



# Accurate dating of spruce budworm infestation using tree growth anomalies

Martin Simard & Serge Payette

To cite this article: Martin Simard & Serge Payette (2003) Accurate dating of spruce budworm infestation using tree growth anomalies, *Écoscience*, 10:2, 204-216, DOI: [10.1080/11956860.2003.11682768](https://doi.org/10.1080/11956860.2003.11682768)

To link to this article: <https://doi.org/10.1080/11956860.2003.11682768>



Published online: 23 Mar 2016.



Submit your article to this journal 



Article views: 20



View related articles 



Citing articles: 1 View citing articles 

# Accurate dating of spruce budworm infestation using tree growth anomalies<sup>1</sup>

Martin SIMARD<sup>2</sup> & Serge PAYETTE, Centre d'études nordiques and Département de biologie, Université Laval,  
Sainte-Foy, Québec G1K 7P4, Canada, e-mail: masimard@cfl.forestry.ca

**Abstract:** Spruce budworm feeding causes stem and branch deformities that alter the architecture of host trees in a permanent way, easily recognized several years after the defoliation event. Dating of budworm-related growth anomalies using tree rings provides a new means to reconstruct recent infestations of this defoliator. We tested this dendro-architectural method in the southernmost black spruce-lichen woodlands in eastern North America, which were affected by spruce budworm from 1976 to 1985. In these open stands, moribund black spruce trees support high loads of the epiphytic lichen *Bryoria* arranged in unusual patterns, a phenomenon known as black spruce decline. Because *Bryoria* was restricted to the dead and deformed parts of the trees, we hypothesized that the lichen only colonized those parts of the trees defoliated by spruce budworm. To test this hypothesis, we dated *i*) three types of growth anomalies associated with spruce budworm feeding (death of terminal buds, death of axes, and reiteration, *i.e.*, production of new leaders and epicormic shoots) and *ii*) maximum extent of *Bryoria* on stem and branches of three spruce trees showing contrasting lichen cover patterns. All trees showed peaks of growth anomalies during periods of known spruce budworm activity. Also, *Bryoria* was almost exclusively located on internodes that were defoliated by spruce budworm. A model is also proposed to explain the different lichen cover patterns observed. Dating of tree growth anomalies (terminal bud mortality) has better resolution in time and space than tree-ring patterns to determine the first year of insect defoliation.

**Keywords:** tree rings, plant architecture, black spruce (*Picea mariana*), spruce budworm (*Choristoneura fumiferana*), insect outbreaks, epiphytic lichens, *Bryoria*, lichen woodland.

**Résumé :** L'alimentation de la Tordeuse des bourgeons de l'épinette cause des déformations des tiges et des branches qui altèrent d'une façon permanente l'architecture des arbres hôtes et qui sont facilement reconnaissables plusieurs années après la défoliation. La datation des anomalies de croissance associées à la Tordeuse, grâce à l'analyse des cernes annuels, offre un nouveau moyen de reconstituer les infestations récentes de ce défoliateur. Nous avons testé cette méthode dendro-architecturale dans les pessières noires à lichens les plus méridionales de l'Est de l'Amérique du Nord, qui ont été affectées par la Tordeuse des bourgeons de l'épinette de 1976 à 1985. Dans ces peuplements ouverts, les Épinettes noires moribondes supportent de grandes quantités du lichen épiphyte *Bryoria* disposé en patrons de recouvrement inhabituels, un phénomène appelé dépérissement de l'Épinette noire. Puisque *Bryoria* est confiné aux parties mortes et déformées des arbres, nous avons émis l'hypothèse que ce lichen ne colonise que les parties des arbres qui ont été défoliées par la Tordeuse. Pour vérifier cette hypothèse, nous avons daté : *i*) trois types d'anomalies de croissance associées à l'alimentation de la Tordeuse (mort de bourgeons terminaux, mort d'axes et réitération, *c'est-à-dire* production de têtes surnuméraires et de pousses adventives) et *ii*) l'étendue maximale de *Bryoria* sur les tiges et les branches de trois épinettes noires affichant des patrons de recouvrement lichéniques différents. Tous les arbres ont montré des pics d'anomalies de croissance pendant les périodes connues d'activité de la Tordeuse des bourgeons de l'épinette. De plus, *Bryoria* était presque exclusivement situé sur les entremeneuds qui avaient été défoliés par la Tordeuse. Un modèle est également proposé pour expliquer les différents patrons de recouvrement lichénique observés. La datation des anomalies de croissance des arbres (mort de bourgeons terminaux) offre une meilleure résolution dans le temps et l'espace que les patrons de croissance radiale pour déterminer la première année de défoliation.

**Mots-clés :** dendrochronologie, architecture des plantes, Épinette noire (*Picea mariana*), Tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana*), épidémies d'insectes, lichens épiphytes, *Bryoria*, pessière à lichens.

**Nomenclature :** Anderson, Crum & Buck, 1990; Esslinger, 1997; Marie-Victorin, 1995.

## Introduction

Recurrent outbreaks of the spruce budworm (*Choristoneura fumiferana*) are major disturbances in the southern boreal forest of eastern North America. Spruce budworm larvae feed primarily on current-year and sometimes 1-year-old foliage of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), red spruce (*P. rubens*), and black spruce (*P. mariana*) (Harvey, 1985; Mattson,

Simmons & Witter, 1988). Massive and repeated defoliations cause radial growth reductions in stems, branches, and roots of host trees (Blais, 1958; MacLean, 1985; Krause & Morin, 1995a; 1999; Filion *et al.*, 1998). Budworm defoliation is heavier at the top of the crown (Alfaro *et al.*, 1982), thus causing height growth reductions (Van Sickle, Alfaro & Thomson, 1983; Piene, 1989b; Piene & Little, 1990), top-kill (Schmiede, 1961; Ferrell & Scharpf, 1982), and mass mortality of host species (MacLean, 1980). Surviving trees with destroyed terminal buds usually develop new leaders from dormant buds (Williams, 1967) or lateral shoots bending upwards

<sup>1</sup>Rec. 2002-05-08; acc. 2002-12-10.

<sup>2</sup>Author for correspondence. Present address: Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du PEPS, P.O. Box 3800, Sainte-Foy, Québec G1V 4C7, Canada.

to assume vertical growth (Bailey, 1925b; Ghent, 1958). Top-killed trees therefore show permanent stem anomalies (curvatures, spikes, crooks, forks, etc.), which are still visible several years after the outbreak (Stillwell, 1956; Ghent, 1958; Ferrell & Scharpf, 1982). Although budworm-caused growth anomalies have mostly been documented for the main stem of trees (*i.e.*, top-killing), they also occur on branches (production of epicormic shoots; Batzer, 1973; Piene, 1989a,b; Ostaff & MacLean, 1995; Piene & Eveleigh, 1996).

To better understand the dynamics and impacts of the spruce budworm, the history of past outbreaks was reconstructed by comparing tree-ring patterns of host and non-host tree species (Blais, 1962; Swetnam & Lynch, 1993; Morin, Laprise & Bergeron, 1993). A shortcoming of this method, however, is the inability to determine the first year of budworm defoliation. This inaccuracy is caused by the time-lag between the first year of insect defoliation and the first year of tree-ring growth reductions near the base of host trees, where wood samples are usually taken (Blais, 1958; Kulman, 1971). The first radial growth reduction occurs at the top of trees, usually one year after the beginning of the defoliation event (Krause & Morin, 1995b), as early wood formation in conifer tree-rings depends on 1-year-old foliage, while current-year foliage mainly contributes to the formation of late wood (Gordon & Larson, 1968; 1970). An additional delay of 1 to 3 years is necessary before growth suppression is observed at the base of the trees (Krause & Morin, 1995a; 1999), probably because of starch reserves that compensate for the diminished photosynthates for a time (Ericsson *et al.*, 1980; Ericsson, Larsson & Tenow, 1980). The total time-lag can extend 2 to 4 years, and thus one has to rely on insect defoliation surveys (when available) to determine the actual beginning of an outbreak. We present here an alternative method for dating recent spruce budworm infestations with high resolution in both space (branch level) and time (exact year). This method combines tree-ring dating and architectural analysis and consists of dating growth anomalies caused by spruce budworm feeding (terminal bud destruction, killing of tops and shoots, and production of epicormic shoots) on branches and stems of trees.

The architecture of a tree refers to its morphology at any given time of its development (Tomlinson, 1983; Bégin & Filion, 1999). It is the result of two different but related morphogenetic processes: the first process is the genetically determined program that guides the organization and development of the tree (Hallé, Oldeman & Tomlinson, 1978); the second process, called reiteration, enables the tree to duplicate a part or the totality of its structure in response to environmental stresses (*e.g.*, stem breakage or defoliation) or increased physiological needs (Oldeman, 1974). Knowing the rules underlying the development of a tree and the way reiteration takes place, it is possible to identify growth anomalies and interpret them in relation to ecological factors. In temperate regions, growth rings are produced yearly in stems, branches, and roots of trees. Tree-ring analysis therefore adds a temporal scale to architectural analysis, so that the exact time of axis (stem, branches, twigs, etc.) formation, mortality, or reiteration can be determined. Dendro-architecture was suc-

cessfully used to reconstruct the development of lichen-black spruce woodland at its northern range limit in Québec (Bégin, 1991) and black spruce clones at treeline (Laberge, Payette & Pitre, 2001).

