another site was established in a balsam fir stand, relatively high in the Laurentian Mountains, Quebec, on a steep, northeast-facing slope, and is subject to the severe climate typical of such areas.

INTRODUCTION

The spruce budworm, *Choristoneura fumiferana* (Clem.), is a very important insect pest in the coniferous forests of eastern North America. Its epidemic behavior and impact are well recognized and have been much studied (Blais 1965, 1983a; Kettela 1983; Hardy et al. 1983, 1986).

In 1981, the Canadian Forestry Service (CFS) initiated a new research program on the population dynamics of the spruce budworm. Study plots were established in six areas: two in New Brunswick (1981, 1986), two in Ontario (1982, 1983), and two in Quebec (1985). Very intensive studies of the demographics, behavior, and reproduction of the spruce budworm and major natural enemies have been undertaken in this limited number of areas. This work is expected to continue over a sufficiently long period to enable the identification of the factors and mechanisms which are responsible for the gradual decline (and eventual buildup) of spruce budworm populations observed during the course of a cycle (Royama 1984).

The influence of host plants, the physical environment, and their interaction, on the performance of this insect is poorly understood. Bess (1946) and Blais (1952) suspected that the flowering of balsam fir, *Abies balsamea* (L.) Mill., in maturing stands favored the development of outbreaks of the spruce budworm. Blais (1983a) has maintained that the expansion of mature balsam fir forests has caused an increase in the frequency of outbreaks of the insect. Simulation models of spruce budworm population dynamics and management (Clark et al. 1979) were based on this concept, and further specified that survival of the insect increased with stand maturity, a poorly documented hypothesis. Hardy et al. (1983) maintained that the apparent increase in outbreak frequency and severity is directly related to the increasing prevalence of coniferous stands in biogeographical areas which would sustain deciduous vegetation associations were it not for human disturbance. Relatively mild outbreaks seem to appear first in the Northern Hardwood Forest Region of Hardy et al. (1986), followed by much more severe ones in the neighboring Boreal Forest Region. Hardy et al.'s hypothesis (1983) rests on the concept of epicenters, from which epidemics of the insect spread through moth dispersal. However, this apparent spread may be the result of inherent regional differences in population-cycle amplitude and frequency, as first suggested by

Stehr (1968). Such regional differences may well be determined, in part, by bioclimatic characteristics.

The vulnerability of forest stands to damage by spruce budworm during outbreaks has been related to their conifer content, particularly balsam fir (Blais 1983b). However, the factors which determine their susceptibility to the development of spruce budworm outbreaks are poorly understood. Simmons et al. (1975) related stand composition and parasitism, but their work did not clarify the reasons for the correlations found. Clearly, biogeographical and phytosociological aspects need to be considered in the development of a thorough understanding of spruce budworm population dynamics.

Climatic factors have also been involved as driving variables determining the appearance or disappearance of spruce budworm outbreaks. Wellington et al. (1950) and Greenbank (1957) favored a climatic release theory, by which spruce budworm outbreaks would follow several years of warm, dry summers. Royama (1984) could not find evidence to support this idea. More recently, Lucuik (1984) suggested that outbreaks tended to collapse in response to high frequency of rain during the spring emergence period. It seems reasonable to believe that climatic conditions have a strong impact on the seasonal history and interaction of all organisms involved in spruce budworm population dynamics (e.g., Pilon and Blais 1961).

Little attention has been focused on the influence of foliage quality on the performance of the insect. Natural levels of variation in fibre content of host-tree foliage, in response to defoliation or water stress, may have an impact on the survival and fecundity of spruce budworm populations (Bauce 1986). Thus, conditions under which trees are growing may have a direct effect on the performance of the insect.

In this report, we describe and compare some important physical and vegetational characteristics of the stands in which the current spruce budworm population dynamics studies of the Canadian Forestry Service are being carried out. The report is intended first as a source of information for later interpretation of results.

MATERIALS AND METHODS

Each study area was located with respect to the major forest regions of Canada (Rowe 1972). Reference is also made to the work of Hardy et al. (1986), which provides a succinct cartographic presentation of the major regions and vegetation associations of northeastern North America. To avoid confusion with the term association also used at lower levels of perception, and to conform with the nomenclature of other authors, the term domain is used in reference to these broad associations.

At the provincial level, reference was made to the ecoregion, a portion of a territory characterized by a distinct regional climate, as expressed by vegetation (Jurdant et al. 1977). Such cartographic units have been recognized by various organizations, under different names (ecoclimatic, land, or site region), in most provinces. Classification below this level was attempted only where adequate information was available in the literature on a particular region, and when sufficient concordance existed between the study area and the described sub-units.

The normal daily and extreme minimum and maximum as well as annual mean air temperatures, total precipitation, frost-free period, and total degree-days above 0°C for each study area were obtained from the records of the nearest weather station (Canadian Climate Program 1982). Potential solar radiation ($kcal/cm^2$) was calculated for each study area from its slope, exposure (azimuth), latitude, as well as the timing and duration of the growing season (Swift 1976).

The phenological development of spruce budworm populations expected in each study area was determined with the simulation model of Régnière (1982, 1983, 1987). Daily minimum [Min(t)] and maximum [Max(t)] as well as extreme minimum [Xmin(t)] and extreme maximum [Xmax(t)] temperature normals were generated for each day of the year (t) by linear interpolation, assuming that the normal values occurred at mid-month. Minimum [Tmin(t)] and maximum [Tmax(t)] temperature data used as model input were generated by assuming that they were normally distributed, around respective mean values Min(t) and Max(t), with standard deviations:

$$SD_{min}(t) = \frac{Min(t) - Xmin(t)}{3}$$

and

$$SD_{max}(t) = \frac{Xmax(t) - Max(t)}{3}$$

Microclimatic modification of temperature regimes was used for diapausing larvae, as initially suggested by Régnière (1982).

The length of development period and average temperature during development (from 50 percent larval emergence in the spring to 50 percent egg hatch) were calculated for each station, as indices of climatic favorability.

A preliminary interpretation was made of the geomorphology, drainage, and homogeneity of the stands from black and white panchromatic aerial photographs at the 1/15000 scale.

Each study area was rambled through with a soil auger. A representative location was chosen for the establishment of a circular sample plot of 500 m^2 (Figure 1) on the basis of dominance of floristic as well as edaphic elements. Whenever significant discordance between the sample plot and certain sections of the study area were present, a complementary general-observation plot (hereafter, observation plot) was set-up in that or those distinct sections.

To avoid confusion, each sample or observation plot was given an identification label bearing: (1) a number beginning by the last two digits of the current year (e.g., 85); (2) the first letter of a nearby locality; (3) a

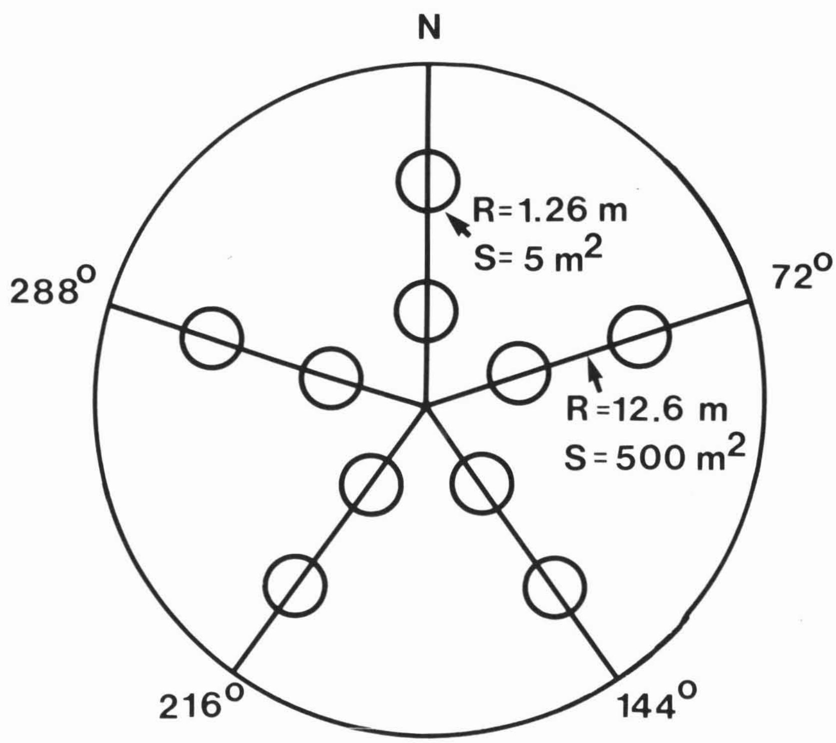

Figure 1. Sample plot, showing the arrangement of circular microplots used to evaluate regeneration.

sequential plot number (e.g., 01); and (4) a letter indicating the type of sampling done in the plot (S for detailed sample plots, O for observation plots).

The criteria retained for the descriptions are essentially the same as those used by Jurdant et al. (1977) and by Jones et al. (1983). Tree diameter was measured at breast height, separately for living and dead trees, by 2 cm diameter-classes with segregation by species. The site index, which is based on the estimated height of dominant trees at a reference age, was used to express the quality or productivity of the sites. The method used was that of Vezina and Linteau (1968). Stem analysis (Curtis 1964) requires removal of prime trees and was not judged necessary. The age of trees was obtained by adding ten years to the age measured at breast height (Zarnovican 1981). For ease of comparison, the site index was determined for balsam fir as it is the only important spruce budworm host species common to all study areas.

Stocking (ratio, in percent, between actual and normal basal area at current age, in m^2/ha) was calculated from normal yield tables (Vezina and Linteau 1968), which were used as a common denominator because they were consistent with local yield tables. The site index, along with other regional ecological factors, was used to estimate a value of the National Capability ratings (McCormack 1967), which is expressed as mean annual increment on a fully stocked hectare at rotation age (in m^3 merchantable volume).

Regeneration was evaluated by counting the number of seedlings (DBH < cm) of each tree species in 10 circular micro-plots of 5 m^2 (Figure 1); the seedlings were divided into two classes with a 30 cm-height cut-point (Jurdant et al. 1972); stems with 1.5 to 9.5 cm in DBH were counted and included in the regeneration. This evaluation was not done when human disturbance was obvious.

A list was compiled of all plant species present in each vegetation stratum of the sample plots, and the abundance-dominance as well as sociability of each species were estimated according to the Braun-Blanquet (1932) scale. Species names used are as in Scoggan (1979) for the vascular plants, Ireland et al. (1980) for mosses, Schuster (1977) for hepatics, and Hale and Culberson (1970) for lichens. Common names used are those of the Canadian Terminology and Documentation Directorate (1974).

A vegetation table was prepared indicating abundance and sociability indices. Species were grouped arbitrarily to facilitate visual comparisons between study areas. Whenever possible, plant communities were compared with published phytosociological vegetation tables corresponding to types occurring in the appropriate regions. In the case of observation plots (except in 85-A-02-0), only the most important differential species were noted.

A soil pit was dug near the center of each sample plot. The soil profile description was done following the Canadian Soil Survey Committee (1978), using the Field Manual for Describing Soils of the Ontario Institute of Pedology (1982). A sample of each horizon of the profile was taken. The following methods, recommended by the Canadian Society of Soil Sciences (1978), were used for the analysis of the reference horizons of each soil profile: Bouyoucos for granulometry, Kjeldahl semi-microanalysis for nitrogen, $CaCl_2$ for pH, Walkley-Black for organic carbon, and pyrophosphate for iron and aluminium. Soils were classified to the subgroup level following the Canadian Commission on Soils Sciences (1978). These analyses and determinations included the evaluation of soil drainage and moisture regime. In the case of observation plots, the soil-profile description was omitted, and only information which could be evaluated in the field was noted.

RESULTS

In the following sections, the study areas are described, in terms of their ecological characteristics, climate, topography, vegetation, and soils. Figure 2 is a map indicating the location of all study areas.

