Bauce *et al. Annals of Forest Science* (2024) 81:40
https://doi.org/10.1186/s13595-024-01260-9

Annals of Forest Science

RESEARCH PAPER Open Access

Biennial aerial application of *Bacillus thuringiensis* Berliner var. *kurstaki* is the most cost-effective approach of protection against spruce budworm (*Choristoneura fumiferana* [Clemens])

Éric Bauce[1], Alain Dupont[2], Christian Hébert[3], Richard Berthiaume[2], Roberto Quezada-García[1] and Alvaro Fuentealba[1*]

Abstract

Key message Aerial application of *Bacillus thuringiensis* Berliner var. *kurstaki* (Btk) every second year to stands of white spruce (*Picea glauca* (Moench)Voss.), black spruce (*Picea mariana* Mill.) and balsam fir (*Abies balsamea* (L.) Mill.) is the most cost-effective spraying scenario for reducing the impact of spruce budworm (*Choristoneura fumiferana* Clemens) on wood production, providing a similar level of forest protection, but at lower cost, to the standard scenario currently used in which 50% of current year's foliage is protected every year.

Context Insect outbreaks can have significant effects on forest productivity and various formulations of *Bacillus thuringiensis* Berliner var. *kurstaki* (*Btk*) are used to reduce their damage. In the Province of Québec, Canada, control programs aim to protect at least 50% of current-year foliage to limit tree mortality, but little information exists on the long-term cost-effectiveness of such programs.

Aims Our goal was to evaluate the benefit/cost ratio and the efficacy of different *Btk* protection scenarios in reducing coniferous tree mortality and growth losses over a 11-year period. We hypothesized that less-intensive protection approaches (*Btk* applications every 2 or 3 years) may provide similar levels of protection but with higher cost-effectiveness ratios than the standard program currently used in Quebec.

Methods In 2007, we established nineteen 100-ha experimental units in Quebec's Côte-Nord region to determine the efficacy and cost-effectiveness of different *Btk* spraying scenarios for reducing tree mortality and volume losses

Handling editor: Aurélien Sallé.

This paper has undergone an Optional Open Peer Review. Read the Peer Review Report (Battisti et al. 2024) at https://hal.inrae.fr/hal-04630314

*Correspondence:
Alvaro Fuentealba
alvaro.fuentealba-morales.1@ulaval.ca
Full list of author information is available at the end of the article

in coniferous stands dominated by mature balsam fir trees (*Abies balsamea* (L.) Mill., with white spruce (*Picea glauca* (Moench) Voss.) and black spruce (*P. mariana* Mill.) as companion species. Tree mortality was monitored annually in three circular plots of 400 m^2 within each experimental unit. Growth losses were evaluated using stem analyses.

Results Mortality was much higher in balsam fir than in black spruce and white spruce (respectively 74.4%, 13.8% and 5.9% in untreated stands) in all protection scenarios. The application of *Btk* every 2 years reduced balsam fir mortality to a level similar to the standard scenario (10.3% vs 7.15%, respectively) at a much lower cost. Growth losses have also been reduced but not to the same extent as in the standard scenario.

Conclusion Spraying *Btk* every 2 years provides effective protection to balsam fir and is the most cost-effective scenario. A less intensive use of *Btk* would mitigate impact on non-target lepidoptera and allow protecting other areas, such as habitat of the woodland caribou, a threatened species which avoids disturbed areas.

Keywords Spruce budworm, *Bacillus thuringiensis*, Spray operations, Tree mortality, Volume losses, Balsam fir, Spruce spp

1 Introduction

Natural disturbances such as insect outbreaks not only significantly affect forest structure, composition, ecosystem function, and services (Anderegg et al. 2015) but can also adversely affect regional economies (MacLean 2016). Globally, insect outbreaks have affected over 29 million ha annually, on average, between 2002 and 2017 (FAO 2020). The cost associated with these outbreaks can be substantial in terms of tree mortality and growth losses. For example, Ayres and Lombardero (2000) estimated that the economic impact of forest pests could account for over one billion USD per year in the USA. Similarly, Chang et al. (2012) projected that uncontrolled outbreak of the spruce budworm (*Choristoneura fumiferana* [Clemens]), which is a native defoliator, could incur economic losses in eastern Canada ranging from 3.3 to 4.7 billion CAD between 2012 and 2041. Therefore, effective management methods to protect stands against insect outbreaks are urgently needed to preserve the integrity of forests and ecosystem services they provide (Wainhouse 2005).

Several methods of direct (insecticide application, biological control and semiochemicals) and indirect (increasing stand diversity, application of silvicultural techniques such as thinning, among others) control have been advocated to protect forests against insect defoliators (Wainhouse 2005; Bentz et al. 2019). The selection of the appropriate combination of pest management methods requires a clear understanding of the manner in which these techniques affect tree and stand resistance, together with a thorough assessment of system responses to the prescriptions so that subsequent decisions are better informed (Wainhouse 2005). Direct control using aerial spraying of pesticides has been utilized since the early twentieth century against insect defoliators (e.g., Trägårdh 1935; Prebble 1975) with positive results in terms of insect mortality (e.g., Blais 1977), foliage protection (e.g., Prebble 1975; Blais 1977) and tree survival after the outbreak (e.g., Fuentealba et al. 2022).

Bacillus thuringiensis var. *kurstaki* (*Btk*) is currently one of the most widely used biological insecticide around the world (van Frankenhuyzen et al. 2016; Hajek and van Frankenhuyzen 2017), due to its specificity for Lepidoptera and its efficacy in reducing the damage they cause. Nevertheless, 25 years ago, aerial applications of *Btk* against the spongy moth *Lymantria dispar* (L.) triggered emotional debates among citizens of the United States, arguing over the specificity of *Btk* for Lepidoptera (Scriber 2001). A few years earlier, abundance and richness of non-target Lepidoptera were shown to decrease after *Btk* applications (Miller 1990; Wagner et al. 1996). However, few years later, another study showed some recovery of non-target Lepidoptera one to four years after the end of spraying operations (e.g., Boulton et al. 2007), indicating that adverse effects of *Btk* on forest ecosystems and non-target organisms were limited and temporary at best (van Frankenhuyzen et al. 2016). This shows the role of scientific research in framing public debate with solid data. However, most studies involving the use of *Btk* were carried out after only 1 year of applications and concerns remain regarding the effects of multi-year applications of *Btk* on non-target Lepidoptera, such as during spruce budworm outbreaks that may last over a decade.

In Canada, commercial formulations of *Btk* have been used since 1980s to reduce spruce budworm-induced damage (Dorais et al. 1995; van Frankenhuyzen et al. 2016). Periodic outbreaks of this native defoliator first result in growth reductions and, eventually, in death of attacked trees after 4 or 5 years of severe defoliation in balsam fir (*Abies balsamea* [L.] Mill.) (Blais 1958; MacLean and Ostaff 1989; MacLean 1980; 2016) or 6 to 7 years in white spruce (*Picea glauca* [Moench] Voss) (Blais 1981). Mortality in black spruce (*Picea mariana* [Mill.] B.S.P.) is marginal and usually limited to over-mature and suppressed trees (Lussier et al. 2002). Growth losses due to spruce budworm defoliation can be observed from the first year of defoliation and onward (Piene 1980; Krause et al. 2012). Growth reductions of up to 20% have been reported during the first year of defoliation (Piene 1980). During the second year of severe defoliation, these reductions can reach 25–56% (Batzer 1973; Piene 1980) and up to 75–95% by the end of the epidemic (Batzer 1973). Growth losses are less severe in spruce species (Piene 1991; Chen et al. 2017). Blais (1964) reported growth losses of 36% in white spruce over a defoliation period of 11 years. In black spruce, growth reductions begin after 1 to 3 years of severe defoliation and can reach up to 40% in volume by the end of the outbreak (Krause et al. 2012).

The main goal of spruce budworm control programs in the Province of Quebec (Canada) is to protect at least 50% of the current-year foliage to limit host tree mortality (Dorais et al. 1995). Despite positive results in terms of foliage protection (e.g., Bauce et al. 2004; Fournier et al. 2010; Fuentealba et al. 2015, 2019), this approach requires repeating *Btk* applications every year for around 10 years in the same stands, making it a costly approach. In addition to high annual costs, this program faces important logistical problems, as it covers a vast territory covering tens of million of hectares. With manpower shortages, limited number of aircraft, and a narrow time window (around 25 days), conducting operations on such large-scale program is a challenge. As a result, only 5–10% of the area infested by the spruce budworm can be protected, which remains insufficient for the various forest users. There is little information on the overall cost of this approach and its long-term effects in terms of reducing tree mortality and growth losses and therefore its cost-effectiveness. Furthermore, it is not known whether the threshold of 50% current-year foliage protection targeted for aerial spraying is justified in all situations, given the observed differences in resistance to budworm attack among host species (Blais 1981, 1983a; Fuentealba et al. 2017). A quantitative evaluation of the impact of spruce budworm and the cost-effectiveness of forest protection programs is essential, not only to determine the best strategy to use but also to improve our ability to predict and maintain stable supplies of wood to the forest industry.

To test whether a less-intensive protection program can provide an adequate level of protection, we initiated a long-term study in 2007, in which we compared four aerial *Btk* spraying scenarios, together with an unsprayed scenario. The scenarios involved a gradient of protection intensity that ranged from no protection (used as control treatment for the experiment) to intensive protection with multiple applications of *Btk* each year to reduce budworm impact at the lowest possible level. Scenarios developed to provide very light and light protection involved respectively *Btk* applications every 3 and 2 years. To assess their efficacy and cost-effectiveness, we compare them to our reference scenario, i.e., the standard scenario, which is the protection approach currently used in Quebec. This approach applies *Btk*, with the aim of protecting at least 50% of current-year foliage after a year of moderate or severe defoliation (≥ 35%) (for more details, see Table 1).

In a previous article, we evaluated the efficacy of the aforementioned protection scenarios in protecting tree residual photosynthetic capacity (RPC) during the first 7 years (2010–2016) of this long-term study (Fuentealba et al. 2019). RPC was estimated using the residual foliage area after defoliation and the estimated contributions to total photosynthetic capacity of foliage of different age classes and spruce budworm defoliation intensities (for further details, please see Fuentealba et al. 2019). Our results showed that a less intensive spraying scenario (*Btk* application every 2 years) than the one currently used in Quebec provided an adequate level of protection by maintaining tree residual photosynthetic capacity (RPC) above the threshold (Fuentealba et al. 2019) associated with low balsam fir mortality (38 to 51% of RPC) (Dorais and Hardy 1976). RPC is a more reliable proxy for assessing tree capacity to recover after an outbreak than is current-year defoliation, given that the former considers effects of current and past defoliation and informs on the physiological status of the defoliated host tree (Dorais and Hardy 1976; Fuentealba et al. 2019). In this study, we used tree mortality and growth data from this long-term study to assess the efficacy of the aforementioned scenarios in protecting Quebec's forests in terms of their effects on wood production (losses of wood fiber through tree mortality and growth reductions). We hypothesized that a less-intensive protection approach might be more cost-effective than the approach currently used in Quebec, referred as the standard scenario. Scenarios involving *Btk* application every 3 and 2 years may provide similar foliage protection and wood losses to the standard scenario but at a much lower cost. The main goal of this study is to evaluate the efficacy of the five previously mentioned *Btk* spray scenarios for reducing tree mortality and growth losses over the 11-year outbreak period (2010–2020) and compare their economic profitability. We aimed at determining if less-intense *Btk* scenarios (*Btk* application every 3 and 2 years) may be profitable alternatives to protect Quebec's forests by providing results similar to the standard approach currently used in terms of tree mortality and growth losses reduction but at a lower cost.