We developed the dendro-architectural method in the southernmost lichen-black spruce woodlands in eastern North America, where the impact of spruce budworm infestations has been recently documented (Payette *et al.*, 2000; Simard & Payette, 2001). Lichen woodlands are open forests (<25% black spruce cover) typically found north of 52° N in eastern Canada. Lichen-spruce woodlands reach their southernmost range limit at a considerably lower latitude (47° N), where they form small patches within the closed-crown spruce-moss forest. Successive spruce budworm infestation and fire disturbances have recently been shown to be causal factors for the inception and maintenance of southernmost lichen-spruce woodlands (Payette *et al.*, 2000). Several lichen woodlands were damaged by the last spruce budworm outbreak that occurred in Québec in the 1970s and 1980s (Simard & Payette, 2001). In these damaged stands, dead and moribund black spruce trees now support large amounts of pendulous epiphytic lichens (mainly *Bryoria* spp.), a phenomenon described as black spruce decline (Simard & Payette, 2001; Figure 1). The presence of *Bryoria* is not exceptional in itself, as it is a common component of mature circumboreal forests (Brodo & Hawksworth, 1977). The particularity of the spruce decline comes from the distribution of *Bryoria* at both stand and tree levels. At the stand level, *Bryoria* is abundant in young and mature stands, irrespective of tree or stand age (Simard & Payette, 2001); this distribution differs from that reported in other studies, which have shown that alectorioid lichen biomass is proportional to stand age (Lang, Reiners & Pike, 1980; McCune, 1993; Arseneau, Sirois & Ouellet, 1997). At the tree level, *Bryoria* shows a variable cover pattern on spruce trees, and it is usually found on dead parts of declining trees (Figures 1 and 2). The distribution patterns of this lichen contrast with the vertical distribution reported in Fennoscandia and the northwestern United States, with greater abundance in the middle, upper, and outer parts of conifers (McCune, 1993; Clement & Shaw, 1999; Liu, Ilvesniemi & Westman, 2000; Lyons, Nadkarni & North, 2000; Campbell & Coxson, 2001).

The mechanisms explaining the distribution and abundance of *Bryoria* on spruce trees are unknown. It is likely that epiphytic lichen distribution is closely linked to budworm defoliation as *i*) the abundance of *Bryoria*, at the stand level, is proportional to severity of radial growth reductions caused by the spruce budworm (Figure 8 in Simard & Payette, 2001), and because *ii*) this lichen seems to be associated with dead and deformed parts of spruce trees.

The first objective of this study was to develop a dendro-architectural method enabling accurate dating of spruce budworm feeding activity at the branch and tree levels. To do so we analyzed three types of growth anomalies associated with budworm feeding: mortality of terminal bud (of both stem and branches), mortality of entire parts of the stem (top-kill) or branches, and reiteration (or duplication) of stems (new leaders) or branches (epicormic



FIGURE 1. Black spruce decline in the lichen woodland of the Parc des Grands-Jardins is characterized by high epiphytic lichen biomass (mainly *Bryoria* spp.) on moribund black spruce trees. Here, most trees show dead tops covered with the blackish lichen *Bryoria*, while their lower branches bear healthy foliage (compare declining tree on the right with healthy tree in the upper left corner).

shoots). Our analysis was based on the architectural model of black spruce recently described by Bégin and Filion (1999). The second objective was to document the relationship in time and space between spruce budworm defoliation and distribution of *Bryoria* on declining black spruce trees. Comparison of these two distribution patterns was used to test the hypothesis that *Bryoria* only grows on parts of trees previously defoliated by spruce budworm.

## Methods

### STUDY AREA

The southernmost lichen woodlands in eastern Canada are located in the Parc des Grands-Jardins (PGJ) ( $47^{\circ} 40' N$ ,  $70^{\circ} 50' W$ ), in the Laurentian Highlands of Charlevoix, 120 km northeast of Québec City. These open black spruce stands (total area of  $\sim 30 \text{ km}^2$ ) are distributed in patches of different size within a matrix of closed-crown, balsam fir-black spruce forests. They grow in a cold climate, with an annual mean temperature of  $0^{\circ}\text{C}$  (mean temperature of January and July are  $-15^{\circ}\text{C}$  and  $14^{\circ}\text{C}$ , respectively), a frost-free period of 42 days, and annual precipitation of  $1,000 \text{ mm year}^{-1}$  on average (Boisclair, 1990). The PGJ area was severely affected by an infestation of the spruce budworm during 1976-1977 and 1981-1985, as shown by aerial defoliation surveys (Gouvernement du Québec, Ministère des Ressources naturelles, Direction de la conservation des forêts) and tree-ring analysis (Simard & Payette, 2001).

### SAMPLING OVERVIEW

To understand the significance of the contrasting lichen-cover patterns in the black spruce decline, a survey was first conducted throughout the study area to document the distribution of *Bryoria* at the tree- and stand-level. Survey data were then used to determine 3 main lichen cover types, and the proportion of these types in each surveyed stand was used as a criterion for selecting a sampling site. Finally, one spruce tree of each lichen-

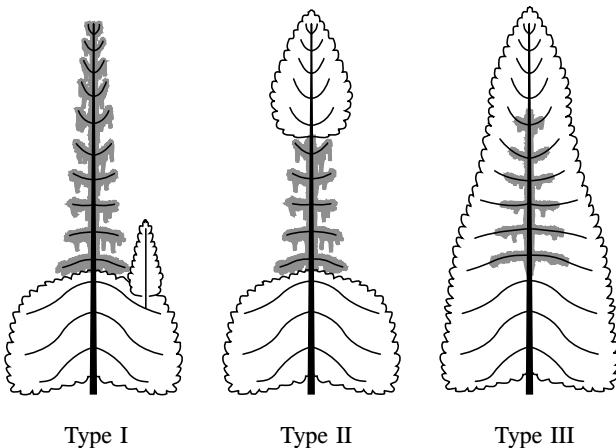


FIGURE 2. Cover patterns (types I-III) of the epiphytic lichen *Bryoria* on moribund black spruce trees. Type X (not shown) represents cover patterns not included in the three main types. Healthy foliage in white; *Bryoria* in gray.

cover type was selected for detailed dendro-architectural analysis, for a total of 3 spruce trees.

#### LARGE-SCALE SURVEY

*Bryoria* abundance was assessed in 28 sites showing different ecological conditions (topography, surface deposits, drainage, stand age, associated vegetation, etc.) within the lichen woodland (Simard & Payette, 2001). At each site, 10 parallel transects (20 m × 1 m, 5-m interval) were positioned at random. Cover and vertical distribution of *Bryoria* were assessed on every tree in the transects, following a simplified version of a method developed by Stevenson (Stevenson & Enns, 1993). Lichen-cover assessment was always made by the same two observers and considered all four aspects of the trees. First, *Bryoria* cover was estimated for the whole tree using pre-established classes (0-4%, 5-24%, 25-49%, 50-74%, 75-99%, and 100%; the last class implied that the tree was dead). The reference area (100%) consisted of the area occupied by tree crown added to the area occupied by pendular portions of the lichens. Secondly, the vertical distribution of *Bryoria* was assessed visually by dividing the crown into four equal parts (upper, upper-middle, lower-middle, and lower). The observers noted which of the 4 quarters showed *Bryoria*, recording separately lichen growing on the distal end of branches from that growing near the trunk. The number and position of new leaders was also noted for each tree.

We analyzed lichen-cover data of all sites (>10,000 trees) for recurring cover patterns of *Bryoria*. Three main types of lichen cover were determined to include most cover patterns (Figure 2). Type I is characterized by complete covering of the tree top, which can extend to more than half of the crown. Lichen-covered tops are dead and usually have one or several new leaders at the base. Dead trees completely covered with *Bryoria* represent the extreme of type I and are thus included in this group. Type II trees show a living apex not covered by *Bryoria*. Lichens cover dead branches of upper-middle or lower-middle parts of the tree, and both upper and lower parts are free of lichens. In type III, *Bryoria* is restricted to the proximal part of branches, so that only inner parts of the crown harbour lichens, with an outer shell of healthy foliage. A large proportion of trees showed cover patterns not included in any of the main types and were thus lumped into a composite group (type X).

#### SITE SELECTION AND SAMPLING

The sampling site was selected based on the fire date at the origin of the stand and maximum numbers of type I, II, and III trees. The selected stand is a lichen-spruce woodland originating from a 1897 fire (dated with fire scars), damaged by spruce budworm during the 1950s and in 1976-1985 (site 4 in Simard and Payette, 2001), with several moribund trees bearing high loads of *Bryoria*. Of the trees covered with *Bryoria*, 59% were type I, 12% were type II, 25% were type III, and 4% were type X (mean for all sites was 31% type I, 5% type II, 54% type III, and 10% type X). The stand shows a typical lichen-woodland vegetation, including a moss stratum dominated by lichens of the genus *Cladina* and a

shrub stratum composed of dwarf birch (*Betula glandulosa*), *Kalmia angustifolia*, and *Vaccinium angustifolium*. The soil is a well-drained (drainage class 2), thin (solum=9 cm), eluviated dystric brunisol (Canadian Soil Survey Committee, 1987) developed on coarse fluvioglacial deposits. At least two species of *Bryoria* (*B. furcellata* and *B. nadvornikiana*) make up the bulk (> 90%) of the arboreal lichen flora; lichens of secondary importance included two species of *Usnea* (*U. subfloridana* and *U. filipendula*), *Evernia mesomorpha*, *Hypogymnia physodes*, and *Vulpicida pinastri*.

Black spruce trees were selected by random stratified sampling. Trees were first identified based on the morphological categories (types I, II, and III; Figure 2) until 6 trees of each type were located; one tree per type was then randomly selected for analysis. Selected trees were hand drawn to scale on millimetric paper, focusing on stem curvatures and new leaders developed on the trunk and branches. Whole branches and stem cross-sections were then sampled according to the following criteria. Stem cross-sections were sampled at 0 m, 0.3 m, at all heights where a branch was sampled, at all heights where the stem was curved, and at the base of all new leaders. Tree tops showing multiple new leaders were sampled entirely and brought to the laboratory. Living branches were selected by random stratified sampling, to take advantage of the contrasts between healthy, lichen-free and lichen-covered sections of the trees, *i.e.*, lower parts of the tree without *Bryoria* (types I, II, and III), partly covered middle sections (type III), and tree tops not lichen covered (types II and III). In every section, branches were systematically sampled at predetermined intervals on the east side of the trunk (aspect randomly selected). In addition, branches bearing new leaders were sampled. Branches and tree tops were stored at 4°C until analyzed.