The Armagh study area (85-A-S, 02-0)

This study area (1 ha) is located at the northern limit of the Green Mountains of the Appalachian system, Québec (46°46'N, 70°30'W, altitude 270 m), in the Eastern Townships section (L5) of the Great Lakes-St. Lawrence Forest Region (Rowe 1972). According to Rowe, there is a close similarity with forests of the Acadian Forest Region. This was recognized by Hardy et al. (1986) who made no distinction between these forest regions on their map.

The study area belongs in Thibeault's (1985) Ecoregion 3e (Beauce), which itself lies in the sugar maple-yellow birch domain of the Northern Hardwood zone. The latter corresponds,

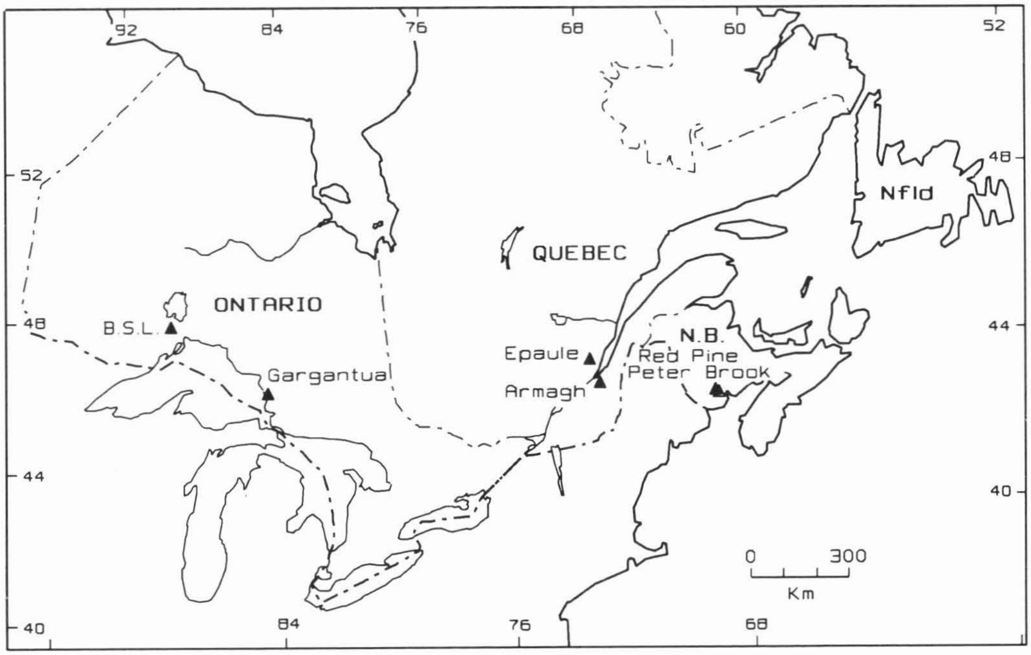

Figure 2. The location of the six study areas currently used by the Canadian Forestry Service for the study of spruce budworm population dynamics.

both in name and boundaries, with Hardy et al.'s (1986) map. Ecoregion 3e is characterized by the high frequency of balsam fir-yellow birch stands on mesoic (neither hydric nor xeric) stations, and balsam fir-white cedar stands on hydric stations.

The climate of the Armagh study area was taken from the Armagh weather station, 3-4 km south (46°43'N, 70°37'W, 312 m altitude). Temperature and precipitation normals are presented in Figure 3a. Mean annual temperature is 3.8°C, with 2575 degree-days above 0°C; the frost-free period is 112 days; total annual precipitation is 1016 mm; and potential solar radiation is 167 kcal/cm².

Simulations indicate that peak spring emergence of spruce budworm larvae should occur around 9 May, and that the development period should last about 73 days at an average temperature of 14.3°C (Figure 4a). Egg hatch should peak around 21 July, a time when mean air temperature is 17.8°C.

The study area is located in a rolling relief controlled by bedrock, covered by glacial till derived from slaty schist, quartzite, and clayey shales. It is in the middle of short 3 to 5 percent slope exposed to the south east. It occupies two different sites (Figure 5a). The sample plot (85-A-01-S) was located in the section that appeared least disturbed. An observation plot

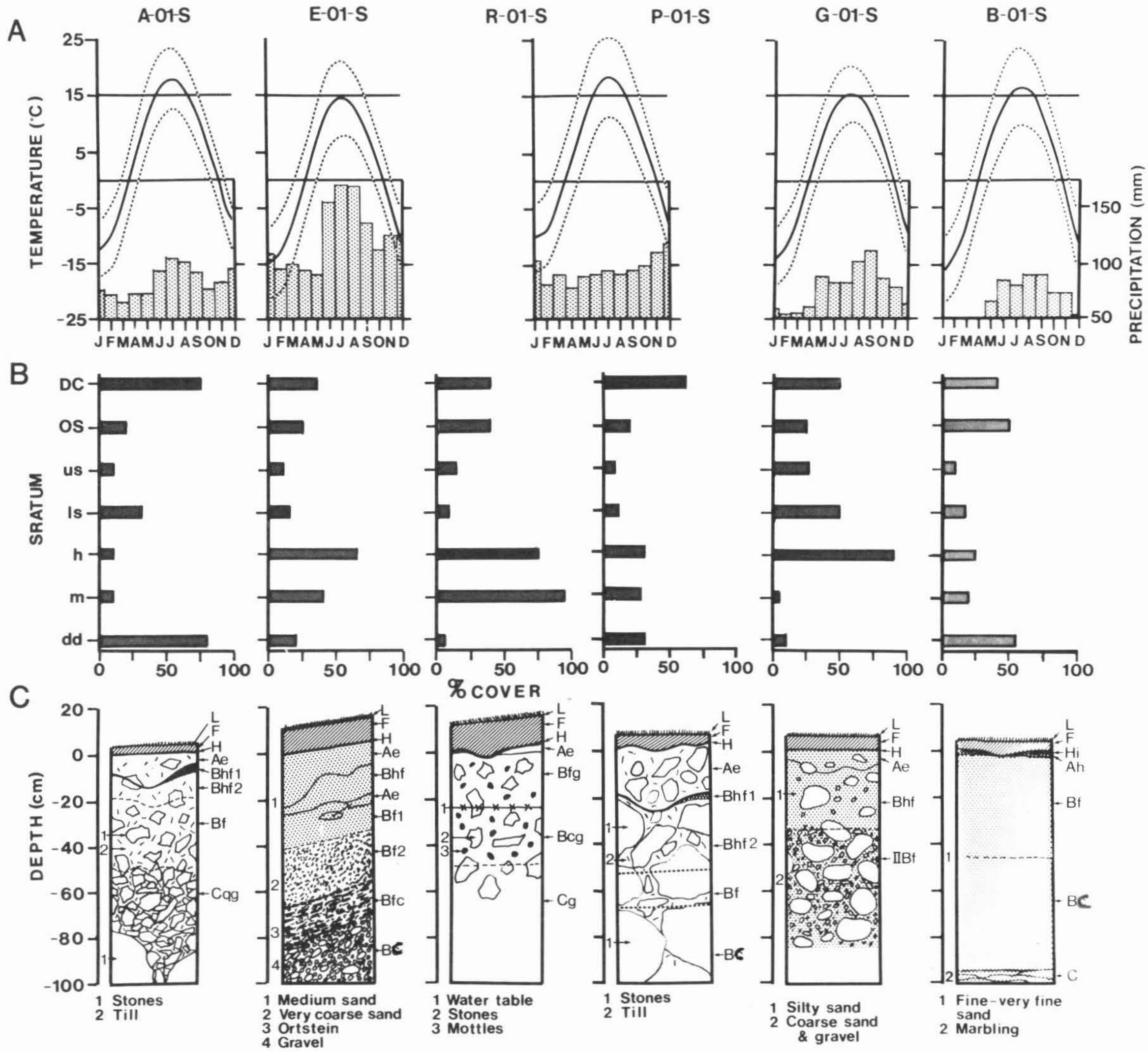

Figure 3. (A) Climatic normals for the study areas. Lines: mean (solid), minimum and maximum (dotted) daily air temperature. Histograms: total monthly precipitation. (B) % cover by vegetation strata in each study area (DC: dominant-codominant and OS: oppressed-suppressed arborescent; us: upper and ls: lower shrubs; h: herbaceous; m: mosses; dd: duff and debris). (C) Soil profile representative of each study area. Depth measured relative to the mineral-soil surface.

(85-A-02-0) was placed in a more open, more humid section which, some 30 years earlier, had been a pastured ecotone bordering an agricultural field. Pieces of old, partly-burried fence wire were found in the section of the sample plot. Thus, part of this area may also have been grazed. The occurrence, in the two sections, of a fair amount of trembling aspen, *Populus tremuloides* Michx., and grey birch, *Betula populifolia* Marsh., both pioneer species after fire

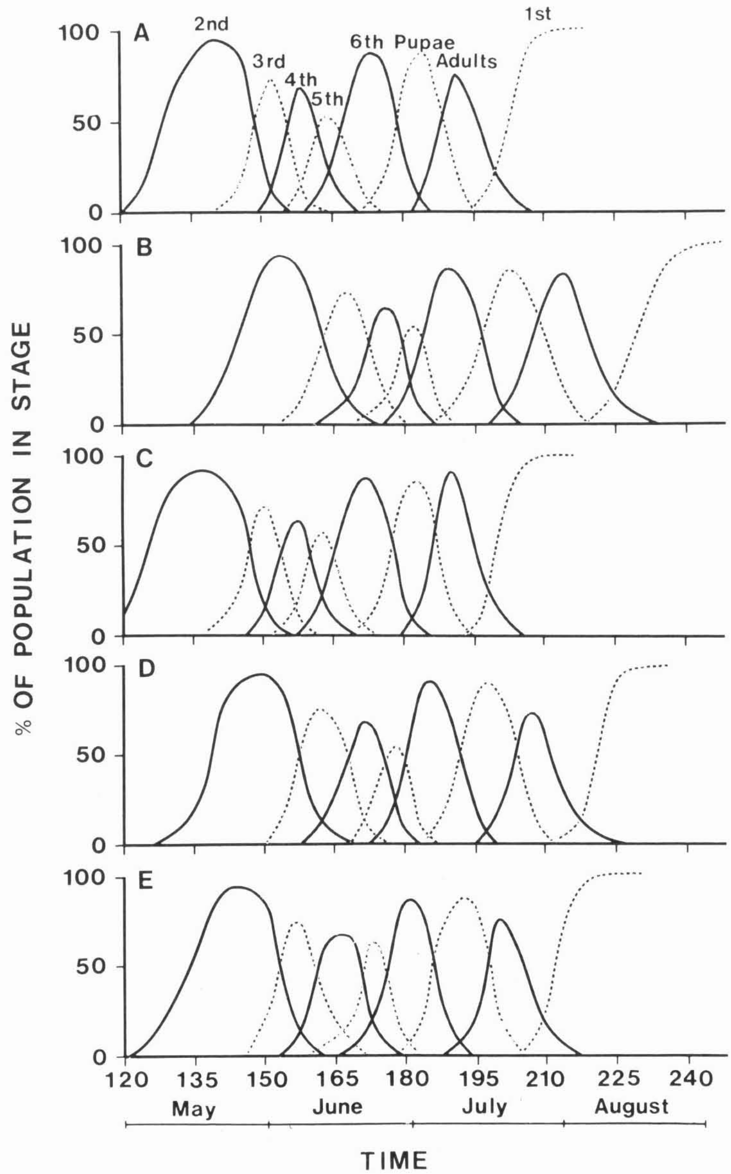

Figure 4. Simulations of spruce budworm seasonal history based on temperature normals for the six study areas. Model of Régnière (1982, 1983, 1987). (A) Armagh. (B) Épaule. (C) Fredericton Red Pine Brook and Peter Brook. (D) Gargantua. (E) Black Sturgeon Lake.

or soil disturbance, is also consistent with recent reforestation of agricultural land. Except for a sugar maple, *Acer saccharum* Marsh., and yellow birch, *Betula alleghaniensis* Britton, (*Betula lutea*) Michx. F., stand on a site with shallower soil, the bordering communities are somewhat similar.