2 Materials and methods

2.1 Study area

The study is located in Quebec's Côte-Nord region (Fig. 1), where the climate is continental humid. Annual precipitation varies between 900 and 1300 mm, while mean annual temperature ranges from − 1.5 °C to 2.5 °C (Robitaille and Saucier 1998). The topography of the region is rugged, with high hills and deep valleys. Till is the main surface deposit, but fluvio-glacial deposits can

Table 1 Description of the *Btk* spray application scenarios that were compared in this study, and efforts invested in each one over 11 years of implementation, as expressed by the overall number of *Btk* spray applications conducted for each scenario, and cost of *Btk* interventions depending on the number of years of treatment and aerial applications for the different protection scenarios

Scenario	Description	Rationale behind each scenario	Number of years of treatment	Number of *Btk* applications	Mean cost (CAD/ha)	Total cost (CAD/ha)
1	No protection	Control (SBW impact when no protection is applied)	0	0	0	0
2	Very light protection (*Btk* applied every 3 years)	It aims to reduce mortality in susceptible hosts. The spruce budworm outbreak could induce certain thinning by killing weak trees, such as those exhibiting a small crown. Such thinning would favor future crop trees, thereby producing an interesting timber volume after the end of the outbreak	4	7	23.31	279.69
3	Light protection (*Btk* applied every 2 years)	The objective of this scenario is to reduce tree mortality and growth losses. This strategy could be allowed to either rotate the areas to be protected or increase the area treated without additional cost	6	11	36.46	437.55
4	Standard protection (*Btk* applied 1 year after moderate to severe defoliation to keep defoliation ≤ 50%)	Standard strategy used in Quebec. It aims to protect at least 50% of current-year foliage to avoid tree mortality	11	20	65.97	791.59
5	Intensive protection (up to three Btk applications per year)	The purpose of this strategy is to keep SBW defoliation at 20% or less to reduce growth losses and tree mortality to a minimum	12	29	89.15	1069.83

be found at the bottoms of broad valleys (Robitaille and Saucier 1998). Forests are dominated by balsam fir and black spruce. Historically, this region had been affected by light spruce budworm outbreaks until the 1970s when a severe outbreak occurred, which caused significant stand and landscape-scale mortality in the southern part (Blais 1983a; Bouchard and Pothier 2010). During the present infestation, spruce budworm populations increased steadily from 2006 to 2020, defoliating 2319 ha in 2006 to over 4.4 million ha in 2020. The area that was affected by this defoliator declined sharply in 2022, to about 340,000 ha, of which around 80% sustained light defoliation (MRNF 2022).

2.2 Experimental design

Nineteen 100-ha experimental units were selected and established in 2007 in balsam fir (*Abies balsamea* (L.) Mill.) dominated stands with disseminated black (*Picea mariana* Mill.) and white spruce (*P. glauca* (Moench) Voss.) according to the following criteria: (1) spruce budworm populations or traces of defoliation had been detected; (2) forest stands were highly susceptible and vulnerable; and (3) no operational constraints were in place and site accessibility was adequate. With regard to the second criterion, the mixed fir-spruce stands in question are composed mainly of balsam fir (average content in the experimental units was 58% of standing volume) and, to a lesser extent, of white spruce (average content in the experimental units was 17% of standing volume) and black spruce (average content in the experimental units was 25% of standing volume). Experimental units were randomly assigned to one of five spraying scenarios (including unsprayed stands) (Table 1), with four replicates per scenario, with the sole exception of the approach currently used in Quebec, to which three units were assigned. One of the experimental units belonging to this scenario was removed from the analysis as spruce budworm populations remained very low and defoliation did not reach the moderate level that is required to trigger *Btk* applications.

2.3 Btk formulations and applications

Btk applications were carried out on an operational basis using all available resources in terms of aircraft and registered products. Foray 76B™ and Bioprotec HP™ are the *Btk* strain HD-1 commercial formulations at a

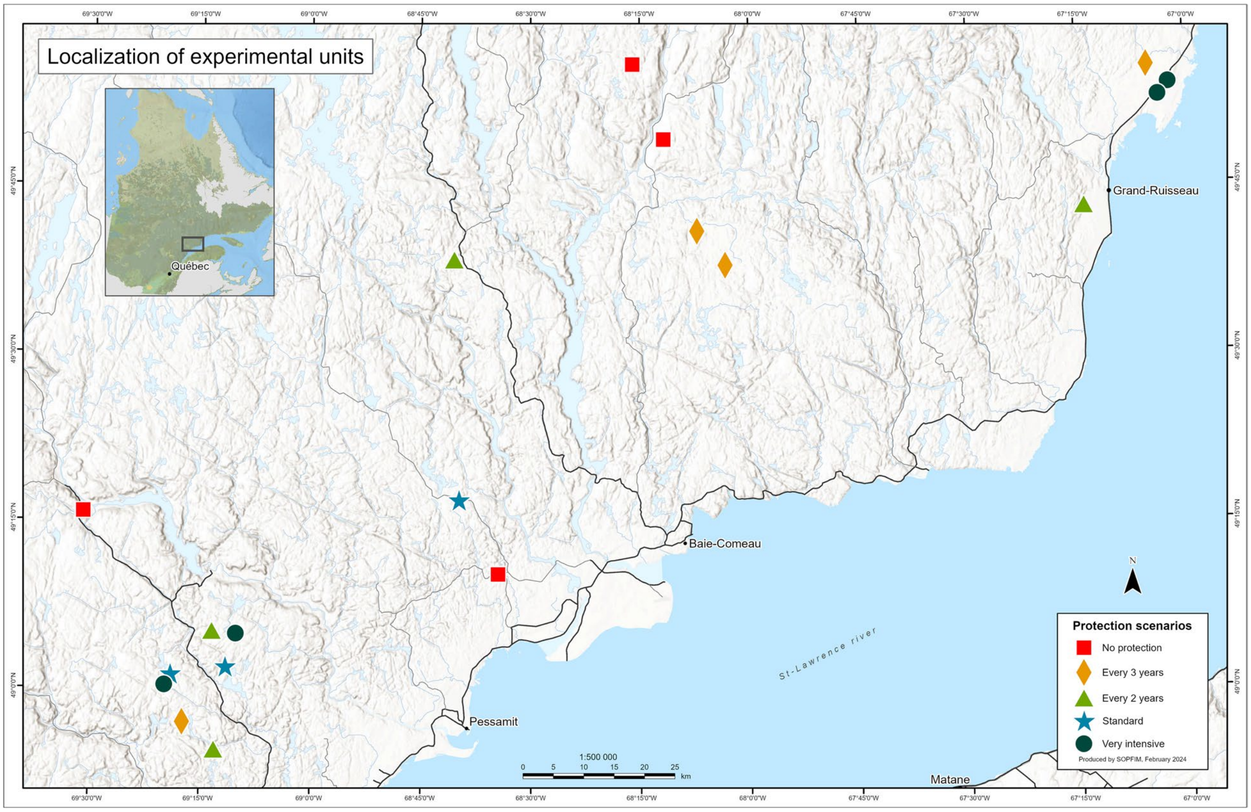

Fig. 1 Experimental unit locations within the study area (Côte-Nord region of Quebec). Nineteen 100-ha experimental units were selected and established in 2007 and were assigned to one of the five protection scenarios tested in this study. Scenarios: no protection, *Btk* applied every 3 years, *Btk* applied every 2 years, *Btk* applied after 1 year of moderate to severe defoliation to keep defoliation ≤ 50% (standard protection in Quebec), *Btk* applied every year to keep spruce budworm impact at a minimum (intensive protection scenario)

nominal potency of 20.0 billion international units per liter (BIU/L) (Abbott Laboratories, Chicago, IL, USA; on behalf of Valent Bio-Sciences Corporation, Libertyville, IL, and AEF Global Inc., Levis, QC, respectively). Both *Btk* formulations were applied to the previously described experimental units. Over the years, many aircraft have been used (Cessna 188; Dromader M-18; Air Tractor 402, 502, 504, 602 and 802), with six or eight Micronair atomizers (Micronair Sprayers Ltd., Bromyard, Herefordshire, UK); the Micronair atomizers, which spin at 8000 rpm, were located within 75% of the total wingspan. These aircraft were flown between 161 and 210 km/h, with 50, 80 or 100-m spray widths. Aerial treatments were performed in the early morning or at dusk under good weather conditions (no rain, maximum wind speed of 16 km/h). The flow rate through the nozzles was calibrated to deliver 1.5 L/ha or 30 BIU/ha. *Btk* was sprayed up to three times yearly to maintain defoliation levels under 20% in the intensive protection scenario and under 50% when the other units were treated. The first aerial application of *Btk* against spruce budworm targeted third- to early fourth-instar larvae (beginning in mid-June), whereas the second and third applications were carried out 5 and 10 days later, respectively, when populations were very high (> 24 larvae per branch; SOPFIM 2022). *Btk* treatments were timed to coincide with early flushing of balsam fir shoots. This timing provides optimal protection for balsam fir but does not substantially affect treatment efficacy in white spruce and black spruce that are found in the mixed fir-spruce stands (Cadogan and Scharbach 1993; Carisey et al. 2004; Fuentealba et al. 2015).

2.4 Evaluation of tree mortality and growth losses

Within each of the 19 experimental units, three circular sample plots of 400 m^2 (radius = 11.28 m) were established in 2011 to monitor tree growth and quantify mortality (expressed in terms of volume, m^3) that was attributable to spruce budworm in each of the different protection scenarios. Starting in 2011, all previously numbered merchantable stems (DBH ≥ 9.1 cm) that were present in the sample plots were measured annually using tree-calipers, then classified as dead or alive. Trees classified as dead in 2011 were considered dead from causes other than spruce budworm and, thus, removed from the analysis. Host trees killed during the outbreak were first identified by the complete absence of needles. Mortality was then confirmed by examining the cambium near breast height for discoloration and dryness (MacLean 1979). Only trees still standing, together with those present on the forest floor with bark and branches, were included in mortality estimates. Given the low annual natural mortality of hosts (MacLean and Ostaff 1989) and that host wood decomposes rapidly (e.g., Campbell and Laroque 2007), the criteria used to select trees greatly reduced the likelihood of including natural mortality occurring prior to the outbreak (Bergeron et al. 1995). Furthermore, to remove suppression-related mortality, only trees with DBH $\geq$ 10 cm were included in the mortality estimates.