#### ARCHITECTURAL ANALYSIS

Architectural analysis relies on drawing as a main tool to prevent the overlooking of morphological details. Sampled branches and tree tops were drawn to scale focusing on the distribution of *Bryoria*, living foliage, and bud scars delimiting annual internodes. In architectural analysis, the growing axes are numbered from the main stem (first order axis,  $A_1$ ), to branches ( $A_2$ ), and twigs ( $A_3$ ,  $A_4$ ) (Bégin & Filion, 1999). In this study, only first and second-order axes ( $A_1$  and  $A_2$ ) were considered, but these included  $A_3$  that transformed into  $A_2$  (Bégin & Filion, 1999). Three particular growth anomalies potentially associated with budworm feeding were identified and dated, *i.e.*, terminal bud mortality, axis mortality, and production of replicas (leaders and epicormic shoots).

#### GROWTH ANOMALIES

In black spruce, terminal shoots of  $A_1$  and  $A_2$  support a terminal bud and three sets of lateral buds in subterminal, median, and basal positions (Figure 3A; Bégin & Filion, 1999). Terminal, subterminal, and median buds are sequential, *i.e.*, they always flush the year following their formation. That is why year of formation of a particular internode can be determined by counting the number of bud scars from the tip of a branch or main stem. On the

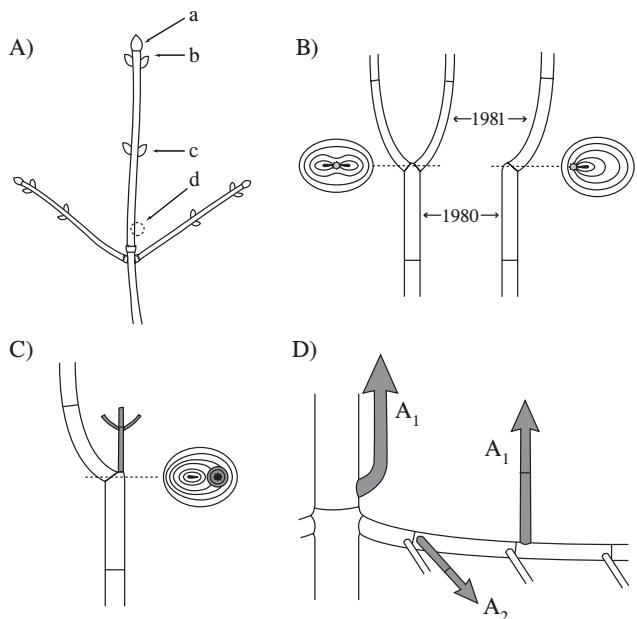


FIGURE 3. A) Position of terminal (a), subterminal (b), median (c), and basal buds (d) along black spruce terminal shoot (modified from Édeline, 1977). B) Axis deviation caused by terminal bud mortality, resulting in a fork or crook, depending on the number of subterminal buds replacing the damaged axis. Because spruce budworm destroys buds in early spring, year of bud mortality (here 1981) was calculated by adding one year to year of formation of the axis bearing the destroyed bud (here 1980). C) Bayonet-shaped axis resulting from axis mortality (in gray), replaced by a surviving subterminal bud. D) Reiteration from dormant buds produces replicas of the main stem ( $A_1$ ) or of branches ( $A_2$ ), called new leaders and epicormic shoots, respectively. Replicas (in gray) are easily identified because they are produced by dormant buds at the base of each internode, in contrast to axes produced by normal tree development (in white), which are produced either by subterminal or median buds. Cross-sections of growth anomalies are shown in B and C.

other hand, basal buds usually remain dormant until environmental stress (e.g., stem breakage or defoliation) or increased physiological needs stimulate their development.

Death of terminal buds occurs when the terminal bud of a shoot is destroyed before flushing in spring (Figure 3B). Spruce budworm causes such damage when second-instar larvae emerge in early spring. Larvae first mine old needles, unopened buds, or feed on staminate cones, and later swollen buds (McGugan, 1954; Mattson, Simmons & Witter, 1988) because there is no new foliage to feed on (budbreak in black spruce occurs 2 to 3 weeks after budworm emergence). Destruction of the terminal bud brings an end to shoot growth, but spared subterminal buds produce new axes to replace the axis that was destroyed. If the terminal bud of the main stem is destroyed, for instance, one or several subterminal buds (designed to become branches) grow upward and transform into  $A_1$  (Bégin & Filion, 1999). This type of growth anomaly appears as forks and crooks on branches and tree tops (Figure 3B).

The second type of growth anomaly is axis mortality (Figure 3C). Repeated, massive defoliation of new and old foliage by spruce budworm causes death of branch tips and stem tops (top-kill). The result is similar to that which follows destruction of the terminal bud: one or sev-

eral neighbouring axes, usually in subterminal position, change orientation to duplicate the damaged axis. The resulting axis eventually takes the shape of a bayonet, which typically develops on top-killed trees (Figure 3C). The extent of the top-kill (or branch tip mortality) can vary from one year to several decades. Therefore, weathering and secondary growth can mask this pattern on 1- to 3-year-old dead tips. Only cross-sections can distinguish death of axis from death of terminal bud (see insets in Figure 3B and 3C).

The third type of growth anomaly corresponds to the production of replicas (new leaders and epicormic shoots) from dormant buds (also called proleptic reiteration; Bégin & Filion, 1999). The loss of foliage, structure, and apical dominance caused by budworm feeding induces flushing of basal buds that were until then dormant. As replicas are necessarily produced by basal buds, the position of different axes relative to others is of primary importance to identify replicas from other sequential axes (originating from subterminal or median buds) associated with normal tree development (Figure 3D). Replicas can replace the main stem, branches, or twigs. In contrast to proleptic reiteration, sylleptic reiteration occurs when an already growing axis changes its spatial orientation to replace a damaged axis. In this study, we did not consider sylleptic reiteration because of dating problems. Therefore, proleptic reiteration will simply be referred to as reiteration in the text.

#### TREE-RING ANALYSIS

Stem and branch cross-sections were finely sanded (1500 grit) and cross-dated with a master frost-ring chronology (Simard, 2000). Frost rings show one or several rows of distorted cells caused by frost during the growing season (Bailey, 1925a; Glerum & Farrar, 1966). Tree-ring counts were compared with counts of annual internodes on living branches (Bégin & Filion, 1999). Special attention was given to detecting incomplete and missing rings, which are numerous during insect infestations (Swetnam & Lynch, 1989; Jardon, Filion & Cloutier, 1994; Simard & Payette, 2001). In addition, internodes formed during years of heavy defoliation are typically narrow (1 mm in length) and secondary growth often masks bud scars with time (Figure 4B). Because small internodes could not be cross-sectioned without being destroyed, they were progressively sanded and regularly checked for change in tree ring count. This process was repeated until the whole series of small internodes was sanded throughout. Drawings were occasionally made to keep record of anatomic characteristics indicative of growth anomalies (e.g., discontinuity of pith due to terminal bud mortality; see cross-sections in Figure 3B and 3C).

Death of an axis at a given level corresponded to year of the last visible ring. Terminal bud mortality was determined by adding one year to the year of formation of the internode bearing the destroyed bud. Year of reiteration was the year of the first ring of a replica; the axis bearing the replica was also dated to validate the identification of the replica, i.e., make sure there was a difference of more than 1 year between the two axes. To evaluate the distribution of *Bryoria* and healthy foliage on axes, we

dated the youngest internode bearing *Bryoria*, the oldest internode free of lichens, and the oldest internode bearing foliage. Dating of stem anomalies was compared to a black spruce chronology (25 trees, 75 radii) constructed for the study site in a previous work (Simard & Payette, 2001), where methods of tree-ring analysis are described.

## Results

### BLACK SPRUCE GROWTH ANOMALIES

Three types of growth anomalies (terminal bud mortality, axis mortality, and reiteration; Figure 3) were identified and dated on branches of three black spruce trees with contrasting lichen covers (Figure 2). As an example, some of these growth anomalies are shown in the tree of type I (Figure 4). The most striking feature was top-killing of more than 75% (nearly 4 m) of main stem and vigorous production of leaders developed from dormant buds (*e.g.*, 1983, 1986) and upward bending of already growing branches (*e.g.*, 1989; Figure 4C). Dead treetops (Figure 4A) showed several growth anomalies,

such as multiple leaders originating from upturned branches and dormant buds (in 1977 and 1979). The terminal bud was killed on several leaders, resulting in forks (*e.g.*, 1978) and crooks (*e.g.*, 1977). Shortly thereafter, individual axes of the treetop died one after the other (1983, 1984, and 1985). Branches also showed forks, bayonets, and axis deviations associated with death of terminal buds and axes, as well as reiteration (Figure 4B). Internodes produced during epidemic years were often small and showed several episodes of death-reiteration. Radial growth was measured on selected sections of the tree to show the relation between architecture and radial growth in the dynamics of axis replacement. The main stem (level F) was affected by two major growth reductions likely caused by budworm defoliation (beginning in 1978 and 1982, respectively; Figure 4F) before it began to die off from the top (1986; Figure 4C, years in brackets) downwards to its present level of maximum top-killing (1988). The tree responded to the loss of foliage, structure, and apical dominance by producing replicas, either from dormant buds (Figure 4D) or upturned branch-