The mean basal area of the Armagh study area is 29.8 m^2/ha, composed of 66 percent balsam fir, 12 percent

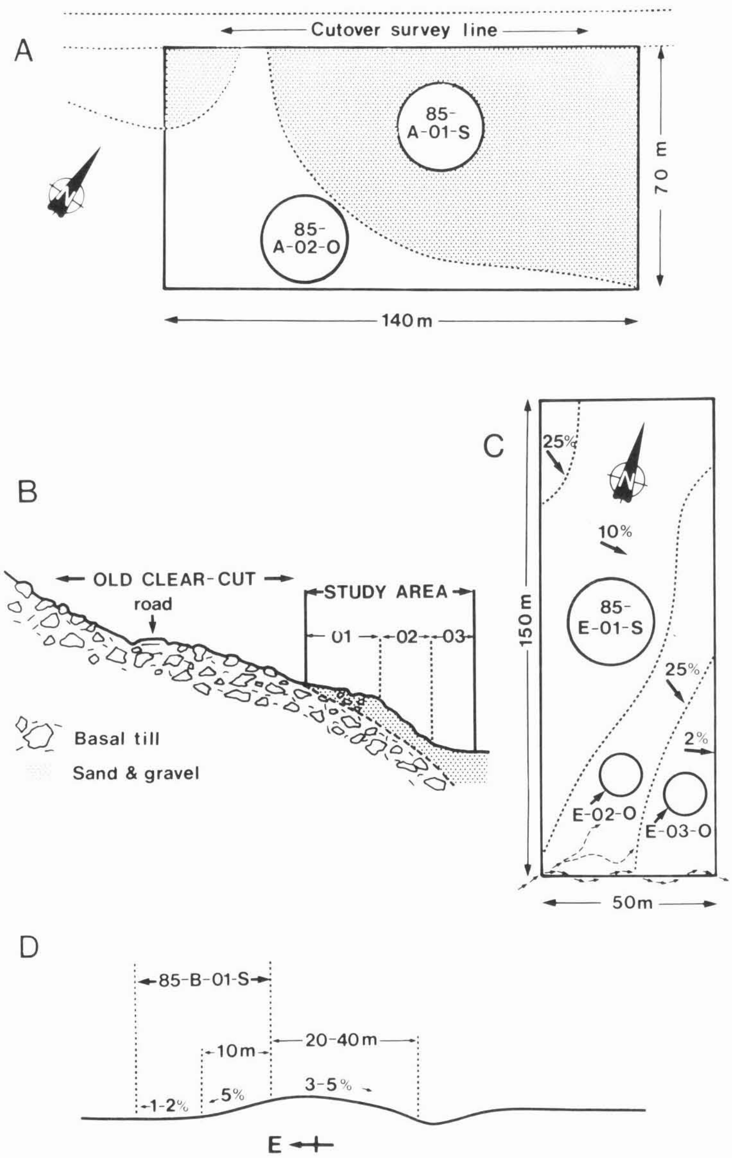

Figure 5. (A) Top view of the Armagh study area, showing position of two stand types, sample and observation plots. (B) Cross-section and (C) Top view of the Épaule study areas. (D) Cross-section of the Black Sturgeon Lake study area, showing the complex 1-5% slopes.

trembling aspen, 11 percent red maple, *Acer rubrum* L., 7 percent red and white spruce, *Picea rubens* Sarg. and *P. glauca* (Moench.) Voss., and other minor species (Figure 6a). The physiognomy of 85-A-01-S is dominated by a young (ca. 42 year-old), closed and fully stocked balsam fir stand. Red maple, trembling aspen, white spruce, grey birch, red spruce, and white birch,

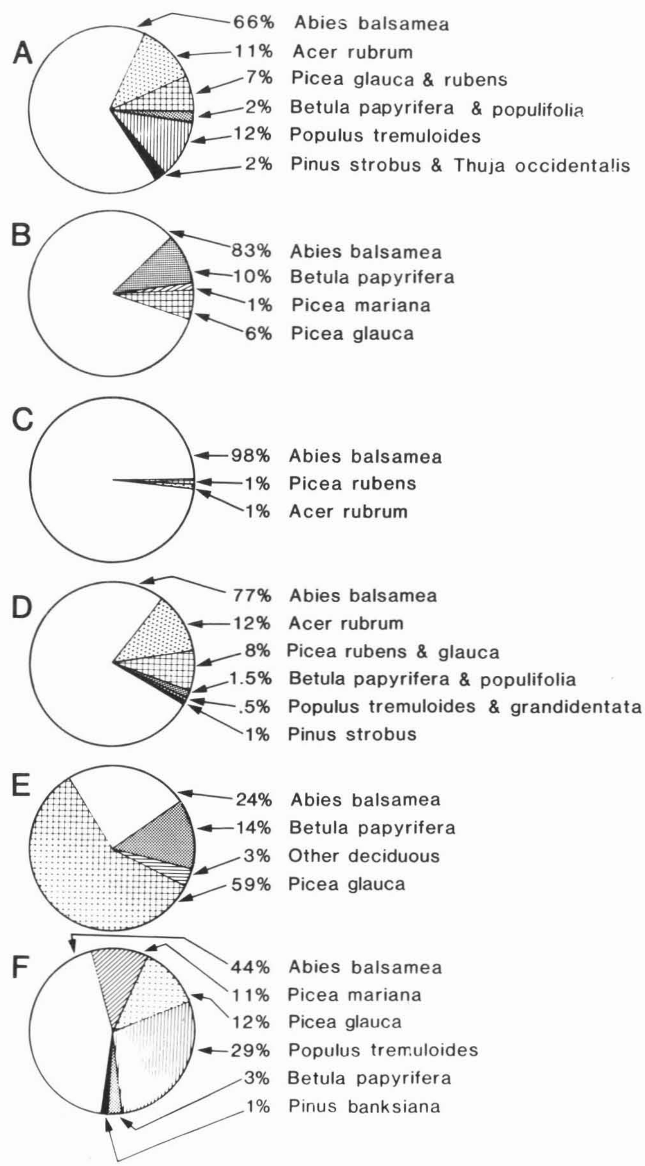

Figure 6. Distribution of stand basal area in the six study areas. (A) Armagh. (B) Épaule. (C) Fredericton Red Pine Brook and (D) Peter Brook. (E) Gargantua. (F) Black Sturgeon Lake.

Betula papyrifera Marsh., are also present in the arborescent stratum. Dominant and codominant balsam fir trees average 14.2 m in height (Figure 7a), and should reach 16 m at age 50, a site index which corresponds to a National Capability rating of 4, with a mean annual increment of 3.6 to 4.9 m³/ ha. The cover of the dominant and codominant as well as suppressed strata is 75 and 20 percent respectively (Figure 3b). The shrub cover is approximately 35 percent and is made-up mostly of balsam fir, red maple, red spruce, white spruce, and witherod, *Viburnum cassinoides* L. The ground cover is composed mainly of

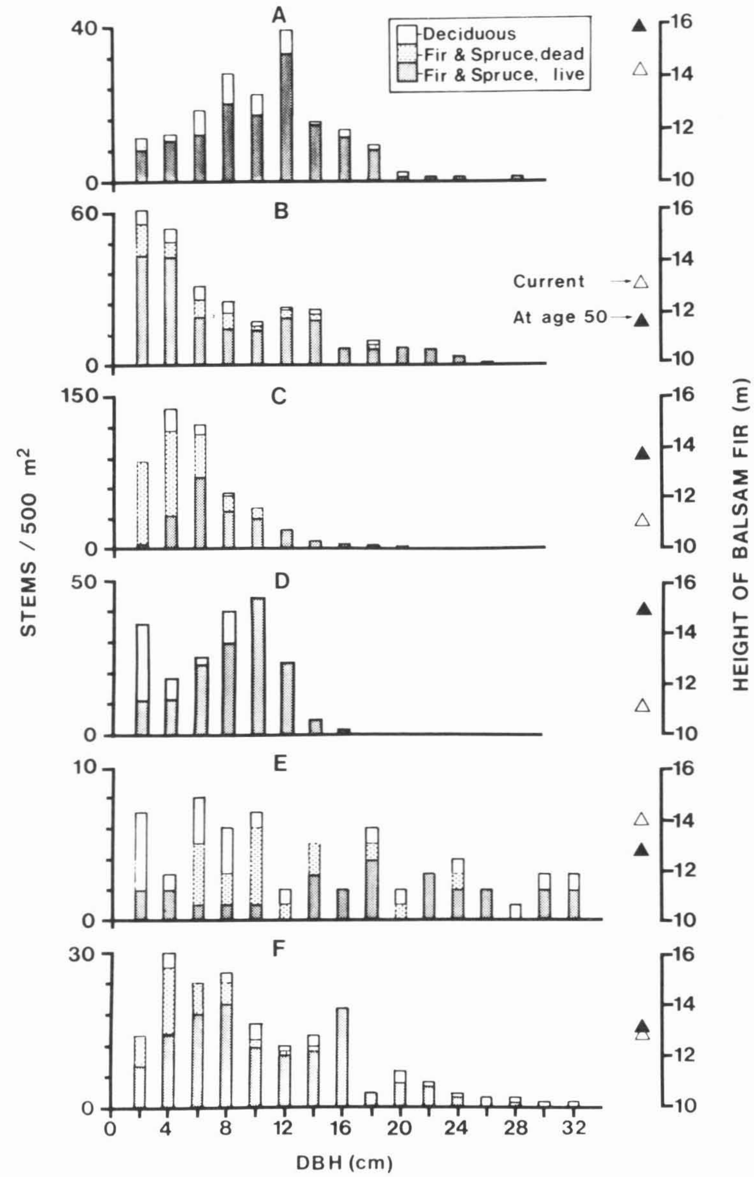

Figure 7. Frequency distribution of tree DBH in the six study areas. Right-hand axis, average height of dominant and codominant trees (Open triangles: current height. Closed triangles: projected height at age 50 years). (A) Armagh. (B) Épaule. (C) Fredericton Red Pine Brook and (D) Peter Brook. (E) Gargantua. (F) Black Sturgeon Lake.

duff and debris (80 percent), with acidiphilic latifoliate vegetation (10 percent) and mosses (10 percent). The distribution of trees, by number of stems, in the various diameter classes, is given in Figure 7a.

Regeneration is dominated by red maple (60 percent) and balsam fir (38 percent), mostly in the seedling (<30 cm-high) category (Table 1). Tree mortality was very low and was not further documented.

Phytosociologically, plot 85-A-01-S (Table 2) is a vegetation-poor, transient stage belonging to the Laurentian balsam fir association (Dicrano-Abietum) of Jurdant and Roberge (1965), described in the southwest part of the same (L5) section (Rowe 1972). This association has many affinities with the balsam fir-red spruce series described by Blouin and Grandtner (1971) on similar soils in the adjacent (L6) forest section.

The soil of the sample plot is an ortic ferro-humic podzol of exceedingly stony, loamy texture (Figure 3c). The results of the physico-chemical analyses of various reference horizons of the soil profile are given in Table 3. The humus is a 2 to 5 cm-thick fibrimor with a pH of 3.1, the pH is 5.2 in the C horizon. The root system is well developed down to 25-30 cm. The soil profile was linked to the well-drained Saint Onesime acid soil series, of the Armagh group (Marcoux 1966). The moisture regime is fresh.