To properly document the effects of the insect and the protection scenarios on volume growth of the three host species, 135 "sentinel trees" (45 balsam fir, 45 white spruce and 45 black spruce individuals) were randomly identified in each of the 19 experimental units, yielding a total of 2565 individuals for the entire system (Bauce et al. 2024). Each of the 2565 trees was monitored annually for current-year defoliation using the Fettes grid (Fettes 1950) and recording their health status (cumulative defoliation, dead or alive). The number of trees selected at the start of the experiment and monitored for more than 10 years made it possible to carry out stem analyses on subjects that were still alive in 2019 and 2020.

During the 2019 and 2020 seasons, a total of 342 trees (6 individuals per host species, yielding 18 trees per experimental unit) were felled to collect a series of discs for stem analyses. These analyses were carried out to assess growth losses according to the different scenarios of protection. After felling and measuring the total length of each stem, a disc was taken at each of the following heights: 30 cm, 80 cm, 1.30 m (DBH), 2.30 m, and at all subsequent meter-intervals until the diameter attained 4 cm at the end. All discs were numbered and returned to the laboratory before being analyzed. Subsequently, all disks were sanded on one face, and, to facilitate analysis, four cross-shaped radii were marked out using a binocular microscope to highlight annual growth rings. Annual ring-widths were measured and cross-dated along these radii using an optical digitizing scanner (Epson Expression 1680, 200–400 dpi resolution), combined with image analysis software (WinDendro, Regent Instruments Inc., Quebec, QC). For each year and tree, the volumetric and cambial surface area growth was determined using XLSTEM macros (Regent Instruments Inc.).

Volume growth estimates were based upon growth expressed as an annual volume increment (AVI) using the methodology proposed by Gross (1992). As treatment began in various years in each experimental unit, scenario efficacy was assessed according to the number of years after the beginning of the treatment of a given scenario rather than by calendar year. Estimated growth losses were calculated for each year since the first treatment based upon the average 5-year pre-treatment growth period using the following formula:

$$\mathrm{AVI}_n(\%)=\frac{VI_n}{VI_p}\times 100$$

where AVI is the annual volume increment expressed as a percentage for the year n since the first treatment, VIn is the volume increment for the year n since the first treatment, and VIp is the mean volume increment of the 5-year pre-treatment period. This index eliminates a considerable portion of variation in growth related to tree size (Gross 1992). A growth index above or below 100% indicates respectively higher growth (growth increase) or lower growth (loss of growth) compared to the average 5-year pre-treatment growth period. Furthermore, specific volume increment (SVI, $\mathrm{m}^3/\mathrm{m}^2$) was calculated for each year since the first treatment using the following formula:

$$S\mathrm{VI}_n=\frac{\mathrm{VI}_n}{(\mathrm{CSA}(\mathrm{n}-1)+\mathrm{CSAn})/2}$$

where SVIn is the specific volume increment for the year n since the first treatment, VIn is the volume increment for the year n since the first treatment, CSAn-*1* is cambial surface area for the year *n-1*, and CSAn is the cambial surface area for the year n since the first treatment. SVI is a measure of tree growth that reflects the net result of a tree's metabolic activities (Shea and Armson 1972) and is correlated to a lesser degree with tree age than with other growth measures. Therefore, it is deemed to be more sensitive to changes in growth that are produced by external stimuli such as defoliation (Piene 1981).

2.5 Cost–benefit analysis

In our cost–benefit analysis, we refer to the indicator ratio throughout the paper, in terms of the benefit/cost ratio (BCR), which was calculated to evaluate the economic profitability of each scenario tested in this study. BCR expresses how much financial value a project may generate in relation to the investment that is required to see through to the end of the project (Keefe et al. 2012). The cost of treatments is derived from real estimates that are included in annual reports of SOPFIM (Société de protection des forêts contre les insectes et maladies) activities linked to aerial applications of *Btk* (e.g., SOPFIM 2022). Costs were estimated using the following premises: (a) the year 2009 was not considered in cost estimation because treatments began in 2010 or later; (b) costs come from regular protection programs conducted in natural forests; (c) 2020 costs were not included, due to extra costs that were incurred by the use of helicopters instead of airplanes as a result of COVID 19 pandemic; (d) the average cost was determined from an average weighted by the area that was treated; (e) costs generated by single, double, and triple application of *Btk* were updated using the consumer price index (CPI), which was calculated annually by the Bank of Canada (Statistics Canada 2021); (f) the second and third applications were 16% less expensive than the first application due to fixed costs that were unrelated to the area being protected. The weighted average cost of the first aerial application of *Btk* for the period 2010–2021 was 42.9 CAD (in 2021 dollars) per hectare, whereas the additional costs of a second and third application of *Btk* were 36.06 CAD (each in 2021 dollars). Based on these estimates, we calculated the total cost of investments made to conduct each protection scenario studied (Table 1). The benefits were estimated as the gains in volume that can be attributed to the protection scenarios by subtracting volume losses through mortality and growth losses per hectare observed in each protection scenario from volume losses observed in the no protection scenario (Table 2). We used a range of timber values (5 to 20 CAD per m^3) to evaluate the effect of this variable on the BCR analysis.

2.6 Statistical analysis

Tree mortality (expressed in m^3) was averaged by host species and experimental unit, and then submitted to repeated-measures analyses of variance (ANOVA) in a completely randomized design, where the number of years after the first treatment was considered as a repeated-measures object. Given the large difference in mortality between balsam fir and spruce species reported in the literature (e.g., MacLean 1980; Fuentealba et al. 2022), mortality was separately evaluated for each host species. The models used to evaluate mortality for each host species contained fixed effects (*Btk* spraying scenarios and number of years after the first treatment) and all possible interactions between these terms and random effects (experimental unit nested within scenario). We performed these analyses using PROC GLIMMIX (SAS Institute Inc., 2003) since the data had a binomial distribution (SAS Institute Inc., 2003). Volume growth losses (AVI and SVI) and current-year defoliation were averaged by host species and experimental unit and then submitted to repeated-measures ANOVA using PROC MIXED in a completely randomized design where the number of years after the first treatment was considered as a repeated-measures object. The MIXED procedure of SAS (SAS Institute Inc. 2003) was used with a repeated statement and the covariance structure (compound symmetry for volume growth losses and first-order autoregressive for defoliation) that minimized the Akaike criterion. The Kenward-Roger method was used to calculate the degrees-of-freedom (Kenward and Roger 1997). Given that the volume growth loss data did not meet assumptions of normality and homoscedasticity, the tests were performed on ranked data. The models contained fixed effects (*Btk* spraying scenarios, host species, and number of years after the first treatment) and all possible interactions between these terms and random effects (experimental unit nested within the scenario). The LSMEANS statement (SAS Institute Inc. 2003) computed least-squares means and performed multiple comparisons (Tukey–Kramer adjustment) for each factor and interaction.

Table 2 Overall volume losses (mortality and growth) linked to the spruce budworm outbreak and volume gains attributable to treatments for the three host species according to the different protection scenarios. This information was used to estimate the benefits used in the cost–benefit analysis. The benefits were estimated as the gains in volume that can be attributed to the protection scenarios by subtracting volume losses through mortality and growth losses per hectare that were observed in each protection scenario from volume losses that were observed in the no protection scenario

	Losses				**Gains**			
Scenario	Balsam fir (m^3/ha)	White spruce (m^3/ha)	Black spruce (m^3/ha)	Total (m^3/ha)	Balsam fir (m^3/ha)	White spruce (m^3/ha)	Black spruce (m^3/ha)	Total (m^3/ha)
No protection	91.4	7.3	13.9	112.6	0	0	0	0
Btk every 3 years	56.6	2.9	4.3	63.8	34.8	4.4	9.6	48.8
Btk every 2 years	21.9	2.2	3.8	28.35	69.5	5.1	10.1	84.3
Standard	6.7	2	3.8	13	84.7	5.3	10.1	99.6
Intensive	5.8	2.2	1.2	9.3	85.6	5.1	12.7	103.3

3 Results

The results of repeated-measures ANOVA indicate that protection scenarios and the number of years since the start of aerial spraying have significant effects on balsam fir mortality. Yet, the interaction of these two factors, in turn, was not significant (Table 3). Balsam fir mortality was higher in unprotected units than in those assigned to other protection scenarios tested in this study (Fig. 2, Tables 4 and 5). Indeed, we observed that unprotected units lost in average 56.1 m^3/ha balsam fir volume, whereas units assigned to the other protections scenarios lost in average between 12.6 to 50.7 m^3/ha less balsam fir volume than the no protection scenario (Table 4). In contrast, cumulative mortality remains low in spruce species and did not exceed 14% of available volume, regardless of the protection scenario being considered (Fig. 3; Table 5). Nevertheless, the protection scenarios had also statistically significant effects on white spruce and black spruce mortality (Table 3). Spruce mortality was significantly higher in unprotected units compared to the other protection scenarios, exhibiting a cumulative mortality of 1.8 m^3/ha in white spruce and 6.1 m^3/ha in black spruce (Table 4). Host cumulative mortality varied from 6.4 to 64 m^3/ha, with the highest mortality being observed in unprotected units (Tables 2 and 4). Balsam fir was the most strongly affected host species. Yet, balsam fir volume loss per hectare was significantly reduced in units subjected to *Btk* treatments every two years, and to the standard and intensive scenarios (Fig. 2).

In terms of relative changes, balsam fir mortality in unprotected units was ~ 34% higher than in the those treated with *Btk* every 3 years, ~ 64% higher than in units treated with *Btk* every 2 years, ~ 67% higher than in those treated using the standard scenario, and ~ 71% higher than in those treated with the intensive protection scenario (Fig. 2, Table 5). It should be noted that cumulative mortality was similar in units treated every two years and in those treated with the standard approach (10.26% and 7.15%, respectively) after 11 years of treatment (Fig. 2, Table 5). Spruce species in turn exhibited cumulative mortality varying between 5.94% and 13.83% in unprotected units whereas it did not surpass 4% in the other protection scenarios (Fig. 3 and Table 5).

Furthermore, balsam fir mortality followed an incremental trend over time regardless of the protection scenario being considered. Indeed, balsam fir mortality was negligible, and this trend remained stable until the sixth year after the start of spraying (Fig. 2). From the sixth year onward, mortality increases continuously over time in the no protection scenario and in units treated with *Btk* every 3 years (Fig. 2). For the other protection scenarios (standard and intensive protection spraying scenarios and in units treated every 2 years), a slight increase in mortality is perceptible from the seventh year onward (Fig. 2). In contrast, the number of years since the start of aerial spraying did not have a significant impact on spruce species mortality (Table 3).