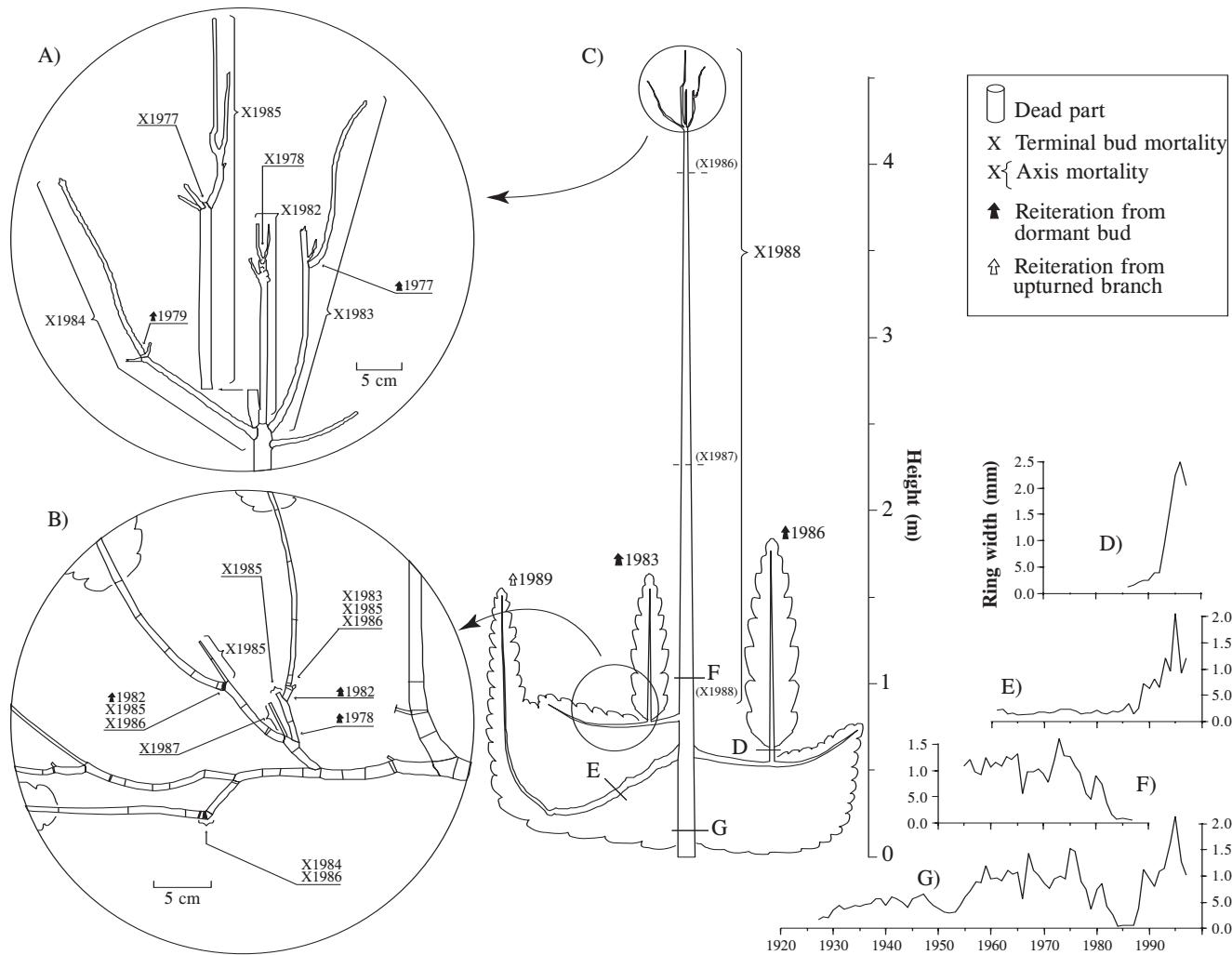


FIGURE 4. Identification and dating of growth anomalies (see legend) on black spruce tree of type I (C). Insets: details of main stem apex (A) and branch (B). For clarity, *Bryoria* is not shown, only A<sub>1</sub> and A<sub>2</sub> are drawn, and not all growth anomalies are identified. Years in brackets along main stem show gradual death of axis, but only the lowermost dating (1988) was included in the growth anomaly frequencies. Reiteration from upturned branches were dated with the first ring showing reaction wood and a concomitant increase in ring width, but were not included in the growth anomaly frequencies. Radial growth was measured on selected axis (D, E, F, G).

es (Figure 4E). Both reiterated axes showed strong initial radial growth when assuming apical dominance. The tree base (Figure 4G) showed the integration of radial growth in the different parts of the tree, *i.e.*, reductions recorded in the original stem followed by a strong increase caused by new replicas.

All growth anomalies were dated in trees of type I, II, and III (Figure 5). The trees experienced a high level of terminal bud mortality between 1976 and 1986, axis mortality through the 1980s, and reiteration between 1978 and 1986. Although growth anomalies peaked in the period of known spruce budworm defoliation (1976–1985), they were observed at lower frequencies outside that range. Frequency distributions ( $A_1$  and  $A_2$  taken together) were the same between the three cover types for each growth anomaly (Kolmogorov-Smirnov two-tailed test,  $\alpha=0.05$ ), suggesting a synchronous response of trees, irrespective of lichen cover.

#### DISTRIBUTION OF *BRYORIA*

The distribution of the arboreal lichen *Bryoria* was determined on the same axes ( $A_1$  and  $A_2$ ) studied for growth anomalies. As an example, the lichen distribution pattern is shown for the tree of type II, which showed an apparently healthy top concealing a dead  $A_1$  covered by lichens (Figure 6A). Dating of the dead part of the tree indicated that it was the original treetop, which died in 1984 (Figure 6B). Before death, it produced a replica in 1983 (which died in 1993), which in turn produced a second replica in 1986, which now forms the present treetop. *Bryoria* now covers the dead parts of the stem, but also the lower part of the living stem. The youngest internode bearing *Bryoria* on the main stem was produced in 1986, indicating that internodes produced after that year were completely lichen-free, despite the fact they were close to the dead, lichen-covered  $A_1$  (Figure 6B). The cover pattern on the main stem was also observed on branches above (Figure 6C) and beneath (Figure 6D) the branchless, lichen-covered parts of the tree: *Bryoria* was growing on dead and deformed parts of branches, whereas younger, lichen-free parts of branches usually showed normal growth, with no crooks or bayonets. There was a zone with no foliage or lichens between lichen-covered and foliated parts of branches.

The cover pattern is more obvious when branches are examined on the same time scale, with superimposed lichen cover and growth anomalies, as in the tree of type III (Figure 7).  $A_2$  were divided into two time periods: before *ca* 1987, covered by *Bryoria* and showing several growth anomalies, and after *ca* 1987, lichen-free with normal growth. The lowermost branch did not bear lichens, even though it showed several growth anomalies.

The maximum extent of *Bryoria* on main stem and branches was determined by compiling the years of formation of the youngest internodes bearing lichens for each studied axis (Figure 8). These lichen limits all occurred between 1975 and 1988, although the frequency distribution on the tree of type I was different from those on the trees of type II and III (Kolmogorov-Smirnov two-tailed test,  $\alpha=0.05$ ). The maximum extent of *Bryoria* was thus 1985 for the tree of type I, and 1988 for the trees of type II and III.

Finally, the number of internodes between the inner, lichen-covered and outer, foliated parts of branches (corresponding to the bare internodes in Figure 7) was calculated (Figure 9). The number of bare internodes varied between 1 and 14, although some branches had none. Again, trees of type II and III had similar frequency distributions but differed from tree of type I (Kolmogorov-Smirnov two-tailed test,  $\alpha=0.05$ ).

## Discussion

### SPRUCE BUDWORM FEEDING REVEALED BY GROWTH ANOMALIES

Spruce budworm feeding can affect black spruce architecture in three different ways: by causing mortality of terminal buds, causing mortality of parts of axes, and inducing the development of replicas replacing damaged axes. We identified and dated growth anomalies on three black spruce trees with contrasting lichen cover (Figure 2) heavily defoliated by the spruce budworm in 1976–1977 and 1981–1985. All trees showed several growth anomalies during epidemic years, whereas endemic years were associated with few or no growth anomalies (Figure 10A). More importantly, terminal bud mortality occurred on the first year of spruce budworm infestation (1976, according to defoliation aerial surveys). Dating of growth anomalies thus proves to be more accurate than tree-ring patterns for dating the onset of an infestation, as radial growth at the base of trees declined only in 1979, *i.e.*, 3 years after the onset of defoliation (Figure 10C). This is consistent with previous studies suggesting that growth reductions at the base of conifers usually occur 2 to 4 years after the first year of insect defoliation (Blais, 1958; Kulman, 1971). Frequencies of growth anomalies before and after the infestation are very low and are probably caused by natural abortion of buds, senescence of branches and twigs, and adaptive reiteration that occurs during the development of black spruce (Bégin & Filion, 1999).

Frequency of terminal bud mortality is the growth anomaly that provides the most accurate means of determining the first year of defoliation, because buds can only be destroyed between the time of their formation (late summer) and budbreak (spring). Therefore, dating of terminal bud mortality determines the exact year of budworm feeding, resulting in a bimodal frequency that closely follows the observed defoliation levels (Figure 10A). However, the last year of high terminal bud mortality (1986) does not correspond to the last outbreak year (1985). It is possible that heavy bud abortion rate in 1986 resulted from depleted starch reserves (Ericsson, Larsson & Tenow, 1980) caused by budworm defoliation in the previous years (Webb & Karchesy, 1977).