The vegetation of the 85-A-02-0 observation plot differs from that of 85-A-01-S. The stand is younger (ca. 30 year-old), more open (45 percent stocking), with a much denser cover of shrubs, mainly witherod, velvet-leaf blueberry, *Vaccinium myrtilloides* Michx., and species related to abandoned fields such as meadow sweet, *Spiraea alba var. latifolia* (Ait.) Borkh. Balsam fir is less abundant and represents 46 percent of the total basal area of 15.4 m^2/ha, as opposed to 71 percent of 37.2 m^2/ha in the 01-S sample plot. The average height of dominant-codominant trees is 8.9 m. This translates into a site index of 12.5 m at age 50 or a National Capability rating of 5 with mean annual increment of 2.2 to 3.5 m^3/ha. The herbaceous layer is composed of more hydrophilic species such as interrupted fern, *Osmunda claytoniana* L., and sun-loving species of more open habitats such as bracken fern, *Pteridium aquilinum* (L.) Kuhn., (Table 2).

The gleyed podzol of the observation plot is linked to the stony-loam Mont Carmel series (Marcoux 1966), representing the imperfect drainage of the same catena. In places, the drainage of 85-A-02-0 is impaired by the presence of a moderately dense, almost impervious fragipan, creating pools until late spring or after heavy rainfall, in the depressions of the hummocky micro-relief. The moisture regime is moist. The humus of this soil type is usually slightly mineralized with a pH of 5-5.1, which increases to 6.3-7 in the C horizon (Marcoux 1966). Stones and blocks are common on the surface.

The Petit Lac à l'Épaule study area (85-E-01-S, 02-0, 03-0)

This 0.75 ha study area (hereafter, Épaule) is located in the Laurentian Wildlife Reserve, Québec (47°18'N, 71°12'W, 750 m altitude). It is part of the Laurentian Onatchiway (B. 1a) section of the Boreal Forest Region (Rowe 1972). Other authors (Thibeault 1985; Hardy et al. 1986) agree on the geographical limits of this region.

At the provincial level (on a purely cartographic basis), the study area might be placed in the 9c Ecoregion of Thibeault (1985) (high Laurentians of the Malbaie river) and in the related balsam fir-black spruce domain. However, the vegetation and other ecological factors led us to link the area to the 8f ecoregion (median Laurentians of the Jacques-Cartier river), and to the upper limit of the related balsam fir-white birch domain (Jurdant 1968; Thibeault 1985; Hardy et al. 1986).

Climatic data for the Épaule study area were obtained from the Montmorency experimental forest research station (Laval University, Québec), some 5 km away (47°19'N, 71°09'W, 670 m altitude). Temperature and precipitation normals are presented in Figure 3a. Mean annual air temperature is 0.2°C, with 1903 degree-days above 0°C; the frost-free period is a brief 47 days; total annual precipitation is 1420 mm; and potential solar radiation is 125 kcal/cm².

Simulations indicate that peak spring emergence of spruce budworm larvae occurs late, around 25 May. The development period should last about 84 days, 11 days longer than in Armagh (Figure 4b). The insect is exposed to an average air temperature of 12.9°C during its active development period, 1.4°C lower than in the Armagh area. Egg hatch is predicted to peak around 17 August when mean air temperature is only 13.3°C.

The study area lies in a broken-hilly relief system. It is at the foot of a long slope exposed to the east-northeast, composed of basal till and culminating at 1000 m. This slope is sectioned by a gravel road, about 40 m above the plot, and ends in a partly eroded fluvio-glacial deposit at the level of the study area (Figure 5b).

The relatively even-aged stand enclosing the study area is of cut-over origin. No traces of fire were found. The presence of a partly hummocky micro-relief, in conjunction with a displaced Ae horizon in the soil profile (Figure

3c), indicate the existence of relatively frequent and severe windfall disturbance.

The Épaule area occupies most of a small, older patch left within a 25 year-old partial clear-cut. It has a mean basal area of 40 m^2/ha, composed of 83 percent balsam fir, 10 percent white birch, and 7 percent white and black spruce, *Picea mariana* (Mill.) B.S.P., (Figure 6b). Three or four secondary, partly re-grown skidding roads still scar the study area. The neighboring community belongs to the balsam fir-white birch association, with a prevalence of young white birch, and pin cherry, *Prunus pensylvanica* L.F. Linked to varying slope and soil drainage, three different sites were perceived (Figures 5b, c). The 85-E-01-S sample plot was established in the dryer section covering the greater part of the study area. The slope of this section is 10 percent.

The physiognomy of 85-E-01-S is a clear, fully stocked 57-year-old balsam fir, white birch stand with an herbaceous and moss ground cover. The mean height of dominant-codominant balsam fir trees is 13.1 m (Figure 7b). This gives a site index of 12 m at age 50, or a National Capability rating of 5, with mean annual increment of 2.2 to 3.5 m^3/ha. The distribution of tree dbh is shown in Figure 7b. Basal area is 37.4 m^2/ha, 89 percent of which is balsam fir. The dominant-codominant and the oppressed-suppressed strata have a crown cover of 35 and 25 percent, respectively (Figure 3b). The upper and lower shrub strata each have a 10 to 15 percent cover. The most abundant species of that layer are balsam fir and mountain ash, *Sorbus americana* Marsh. The herbaceous layer covers 60 percent and is composed of 40 percent latifoliates, 15 percent ferns (mostly spinulose wood-fern, *Dryopteris austriaca* var. *spinulosa*, and 5 percent brownish sedge, *Carex brunnescens* (Pers.) Poir. The moss layer covers 40 percent of the ground and is dominated by hypnaceous and dricanaceous mosses. The total integrated ground cover is constituted of 80 percent vegetation, 18 percent duff, and 2 percent debris.

The mortality of balsam fir, by stem numbers, was 17.5 percent and was concentrated in the shrub and oppressed-suppressed categories (Figure 7b). The regeneration is highly dominated by balsam fir (Table 1).

The vegetation of the Épaule study area is listed in Table 2. A detailed, integrated vegetation-soil-landform study in this locality by Jurdant (1968) allowed us to further classify the Épaule study area, phytosociologically, in the balsam fir-white birch association of Jurdant (1968). This author set the altitudinal limits for his D Ecoregion (Thibeault's 8f) between 530 and 760 m, and characterized the vegetetation by the constant dominance of balsam fir, with variable proportions of white birch, white spruce, black spruce, and hazelnut. The structure of the vegetation may vary but the undisturbed, mature stands are generally even-aged. The greater part of the Épaule study area was linked to a mossy transient stage of the balsam fir, white birch, *Dryopteris* type.

The soil supporting the above vegetation is a rapidly-drained, sandy, ferro-humic podzol with a consolidated iron layer (Ortstein) in the lower Bf horizon (Figure 3c). The surface material is deposited in layers varying in texture from medium sand to very coarse sand or gravel (Table 3). The pH ranges from 3.5 to 4.32. The root system is developed down to the middle of the Bf1 horizon of the soil profile. The surface organic horizon is a 10 cm-thick fibrimor with a pH of 3.2. The moisture regime is dry.

Two other distinct sections were detected in the Épaule study area. Observation plots of 100 m^2 were used in both cases, because of the small size of each section (Figure 5c). The portion represented by the 85-E-02-0 observation plot occupies a well to moderately well drained transition zone on a steeper slope (25 percent) between the upper, dryer site represented by the 85-E-01-S sample plot and the lower section of the study area. A small stream running along the southern edge of the study area forms several underground ramifications which skim some 25-30 cm below the surface (Figure 5c). Elsewere, the water table is much deeper, and moderate seepage exists throughout the section, in which the moisture regime is fresh.

The vegetation of 85-E-02-0 incorporates elements of both the upper and the lower parts of the study area but is distinguished by the abundance of hypnaceous mosses. The better drainage, coupled to the presence of seepage, has allowed balsam fir to grow quite well in this section: mean height of dominant and codominant trees is 15.2 m, for a site index of 14 m at age 50. This places it at the upper limit of a National Capability rating of 5, with mean annual increment near 3.5 m^3/ha. The basal area of this observation plot totalled 54.9 m^2/ha, and was made up of 76 percent balsam fir, 13 percent white birch, and 11 percent white spruce.

Stocking was 140 percent mainly because of large dbh's (the number of stems was normal). According to Jurdant (1968), such rapidly and well drained sites are quite stable and, after clear cutting, regenerate quickly into balsam fir stands.

The 85-E-03-0 observation plot (Figure 5c) is a clear to open, fully stocked balsam fir stand growing on a poorly drained soil covered by a carpet of mosses, mostly *Sphagnum* spp., intermixed with sedge colonies (mostly three-seeded sedge, *Carex trisperma* Dewey. Speckled alder, *Alnus rugosa* (Du Roi) Spreng., dominates the shrub layer. The 35.5 m^2 basal area is composed of 75 percent balsam fir, 15 percent white birch, and 10 percent white spruce. Black spruce occurs sporadically in this section.

The moisture regime of 85-E-03-0 is very moist to wet. Small springs emerge here and there causing surface runoff in the spring or after heavy rain. This waterlog condition, along with the generally poor drainage, has restrained the growth of balsam fir, as reflected by a mean height of only 10.7 m for dominant and codominant trees. This represents a site index of only 9-10 m at age 50, corresponding to the limit between National Capability ratings 5 and 6, with a maximum mean annual increment of 2.1 to 2.2 m^3/ha.

This section of the Épaule study area was linked to the balsam fir-white birch-Carex (*Betulo-Abietum caricetosum*) BA.c type of Jurdant (1968). Logging in stands of this type may lead to the development of a transition alder-balsam fir type which may take a very long time to evolve back into the balsam fir-white birch-Carex type (Jurdant 1968).

The Red Pine Brook study area (85-R-01-S)

This study area (1 ha) is situated in the Acadia Forest Experiment Station, New Brunswick (46°0'N, 66°16'W, 60 m altitude), in the Eastern Lowlands section (A.3) of the Acadian Hardwood Forest Region (Rowe 1972). Because similar major vegetation associations are found as far west as Lake Superior, Hardy et al. (1986) merged most of Rowe's Acadian and Great Lakes-St. Lawrence Forest Regions into their Northern Hardwoods Forest Region. The study area lies in the sugar maple-red spruce domain of the latter region. In New Brunswick, the boundaries of this domain correspond to Loucks' (1962) Maritime Lowlands

Ecoregion, which he characterized by the distinctive association of red spruce, black spruce, balsam fir, sugar and red maple hemlock, *Tsuga canadensis* (L.) Carr., and white pine, *Pinus strobus* (L.), growing in a gentle relief of generally poor drainage. Red maple and grey birch predominate after fire. Witherod and rhodora, *Rhododendron canadense* (L.) Torr., are common shrubs in areas of repeated cutting and burning disturbances. Mountain maple, *Acer spicatum* Lam., and spinulose shield-fern, *Dryopteris austriaca* (O.F. Muell.) Fiori., are not as abundant as in the more humid ecoregions.

The climate for the study area was compiled from the Acadian Forest Experiment Station, 8 km to the west (45°59'N, 66°22'W, 61 m altitude). Temperature and precipitation normals are given in Figure 3a. Average annual air temperature is 4.5°C, with 2692 degree-days above 0°C; there are 91 frost-free days; total annual precipitation is 1143 mm; and potential solar radiation is 158 kcal/cm².

As indicated by simulations, 50 percent of larval emergence from diapause should be complete by 5 May (Figure 4c). Development should require about 75 days, and should occur at an average air temperature of 13.9°C. Peak egg hatch is predicted to occur around 19 July when mean air temperature is about 18.3°C.

The gentle relief is controlled by horizontally-bedded sandstones and shales with occasional conglomerates and limestones. Loucks (1962) subdivided the Maritime Lowlands Ecoregion into 12 districts based on the pattern of relief, drainage, and type of bedrock. The Red Pine Brook study area is located at the southern border of his Bantalor District, which consists mainly of flat, slightly elevated, undissected land, with a prevalance of black spruce or bogs in the wetter sites, and mixed softwood forests on the moist sites. Grey birch, red maple, and white birch predominate locally after fire. The bedrocks are flat sandstones and mudstones smeared-over by a heavy till allowing little internal drainage.