Defoliation level during the study period varied significantly between host species as well as among spraying scenarios and number of years after the first treatment (Table 6). Balsam fir sustained greater defoliation than spruce species throughout the study period (Fig. 4). In general, experimental units assigned to more intensive spraying scenarios sustained less defoliation, but it varied greatly through time (Fig. 4). Cumulative volume growth losses varied among host species from 2.8 to 48.7 m^3/ha (Table 4). Indeed, cumulative volume growth losses are very low for balsam fir in units subjected to the standard and intensive scenarios (0.55 and 1.50%, respectively; Table 5) and low in those protected every 2 or 3 years (Table 5). In the case of spruce species, cumulative volume growth losses ranged from 0.8 to 3.8 m^3/ha (Table 4) which represent relative losses ranging from 14.80 to 42.40% of volume growth (Table 5), depending upon the protection scenario.

Protection scenario, host species, years after the first treatment and the interactions between protection scenario and host species, and protection scenario and years after the first treatment had significant effects on AVI (Table 6). Indeed, marked reductions in AVI were observed for the three host species in unprotected units and in those treated every three years (Fig. 4). AVI losses are first noted 3 years after the first treatment in black spruce and 4 years after the first treatment in balsam fir and white spruce in unprotected units. White spruce shows the least significant AVI reductions in unprotected units, while black spruce and balsam fir show similar AVI reductions by the end of the study. In units treated every 3 years, the three species show a similar reduction in AVI after 10 years of treatment (Fig. 4).

The units treated every 2 years also showed reductions in AVI, but these were less important than those observed in unprotected units and those treated every 3 years in balsam fir and black spruce (Fig. 4). In contrast, white spruce showed similar losses to those observed in units treated every 3 years (Fig. 4). The standard protection scenario, in turn, appears to be effective in reducing AVI losses in balsam fir only. AVI reductions were observed in this species only at the end of the study period, whereas spruce species sustained AVI losses throughout the study period. These were less important when compared to less intense protection scenarios (Fig. 4). The intensive scenario is effective in reducing AVI losses in balsam fir, given that no growth losses were observed during the study period. Furthermore, this scenario seems to protect black spruce reasonably well, given that AVI reductions

Table 3 Summary of repeated-measures ANOVA using PROC GLIMMIX showing the effects of various *Btk* spray scenarios and number of years after the first treatment on balsam fir and spruce mortality

Source of variation	**Balsam fir**			**White spruce**			**Black spruce**		
	F	*df*	*p*	*F*	*df*	*P*	*F*	*df*	*p*
Protection scenario	7.16	4,110	**<0.0001**	2.90	4,82	**0.0266**	3.67	4,82	**0.0084**
Years after 1st treatment	6.77	7,110	**<0.0001**	0.83	5,82	0.8331	0.62	5,82	0.6857
Interaction	0.44	28,110	0.9933	0.22	20,82	0.9998	0.48	20,82	0.9655

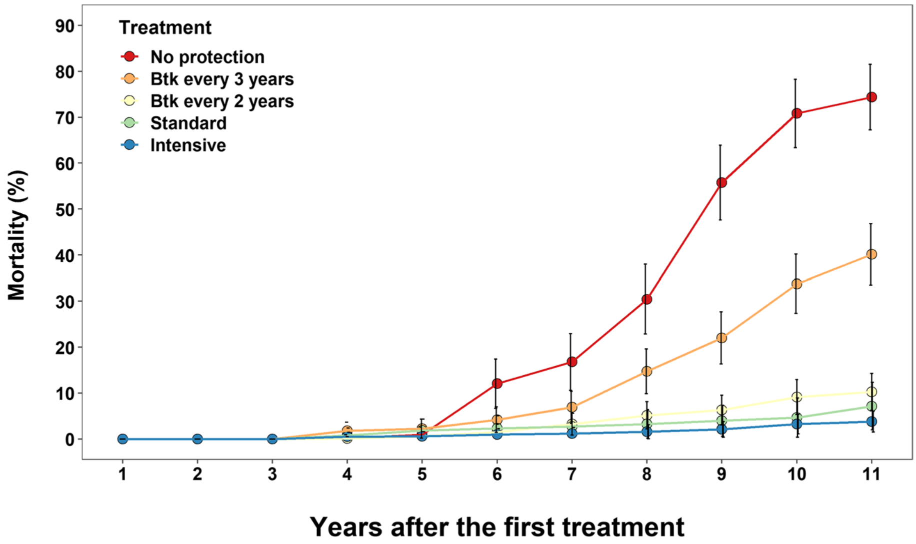

Fig. 2 Balsam fir cumulative mortality (%) according to protection scenario and years after the first treatment (lsmeans ± SEM). Scenarios: no protection, *Btk* applied every 3 years, *Btk* applied every 2 years, *Btk* applied after 1 year of moderate to severe defoliation to keep defoliation ≤ 50% (standard protection in Quebec), *Btk* applied every year to keep spruce budworm impact at a minimum (intensive protection scenario)

Table 4 Cumulative volume losses (mortality and volume growth reductions) in m^3/ha according to host species and protection scenario

	Mortality (m^3/ha)				**Volume growth losses (m^3/ha)**			
Scenario	Balsam fir	White spruce	Black spruce	Total	Balsam fir	White spruce	Black spruce	Total
No protection	56.1 ± 7	1.8 ± 0.8	6.1 ± 4	64.0 ± 7	35.3 ± 2.1	5.5 ± 2.1	7.8 ± 2.1	48.7 ± 2.1
Btk every 3 years	43.5 ± 7	1.1 ± 0.8	0.5 ± 0.5	45.1 ± 7	13.1 ± 2.1	1.8 ± 2.1	3.8 ± 2.1	18.7 ± 2.1
Btk every 2 years	11.9 ± 7	0.6 ± 0 4	0.9 ± 0.6	13.4 ± 7	9.1 ± 2.1	1.5 ± 2.1	2.8 ± 2.1	13.5 ± 2.5
Standard	7.1 ± 9	0.2 ± 0.15	0.0 ± 0.0	7.3 ± 9	0.2 ± 2.1	1.9 ± 2.5	3.8 ± 2.5	6.0 ± 2.5
Intensive	5.4 ± 7	0.6 ± 0.3	0.4 ± 0.3	6.4 ± 7	0.4 ± 2.1	1.6 ± 2.1	0.8 ± 2.1	2.0 ± 2.1

Table 5 Cumulative volume losses (mortality and volume growth reductions) as percentages according to host species and protection scenario

	Mortality (%)				**Volume growth losses (%)**			
Scenario	Balsam fir	White spruce	Black spruce	Total	Balsam fir	White spruce	Black spruce	Total
No protection	74.38 ± 7.4	5.94 ± 1.7	13.83 ± 2.9	42.75 ± 6.2	54.40 ± 6.0	48.70 ± 6.0	55.90 ± 6.0	53.10 ± 6.0
Btk every 3 years	40.17 ± 6.7	4.11 ± 1.5	1.27 ± 1.0	25.84 ± 5.1	44.10 ± 6.0	35.10 ± 6.0	42.40 ± 6.0	39.50 ± 6.0
Btk every 2 years	10.26 ± 4.0	1.65 ± 0.8	2.25 ± 1.3	6.99 ± 2.8	22.86 ± 6.0	33.60 ± 6.0	20.91 ± 6.0	24.80 ± 6.0
Standard	7.15 ± 5.2	0.40 ± 0.6	0.0 ± 0.0	3.69 ± 2.9	0.55 ± 7.0	26.80 ± 7.0	25.20 ± 7.0	17.60 ± 7.0
Intensive	3.80 ± 2.3	1.82 ± 0.9	0.96 ± 0.8	2.95 ± 1.8	1.50 ± 6.0	27.90 ± 6.0	14.80 ± 6.0	14.80 ± 6.0

did not often exceed 16% (Fig. 4). Finally, even if white spruce exhibited AVI losses in units assigned to the intensive scenario, these were less significant when compared to growth losses observed in units treated with the standard scenario (Fig. 4).

Host species, years after the first treatment, and the interactions between protection scenario and host species, and protection scenario and years after the first treatment had significant effects on SVI (Table 5). Balsam fir exhibited a higher SVI compared to spruce species,

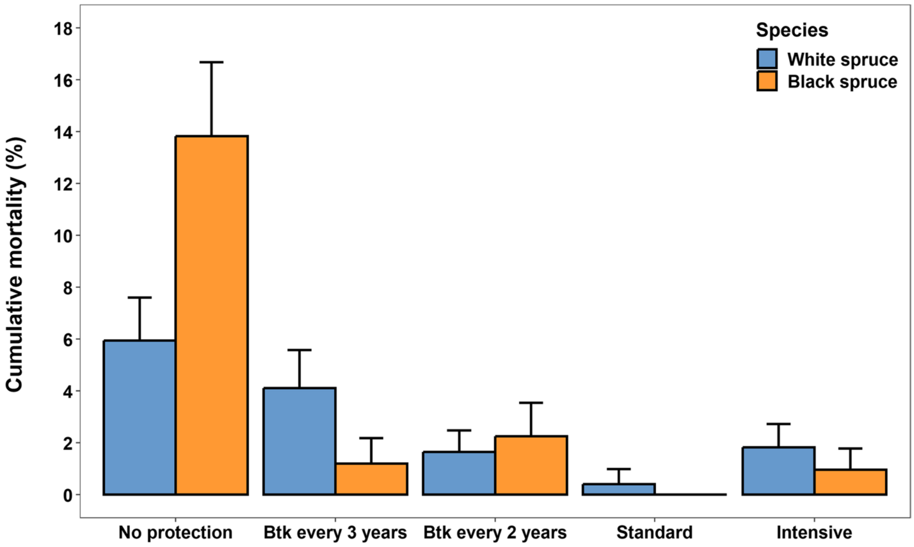

Fig. 3 Spruce spp. cumulative mortality according to protection scenario. Scenarios: no protection, *Btk* applied every 3 years, *Btk* applied every 2 years, *Btk* applied after 1 year of moderate to severe defoliation to keep defoliation ≤ 50% (standard protection in Quebec), *Btk* applied every year to keep spruce budworm impact at a minimum (intensive protection scenario)

Table 6 Summary of repeated-measures ANOVA using PROC MIXED showing the effects of various *Btk* spray scenarios, host trees (balsam fir, white spruce and black spruce), and number of years after the first treatment on annual volume increment (AVI), specific volume increment (SVI), and current-year foliage defoliation

Source of variation	AVI*			SVI*			Defoliation		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
Protection scenario	4.67	4,14	**0.0131**	1.27	4,14	0.3263	47.32	4,14	**< 0.0001**
Host species	38.86	2,395	**< 0.0001**	56.66	2,395	**< 0.0001**	115.21	2,104	**< 0.0001**
Scenario × host species	11.27	8,395	**< 0.0001**	8.74	8,395	**< 0.0001**	1.56	8,124	0.144
Years after 1st treatment	76.25	9,394	**< 0.0001**	118.03	9,395	**< 0.0001**	47.14	10,368	**< 0.0001**
Scenario × years after 1st treatment	3.7	36,394	**< 0.0001**	2.69	36,394	**< 0.0001**	7.8	39,388	**< 0.0001**
Host species × years after 1st treatment	0.94	18,394	0.525	0.89	18,394	0.5879	1.56	20,333	0.0609
Scenario × host species × years after 1st treatment	0.77	72,394	0.9173	0.43	72,394	1	0.78	78,353	0.9129

[*] Variables were rank-transformed

in both unprotected units and those that had been subjected to the standard and intensive scenarios. No difference was observed in the units treated every two and three years (Fig. 4). In general, decreases in SVI were observed in all spraying scenarios tested in this study, but they were more important in spruce species than in balsam fir, especially in experimental units assigned to the standard and intensive protection scenarios (Fig. 4).