On the other hand, dating of axis mortality does not necessarily determine actual year of defoliation, as an axis can survive defoliation several years before it dies (see gradual death of main stem in Figure 4C). This explains why axis mortality continues after the infestation, as it does for whole trees, which sometimes die several years after an outbreak (MacLean, 1980; MacLean & Ostaff, 1989). The reiteration frequency distribution was almost the same as the frequency of terminal bud mortality, but with a 1-year lag (Figure 10A), as dormant buds

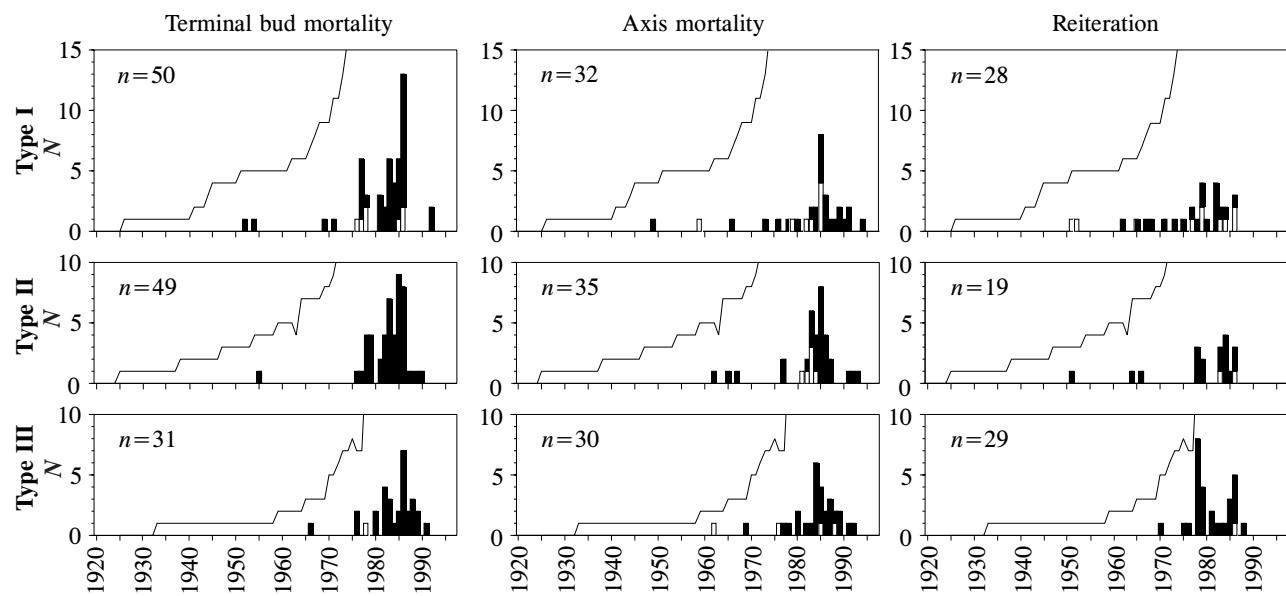


FIGURE 5. Frequency distributions of internodes showing growth anomalies (terminal bud mortality, axis mortality, and reiteration) on main stem, A<sub>1</sub> (white bars) and branches, A<sub>2</sub> (black bars) of three black spruce trees with different cover type (Types I, II, and III). Solid line indicates sample depth (*i.e.*, the total number of internodes). Frequency distributions are similar between types for the same growth anomaly (A<sub>1</sub> and A<sub>2</sub> taken together, Kolmogorov-Smirnov two-tailed test,  $\alpha=0.05$ ).

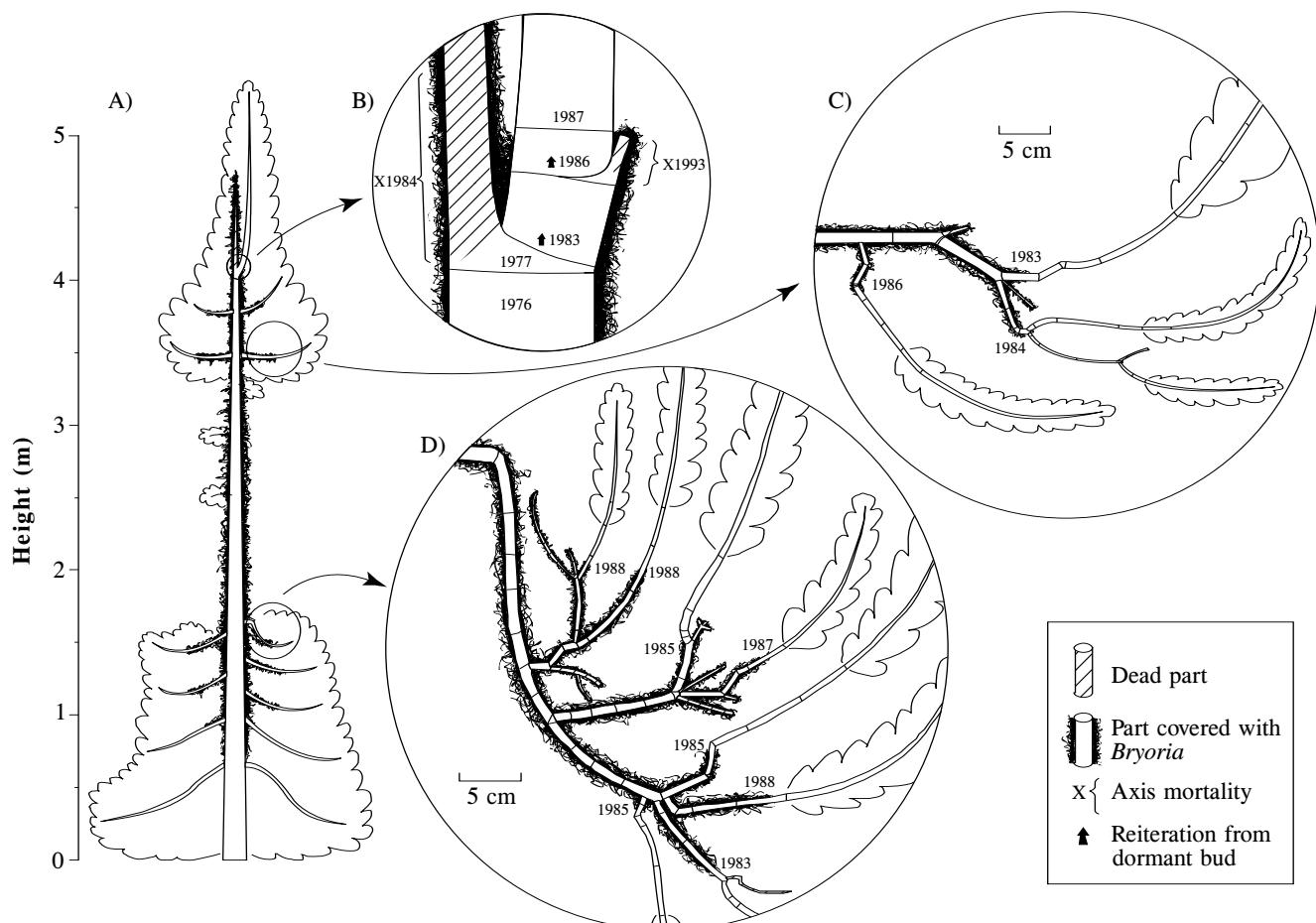


FIGURE 6. Distribution of *Bryoria* on tree of type II (A). Insets: details of main stem at the base of top-kill (B), and branches over (C) and below (D) the branchless, lichen-covered tier of the tree. In B, date of formation of some internodes are shown. In C and D, only A<sub>2</sub> are drawn, and dates of the youngest internodes bearing lichen (maximum extent of *Bryoria* or lichen limits) are shown.

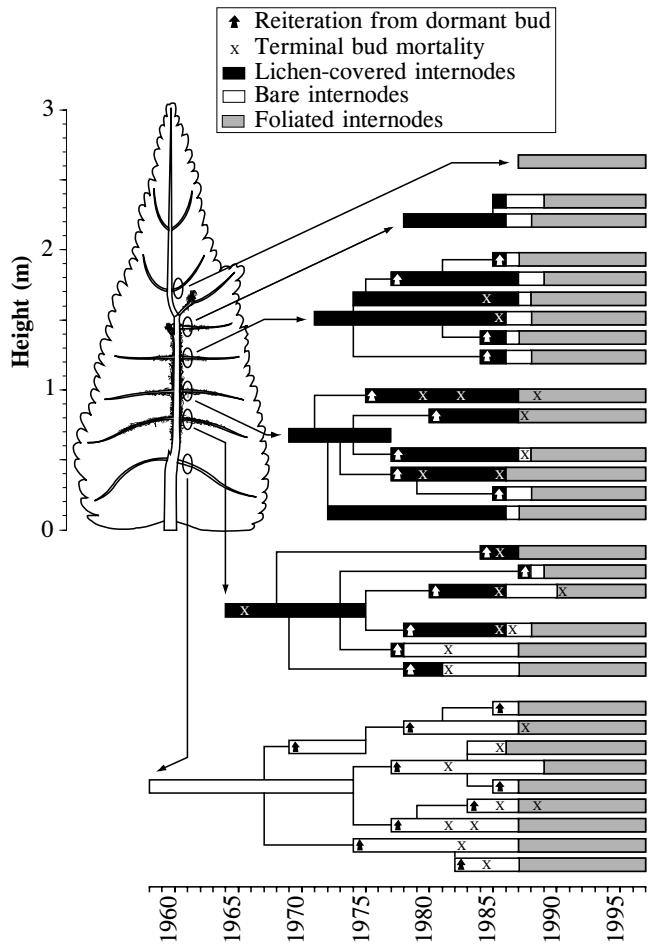


FIGURE 7. Selected branches (bars) along type III tree stem. All internodes are represented with the same length, aligned according to date of formation, and superimposed with corresponding terminal bud mortality and reiteration events.

necessarily flush in the spring following destruction of meristems or with a delay of 1 year or more (Bégin, 1991). The high frequency of reiteration in 1986 is thus in direct response to the damage caused in 1985.