The Red Pine Brook study area is situated at the foot of a medium-length, 4 percent slope exposed to the southeast, draining into a small brook at its south-east limit. It occupies half of a young (ca. 35 year-old), closed, 9 to 15 m-high stand, which contrasts sharply from surrounding vegetation as a result of its cut-over origins. Neighboring plant communities are: red spruce to the northwest; trembling aspen, white birch, and scattered white pine to the northeast; young trembling aspen and balsam fir to the southeast; and a grass-sedge prairie to the southwest.

The 60 to 80 percent crown-cover of the arborescent strata of the 85-R-01-S sample plot is greatly dominated by balsam fir, which occupies 98 percent of the total 21.6 m^2/ha basal area (Figure 6c). Stocking was only 60 percent, due to high mortality. The average height of dominant and codominant trees of this species is 11.1 m (Figure 7c), a site index of 14 m at age 50. This places the stand at the lower limit of a National Capability rating of 4, representing a mean annual increment of 3.6 to 4.0 m^3/ha. Red maple and red spruce occupy only 1 percent of basal area each, and are confined to the lower levels. Scattered white birch and trembling aspen occur throughout the study area. The upper shrub stratum covers 15 percent of the sample plot (Figure 3b) and is composed primarily of speckled alder and balsam fir, with scattered red spruce and mountain ash. The presence of mountain holly, *Nemopanthus mucronatus* (L.) Trel., was also noted. The lower shrub stratum covers only 5 percent, and is made-up of several species, including lambkill, *Kalmia angustifolia* L., and red raspberry, *Rubus idaeus* L. The herbaceous plants cover 75 percent of the area, with 25 percent ferns, mostly interrupted fern, 45 percent latifoliates, and 5 percent graminoids. Girgensohn sphagnum, *Sphagnum girgensohnii* Russ., covers more than 25 percent of the 85 percent moss layer cover. About 85 percent of the ground is covered by vegetation, 10 percent by duff and debris, and 5 percent by blocks.

Insect defoliation of balsam fir was very high, and 55 percent of the 423 boles of this species in 85-R-01-S were dead, mostly in the smaller (<12 cm) dbh-classes (Figure 7c). About 4 percent of this mortality could be attributed to porcupine, *Erithizon dorsatum* L., damage, and very little directly to suppression. Mortality of red spruce was also high (four of the seven red spruce trees in the sample plot were dead). In terms of regeneration (Table 1), red maple seedlings (<30 cm-high) were 3 times more abundant than balsam fir. The >30 cm-high, <2 cm-DBH regeneration was practically nonexistant in the sample plot, and red spruce regeneration was limited to the 2-9 cm-dbh category.

The vegetation of the 85-R-01-S sample plot (Table 2) is differentiated by the relative abundance of hygrophilic species such as speckled alder, interrupted fern, and Girgensohn sphagnum. Long (1952) classified the vegetation of the Acadia Forest Experiment Station. Because of the destruction of original types and the absence of climax vegetation, he based his classification on the three most evolved and stable tree associations, which he subdivided into four types based on the apparent moisture requirements of the vegetation (i.e., dry, fresh, moist, and wet sites). The 85-R-01-S sample plot is a transitional type of Long's red spruce-balsam fir association, linked by its vegetation and productivity to his moist site. Long (1952) stated that, in the region studied, the succession of the balsam fir stands should proceed towards red spruce stands.

The soil of the sample plot is an imperfectly-drained, gleyed humo-ferric podzol, of stony clay loam texture (Figure 3c). The water table was at 22 cm below the mineral surface and the soil moisture regime is very moist. The pH of the Bf horizon is 3.4 (Table 3). The humus is a 8 to 12 cm-thick fibrimor with a pH of 3.4.

The Peter Brook study area (87-P-01-S, 02-0, 03-0, 04-0)

This 1.5 ha study area is located only 10.5 km from the Red Pine Brook study area (46°0'N, 66°24'W, 107 m altitude), and shares its broad ecological context and climate.

The Peter Brook plot lies in the lower portion of a long and gentle (2-4%) slope exposed to the southeast. A secondary road crosses this slope diagonally above the study area, and a network of access roads dissects the plot and occupies 10 percent of the area (Figure 8). Erosion around a dry creek bed running through the study area, created steeper (10-15 percent), short slopes exposed to the southwest and northeast.

The young (30 year-old) balsam fir stand occupying this plot is closed, and most likely originated from a cut made in a red maple stand similar to that occupying most of the remaining hillside (α in Figure 8). In that original stand, mature red maple represents 60 percent of the 37 m^2/ha basal area, with 20 percent white birch and 20 percent dense, young understory of balsam fir and white

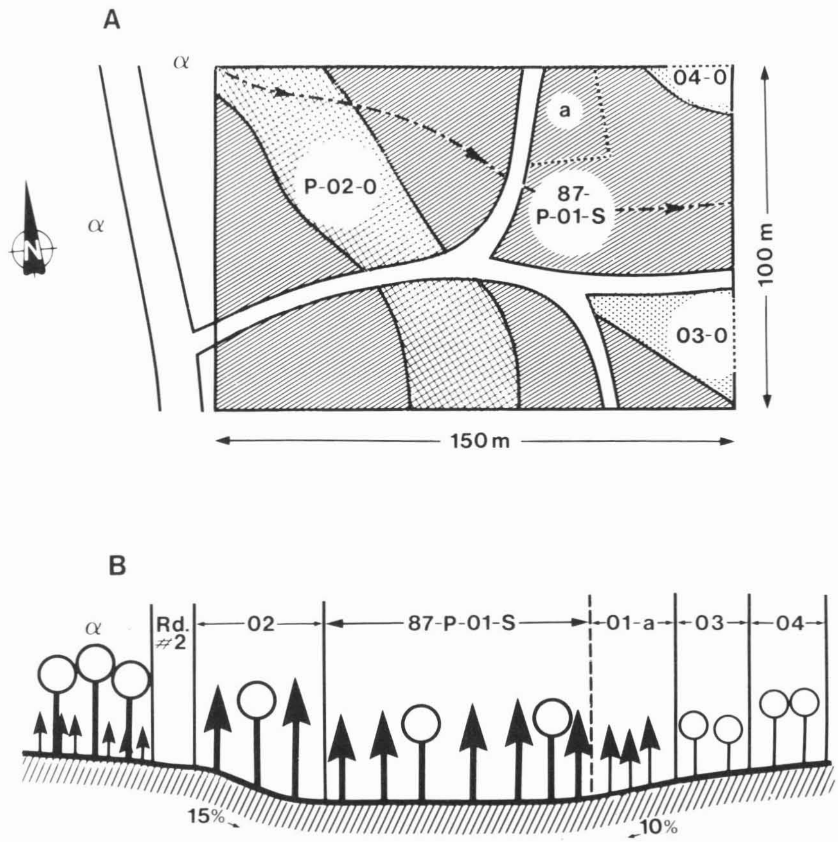

Figure 8. (A) Top view and (B) cross section of the Fredericton Peter Brook study area.

spruce. Ground cover is mostly duff, due to closure of the lower canopy. With the exception of white spruce and Jack pine, *Pinus banksiana* Lamb., plantations, the area has been thinned at the lower understory level, prohibiting an evaluation of regeneration.

The study area is heterogeneous and has a mean basal area of 28 m²/ha, composed of 77 percent balsam fir, 12 percent red maple, and traces of several other hardwood species (Figure 6d). Based on stand composition, age, microrelief, and density, we have subdivided the Peter Brook study area into four units (Figure 8).

The 01-S unit occupies the major part of the study area, in which most spruce budworm sampling is carried-out. Due to the extensive sectioning created by the road network, several samples were combined to the 01-S sample-plot data. Except for a small subsection (a in Figure 8), the 01-S unit has a mean density of 31 m²/ha, composed of 86 percent balsam fir, 6 percent red maple, and small amounts of grey birch and white pine. Traces of sugar maple and white birch are also present.

This part of the stand has a 90 percent stocking. The crown-cover of the dominant and codominant arborescent stratum varies between 50 and 75 percent (Figure 3b) with an average height of 10.9 m (a site index of 15 m at age 50). The small sub-section (Figure 8: a) occupies a 10 percent slope and is much denser, with a basal area of 39 m^2/ha and 110 percent stocking. White spruce and red maple are more abundant (10 and 8 percent of basal area, respectively). Scattered white pine are also present. Dominant and codominant trees are shorter (9 m), for a site index of less than 14 m at age 50. Because of more closed cover, lower vegetation is scarcer in these patches. The oppressed-suppressed stratum covers 20 percent, and is also dominated by balsam fir, with some red maple. The upper shrub stratum covers 10 percent, and is made-up mostly of red maple. The lower shrub layer varies from 5 to 15 percent, possibly due to uneven thinning, and is composed of red maple, whiterod, balsam fir, and blueberry. Bunchberry, *Cornus canadensis* L., and clubmoss, *Lycopodium* L., are the most abundant in the herbaceous layer, which covers 30 percent of the area. The moss cover is dominated by *Dicranum* spp. and varies from 5 to 50 percent.

The 02-0 unit (Figure 8) is more open, with a 27.5 m^2/ha basal area and 80 percent stocking. Although no marked difference was noted in the soil profile, the abundance of ferns (particularly *Dennstaedia punctilobula* (Michx.) Moore) indicates a slightly moister site (Long 1952). The dominant, codominant trees reach 12 m, a site index of 16 m at age 50. Balsam fir accounts for 63 percent of the basal area, red maple (29 percent), and red spruce (8 percent) make up the rest.

The 03-0 unit (Figure 8) is a younger, 25 year-old, stand regenerated from a cutover strip, in which balsam fir occupies only 29 percent of the 32 m^2/ha basal area. Other dominant species are red maple (57 percent), red spruce, and trembling aspen (7 percent each). A few scattered veteran trees are still present. Like elsewhere in the area, the shrub layer is underdeveloped. The vegetation is dominated by bunchberry and clubmoss.

The 04-0 unit, which barely enters the study area (Figure 8) is dominated by white birch, which accounts for 68 percent of the 25 m^2/ha basal area. Balsam fir and red maple occupy 16 percent each. The more open physiognomy of this strip has favored bracken fern. Otherwise, the vegetation is similar to the rest of the study area.

The Peter Brook area has a National Capability rating of 4 (3.6 to 4.9 m^3/ha), varying from the lower limit in subsection 01-S(a) to the upper limit in the 02-0 unit. The better growth in the latter section is probably due to higher moisture and nutrient availability caused by a steeper slope. Overcrowding may have caused the poor growth in subsection 01-S(a).

The study area is linked to Long's Red maple association. The varying composition is the result of silvicultural interventions. Most of the Peter Brook area was found to be related to Long's fresh red maple type, with some elements of his moist maple type in the 02-0 unit.

The soil of the study area is a well drained ferro-humic podzol of sandy loam texture, becoming exceedingly stony and compact in the lower horizon, in which root establishment is scarce (Figure 3c).

The Gargantua study area (85-G-01-S)

This study area (2 ha) is located in Lake Superior Provincial Park, Ontario (47°35'N, 84°49'W, 305 m altitude), 10 km from the north shore of Lake Superior. it is in the Algoma section (L.10) of the Great Lakes-St. Lawrence Forest Region (Rowe 1972). This region corresponds to the Northern Hardwoods Forest Region of Hardy et al. (1986), and the study area lies in their sugar maple-yellow birch domain.

At the provincial level, the Gargantua area is in the Humid Eastern Ontario (4e) Lake Tamagami ecoregion (Hills 1959). On the basis of variations in relief and minor vegetation differences, Hills (1959) subdivided this region into 5 districts. The district of concern here is the Michipicoten district, which is characterized by a deeply incised upland of gentle slopes with steep-walled, narrow valleys. The most common species are white spruce, red pine, *Pinus resinosa* Ait., and white pine on the shallow uplands, and white spruce in the cooler valleys. White and red pine occur on slopes, along with scattered yellow birch and sugar maple.