BCR shows that all protection scenarios tested proved to be profitable when timber values ranged between 10 and 20 CAD/m^3, assuming that harvesting occurs shortly after the end of spraying operations (Fig. 5). However, a loss of profitability is observed for all protection scenarios when the timber value was 5 CAD/m^3. Furthermore, the light protection scenario exhibited the highest BCR value (3.85), confirming that applying *Btk* every 2 years is the most profitable approach to manage forests affected by a spruce budworm outbreak. Furthermore, the operational cost associated to the different scenarios differed significantly. Deploying the intensive scenario resulted in a cost of 1069.83 CAD/ha, whereas the standard scenario cost 791.59 CAD/ha during the study period. These operational expenses are around 2.4 and 1.8 times higher than the cost of applying *Btk* every 2 years (437.55 CAD/ha) (Table 1). Consequently, applying Btk every 2 years is not only the most profitable approach to protect forest against spruce budworm but also its lower operational cost as compared with the two aforementioned scenarios would allow to protect additional area without the need to increase the budget allocated to forest protection.

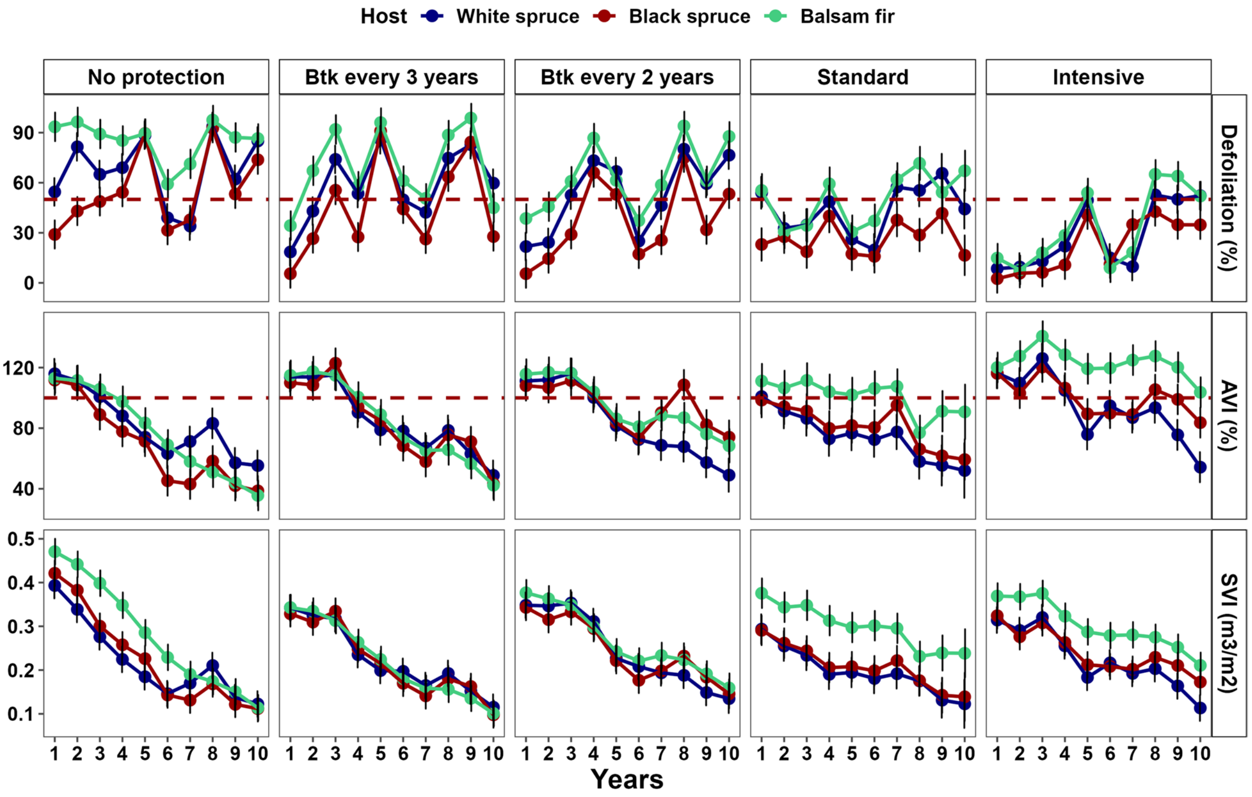

Fig. 4 Current-year defoliation (%), annual volume increment (AVI) of the tree (estimated using stem analysis data), and specific volume increment (SVI) according to host species, protection scenario and years after the first treatment (lsmeans ± SEM). Scenarios: no protection, *Btk* applied every 3 years, *Btk* applied every 2 years, *Btk* applied after 1 year of moderate to severe defoliation to keep defoliation ≤ 50% (standard protection in Quebec), *Btk* applied every year to keep spruce budworm impact at a minimum (intensive protection scenario)

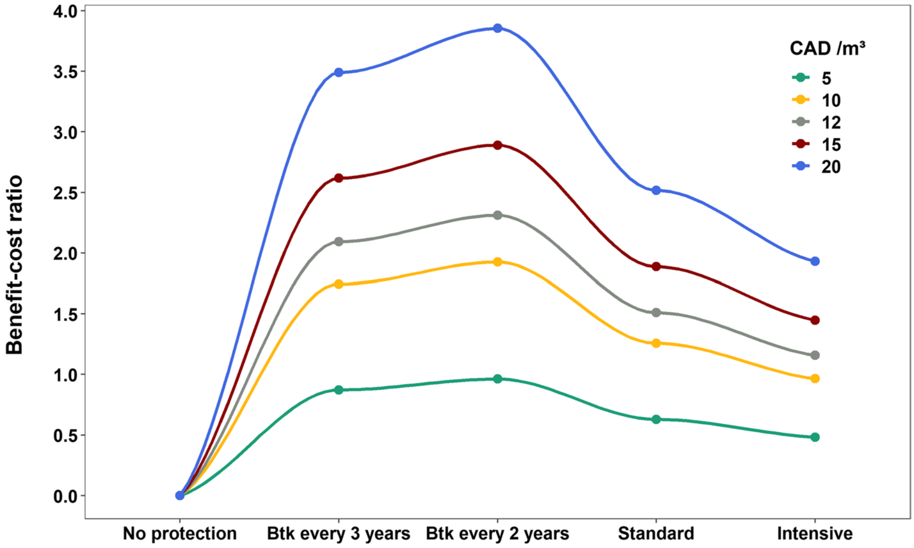

Fig. 5 Benefit–cost ratios for the different protection scenarios tested based on simulations varying the monetary value of standing softwood timber. The weighted average cost of the first aerial application of *Btk* for the period 2010–2021 was CAD 42.9 (2021 dollars), whereas the additional costs of a second and third application of *Btk* were CAD 36.06 (each in 2021 dollars). Based on these estimates, we calculated total cost of investments that were made to conduct each protection scenario studied. The benefits were estimated as the gains in volume that can be attributed to the protection scenarios by subtracting volume losses through mortality and growth losses per hectare that were observed in each protection scenario from volume losses that were observed in the no protection scenario

4 Discussion

Our results show that the most cost-effective protection scenario for reducing wood losses caused by a SBW outbreak is spraying *Btk* every two years. At a lower cost, it reduces tree mortality to a level similar to that of the standard scenario, which is the protection scenario that has been deployed in Quebec over the last 35 years. Balsam fir cumulative mortality (expressed as m^3/ha) in units protected with a *Btk* application scenario ranged from 3.80 to 40.17% depending upon protection intensity, whereas unprotected units exhibited 74.38% mortality. In other words, the protection scenarios tested in this study saved an average of 12.6 to 50.7 m^3/ha of balsam fir volume by preventing spruce budworm-related mortality as compared with unprotected units. These results are consistent with the literature, confirming that aerial spraying can substantially reduce balsam fir mortality (e.g., Batzer 1973; MacLean et al. 1984; Fournier et al. 2010; Fuentealba et al. 2022). Reduction in wood volume losses from balsam fir mortality observed in stands sprayed with *Btk* every 2 years, compared to the no protection scenario (average of 44.2 m^3/ha), is noticeably higher than that reported in a previous study, conducted in the Ottawa River Valley and which used the standard scenario (20.5 m^3/ha; Fournier et al. 2010). Our study area belongs to the boreal forest and is dominated by highly vulnerable coniferous stands, while the Ottawa River Valley belongs to the temperate forest in which deciduous trees dominate and where conifers grow in less vulnerable mixed stands. Thus, the volume of vulnerable trees to the spruce budworm was much higher in our study area than in Fournier et al. (2010). Nevertheless, the reduction in wood volume losses from balsam fir mortality in our study is also higher than that reported during the previous outbreak when both chemical and biological insecticides were used in several regions of Quebec (34.8 m^3/ha; Fuentealba et al. 2022), attesting for the efficacy of this less-intensive scenario but also suggesting that aerial application technology has improved since the last outbreak. The application of *Btk* every 2 years reduced balsam fir mortality in highly vulnerable forests affected by a very severe spruce budworm outbreak. Moreover, among all the scenarios tested, the application of *Btk* every 2 years had the highest benefit/cost ratio, regardless of the monetary value of the wood used in the simulations. This shows that the application of *Btk* every 2 years is the most cost-effective approach for mitigating the impacts of spruce budworm outbreaks. This conclusion is further supported by the similar levels of mortality observed in units assigned to these two scenarios (10.26 vs 7.15% in units treated every 2 years and treated with the standard approach, respectively), together with the findings that this strategy maintained defoliation at a moderate intensity level (≤75%) for most of the study period, thereby providing reasonable protection in terms of maintaining balsam fir photosynthetic capacity (Fuentealba et al. 2019). These results also corroborate the conclusion of Fuentealba et al. (2022) that it is not necessary to reach the target of protecting 50% of the current-year foliage every year to substantially reduce balsam fir mortality.