Although our data are retrospective in scope and not derived from direct observations of insect feeding, it is likely that dated growth anomalies were caused by budworm feeding because 1) spruce budworm feeding behaviour is well documented, 2) black spruce architecture is also well established and highly predictable, and 3) growth anomaly frequencies and the aerial defoliation survey data match almost perfectly in time. Even though our sampling design (3 trees in 1 site) was adequate to demonstrate fine-scale relationships between budworm defoliation and black spruce architecture at the tree level, it may not be well suited for population-level studies. We propose that if dendro-architecture is to be used for dating outbreaks, the analysis should focus on growth anomalies occurring on the main stem ( $A_1$ ), including new leaders growing on branches, so that more trees can be studied in several stands. Also, it is difficult to estimate how far back in time the method can detect growth anomalies, because secondary growth will eventually mask small growth anomalies (such as death of small branch tips).

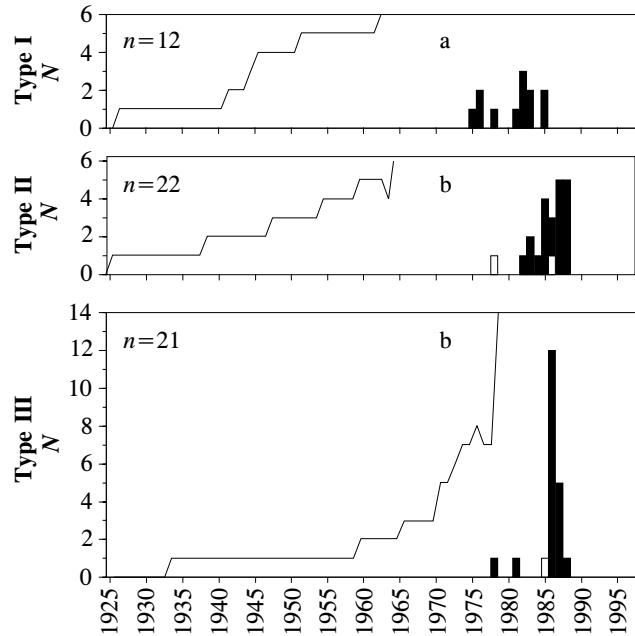


FIGURE 8. Year of formation of the youngest internode covered with *Bryoria* (maximum extent of *Bryoria*, or lichen limits) on  $A_1$  (white bars) and  $A_2$  (black bars) of three spruce trees of different cover type. Solid line indicates sample depth (i.e., total number of internodes). Frequency distributions with same letter are identical ( $A_1$  and  $A_2$  taken together, Kolmogorov-Smirnov two-tailed test,  $\alpha=0.05$ ).

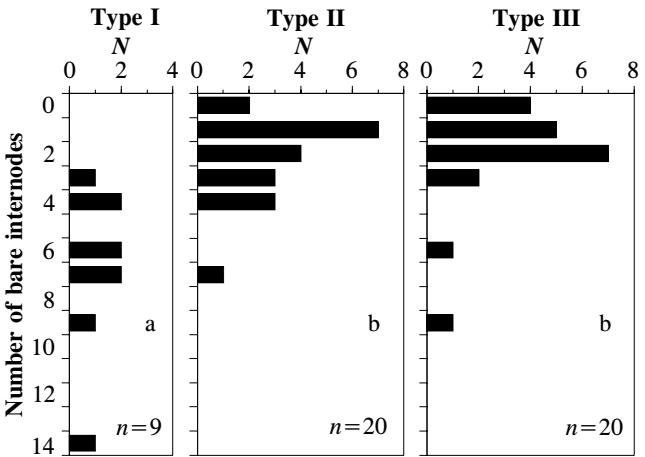


FIGURE 9. Number of bare internodes between lichen-covered internodes and foliated internodes on  $A_2$  of studied trees. Frequency distributions with same letter are identical (Kolmogorov-Smirnov two-tailed test,  $\alpha = 0.05$ ).

Again, focusing on the main stem's growth anomalies would overcome this problem: as growth anomalies (such as top-killing and forked tops) tend to be larger and more obvious on the main stem, it is likely that they would be detectable for several decades (Ferrell & Scharpf, 1982) or even centuries (Bégin, 1991).

#### PATTERNS OF LICHEN COVER

The epiphytic lichen *Bryoria* was mostly found on parts of trees defoliated by the spruce budworm, which supports our initial hypothesis (Figures 6, 7, and 10B). However, *Bryoria* also covered internodes produced after the infestation (last year = 1985), as most lichen limits

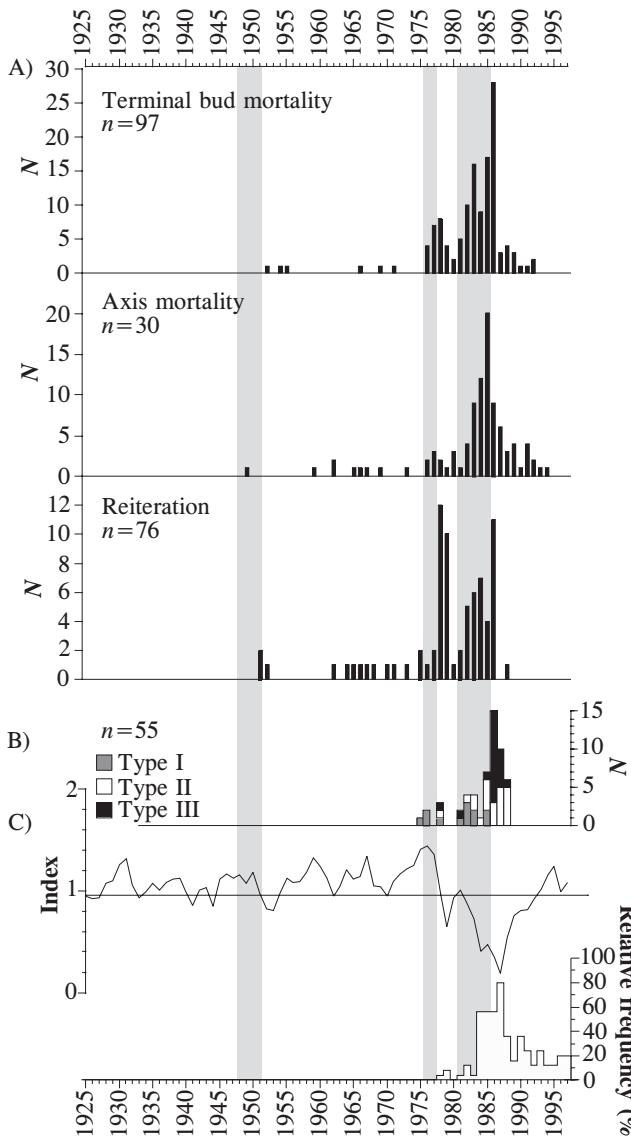


FIGURE 10. Growth anomaly frequency (A), and year of formation of the youngest internode covered with *Bryoria* (maximum extent of *Bryoria*, or lichen limits) (B) on  $A_1$  and  $A_2$  of three spruce trees of different cover type. C) Standardized chronology of black spruce in the study site ( $n = 25$ ; 3 radii per tree); bars represent relative frequency of incomplete rings. Vertical gray bands correspond to periods of severe spruce budworm defoliation, according to aerial defoliation surveys (Gouvernement du Québec, Ministère des Ressources naturelles, Direction de la conservation des forêts).

(i.e., year of formation of the youngest internode bearing lichens) occurred in 1986, 1987, and 1988 (Figure 10B). Unfortunately, the dendro-architectural approach cannot actually determine the year of establishment of *Bryoria* on the axes, as it provides only a static view of lichen distribution and a minimum establishment year. Even though it is not possible to know for certain whether post-epidemic internodes (1986-88) had foliage or not when they were colonized by *Bryoria*, it is likely they had none, as *Bryoria* was never found on living foliage of the studied trees (as in Goward, 1998). This suggests that the internodes were colonized by *Bryoria* only after shedding their senescent needles. Needles stayed on average 9 years on

branches ( $9.3 \pm 0.9$  years; minimum=7 years, maximum=11 years;  $n=77$ ). On the other hand, lichens did not always occupy lichen-free internodes, as there was often one to several bare internodes between lichen-covered and foliated parts of the branches (Figures 7 and 9). These results suggest that *Bryoria* first established on insect-defoliated axes, and colonized nearby internodes only after natural senescence of needles provided new substrate. The rate of colonization seems to be slower than the rate at which new substrate becomes available, however, as *Bryoria* does not occupy all needle-free internodes.

Lichen distribution on type I differs from that of the other two types (Figure 8 and 9), probably because all living branches (Figure 4) are located near maximum snow depth (1 m to 1.5 m; measured every two weeks [Vandal, 1985] during 1980-81 and 1981-82 winters, which had snowfall representative of the 1957-1997 mean). *Bryoria* decomposes rapidly under the snowpack (Taylor & Jones, 1990; Esseen & Renhorn, 1998; Coxson & Curteanu, 2002), as evidenced by the lack of epiphytic lichen in the first meter from the ground on all standing spruce trees in the study area. Furthermore, all lichen-covered trees cut down in a previous study (Simard & Payette, 2001) and left on the ground were completely devoid of *Bryoria* the following summer. Lichen limits in the type I tree were all located near the snowpack, which may have destroyed lichens, therefore resulting in older lichen limits (and concomitantly in a greater number of bare internodes in Figure 9). In contrast, trees of type II and III had several branches well above the snowpack, probably reflecting more accurately the "natural" extent of lichens.