Acidic medium and coarse sands of granitic origin are dominant, with fine sand and silt loams occurring occasionally in the valleys. In general, the surface materials are water- or ice-laid deposits. Drainage is often excessive, with good drainage occurring where the water table is held up by bedrock or other impervious materials.

Climatic data were compiled from the Wawa weather station, 40 km north of the study area (48°00'N, 84°48'W, 297 m altitude). Temperature and precipitation normals are shown in Figure 3a. Mean annual air temperature is 2.0°C, with 2274 degree-days above 0°C; there are 100 frost-free days; total precipitation is 946 mm; and potential solar radiation is 149.0 kcal/cm².

Simulated emergence of spruce budworm larvae from diapause peaks around 19 May (Figure 4d). Development in Gargantua should require about 82 days and should occur at an average air temperature of 13.6°C, only 0.7°C higher than in the Épaule area. Peak egg hatch should occur around 9 August, when mean air temperature is 15.3°C.

The Gargantua study area occupies a relatively small fluvio-glacial outwash valley of almost flat relief (< 2% slope) with a slight northwest exposure. The surrounding hills in which it is nested average 100 m in vertical drop above the valley floor. The study area is positioned at the intersection of the Trans-Canada Highway and the Gargantua Harbour road, which form its eastern and southern boundaries. A small river flows on the northwest side. The surrounding vegetation is fairly homogeneous.

Except for scattered veteran white spruce, the relatively even-aged stand is of partial cut-over origin. No traces of fire or other major disturbance were observed. More or less recent, partial cuts have created small clearings that are invaded by hazelnut and mountain maple. The stand has a 24 m²/ha basal area, composed of 59 percent white spruce, 24 percent balsam fir, 14 percent white birch, and 3 percent other deciduous species (Figure 6e).

The physiognomy of the 85-G-01-S sample plot is a clear 60 year-old white spruce, white birch, balsam fir stand, with latifoliate and fern herbaceous ground cover. Stocking is only 60 percent. The arborescent stratum covers approximately 65 percent of the area (Figure 3b). Dominant and codominant balsam fir trees average 14.0 m in height (Figure 7e). This is a site index of 13 m at age 50, a National Capability rating of 5 with mean annual increment in the 2.2 to 3.5 m³/ha range. The upper and lower shrubs cover about 25 to 30 percent each and are dominated by hazelnut, mountain ash, and pin cherry, with clumps of red raspberry and mountain maple in more open areas. The 90 percent cover of the herbaceous layer is dominated by common wood-sorrel, *Oxalis montana* Raf., and spinulose woodfern, *Dryopteris austriaca* var. *spinulosa* (O.F. Muell.) Fiori. The moss layer, mostly broom moss, *Dicranum scoparium*, covers less than 5 percent. About 10 percent of the sample plot was covered by duff and debris.

Based on the number of stems, mortality reached 53 percent in balsam fir, mostly in the > 10 cm DBH-classes, and 28 percent in white spruce, mostly in the < 10 cm DBH regeneration classes (Figure 7e). The regeneration was very low for all species, with a dominance of balsam fir (Table 1).

The vegetation of 85-G-01-S is listed in Table 2. However, further classification is not possible at this time. Indeed, no phytosociological or ecological studies at the type or phase level were found in literature for this part of Ontario.

The soil of the study area is a rapidly-drained ortic ferro-humic podzol (Figure 3c). Particle size increases from a loam above 35 cm-depth, gradually to coarse sand and gravel at 70 cm. Some less stony (sandy) pockets were found on the river-side of the study area. The moisture regime is dry. The pH ranged between 4 and 4.3. The humus is a 5 to 10 cm-thick fibrimor with a pH of 3.3.

The Black Sturgeon Lake study area (85-B-01-S)

This long-standing study area (10.4 ha) is located 45 km from the northwestern shore of Lake Superior, Ontario (49°18'N, 88°52'W, 260 m altitude) in the Superior (B9) Boreal Forest Region of Rowe (1972). Spruce budworm populations in this study area have been sampled since the mid-1960s. It lies in the balsam fir-white birch domain (Hardy et al. 1986).

At the ecoregion level, the study area is in the Humid Western Ontario, Lake Nipigon (3w) ecoregion (Hills 1959). This author characterized the region by the common regional occurrence of white spruce, balsam fir, trembling aspen, and white birh on well-drained sites, with white and red pine locally common on the uplands.

The study area lies in the Black Sturgeon District (Hills 1959), which is characterized by flat-topped basaltic ridges with deeper deposits of granitic and clay-forming sand, silt, and limy clay in the depressions. The vegetation surrounding the study area is boreal mixedwood, composed of a white spruce, balsam fir, white birch, and trembling aspen. This species mix is relatively stable and covers great expanses in valleys and on lake shores (Rowe 1972). High proportions of trembling aspen and white birch are usually indicative of fire disturbance.

Climatic records used were from the Cameron Falls weather station, 42 km to the southeast of the study area (49°08'N, 88°21'W, 229 m altitude), at the southern tip of Lake Nipigon. Temperature and precipitation normals are illustrated in Figure 3a. Mean annual air temperature is 1.7°C, with 2320 degree-days above 0°C; frost-free days total 101; total annual precipitation is 793 mm; and potential solar radiation is 129.0 kcal/cm².

Simulations of spruce buworm phenology under a normal temperature regime suggest that peak spring emergence occurs around 14 May (Figure 4e). Development should be about 77 days, with air temperature during that period averaging 13.6°C. Egg hatch should peak around 30 July, at a time when mean air temperature is 16.5 C.

The Black Sturgeon Lake study area occupies a large, undulating to flat relief on a deep, lacustrin-deltaic deposit left behind by the late Algonquin glacial lake. The micro relief of the study area is flat to hummocky, with complex 10 to 40 m-long 1 to 5 percent slopes (Figure 5d). The 85-B-01-S sample plot has a slight overall southeast aspect.

The stand of the study area originated from a salvage cut-over after a spruce budworm outbreak in a reconstitution stand, itself originating from fire, as indicated by traces found in the soil profile. It has a basal area of 42 m²/ha, composed of 44 percent fir, 29 percent trembling aspen, 12 percent each of white and black spruce, and other minor species (Figure 6f). The distribution of balsam fir in the study area is uneven.

The physiognomy of 85-B-01-S is a somewhat closed 42 year-old balsam fir, trembling aspen and white spruce stand, with normal stem density and 110 percent stocking. The basal area in that part of the stand is 40.4 m²/ha, with 60 percent balsam fir. The dominant-codominant and oppressed-suppressed strata of the stand has 35 and 50 percent cover, respectively (Figure 3b). There was about 25 percent cover by understory shrubs, 20-25 percent by latifoliate herbaceous vegetation, a 20 percent moss layer, and 50 to 60 percent of the ground is covered by duff and debris. Dominant and codominant balsam fir trees average 12.8 m in height

(Figure 7f). This represents a site index of 13 m at age 50, a National Capability rating of 5, with mean annual increment in the range of 2.2 to 3.5 m^3/ha.

Relatively recent balsam fir mortality amounted to 20 percent of stems of this species (Figure 7f), close to that observed in trembling aspen. Thus, mortality could not be linked to spruce budworm damage. The regeneration was found almost exclusively in the < 30 cm height-class, balsam fir representing 92 percent of the seedlings (Table 1).

The vegetation recorded in the various strata of 85-B-01-S is listed in Table 2. The upper shrub stratum is dominated by speckled alder, an unusual species for the type of vegetation and soil drainage of the area. This species normaly colonizes poorly to very poorly drained soils (usually with seepage), although it is also apparently found on drier sites in adjacent 3e ecoregion (Jones et al. 1983). Among other shrub species, hazelnut, balsam fir, and black spruce were also important. Bush honey suckle, *Diervilla lonicera* Mill., hazelnut, and speckled alder were the most common species of the lower shrub stratum. Of the 22 species noted in this stratum, three were transgressive of the sugar maple-yellow birch domain: hazelnut, fly honeysuckle, *Lonicera canadensis* Bartr., and choke cherry, *Prunus virginiana* L.. The herbaceous layer is composed of the usual balsam fir-white birch association differentials and companion species, with the exception of twisted-stalk, *Streptopus roseus* Michx., and poisonberry, *Actea rubra* (Ait.) Willd., two transgressive species of the sugar maple-yellow birch domain, and a peculiar species: palmate-leaved coltsfoot, *Petasites palmatus* (Ait.) Gray., which is usually found in lowwoods, clayey soils, and sub-alpine regions. Jones et al. (1983) also found this species in sites somewhat similar to the study area. Schreber's moss, *Pleurozium schreberi* (Brid.) Mitt., makes-up most of the 20 percent moss-cover.

Although no detailed ecological studies at the type level were found for this region, some similarities were found with the mixedwood, herb-rich Operational Group 7 described in the adjacent clay belt (3e) ecoregion by Jones et al. (1983).

The soil of the sample plot is a silty sand, well drained, ortic humo-ferric podzol (Figure 3c). The pH ranged from 4.7 in the Bf horizon to 6.1 in the C horizon (Table 3). The humus is a transition between a fibrimor and a raw moder, less than 5 cm thick, with a pH of 4.6. Traces of fire were found in the soil profile. Root systems were present down to the bottom of the soil profile (1 m). The moisture regime was fresh.

DISCUSSION AND CONCLUSION

Basic information on the physical and vegetational characteristics of the sample plots representing the study areas is summarized in Table 4. The research sites are aligned along a narrow band spanning 17°40' longitudinally, and only 3°18' latitudinally, between Fredericton and Black Sturgeon (Figure 2). The small range in latitudes is partly compensated for by a wide range in altitudes: the Fredericton and Épaule areas are 60 and 750 m above sea-level, respectively. Other study areas are between 110 and 305 m.

The climate of the Armagh area is warm, with a long frost-free period (112 days) and a moderate amount of precipitation falling mostly during the summer months. Because of its southerly latitude and significant southeast exposure, potential solar radiation in the Armagh site is the highest among the study areas (167 kcal/m²/year).

The Épaule area is particularly cold and rainy. Mean annual temperature is just above 0°C, the frost-free period is only 40 percent and precipitation 140 percent of those in Armagh. Potential solar radiation is very low (75 percent of that in Armagh), because of the pronounced east-northeast slope.

The Fredericton sites are the warmest, although the frost-free period is only 80 percent of that in Armagh. Daily maximum temperature extremes in summer are likely to be more frequent and pronounced there than in the other areas. Precipitation is abundant and peaks in the winter months. Potential solar radiation is also high because of the southerly latitude.

In the Gargantua and Black Sturgeon areas, mean annual temperature is 2.0 to 2.8°C lower than in Armagh or Fredericton. The frost-free period is similar to that in Fredericton. Total precipitation is relatively low and is most abundant in the summer months, during which it is comparable to that in Armagh or Fredericton. Potential solar radiation is low in Black Sturgeon, because of its northerly latitude.

Although the effects of weather factors on the population dynamics of the spruce budworm are poorly understood, it is widely recognized that the phenology and activity levels of most organisms involved are determined, in part, by weather variables. It is reasonable to believe that the duration of the development period determines the length of exposure of the insect to various mortality factors. In this respect, populations living in the Épaule and Gargantua areas are somewhat at a disadvantage. However, this difference in development period is only 10 to 12 days. Differences in average air temperature during active development are also relatively minor, considering the range of climatic conditions represented. This is in part the result of the non-linear relationship between temperature and the post-diapause, pre-emergence development rates of second-instar larvae, which ensures that emergence occurs only once sufficiently warm temperatures are firmly established.