Considering that around 5% of the spruce budworm infested area is protected with *Btk* at the peak of the outbreak, spraying every 2 years instead of every single year may also allow protecting a greater forest area every year and reduce the need to implement salvage logging plans. When several million hectares are affected by an outbreak (13 M ha in 2020, at the peak of the outbreak), the scale at which salvage logging must be done largely exceeds the harvesting capacity of the forest industry and the annual allowable cut defined by the Québec's Chief Forester. The benefit/cost ratio of spraying *Btk* every 3 years indicates that this scenario is also more profitable than the standard scenario. Yet, the high balsam mortality (40.17%) observed in stands sprayed with *Btk* every 3 years renders this scenario less appealing than applying *Btk* every 2 years for maintaining the wood supply needed by the forest industry.

A similar assessment applies to volume growth losses in balsam fir since the debut of spraying operations. The extent of AVI losses is inversely related to protection intensity. Indeed, AVI losses in trees still alive at the end of the study period attained a maximum annual reduction of about 65% of the average 5-year pre-defoliation annual volume increment and a cumulative volume growth loss of 54.4% by the end of the study period in unprotected blocks. This trend concurs with previous studies reporting severe reductions in annual increment caused by spruce budworm defoliation in unprotected stands, which may range from 20 to 80% of the pre-defoliation volume increment (e.g., MacLean 1981; MacLean et al. 1996; Fournier et al. 2010). Stands treated every 3 years also showed poor performance in terms of volume growth protection, confirming that this scenario is less suitable for protecting balsam fir stands from spruce budworm attack, from a wood production perspective. In contrast, balsam fir individuals in units assigned to the intensive and standard scenarios exhibited very low cumulative AVI losses after 10 years of defoliation, demonstrating the high efficacy of these scenarios for protecting volume growth during outbreaks. These scenarios would be favorable in highly productive balsam fir stands, if the goal was to protect tree growth, regardless of protection costs. However, even if applying *Btk* every 2 years is not as efficient as standard and intensive scenarios in protecting balsam fir tree growth, it should be recommended for protecting most balsam fir stands as it is the most profitable scenario, based on BCR.

SVI decreased under all protection scenarios, but the magnitude of SVI reductions was related to protection intensity. This response is consistent with a previous study reporting that the extent of SVI reduction was generally related to defoliation intensity (MacLean et al. 1996). Indeed, trees in unprotected units exhibited a steady reduction in SVI over the study period. This trend is consistent with effects of severe defoliation on SVI in unprotected stands (Piene 1980; MacLean et al. 1996). Piene (1980) had reported SVI reduction of about 20% after the complete removal of current-year foliage in balsam fir during the first year of severe defoliation. It is also noteworthy that SVI was higher in the unprotected stands than it was in the protected ones at the beginning of the study. This phenomenon may be explained by the fact that only the most vigorous trees survived the severe defoliation observed in unprotected stands. Trees growing in stands treated every 3 and 2 years show similar trends in SVI reductions. Furthermore, the standard and intensive scenarios were more effective than the other scenarios in attenuating SVI reductions during the study period. Similar trends in SVI reductions (4 to 26%) resulted after 2 years of partial defoliation in New Brunswick (MacLean et al. 1996).

Mortality sustained by spruce species was much less important than mortality exhibited by balsam fir, which is consistent with the literature (MacLean 1980, 2016). Indeed, cumulative mortality sustained by spruce species was very low in all protection scenarios, not exceeding 14% in unprotected units. Tree mortality continues for several years after the cessation of defoliation (Blais 1981). Therefore, more spruce mortality would be expected, but it is very unlikely that it would reach levels as high as those observed in balsam fir. For example, MacLean (1980) reported that spruce mortality ranged between 13 and 36% depending upon stand age. Blais (1981) observed a 17% mortality rate for white spruce in the last year of defoliation, but it increased to 52% 4 years after cessation of defoliation. In contrast, Fuentealba et al. (2022) reported low spruce mortality at the end of the previous outbreak in Quebec within unprotected stands. Here, white and black spruce experienced 5.62 and 3.64% mortality, respectively. Information regarding volume losses in spruce species is scarce, given that most studies have focused upon spruce budworm's most vulnerable host, i.e., balsam fir (MacLean 1981). The few available studies report growth volume losses ranging from 9 to 27% in young white spruce trees after 2 years of severe defoliation (Piene 1991), 78% in white spruce plantations (D'Amato et al. 2011), and 1 to 34% in dominant black spruce individuals (Morin et al. 2008). Our results show that AVI losses were more important than mortality in spruce species. Indeed, respective AVI reductions of about 49% in white spruce and 60% in black spruce of the average 5-year pre-defoliation annual volume increment were observed in unprotected stands. Although all protection scenarios were effective in stemming AVI losses, especially the standard and intensive scenarios, the efficacy of all protection scenarios was lower in spruce species than it was in balsam fir. It should be noted that black spruce exhibited a more positive response than did white spruce to spraying operations. A similar tendency was observed for SVI losses.

The difference in efficacy of protection scenario observed between spruce species and balsam fir may be due to species-specific characteristics. White spruce foliage exhibits faster growth, greater development, and more foliage per unit area compared to balsam fir foliage (Greenbank 1963; Wu et al. 2020). Furthermore, white spruce is extremely sensitive to losses of current-year foliage. Even low spruce budworm defoliation intensities may increase its shoot production relative to balsam fir, which exhibits strong epicormic shoot development only after severe defoliation and bud destruction (Piene 1998). Moreover, Wu et al. (2020) found that spruce species respond more strongly to cumulative defoliation than does balsam fir. Black spruce produced 41% more current-year shoots than did white spruce, which in turn produced 38% more current-year shoots than did balsam fir after 3 years of defoliation (Wu et al. 2020). Foliar chemistry and shoot phenological development, have also been identified as factors that may affect *Btk* efficacy (Carisey et al. 2004). For example, the lower *Btk* efficacy in white spruce trees in terms of larval mortality and foliage protection has been related to higher tannin concentrations in its foliage compared with that of balsam fir (Carisey et al. 2004). In addition, white spruce shoots retain their bud cap for a few weeks following bud-break, unlike balsam fir. Consequently, larvae that are feeding upon white spruce needles may be protected by the bud cap when the first *Btk* application against spruce budworm is performed, which may lower *Btk* efficacy (e.g., Volney and Cerezke 1992). Black spruce bud-break occurs up to two weeks after balsam fir bud-break (Blais 1957). This situation can force young larvae to mine old foliage, which may protect them from *Btk* applications. Furthermore, the current approach used in Quebec (standard scenario) was developed to protect balsam fir stands and the first application is synchronized with balsam fir phenology (Bauce et al. 2004; SOPFIM 2022). Consequently, the timing of spraying operations would not be appropriate for protecting spruce species in mixed spruce-fir stands. A recent study testing the efficacy of three *Btk* application treatments on white spruce and balsam fir in mixed stands found that efficacy of all treatments was low in terms of foliage protection and larval mortality in the former species (Fuentealba et al. 2023). The three treatments tested were (1) early applications timed to coincide with balsam fir bud-break, (2) delayed application 6 days later, and (3) double applications. The results of this study suggest that spruce characteristics may be more important than timing of treatment applications in explaining the efficacy of the *Btk* treatments observed in spruce species.

Another potential benefit of biennial *Btk* applications is the reduction of the effects that spraying operations and outbreaks of major defoliators may have on non-target Lepidoptera. Several studies have reported a reduction in the abundance and richness of non-target Lepidoptera after *Btk* spraying operations (e.g., Miller 1990; Wagner et al. 1996; Boulton et al. 2007). Population densities of most non-target Lepidoptera, however, tend to return to the pre-spraying levels 1 to 4 years following the end of spraying operations (e.g., Boulton et al. 2007). Consequently, a less intense spraying scenario could reduce the pressure that *Btk* may exert on non-target Lepidoptera, thereby attenuating the impact of this protection approach on their population densities. It is also important to consider how non-target Lepidoptera may be affected by outbreaks of major defoliators such as spruce budworm. Not protecting stands with *Btk* against the spruce budworm is also a management decision, and it may have important effects on Lepidoptera as important mortality of balsam fir occurs, which lead to new successions, dominated by deciduous trees and shrubs. Preliminary results showed that Lepidoptera communities found in unprotected stands were typical of post-harvest stands, indicating that the ecological integrity of mature balsam fir forest had been lost. (Hébert et al. 2023; Béland et al. 2024). Furthermore, this type of habitat is no longer appropriate to support the woodland caribou, a threatened species in Canada which avoids stands severely affected by the spruce budworm (Labadie et al. 2021). To make informed decisions, forest managers thus need to consider the impacts of all possible management options and discuss them with the various stakeholders.

Efficacy of protection programs may be further influenced by stand characteristics such as drainage quality, stand age, and species composition through their effects on tree vulnerability to spruce budworm (MacLean 1980, 2016; Fuentealba et al. 2022). Given that insect outbreaks always have stochastic elements that may produce unusually severe tree mortality regardless of stand characteristics (Blais 1983b; MacLean 2016), implementation of effective control programs requires not only a general knowledge of the effects of stand characteristics on stand vulnerability but also the manner in which distinctive features at landscape and regional scale can alter its vulnerability. Increasing evidence confirms that landscape biodiversity and heterogeneity play an important role in the duration and spatial extent of insect outbreaks and in forest vulnerability to these biotic disturbances (Kneeshaw et al. 2021). Furthermore, climate effects should also be incorporated into the decision process, as adverse climate may affect tree growth, resulting in loss of vigor and greater vulnerability to spruce budworm attack (e.g., de Grandpré et al. 2019). This knowledge may help to improve forest protection efficacy not only by allowing the criteria that are used to be refined when establishing priority areas for protection using aerial applications of *Btk* but also in effectively using silviculture tools that are aimed at implementing pest-resistant forest landscapes.