#### BRYORIA AND BLACK SPRUCE DECLINE

Trees chosen for their contrasting lichen cover (types I, II, and III) surprisingly showed similar growth anomaly frequencies and similar lichen limit distributions (except type I: see section above). We propose a model that explains this with three successive processes: defoliation by the spruce budworm, reiteration, and colonization of defoliated tree parts by *Bryoria* (Figure 11). Black spruce trees were first defoliated during the 1976-1985 outbreak. Budworm feeding is recorded in the tree's architecture (destruction of terminal buds and axis) and growth rings (drastic radial growth decrease and incomplete rings) (Figure 10). The morphological response of the tree to defoliation was reiteration. The reiteration process is variable between trees and is determined by the intensity of defoliation and bud mining, physiological conditions of the tree, and genetics. Depending on reiteration success of the main stem and branches, defoliated trees showed different patterns of branch and top mortality (Figure 11B). The subsequent covering of the dead tree parts by *Bryoria* resulted in lichen distribution patterns of types I, II, III, and several others (type X) (Figure 11C). The different cover patterns that were separated into distinct types are thus caused by the same three processes.

Because *Bryoria* grows on tree parts attacked by the spruce budworm, the distribution of the lichen likely corresponds to the cumulative defoliation area on spruce trees. *Bryoria* could therefore be used as a marker of

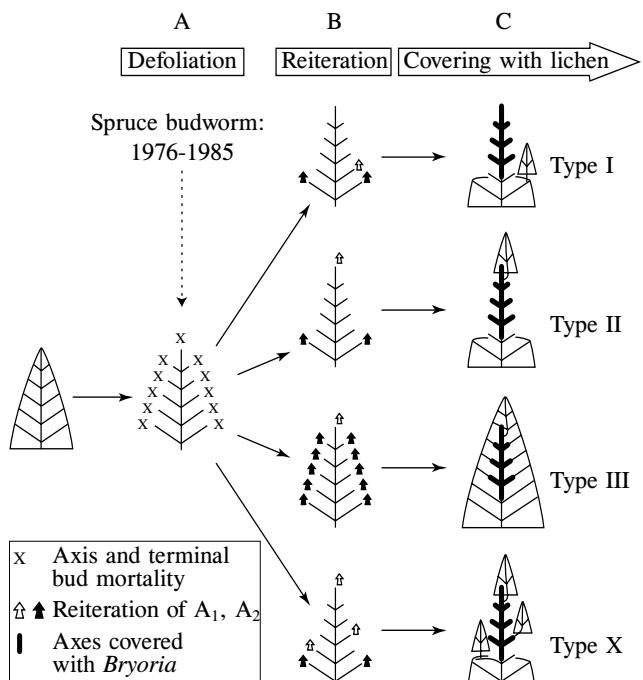


FIGURE 11. Model of defoliation - reiteration - covering explaining the different lichen cover patterns observed in the black spruce-lichen woodland in the Parc des Grands-Jardins area. Spruce budworm defoliation causes death of axes and terminal buds (A); production of new leaders (white arrows) and epicormic shoots (black arrows) by reiteration (B) and subsequent covering of defoliated parts by *Bryoria* (C) generate the main cover patterns observed (types I, II, and III) as well as many other patterns (type X). Note that *Bryoria* is never observed in the lowermost part of trees, even though defoliated, probably because of snowpack influence.

defoliation. This is supported by the fact that *i*) there is a positive relationship between growth reduction and lichen abundance in budworm-defoliated stands of the PGJ area (Figure 8 in Simard & Payette, 2001) and *ii*) this relationship is the same as the one between growth reduction and cumulative defoliation by spruce budworm in balsam fir stands (Figure 4B in MacLean *et al.*, 1996).

*Bryoria* abundance on defoliated trees has not been reported elsewhere in the closed crown boreal forest, which is periodically defoliated by spruce budworm. Thus, the high lichen biomass associated with black spruce decline (Simard & Payette, 2001) is likely a result of the open structure of the lichen woodland. Higher lichen biomass in open stands could result from high irradiance promoting increased lichen growth rates (Kershaw, 1985) and greater ventilation that favours propagule dispersion (Goward, 1998; Dettki, Klintberg & Esseen, 2000). Therefore, it is likely that epiphytic lichen invasion of insect-defoliated trees occurs in other *Bryoria*-rich, open coniferous forests that are subjected to phytophagous insect outbreaks (Goward, 1998).

## Conclusion

In the lichen woodland of the Parc des Grands-Jardins area, the arboreal lichen *Bryoria* colonized parts of spruce trees defoliated during the last spruce budworm outbreak. Our study outlines the high reiterative capacity of black

spruce, able to survive spruce budworm infestation by producing new axes and foliage as they were destroyed. The higher reiterative capacity of black spruce, compared to balsam fir, could partly explain its lesser vulnerability to spruce budworm (D. MacLean, unpubl. data). Moreover, because budburst in black spruce is about 2 weeks later than balsam fir, emerging second-instar larvae have a higher probability of feeding on unopened buds when on black spruce than on balsam fir. As the destruction of buds seems to stimulate reiteration more than simple defoliation does (Piene & Little, 1990), black spruce reiteration could be further favoured. Dendro-architectural analysis allowed us to detect spruce budworm impact at the branch level and at the exact year of feeding. However, this method is time-consuming, and thus few trees can be thoroughly studied. On the other hand, its high resolution at both spatial and temporal scales makes it a powerful tool when this level of precision is needed.

## Acknowledgements

This study was supported financially by the Ministère des Ressources naturelles (Québec), Direction de la recherche forestière and the Natural Sciences and Engineering Research Council of Canada. We are grateful to C. Zimmermann, M. Lafortune, and A. Delwaide for field and laboratory assistance, C. Roy (Herbier Louis-Marie, Université Laval) for lichen identification, and P. Jasinski for useful comments on the manuscript.

## Literature cited

- Alfaro, R. I., G. A. Van Sickle, A. J. Thomson & E. Wegwitz, 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. Canadian Journal of Forest Research, 12: 780-787.
- Anderson, L. E., H. A. Crum & W. R. Buck, 1990. List of mosses of North America north of Mexico. Bryologist, 93: 448-499.
- Arseneau, M.-J., L. Sirois & J.-P. Ouellet, 1997. Effects of altitude and tree height on the distribution and biomass of fruticose arboreal lichens in an old growth balsam fir forest. Écoscience, 4: 206-213.
- Bailey, I. W., 1925a. The "spruce budworm" biocoenose. I. Frost rings as indicators of the chronology of specific biological events. Botanical Gazette, 80: 93-101.
- Bailey, I. W., 1925b. Notes on the "spruce budworm" biocoenose. II. Structural abnormalities in *Abies balsamea*. Botanical Gazette, 80: 300-313.
- Batzer, H. O., 1973. Defoliation by the spruce budworm stimulates epicormic shoots on balsam fir. Environmental Entomology, 2: 727-728.
- Bégin, C., 1991. Analyse architecturale et dendrochronologique d'une pessière à lichens à la limite des forêts. Ph.D. thesis, Université Laval, Sainte-Foy, Québec.
- Bégin, C. & L. Filion, 1999. Black spruce (*Picea mariana*) architecture. Canadian Journal of Botany, 77: 664-672.
- Blais, J. R., 1958. Effects of defoliation by spruce budworm on radial growth at breast height of balsam fir and white spruce. Forestry Chronicle, 34: 39-47.
- Blais, J. R., 1962. Collection and analysis of radial-growth data from trees for evidence of past spruce budworm outbreaks. Forestry Chronicle, 38: 474-484.