Few insects may normally be killed by extreme weather conditions, but the frequency and severity of such events probably varies greatly over the range of the species. Insects in the Épaule area are most likely to experience untimely frosts. The relatively low air temperature during egg hatch in this locality emphasizes the harsh climatic conditions and high probability of frost-kill prevailing during this particularly fragile part of the insect's life cycle. Spruce budworm living in the Fredericton and Black Sturgeon sites may encounter very hot temperatures more frequently than those in the other areas.

Climatic conditons also affect the phenology, growth rate, and vigor of host trees. This, in turn, may determine the vulnerability of stands to spruce budworm damage, and perhaps also the performance of populations of the herbivore. Blais (1985) reported that the mortality rate of balsam fir growing in stands above 700 m was much lower than in stands below this altitude, after a spruce budworm outbreak.

Soil moisture regimes range from dry in part of the Épaule and the Gargantua areas, to moist in the Fredericton Red Pine Brook site. Because of the abundant summer rainfall in Épaule, water stress is not likely to occur frequently. This is not the case for the Gargantua study area, where rainfall is much less abundant, and where the gravelly, coarse soil texture leads to rapid drainage. The frequency of water stress may help explain the high mortality of balsam fir

(53 percent) in Gargantua, despite relatively mild spruce budworm defoliation. Waterlog conditions occur frequently in the lower section of the Épaule area, and occasionnally in part of the Armagh area as well as throughout the Fredericton Red Pine Brook site, where the water table is only 30 cm below the mineral-soil surface. Water stress is known to affect the fiber content of conifer needles, and this, in turn, can have an effect on the performance of spruce budworm populations (Bauce 1986).

The six study areas represent a range of stand conditions and vegetation structure. Of the 135 species listed in Table 2, only 9 are common to all areas. The Armagh area has the most diversified vegetation, because of varying soil conditions and because of the agricultural origin of part of the stand. The Jaccard coefficient of similarity (Gérardin 1980) between the vegetation lists of the 85-A-01-S and 85-A-02-0 plots is only 35, comparable to the value of 36 calculated between 85-A-01-S and the remote, and very different 85-G-01-S in the Gargantua study area. A combined list of 65 plant species were recorded in the Armagh study area. A coefficient of similarity of 40 was calculated between this combined species list and the vegetation of the Fredericton Red Pine Brook study area. The arborescent strata of the Armagh stand are more homogeneous and cover most of the available surface area. Balsam fir is abundant, healthy, and fast-growing. Only mild spruce budworm defoliation and very little balsam fir mortality were recorded. Regeneration is abundant, and is composed mostly of balsam fir and red maple seedlings. There is a fairly, abundant layer of shrubs, which have a 35 percent ground cover. The soils is relatively fertile but stoniness, fragipan, and excess water are factors limiting growth in localized areas.

The Épaule study area is also heterogeneous, but more from topographical and drainage points-of-view than relative to its vegetation. Only 37 plant species were recorded in the area. The vegetation is most similar to that of the Gargantua area (Jaccard coefficient of similarity = 36). The stand is greatly dominated by balsam fir. Deciduous species are also present in the dominant-codominant stratum, which has less than 50 percent ground cover. Balsam fir is slow-growing, but is relatively healthy (only 17 percent mortality, despite relatively heavy spruce budworm defoliation). Regeneration is also dominated by balsam fir, with 10 percent white birch. The upper and lower shrub strata cover 10 to 15 percent of the ground, respectively.

The vegetation of the Fredericton Red Pine Brook area comprises 58 plant species, and shares the largest number of these with the Armagh site (Jaccard coefficients of similarity = 40 with the combined species list of the latter area). The dense arborescent strata are greatly dominated by small-diameter balsam fir, which represents 98 percent of the relatively low live basal area of the stand. Stocking, and ground crown cover are low because of mortality due, for the most part, to spruce budworm defoliation. This stand is fairly productive, despite the crowded tree population and imperfect drainage. Long (1952) observed that some of the most productive stands in the Acadia Forest Experiment Station were of this type. Regeneration is limited and is composed of suppressed balsam fir and red maple. The upper and lower shrub strata have only 15 and 5 percent ground cover, respectively.

The Fredericton Peter Brook area has a site index comparable to that of the Armagh area, putting them both in National Capability rating category 4. These two areas have very similar stand compositions (Figure 6), tree sizes (Figure 7), soils (Figure 3c), and upper canopy cover (Figure 3b). The coefficient of similarity between overall vegetation lists of these sites is 37 (Table 2). However, when only the species found in the fresh section of the Armagh study area are considered, the coefficient of similarity rises to 45, probably because both sites have very similar moisture regimes. The heterogenesity of the surrounding community is high in both cases.

In the Gargantua site, only 39 plant species were recorded. The vegetation list is most similar to that of the Épaule study area (Jaccard coefficient = 36). However, the arborescent strata are quite different from those in the other research stands. White spruce, not balsam fir, dominates these strata, which cover 65 percent of the ground. Stocking is low, but trees are very large. Balsam fir is relatively slow-growing, probably because of the dry soil-moisture regime. Mortality of this species reached 53 percent. Regeneration is composed of balsam fir, pin cherry, and white birch. The shrub strata, are well developed and contain a fair amount of hazelnut, mountain maple, and raspberry.

The Black Strugeon area is a homogeneous, species-rich (62 taxa) stand growing on a fine-textured, well-drained soil. The diversity of species may be the result of a fertile soil and of a transitional position between the Great Lakes-St. Lawrence and Boreal forest regions. The transitional nature of the vegetation in 85-B-01-S is indicated by the presence of transgressive species from the sugar maple-yellow birch association of the Northern Hardwood region. The arborescent strata each cover 35 to 50 percent of the ground, and are dominated by balsam fir and trembling aspen, which represent 45 and 30 percent of the high basal area, respectively. Stocking was very high, mainly because of large tree diameters. Balsam fir is relatively slow-growing. Only 20 percent mortality was observed in this species. This mortality was not attributed to insect damage. Regeneration is greatly dominated by balsam fir. The shrub strata cover only 5 to 15 percent of the ground each.

The composition of the plant community of forest stands may be an important factor determining the abundance of several species of natural enemies of the spruce budworm. This influence may come into play by determining the availability, abundance, and distribution of food for many dipteran and other parasitoids. The abundance and distribution of host plants for the alternate hosts of several multivoltine parasitoids may also be a critical consequence of stand structure. A good example is the obliquebanded leafroller, *Choristoneura rosaceana* (Harris), found on shrubs like *Acer spicatum*, *Rubus* spp., *Corylus cornuta* and several other deciduous species, which has recently been identified as an overwintering host of the braconid *Meteorus trachynotus* Vier. (Maltais et al. unpublished results). At this point, this parasite seems to play a role during the decline phase of spruce budworm populations, the importance of which is probably a function of alternate-host availability. Vegetation structure may also determine the diversity and density of vertebrate predator populations, which also play a role in declining spruce budworm populations (Régnière et al. unpublished results). Stand structure may also affect the vulnerability of host-trees to spruce budworm damage. There is a possibility that host-tree distribution, density, and health influence the survival rates of dispersing larvae (Mott 1963), and the migratory tendencies of adults of this insect (Royama 1984).

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APPENDIX

Table 1. Regeneration, based on the total number of stems in ten circular microplots of 5 m^2, placed inside each sample plot, except for the Peter Brook study area, where regeneration was not recorded

Tree species	Sample plot									
	A-01-S		E-01-S		R-01-S		G-01-S		B-01-S	
	%	Class[1]	%	Class	%	Class	%	Class	%	Class
Abies balsamea	44	C	90	C	41	A	39	C	92	C
Picea glauca	-	-	-	-	-	-	2	A	<1	A
Picea rubens	1	B	-	-	1	A	-	-	-	-
Picea mariana	-	-	<1	A	-	-	-	-	4	C
Acer rubrum	52	C	-	-	48	C	-	-	-	-
Acer saccharum	-	-	-	-	-	-	8	B	-	-
Betula papyrifera	<1	A	10	C	8	C	20	C	2	C
Betula populifolia	1	A	-	-	-	-	-	-	-	-
Populus tremuloides	1	A	-	-	-	-	-	-	<1	A
Prunus pensylvanica	-	-	-	-	2	C	31	B	<1	A
Fagus grandifolia	<1	C	-	-	-	-	-	-	-	-
Total Stems/500 m^2	4030		1192		489		137		505	

[1] Class indicates regeneration category in which species is most abundant.
A: 2-9 cm-dbh. B: < 2 cm-dbh, height > 30 cm. C: < 2 cm-dbh, height < 30 cm.

Table 2. Vegetation list of the sample plots. First digit is abundance-dominance index (r: rare, + : present, < 1% cover, 1: 1 - 5%, 2: 6 - 25%, 3: 26 - 50%, 4: 51 - 75%, 5: 76 - 100% cover). Second digit is sociability index (1: individuals, 2: tufts, 3: patches, 4: colonies, 5: pure populations)

Species name	Stratum[1]	Sample plot					
		A-01,02[2]	R-01-S	P-01-S	B-01-S	G-01-S	E-01-S
Arborescent species							
Abies balsamea	DC	4-4	3-5	4-5	3-4	1-1	2-5
	OS	1-1	3-5	2-1	3-1	2-1	2.2
	us	2-2	2-2	1-1	1-1	+1	2.2
	ls	2-2	+1	1-2	1-1	+1	2.2
Betula papyrifera	DC	+1	(+1)[3]	(+1)	(1-1)	2-2	2-1
	OS	-	(+1)	+1	(+1)	1-1	2-1
	us	[+1][3]	-	-	r	1-2	-
	ls	-	+1	r	r	1-2	1-1
Picea glauca	DC	2-1	-	+1	2-1	2-5	1-1
	OS	1-1	-	+1	2-1	2-1	1-1
	us	1-1	-	-	+1	+1	1-1
	ls	[+1]	-	-	+1	+1	-
Populus tremuloides	DC	2-2	(+1)	+1	2-3	-	-
	OS	1-2	(+1)	+1	1-1	-	-
	us	-	-	-	+1	-	-
	ls	+1	-	-	-	-	-
Picea rubens	DC	1-1	-	1-1	-	-	-
	OS	1-1	+1	1-1	-	-	-
	us	+1	+1	-	-	-	-
Acer rubrum	DC	2-2	1-1	-	-	-	-
	OS	1-1	1-2	1-2	-	-	-
	us	[1-1]	-	2-2	-	+2	-
	ls	2-2	1-2	2-2	-	+2	-
Picea mariana	DC	-	-	-	(+1)	-	-
	OS	-	-	-	1-1	-	+1
	us	-	-	-	1-1	-	+1
	ls	-	-	-	+1	-	-
Betula populifolia	DC	1-2	-	-	-	-	-
	OS	1-2	-	-	-	-	-
	us	-	-	+1	-	-	-
Thuja occidentalis	OS	[+1]	-	-	-	-	-
Pinus strobus	OS	[+1]	-	(+1)	-	-	-

Table 2 (continued)