5 Conclusion and recommendations

The protection approach that has been used over past decades in the Province of Quebec has proven to be effective in protecting balsam fir stands from spruce budworm defoliation (e.g., Bauce et al. 2004; Fournier et al. 2010; Fuentealba et al. 2015, 2019; and this study). Yet, little information is available regarding the efficacy of spraying operations in reducing not only tree mortality but also growth losses or whether less expensive and intensive protection scenarios could be employed to protect our forests. Our experiment, which is unique in terms of its spatial and temporal coverage, makes an important contribution to filling the gaps regarding efficacy of different protection scenarios based upon aerial applications of *Btk*. Our results show that the extent of balsam fir wood losses is inversely related to the frequency and intensity of *Btk* aerial spraying. Indeed, the standard and intensive protection scenarios provide a substantial level of protection by reducing defoliation, tree mortality, and growth reductions, but these goals are achieved at relatively high costs (791.59 and 1069.83 CAD/ha for the study period) that would otherwise prevent their application at large scales. As such, spraying *Btk* every 2 years is a good alternative because it reduces tree mortality to a level similar to the standard approach that is currently used in Quebec, while also diminishing annual volume losses. Even though this scenario is more effective in reducing volume growth losses in spruce species than it is in balsam fir, this scenario reduced volume growth losses by half compared with unprotected units in the latter host species. This scenario is 45% less expensive over an 11-year period than the standard scenario (437.55 vs 791.59 CAD/ha respectively), which may allow to increase the area covered by the protection program given the narrow window of time (4 to 5 weeks of aerial spraying operations per year) and the limited availability of aircraft, helicopters, and manpower required for aerial spraying. This scenario may mitigate impact of *Btk* on non-target Lepidoptera and allow maintaining the integrity of mature balsam fir forests for biodiversity, including the woodland caribou, a threatened species in Canada which avoids disturbed areas, including stands affected by the spruce budworm (Labadie et al. 2021). Furthermore, protection programs could be proposed to protect other resources such as wildlife habitats and natural attractions which are currently not part of protection efforts in the Province of Quebec. Given the low levels of mortality observed in white spruce and black spruce in mixed spruce-fir forests, aerial spraying of *Btk* should concentrate further upon balsam fir, which is the most vulnerable host as demonstrated by its high observed mortality in unprotected units in both present and past studies (e.gBlais 1981; Fournier et al. 2010; Fuentealba et al. 2022). This recommendation may not be relevant to mono-specific spruce plantations or to spruce-dominated natural stands prior to the studied scenario being tested in such situations where adequate timing of spraying has been adapted to spruce tree phenology. The low mortality observed in white and black spruce in stands treated with the different protection scenarios tested in this study suggests that less intensive protection would be sufficient to safeguard these two species in natural balsam fir-dominated boreal forest. Results from the current study demonstrate that aerial spraying of *Btk* every 2 years against spruce budworm is an effective and the most cost-efficient silvicultural tool for maintaining tree growth and overall volumes of wood for the forest industry.

Acknowledgements
We thank the Board of Directors of the Société de protection des forêts contre les insectes et maladies (SOPFIM) and the MRNFQ for their sustained interest in the project. We also thank SOPFIM laboratory and field teams for all work done over the years, two anonymous reviewers for their useful suggestions, and W.F.J. Parsons for reviewing and editing the manuscript.

Code availability
Not applicable.

Authors' contributions
Conceptualization: Alain Dupont, Éric Bauce, Christian Hébert; methodology: Alain Dupont, Éric Bauce, Christian Hébert, Richard Berthiaume; formal analysis and investigation: Alvaro Fuentealba, Éric Bauce, Roberto Quezada-García; writing—original draft preparation: Éric Bauce, Alvaro Fuentealba; writing—review and editing: Alain Dupont, Christian Hébert, Richard Berthiaume, Roberto Quezada-García, Alvaro Fuentealba, Éric Bauce; funding acquisition: Alain Dupont, Éric Bauce; resources: Alain Dupont, Richard Berthiaume, Éric Bauce; supervision: Alain Dupont, Richard Berthiaume, Éric Bauce, Christian Hébert; visualization: Alvaro Fuentealba, Roberto Quezada-García; project administration: Alain Dupont, Éric Bauce. All authors read and approved the final manuscript.

Funding
We are grateful to the Spray Efficacy Research Group International (SERG-I) members (USDA Forest Service, Newfoundland and Labrador Department of Natural Resources, Ministère des Ressources naturelles et des Forêts du Québec [MRNFQ], Société de Protection des Forêts contre les Insectes et Maladies [SOPFIM], Forest Protection Limited, Valent BioSciences Corp., AEF Global Inc., Nova Scotia Department of Natural Resources) for their financial and in-kind contributions to this study. Research funding was also provided by a Research Development and Collaboration Grant to É.B. from the Natural Sciences and Engineering Research Council of Canada (NSERC) and involving industrial members of SOPFIM (Arbec, Cedrico and Resolute Forest Products), MRNFQ, SOPFIM, and an NSERC Discovery grant to É. B.

Availability of data and materials
The data described in this article can be freely and openly accessed at BOREALIS: https://doi.org/10.5683/SP3/TTWHHF.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
All authors gave their informed consent to this publication and its content.

Competing interests
The authors declare no competing interests.

Author details
[1]Centre d'étude de la Forêt (CEF) and Département des Sciences du Bois et de la Forêt, Université Laval, Faculté de Foresterie, de Géographie Et de Géomatique, Québec, QC G1V 0A6, Canada. [2]Société de Protection des Forêts contre les Insectes et Maladies (SOPFIM), Québec, QC G1N 4B8, Canada. [3]Natural Resources Canada, Canadian Forest Service, Québec, QC G1V 4C7, Canada.

Received: 1 February 2024 Accepted: 3 September 2024

References

Anderegg WRL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, Hood S, Lichstein JW, Macalady AK, McDowell N, Pan Y, Raffa K, Sala A, Shaw JD, Stephenson NL, Tague C, Zeppel M (2015) Tree mortality from drought, insects, and their interactions in a changing climate. New Phytol 208:674–683. https://doi.org/10.1111/nph.13477

Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci Total Environ 262:263–286. https://doi.org/10.1016/S0048-9697(00)00528-3

Battisti A, Coyle D, Sallé A, Dreyer E, Bauce E, Dupont A, Hébert C, Berthiaume R, Quezada-García R, Fuentealba A (2024) Review of "Biennial aerial application of *Bacillus thuringiensis* var. *kurstaki* provides good protection against spruce budworm (*Choristoneura fumiferana* [Clemens])". [Open Peer Review Report]. HAL https://hal.inrae.fr/hal-04630314

Batzer HO (1973) Net effect of spruce budworm defoliation on mortality and growth of balsam fir. J Forest 71:34–37. https://doi.org/10.1093/jof/71.1.34

Bauce É, Carisey N, van Frankenhuyzen K, Dupont A (2004) *Bacillus thuringiensis* subsp. *kurstaki* (*Btk*) aerial spray prescriptions for balsam fir protection against spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). J Econ Entomol 97:624–634. https://doi.org/10.1603/0022-0493-97.5.1624

Bauce É, Dupont A, Hébert C, Berthiaume R, Quezada- García R, Fuentealba A (2024) Data from Biennial aerial application of *Bacillus thuringiensis* Berliner var. *kurstaki* is the most cost-effective approach of protection against spruce budworm (*Choristoneura fumiferana* [Clemens]). Borealis. https://doi.org/10.5683/SP3/TTWHHF

Béland JM, Handfield D, Morneau MS, Bédard N, Hébert C (2024) Uncontrolled vs-controlled spruce budworm (SBW) populations with increasing intensity of *Btk* applications: impact on non-target Lepidoptera. Proceedings of the 2023 SERG-i Workshop, Winnipeg, MB, 12 p.

Bergeron Y, Leduc A, Morin H, Joyal C (1995) Balsam fir mortality following the last spruce budworm outbreak in North-Western Quebec. Can J for Res 25:1375–1384. https://doi.org/10.1139/x95-15

Bentz B, Bonello P, Delb H, Fettig C, Poland T, Pureswaran D, Seybold S (2019) Advances in understanding and managing insect pests of forest trees. In: Stanturf JA (ed.) Achieving sustainable management of boreal and temperate forests, Burleigh Dodds Science Publishing, Cambridge, UK.

Blais JR (1957) Some relationships of the spruce budworm, *Choristoneura fumiferana* (Clem.) to black spruce, *Picea mariana* (Moench) Voss. Forestry Chronicle 13:364–372. https://doi.org/10.5558/tfc33364-4

Blais JR (1958) The vulnerability of balsam fir to spruce budworm attack in northwestern Ontario, with special reference to the physiological age of the tree. Forestry Chronicle 34:405–422. https://doi.org/10.5558/tfc34405-4

Blais JR (1964) Account of a recent spruce budworm outbreak in the Laurentide Park region of Quebec and measures for reducing damage in future outbreaks. Forestry Chronicle 40:313–323

Blais JR (1977) Comparative appraisal of insecticidal operations against spruce budworm in Quebec during two outbreaks. Forestry Chronicle 53:71–76. https://doi.org/10.5558/tfc53071-2

Blais JR (1981) Mortality of balsam fir and white spruce following a spruce budworm outbreak in the Ottawa River watershed in Quebec. Can J for Res 11:620–629. https://doi.org/10.1139/x81-085

Blais JR (1983a) Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can J for Res 13:539–547. https://doi.org/10.1139/x83-079

Blais JR (1983b) Predicting tree mortality induced by spruce budworm: a discussion. Forestry Chronicle 59:294–297. https://doi.org/10.5558/tfc59294-6

Boulton TJ, Otvos LS, Halwas KL, Rohlfs DA (2007) Recovery of nontarget Lepidoptera on Vancouver Island, Canada: one and four years after a gypsy moth eradication program. Environ Toxicol Chem 26:738–748. https://doi.org/10.1897/06-079R1.1

Cadogan BL, Scharbach RD (1993) Efficacy of Foray 48B (*Bacillus thuringiensis* Berliner) applications against the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), timed for phenological development of balsam fir and black spruce. Can Entomol 125:479–488. https://doi.org/10.4039/Ent125479-3

Campbell LJ, Laroque CP (2007) Decay progression and classification in two old-growth forests in Atlantic Canada. For Ecol Manage 238:293–301. https://doi.org/10.1016/j.foreco.2006.10.027

Carisey N, Bauce É, Miron S, Dupont A (2004) Effects of bud phenology and foliage chemistry of balsam fir and white spruce trees on the efficacy of *Bacillus thuringiensis* against the spruce budworm, *Choristoneura fumiferana*. Agric for Entomol 6:55–69. https://doi.org/10.1111/j.1461-9555.2004.00204.x

Chang W-Y, Lantz VA, Hennigar CR, MacLean DA (2012) Economic impacts of forest pests: a case study of spruce budworm outbreaks and control in New Brunswick, Canada. Can J for Res 42:490–505. https://doi.org/10.1139/x11-190

Chen C, Weiskittel A, Bataineh M, MacLean DA (2017) Evaluating the influence of varying levels of spruce budworm defoliation on annualized individual tree growth and mortality in Maine, USA and New Brunswick, Canada. For Ecol Manage 396:184–194. https://doi.org/10.1016/j.foreco.2017.03.026

D'Amato AW, Troumbly SJ, Saunders MR, Puettmann KJ, Albers MA (2011) Growth and survival of *Picea glauca* following thinning of plantations affected by eastern spruce budworm. North J Appl for 28:72–78. https://doi.org/10.1093/njaf/28.2.72

DeGrandpré L, Kneeshaw DD, Perigon S, Boucher D, Marchand M, Pureswaran D, Girardin MP (2019) Adverse climatic periods precede and amplify defoliator-induced tree mortality in eastern boreal North America. J Ecol 107:452–467. https://doi.org/10.1111/1365-2745.13012

Dorais LG, Hardy YJ (1976) Méthode d'évaluation de la protection accordée au sapin baumier par les pulvérisations aériennes contre la tordeuse des bourgeons de l'épinette. Can J for Res 6:86–92. https://doi.org/10.1139/x76-011

Dorais L, Auger M, Pelletier M, Chabot M, Bordeleau C, Cabana J (1995) Insect control in Quebec, 1974–1987. In: Armstrong JA, Ives WGH (Eds.) Forest Insect Pests in Canada. Ottawa, Canada: Canadian Forest Service, Science and Sustainable Development Directorate, pp 667–678.