- Boisclair, J., 1990. Parc des Grands-Jardins. Le Plan Directeur. Gouvernement du Québec. Ministère du Loisir, de la Chasse et de la Pêche. Direction du plein air et des parcs, Québec.
- Brodo, I. M. & D. L. Hawksworth, 1977. *Alectoria* and allied genera in North America. *Opera Botanica*, 42: 1-164.
- Campbell, J. & D. S. Coxson, 2001. Canopy microclimate and arboreal lichen loading in subalpine spruce-fir forests. *Canadian Journal of Botany*, 79: 537-555.
- Canadian Soil Survey Committee, 1987. The Canadian System of Soil Classification. 2<sup>nd</sup> edition. Publication 1646, Agriculture Canada, Ottawa, Ontario.
- Clement, J. P. & D. C. Shaw, 1999. Crown structure and the distribution of epiphyte functional group biomass in old-growth *Pseudotsuga menziesii* trees. *Écoscience*, 6: 243-254.
- Coxson, D. S. & M. Curteanu, 2002. Decomposition of hair lichens (*Alectoria sarmentosa* and *Bryoria* spp.) under snow-pack in montane forest, Cariboo Mountains, British Columbia. *Lichenologist*, 34: 395-402.
- Dettki, H., P. Klintberg & P.-A. Esseen, 2000. Are epiphytic lichens in young forests limited by local dispersal? *Écoscience*, 7: 317-325.
- Édelin, C., 1977. Images de l'architecture des conifères. Ph.D. thesis, Université Montpellier II, Montpellier.
- Ericsson, A., J. Hellkvist, K. Hillerdal-Hagströmer, S. Larsson, E. Mattson-Djos & O. Tenow, 1980. Consumption and pine growth: Hypotheses on effects on growth processes by needle-eating insects. Pages 537-545 in Persson, T. (ed.). *Structure and Function of Northern Coniferous Forests: An Ecosystem Study*. Ecological Bulletins (Stockholm) 32.
- Ericsson, A., S. Larsson & O. Tenow, 1980. Effects of early and late season defoliation on growth and carbohydrate dynamics in Scots pines. *Journal of Applied Ecology*, 17: 747-769.
- Esseen, P.-A. & K.-E. Renhorn, 1998. Mass loss of epiphytic lichen litter in a boreal forest. *Annales Botanici Fennici*, 35: 211-217.
- Esslinger, T. L., 1997. A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. In North Dakota State University web site. [Online]: <http://www.ndsu.nodak.edu/instruct/esslinge/chcklst7.htm> (first posted 1 december 1997, most recent update 17 July 2002). Fargo, North Dakota.
- Ferrell, G. T. & R. F. Scharpf, 1982. Stem volume losses in grand firs topkilled by western spruce budworm in Idaho. United States Department of Agriculture, Forest Service, Pacific Southwest Research Station Research Paper PSW-164, Albany, California.
- Filion, L., S. Payette, A. Delwaide & N. Bhiry, 1998. Insect defoliators as major disturbance factors in the high-altitude balsam fir forest of Mount Mégantic, southern Québec. *Canadian Journal of Forest Research*, 28: 1832-1842.
- Ghent, A. W., 1958. Studies of regeneration in forest stands devastated by the spruce budworm. 2. Age, height growth, and related studies of balsam fir seedlings. *Forest Science*, 4: 135-146.
- Glerum, C. & J. L. Farrar, 1966. Frost rings in the stems of some coniferous species. *Canadian Journal of Botany*, 44: 879-886.
- Gordon, J. C. & P. R. Larson, 1968. Seasonal course of photosynthesis, respiration, and distribution of <sup>14</sup>C in young *Pinus resinosa* trees as related to wood formation. *Plant Physiology*, 43: 1617-1624.
- Gordon, J. C. & P. R. Larson, 1970. Redistribution of <sup>14</sup>C-labeled reserve food in young red pines during shoot elongation. *Forest Science*, 16: 14-20.
- Goward, T., 1998. Observations on the ecology of the lichen genus *Bryoria* in high elevation conifer forests. *Canadian Field-Naturalist*, 112: 496-501.
- Hallé, F., R. A. A. Oldeman & P. B. Tomlinson, 1978. *Tropical Trees and Forests: An Architectural Analysis*. Springer-Verlag, Berlin.
- Harvey, G. T., 1985. The taxonomy of the coniferophagous *Choristoneura* (Lepidoptera: Tortricidae): A review. Pages 16-48 in C. J. Sanders, R. W. Stark, E. J. Mullins & J. Murphy (ed.). *Recent Advances in Spruce Budworms Research. Proceedings of the CANUSA Spruce Budworms Research Symposium*. Bangor, Maine. Canadian Forestry Service, Ottawa, Ontario.
- Jardon, Y., L. Filion & C. Cloutier, 1994. Tree-ring evidence for endemicity of the larch sawfly in North America. *Canadian Journal of Forest Research*, 24: 742-747.
- Kershaw, K. A., 1985. *Physiological Ecology of Lichens*. Cambridge University Press, Cambridge.
- Krause, C. & H. Morin, 1995a. Changes in radial increment in stems and roots of balsam fir after defoliation by spruce budworm. *Forestry Chronicle*, 71: 747-754.
- Krause, C. & H. Morin, 1995b. Impact of spruce budworm defoliation on the number of latewood tracheids in balsam fir and black spruce. *Canadian Journal of Forest Research*, 25: 2029-2034.
- Krause, C. & H. Morin, 1999. Tree-ring patterns in stems and root systems of black spruce (*Picea mariana*) caused by spruce budworms. *Canadian Journal of Forest Research*, 29: 1583-1591.
- Kulman, H. M., 1971. Effects of insect defoliation on growth and mortality of trees. *Annual Review of Entomology*, 16: 289-324.
- Laberge, M.-J., S. Payette & N. Pitre, 2001. Development of stunted black spruce (*Picea mariana*) clones in the subarctic environment: A dendro-architectural analysis. *Écoscience*, 8: 489-498.
- Lang, G. E., W. A. Reiners & L. H. Pike, 1980. Structure and biomass dynamics of epiphytic lichen communities of balsam fir forests in New Hampshire. *Ecology*, 61: 541-550.
- Liu, C., H. Ilvesniemi & C. J. Westman, 2000. Biomass of arboreal lichens and its vertical distribution in a boreal coniferous forest in central Finland. *Lichenologist*, 32: 495-504.
- Lyons, B., N. M. Nadkarni & M. P. North, 2000. Spatial distribution and succession of epiphytes on *Tsuga heterophylla* (western hemlock) in an old-growth Douglas-fir forest. *Canadian Journal of Botany*, 78: 957-968.
- MacLean, D. A., 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: A review and discussion. *Forestry Chronicle*, 56: 213-221.
- MacLean, D. A., 1985. Effects of spruce budworm outbreaks on forest growth and yield. Pages 148-175 in C. J. Sanders, R. W. Stark, E. J. Mullins & J. Murphy (ed.). *Recent Advances in Spruce Budworms Research. Proceedings of the CANUSA Spruce Budworms Research Symposium*. Bangor, Maine. Canadian Forestry Service, Ottawa, Ontario.
- MacLean, D. A., T. L. Hunt, E. S. Eveleigh & M. G. Morgan, 1996. The relation of balsam fir volume increment to cumulative spruce budworm defoliation. *Forestry Chronicle*, 72: 533-540.
- MacLean, D. A. & D. P. Ostaff, 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. *Canadian Journal of Forest Research*, 19: 1087-1095.
- Mattson, W. J., G. A. Simmons & J. A. Witter, 1988. The spruce budworm in eastern North America. Pages 310-330 in A. A. Berryman (ed.). *Dynamics of Forest Insect Populations*. Plenum Press, New York.
- Marie-Victorin, 1995. *Flore laurentienne*, 3<sup>rd</sup> edition. Les Presses de l'Université de Montréal, Montréal, Québec.

- McCune, B., 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. *Bryologist*, 96: 405-411.
- McGugan, B. M., 1954. Needle-mining habits and larval instars of the spruce budworm. *Canadian Entomologist*, 86: 439-454.
- Morin, H., D. Laprise & Y. Bergeron, 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Québec. *Canadian Journal of Forest Research*, 23: 1497-1506.
- Oldeman, R. A. A., 1974. L'Architecture de la Forêt Guyanaise. ORSTOM Report No. 73. ORSTOM, Paris.
- Ostaff, D. P. & D. A. MacLean, 1995. Patterns of balsam fir foliar production and growth in relation to defoliation by spruce budworm. *Canadian Journal of Forest Research*, 25: 1128-1136.
- Payette, S., N. Bhiry, A. Delwaide & M. Simard, 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: The catastrophic impact of insect defoliators and fire on the spruce-moss forest. *Canadian Journal of Forest Research*, 30: 288-305.
- Piene, H., 1989a. Spruce budworm defoliation and growth loss in young balsam fir: Defoliation in spaced and unspaced stands and individual tree survival. *Canadian Journal of Forest Research*, 19: 1211-1217.
- Piene, H., 1989b. Spruce budworm defoliation and growth loss in young balsam fir: Recovery of growth in spaced stands. *Canadian Journal of Forest Research*, 19: 1616-1624.
- Piene, H. & E. S. Eveleigh, 1996. Spruce budworm defoliation in young balsam fir: The 'green' tree phenomenon. *Canadian Entomologist*, 128: 1101-1107.
- Piene, H. & C. H. A. Little, 1990. Spruce budworm defoliation and growth loss in young balsam fir: Artificial defoliation of potted trees. *Canadian Journal of Forest Research*, 20: 902-909.
- Schmiege, D. C., 1961. Mortality and top killing of spruce-fir caused by repeated budworm defoliation. United States Department of Agriculture, Forest Service, Lakes States Forest Experimental Station, Technical Note No. 597, St-Paul, Minnesota.
- Simard, M., 2000. Dépérissement de l'épinette noire dans la pessière à lichens du parc des Grands-Jardins : une analyse dendroécologique et dendroarchitecturale. M.Sc. thesis, Université Laval, Sainte-Foy, Québec.
- Simard, M. & S. Payette, 2001. Black spruce decline triggered by spruce budworm at the southern limit of lichen woodland in eastern Canada. *Canadian Journal of Forest Research*, 31: 2160-2172.
- Stevenson, S. K. & K. A. Enns, 1993. Quantifying arboreal lichens for habitat management: A review of methods. British Columbia Ministry of Forests, Research Branch, Report IWIFR-42, Victoria, British Columbia.
- Stillwell, M. A., 1956. Pathological aspect of severe spruce budworm attack. *Forest Science*, 2: 174-180.
- Swetnam, T. W. & A. M. Lynch, 1989. A tree-ring reconstruction of western spruce budworm history in the southern Rocky Mountains. *Forest Science*, 35: 963-986.
- Swetnam, T. W. & A. M. Lynch, 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs*, 63: 399-424.
- Taylor, B. R. & H. G. Jones, 1990. Litter decomposition under snow cover in a balsam fir forest. *Canadian Journal of Botany*, 68: 112-120.
- Tomlinson, P. B., 1983. Tree architecture. *American Scientist*, 71: 141-149.
- Van Sickie, G. A., R. I. Alfaro & A. J. Thomson, 1983. Douglas-fir height growth affected by western spruce budworm. *Canadian Journal of Forest Research*, 13: 445-450.
- Vandal, D., 1985. Écologie comportementale du caribou du parc des Grands-Jardins. M.Sc. thesis, Université Laval, Sainte-Foy, Québec.
- Webb, W. L. & J. J. Karchesy, 1977. Starch content of Douglas-fir defoliated by the tussock moth. *Canadian Journal of Forest Research*, 7: 186-188.
- Williams, C. B., Jr., 1967. Spruce budworm damage symptoms related to radial growth of grand fir, Douglas-fir, and Engelmann spruce. *Forest Science*, 13: 274-285.