Species name	Stratum[1]	Sample plot					
		A-01,02[2]	R-01-S	P-01-S	B-01-S	G-01-S	E-01-S
Arborescent species							
Acer saccharum	os	-	-	+1	-	-	-
	us	-	-	-	-	+1	-
	ls	-	-	(+2)	-	r	-
Shrub species							
Sorbus americana & decora		r	1-1	-	r	2-2	2-1
Rubus ideaus & sp.		[1-2]	1-2	r	+1	2-3	1-2
Amelanchier bartramiana		1-2	-	r	+1	+2	-
Prunus pensylvanica		[+1]	-	-	+1	2-1	1-2
Viburnum cassinoides		2-3	1-2	1-2	-	-	-
Vaccinium angustifolium		1-2	-	1-2	+1	-	-
Amelanchier sp.		+2	-	-	+2	-	-
Corylus cornuta		+2	-	(+2)	2-3	2-3	-
Ribes glandulosum		-	-	-	+1	1-2	1-2
Acer pensylvanicum		r	-	r	r	-	-
Vaccinium myrtilloides		[3-3]	-	+2	+1	-	-
Cornus stolonifera		[+3]	-	-	+2	-	-
Alnus rugosa		-	2-2	-	2-3	-	[2-3]
Acer spicatum		-	-	-	+2	2-3	-
Lonicera canadensis		-	-	-	1-2	1-2	-
Sambucus pubens & canadensis		-	-	r	-	-	+1
Viburnum edule		-	-	-	(+2)	-	(+1)
Spirea latifolia		[1-3]	-	-	-	-	-
Salix humilis		[+2]	-	-	-	-	-
Nemopanthus mucronatus		-	(+1)	-	-	-	-
Kalmia angustifolia		-	1-2	r	-	-	-
Ilex verticillata		-	-	+2	-	-	-
Taxus canadensis		-	-	r	-	-	-
Rhododendron canadensis		-	-	r	-	-	-
Diervilla lonicera		-	-	-	2-1	-	-
Ribes triste		-	-	-	+1	-	-
Prunus virginiana		-	-	-	(r)	-	-
Rosa acicularis		-	-	-	1-1	-	-
Symphoricarpos albus		-	-	-	1-1	-	-
Ribes lacustre		-	-	-	-	-	(+1)
Herbaceous species							
Cornus canadensis		2-1	+1	2-3	1-1	2-1	1-2
Maianthemum canadensis		1-1	+1	+1	1-1	1-2	+1
Trientalis borealis		+1	+1	+1	+1	1-1	+1

Table 2 (continued)

Species name	Stratum[1]	Sample plot					
		A-01,02[2]	R-01-S	P-01-S	B-01-S	G-01-S	E-01-S
Herbaceous species							
Lycopodium obscurum		+2	+1	2-3	+2	1-2	-
Lycopodium clavatum		1-2	+2	+2	r	+2	-
Dryopteris austriaca		[+2]	+3	+2	r	3-2	2-3
Pteridium aquilinum		1-2	1-3	[1-2]	-	2-2	-
Aralia nudicaulis		-	2-1	1-1	2-1	1-2	+1
Coptis trifolia		[+2]	1-2	-	1-2	-	-
Carex arctata		[r]	1-2	+2	-	1-2	-
Viola incognita		-	1-3	r	-	+2	(+1)
Carex brunescens		-	1-2	-	-	1-2	1-2
Clintonia borealis		-	-	+1	1-1	2-2	2-3
Trillium undulatum		+1	+1	+1	-	-	-
Goodyera repens		r	r	-	-	-	-
Aster macrophyllus		+1	-	-	2-1	-	-
Osmunda claytonii & cinnamomea		[1-2]	2-3	[1-2]	-	-	-
Fragaria virginiana		[r]	r	-	-	-	-
Carex sp.		[+1]	-	+2	-	1-2	-
Rubus pubescens		-	+2	-	1-1	-	-
Linnea borealis		-	1-2	+2	+2	-	-
Solidago macrophylla		-	+1	-	-	-	1-2
Apocynum androsaemifolium		-	-	-	r	r	-
Streptopus roseus		-	-	r	+1	-	+1
Cinna latifolia		-	-	-	-	+1	(+2)
Oxalis montana		-	-	-	-	4-4	2-4
Erythronium americanum		+3	-	-	-	-	-
Aster umbellatus		[1-1]	-	-	-	-	-
Solidago rugosa		[1-1]	-	-	-	-	-
Lycopodium complanatum		[+2]	-	+2	-	-	-
Hieracium vulgatum		[r]	-	-	-	-	-
Iris versicolor		[r]	-	-	-	-	-
Aster acuminatus		-	1-2	+1	-	-	-
Anaphalis margaritacea		-	r	(+2)	-	-	-
Thelipteris noveboracensis		-	1-3	-	-	-	-
Calamagrostis canadensis		-	+2	-	-	-	-
Circea alpina		-	+2	-	-	-	-
Dalibarda repens		-	+2	-	-	-	-
Agrostis hyemalis		-	+2	-	-	-	-
Galium triflorum		-	+2	-	-	-	-

Table 2 (continued)

Species name	Stratum[1]	Sample plot					
		A-01,02[2]	R-01-S	P-01-S	B-01-S	G-01-S	E-01-S
Herbaceous species							
Lycopodium annotinum		-	-	1-3	-	-	-
Dennstaedtia punctilobula		-	-	2-4	-	-	-
Equisetum pratense		-	-	-	1-1	-	-
Viola renifolia		-	-	-	+2	-	-
Actea rubra		-	-	-	1-1	-	-
Monesses uniflora		-	-	-	+2	-	-
Petasithes palmatus		-	-	-	1-2	-	-
Pyrola virens		-	-	-	+2	-	-
Mitella nuda		-	-	-	1-3	-	-
Oryzopsis asperifolia		-	-	-	+1	-	-
Corallorhyza maculata		-	-	-	(+2)	-	-
Brachylitrum erectum		-	-	-	-	1-3	-
Carex communis		-	-	-	-	1-2	-
Thelypteris phegopteris		-	-	-	-	-	(+2)
Epilobium angustifolium		-	-	-	-	-	(r)
Carex trisperma		-	-	-	-	-	[2-2]
Moss species							
Pleurozium schreberi		1-3	1-3	1-2	2-3	+2	2-4
Dicranum polysetum		+2	1-2	1-2	1-2	+2	-
Ptilium crista castrensis		r	1-3	r	+2	r	-
Brachythecium reflexum		+2	+2	1-2	+2	+2	-
Brachythecium curtum		+2	1-2	1-2	1-3	-	-
Dicranum scoparium		1-2	1-2	1-2	-	1-2	2-2
Pohlia nutans		+2	r	r	-	-	-
Plagiothecium laetum		+2	r	+2	-	-	-
Polytrichum commune & formosum		1-2	-	+2	-	+3	1-3
Hylocomium splendens		[+3]	r	-	+2	-	r
Rhytidiadelphus triquetrus		[+3]	r	-	+2	-	-
Sphagnum girgensohnii		[+3]	3-3	-	-	-	[3-4]
Mnium spinulosum		r	-	-	1-3	-	-
Dicranum montanum		r	-	-	-	+2	-
Aulacomnium palustre		[+2]	r	-	-	-	-
Plagiothecium denticulatum		[+2]	r	-	-	-	-
Cladonia cornuta		r	+2	-	-	-	-
Drepenocladus uncinatus		-	r	+2	+2	-	-
Dicranum flagellare		-	+2	-	1-2	-	-

Table 2 (concluded)

Species name	Stratum[1]	Sample plot					
		A-01,02[2]	R-01-S	P-01-S	B-01-S	G-01-S	E-01-S
Moss species							
Dicraum fuscescens		-	-	1-2	1-3	-	1-2
Ptilidium pulcherimum		r	-	-	-	-	-
Callicladium haldanianum		r	-	-	-	-	-
Bryum sp.		[+2]	-	-	-	-	-
Ptilidium ciliare		[r]	-	-	-	-	-
Thuidium recognitum		[r]	-	-	-	-	-
Plagiomnium cuspidatum		-	+2	-	-	-	-
Polytrichum juniperinum		-	+3	+2	-	-	-
Hypnum pallescens		-	-	+2	-	-	-
Dicranum ontariense		-	-	+2	-	-	-
Cladina rangiferina		-	-	+2	(r)	-	-
Plagiomnium drummondii		-	-	-	+2	-	-
Eurhynchium pulchellum		-	-	-	+2	-	-
Sphagnum russowii		-	-	-	-	-	+2
Hylocomnium umbratum		-	-	-	-	-	1-2
Sphagnum squarrosum		-	-	-	-	-	[1-2]
Rhysomnium punctatum		-	-	-	-	-	[+2]
TOTAL SPECIES		65	58	55	62	39	37
Jaccard Coefficients of similarity (Gérardin 1980b):							
85-A-01,02		-	40	37	30	30	17
85-R-01-S		-	-	34	26	28	22
87-P-01-S		-	-	-	29	33	23
85-B-01-S		-	-	-	-	31	25
85-G-01-S		-	-	-	-	-	36

[1] DC: dominant-codominant. OS: oppressed-suppressed. us: upper shrub
ls: lower shrub.

[2] Combined vegetation list of 85-A-01-S and 85-A-02-0.

[3] ( ) indicate species recorded outside of a sample plot, but on same site.
[ ] indicate species recorded in a secondary site.

Table 3. Physico-chemical analysis of reference horizons in the soil profiles

	Humus					< 2 mm Fraction						
Sample plot	% N	C/N ratio	Horizon	Thickness cm	% gravel	% sand	% silt	% clay	pH	% OC	% Fe	% Al
85-A-01-A	1.34	26.9	Bhf	12	-	-	-	-	3.41	10.82	5.41	1.19
			Bf	30	25	47	43	10	3.90	3.98	1.93	1.11
85-E-01-S	2.09	20.6	Bhf	10	-	-	-	-	3.49	5.95	1.73	1.02
			Bf1	15	5	67	24	9	4.24	2.17	0.68	1.03
			Bf2	30	42	76	17	7	4.32	1.76	0.55	0.95
85-R-01-S	1.69	22.6	Bfg	20	15	33	37	30	3.38	3.07	0.98	0.40
87-P-01-S	1.19	31.2	Bhf2	30	50	62	23	15	4.45	5.13	0.96	1.43
			Bf	20	56	74	13	13	4.72	2.65	0.54	0.91
85-G-01-S	1.72	21.8	Bhf	29	33	44	47	9	4.05	5.15	0.18	1.96
			IIBf>	35	61	90	6	4	4.29	1.70	0.11	0.58
85-B-01-S	1.04	26.9	Bf	44	0	72	23	5	4.68	0.54	0.98	0.15

Table 4. Summary of dominant-site caracteristics for each study area

	Armagh	Épaule	Red Pine Brook	Peter Brook	Gargantua	Black Sturgeon
Latitude (N)	46°46'	47°18'	46°00'	46°59'	47°35'	49°18'
Longitude (W)	70°39'	71°12'	66°16'	66°23'	84°49'	88°52'
Altitude (m)	270	750	60	107	305	260
Mean air temperature (°C)	3.8	0.2	4.5		2.0	1.7
Degree-days (<0°C)	2575	1903	2692		2274	2320
Frost-free period (days)	112	47	91		100	101
Precipitation (mm)	1016	1420	1143		946	793
Solar radiation (Kcal/m^2)	167	125	158		149	129
Development period (days)	73	84	75		82	77
Development temp. (°C)	14.3	12.9	13.9		13.6	13.6
Hatch temperature (°C)	17.8	13.3	18.3		15.3	16.5
Relief (regional)	Rolling	Hilly	Flat	Undulating	Flat	Undulating
Slope (local)	3-5	10-25	4	3-15	<2	1.5
Exposure	SE	E-NE	SE	SE	-	SE
Drainage	Well	Rapid	Imperfect	Well	Rapid	Well
Moisture regime	Fresh	Dry	Moist	Fresh	Dry	Fresh
C/N ratio (humus)	26.9	20.6	22.6	35.0	21.8	26.9
Homogeneity (sub-sites)	2	3	1	4	1	1
Stocking (%)	100	100	60	90	60	107
Total basal area (m^2/ha)[1]	29.8	40	21.6	28	24	42
% balsam fir (basal area)[1]	66	83	98	77	24	44
% mortality of balsam fir	0[2]	17	55	0[2]	53	20
Age of balsam fir (years)	42	57	35	30	60	42
Height of balsam fir (m)	14.2	13.1	11.1	10.9	14.0	12.8
Height at age 50 (m)	16	12	14	15	13	14
Growth-limiting factors	Stoniness Fragipan	Climate Hortstein	Water excess	Stoniness Compaction	Water deficiency	Climate

[1]Average for the whole study area

[2]Balsam fir mortality in this stand was very low and was not documented.

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