FAO (2020) Global Forest Resources Assessment 2020: Main report. Italy, Rome

Fettes JJ (1950) Investigations of sampling techniques for population studies of the spruce budworm on balsam fir in Ontario. Forest Insect Laboratory, Sault Ste. Marie, Annual Technical Report 4:163–401

Fournier C, Bauce É, Dupont A, Berthiaume R (2010) Wood losses and economical threshold of *Btk* aerial spray operation against spruce budworm. Pest Manag Sci 66:319–324. https://doi.org/10.1002/ps.1878

Fuentealba A, Bauce É, Dupont A (2015) *Bacillus thuringiensis* efficacy in reducing spruce budworm damage as affected by host tree species. J Pest Sci 88:593–603. https://doi.org/10.1007/s10340-014-0629-8

Fuentealba A, Dupont A, Hébert C, Berthiaume R, Quezada-Garcia R, Bauce É (2019) Comparing the efficacy of various aerial spraying scenarios using *Bacillus thuringiensis* to protect trees from spruce budworm defoliation. For Ecol Manage 432:1013–1021. https://doi.org/10.1016/j.foreco.2018.10.034

Fuentealba A, Dupont A, Quezada-Garcia R, Bauce É (2022) Efficacy of insecticide aerial spraying programs to reduce tree mortality during a spruce budworm outbreak (1967–1992) in the province of Quebec. Agric for Entomol 24:589–599. https://doi.org/10.1111/afe.12523

Fuentealba A, Pelletier-Beaulieu É, Dupont A, Hébert C, Berthiaume R, Bauce É (2023) Optimizing *Bacillus thuringiensis* (*Btk*) aerial spray prescriptions in mixed balsam fir-white spruce stands against the eastern spruce budworm. Forests 14(7):1289. https://doi.org/10.3390/f14071289

Fuentealba A, Pureswaran D, Bauce É, Despland E (2017) How does synchrony with host plant affect the performance of an outbreaking insect defoliator? Oecologia 184:847–857. https://doi.org/10.1007/s00442-017-3914-4

Greenbank DO (1963) Host species and the spruce budworm. Memoirs of the Entomological Society of Canada 31:219–223. https://doi.org/10.4039/entm9531219-1

Gross HL (1992) Impact analysis for a jack pine budworm infestation in Ontario. Can J for Res 22:818–831. https://doi.org/10.1139/x92-111

Hajek AE, van Frankenhuyzen K (2017) Use of entomopathogens against forest pests. In: Lacey LA (ed) Microbial Control of Insect and Mite Pests: From Theory to Practice. Academic Press, Amsterdam, The Netherlands, pp 313–330. https://doi.org/10.1016/B978-0-12-803527-6.00021-4

Hébert C, Bédard N, Bloin P, Béland JM, Pothier D (2023) Uncontrolled vs-controlled spruce budworm (SBW) populations with increasing intensity of Btk applications: impact on non-target Lepidoptera, SBW parasitism and overall arthropod diversity. Proceedings of the 2023 SERG-i Workshop, Victoria, BC, 15 p.

Kenward MG, Roger JH (1997) Small sample inference for fixed effects from restricted maximum likelihood. Biometrics 53:983–997. https://doi.org/10.2307/2533558

Keefe K, Alavalapati JAA, Pinheiro C (2012) Is enrichment planting worth its costs? A financial cost-benefit analysis. Forest Policy Econ 23:10–16. https://doi.org/10.1016/j.forpol.2012.07.004

Kneeshaw DD, Sturtevant BR, DeGrandpré L, Doblas-Miranda E, James PMA, Tardif D, Burton PJ (2021) The vision of managing for pest-resistant landscapes: realistic or utopic? Current Forestry Reports 7:97–113. https://doi.org/10.1007/s40725-021-00140-z

Krause C, Luszczynski B, Morin H, Rossi S, Plourde P-Y (2012) Timing of growth reductions in black spruce stem and branches during the 1970 spruce budworm outbreak. Can J for Res 42:1220–1227. https://doi.org/10.1139/x2012-048

Labadie G, McLoughlin PD, Hebblewhite M, Fortin D (2021) Insect-mediated apparent competition between mammals in a boreal food web. Proc Natl Acad Sci 118(30):e2022892118. https://doi.org/10.1073/pnas.2022892118

Lussier J-M, Morin H, Gagnon R (2002) Mortality in black spruce stands of fire or clear-cut origin. Can J for Res 32:539–547. https://doi.org/10.1139/x01-201

MacLean DA (1979) Spruce budworm-caused balsam fir mortality on the Cape Breton Highlands 1974–1978. Canadian Forestry Service, Maritimes Forest Research Centre, Fredericton, New Brunswick. Information Report No. MX-97.

MacLean DA (1980) Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. Forestry Chronicle 56:213–221. https://doi.org/10.5558/tfc56213-5

MacLean DA (1981) Impact of defoliation by spruce budworm populations on radial and volume growth of balsam fir: a review of present knowledge. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 142:293–306

MacLean DA (2016) Impacts of insect outbreaks on tree mortality, productivity, and stand development. Can Entomol 148:S138–S159. https://doi.org/10.4039/tce.2015.24

MacLean DA, Hunt TL, Eveleigh ES, Morgan MG (1996) The relation of balsam fir volume increment to cumulative spruce budworm defoliation. Forestry Chronicle 72:533–540. https://doi.org/10.5558/tfc72533-5

MacLean DA, Kline AW, Lavigne DR (1984) Effectiveness of spruce budworm spraying in New Brunswick in protecting the spruce component of spruce-fir stands. Can J for Res 14:163–176. https://doi.org/10.1139/x84-033

MacLean DA, Ostaff DP (1989) Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. Can J for Res 19:1087–1095. https://doi.org/10.1139/x89-165

Miller JC (1990) Effects of a microbial insecticide, *Bacillus thuringiensis kurstaki*, on nontarget Lepidoptera in a spruce budworm-infested forest. Journal of Research on the Lepidoptera 29:267–276

Ministère des Ressources Naturelles et des Forêts (MRNF) (2022) Aires infestées par la tordeuse des bourgeons de l'épinette au Québec en 2022. Ministère des Ressources Naturelles et des Forêts. Direction de la protection des forêts. Novembre 2022, Quebec, Canada. https://mffp.gouv.qc.ca/documents/forets/RA_Aires_infesteesTBE_2022_MRNF.pdf. Accessed 13 March 2023.

Morin H, Laprise D, Simard A-A, Amouch S (2008) Régime des épidémies de la tordeuse des bourgeons de l'épinette dans l'Est de l'Amérique du Nord. In: Gauthier S, Vaillancourt M-A, Leducet A, De Grandpré L, Kneeshaw D, Morin H, Drapeau P, Bergeron Y (eds) Aménagement écosystémique en forêt boréale. Presses de l'Université du Québec, Montréal, Québec, pp 165–192

Piene H (1980) Effects of insect defoliation on growth and foliar nutrients by young balsam fir. Forest Science 26:665–673. https://doi.org/10.1093/forestscience/26.4.665

Piene H (1981) Early growth responses to operational spacing in young balsam fir stands on the Cape Breton Highlands, Nova Scotia. Canadian Forestry Service, Maritimes Forest Research Centre, Fredericton, New Brunswick. Information Report M-X-125. 29 p.

Piene H (1991) The sensitivity of young white spruce to spruce budworm defoliation. North J Appl for 8:167–171. https://doi.org/10.1093/njaf/8.4.168

Piene H (1998) Spruce budworm defoliation-foliage production: differences between white spruce and balsam fir. In McManus ML, Liebhold AM (eds) Population dynamics, impacts, and integrated management of forest defoliating insects, Proceedings: IUFRO Working Parties S7.03–06 and S7.03.07. September 18–23, 1996, Banska Stiavnica, Slovak Republic. USDA Forest Service, Hamden, Connecticut, General Technical Report NE-247, Pages 247–252.

Prebble ML (ed.) (1975) Aerial control of forest insects in Canada. Environment Canada, Canadian Forestry Service, Headquarters, Ottawa, Ontario. 330 p.

Robitaille A, Saucier JP (1998) Paysages régionaux du Québec méridional. Direction de la gestion des stocks forestiers et Direction des relations publiques, Ministère des Ressources Naturelles du Québec. Les publications du Québec, Québec.

SAS Institute Inc. 2003. SAS/STAT User's Guide. Release 9.1 edn. Cary, NC, USA, SAS Institute Inc.

Scriber JM (2001) Bt or not Bt: is that the question? PNAS 98:12328–12330. https://doi.org/10.1073/pnas.241503398

Shea SR, Armson KA (1972) Stem analysis of jack pine (*Pinus banksiana* Lamb.): techniques and concepts. Can J for Res 2:392–406. https://doi.org/10.1139/x72-061

SOPFIM (2022) Programmes de Pulvérisation Aérienne d'Insecticide Biologique (*Btk*) Contre la Tordeuse des Bourgeons de l'épinette; Rapport de Réalisation des Travaux; SOPFIM: Quebec, QC, Canada, 2022; 127p. https://sopfim.qc.ca/wp-content/uploads/2022/11/Rapport-TBE-2022-1.pdf. Accessed 13 March 2023.

Statistics Canada (2021) Table 18–10–0005–01 Consumer Price Index, annual average, not seasonally adjusted. https://doi.org/10.25318/1810000501-eng. Accessed 13 March 2023.

Trägårdh I (1935) The economic possibilities of aeroplane dusting against forest insects. Bull Entomol Res 26:487–495. https://doi.org/10.1017/S0007485300036828

van Frankenhuyzen K, Lucarotti C, Lavallée R (2016) Canadian contributions to forest insect pathology and to the use of pathogens in forest pest management. Can Entomol 148:S210–S238. https://doi.org/10.4039/tce.2015.20

Volney WJA, Cerezke HF (1992) The phenology of white spruce and the spruce budworm in northern Alberta. Can J for Res 22:198–205. https://doi.org/10.1139/x92-026

Wainhouse D (2005) Ecological methods in forest pest management. Oxford University Press, Oxford

Wagner DL, Peacock JW, Carter JL, Talley SE (1996) Field assessment of *Bacillus thuringiensis* on nontarget Lepidoptera. Environ Entomol 25:1444–1454. https://doi.org/10.1093/ee/25.6.1444

Wu Y, MacLean DA, Hennigar C, Taylor AR (2020) Interactions among defoliation, species, and soil richness determine foliage production during and after simulated spruce budworm attack. Can J for Res 50:565–580. https://doi.org/10.1139/cjfr-2019-0449

Publisher's Note