NRC Research Press

ARTICLE

Estimating forest vulnerability to the next spruce budworm outbreak: will past silvicultural efforts pay dividends?

Guillaume B. Sainte-Marie, Daniel D. Kneeshaw, David A. MacLean, and Chris R. Hennigar

Abstract: Silvicultural treatments recommended to reduce damage by spruce budworm (SBW; *Choristoneura fumiferana* Clemens) include reducing balsam fir (*Abies balsamea* (L.) Mill.) abundance and age and increasing spruce (*Picea* spp.) and hardwood content. To evaluate the effect of these measures on forest timber supply, we assessed stand characteristics, disturbance history, and timber supply for an intensively managed eastern Quebec forest from 1985 to 2004, encompassing a major SBW outbreak. During this time, mean stand age declined from 55 to 51 years, and proportions of areas in balsam fir stands declined (42% to 27%), spruce–fir stabilized (12% to 11%), and mixedwoods increased (32% to 52%). We estimated forest vulnerability using softwood volume reductions following simulated outbreak scenarios of different severity (low, moderate, and high) and different effects of hardwood content in reducing spruce–fir defoliation. Volume reductions for outbreaks simulated to begin in either 1985 or 2004 were similar, ranging from 15%–46% (no hardwood effect in reducing defoliation) to 13%–39% (given a maximum hardwood content effect) for light and severe outbreaks, respectively. Considering the net detrimental effect of increased hardwood content on softwood timber supply, we question the dividends of promoting hardwoods and recommend increasing the combined use of plantations and weeding treatments to increase spruce content.

Key words: spruce budworm outbreak, silviculture, protective effects of hardwoods, softwood timber supply, forest protection.

Résumé : Les traitements sylvicoles recommandés pour réduire les dommages lors d'épidémies de la tordeuse des bourgeons de l'épinette (TBE; *Choristoneura fumiferana* Clemens) incluent la réduction de l'abondance et de l'âge du sapin (*Abies balsamea* (L.) Mill.) et l'augmentation de l'abondance d'épinettes (*Picea* spp.) et de feuillus. Afin d'évaluer l'effet de ces mesures sur l'approvisionnement en bois, nous avons évalué de 1985 à 2004 les caractéristiques, l'historique des perturbations et l'approvisionnement en résineux d'une forêt de l'est du Québec sous aménagement intensif et pendant une épidémie majeure de TBE. Pendant cette période, l'âge moyen des peuplements a chuté de 55 à 51 ans, la proportion de peuplements de sapin a chuté (42 % à 27 %), celle d'épinette–sapin s'est maintenue (12 % à 11 %) et celle mixte a augmenté (32 % à 52 %). La vulnérabilité des forêts a été estimé à partir des réductions de volume résineux suivant des simulations d'épidémies de différentes sévérité (faible, modérée et sévère) et effet des feuillus sur la réduction de la défoliation des hôtes. Les pertes de bois des épidémies débutant en 1985 ou 2004 se sont avérées similaires et s'élevaient de 15 %–46 % (aucun effet des feuillus) à 13 %–39 % (effet des feuillus maximal) pour les épidémies légères et sévères. Étant donné la difficulté d'augmenter l'abondance d'épinettes et les pertes nettes de production résineuse liées au contenu élevé en feuillus, nous remettons en question les bénéfices liés à la préservation des feuillus et recommandons une utilisation accrue du contrôle de la végétation en plantation pour augmenter l'abondance d'épinette.

Mots-clés : épidémie de tordeuse des bourgeons de l'épinette, sylviculture, effet de protection des feuillus, approvisionnement en bois résineux, protection des forêts.

Introduction

The last spruce budworm (*Choristoneura fumiferana* Clemens; SBW) outbreak, which occurred from 1967 to 1992 in eastern Canada and in the United States (US), generated an estimated annual loss of 44×10^6 m^3 of timber volume at the peak of the outbreak, i.e., from 1977 to 1981 (Power 1991). Several studies have examined forest management treatments that could help prevent or reduce losses to future SBW outbreaks (Baskerville 1975; Blum and MacLean 1984; MacLean 1996). Evidence suggests that silvicultural treatments and forest management planning can reduce forest vulnerability through stand age reduction, or species composition manipulations, or prioritized harvesting of the most susceptible stands (MacLean 1996). Forest susceptibility is defined here as the probability of a forest being defoliated by the SBW, and forest vulnerability is defined as the probability of growth reduction and mortality resulting from defoliation (MacLean and MacKinnon 1997). The logic of silvicultural manipulations to reduce vulnerability is to decrease the abundance of mature (>40 years) balsam fir (*Abies balsamea* (L.) Mill.) dominated stands (MacLean 1980) in favor of younger, less vulnerable spruce species. Yet, the impact of silvicultural manipulations to reduce SBW impacts on stand dynamics and softwood timber supply has not been assessed.

The effect of species composition on forest vulnerability to the SBW led to the emergence of the silvicultural hypothesis, which posits that past forest management has increased SBW outbreak severity by increasing balsam fir abundance and that appropriate management can reduce fir abundance and, consequently, decrease the damage caused by the SBW (Blais 1983; Miller and Rusnock 1993). Despite being contested on the basis of missing detailed historical data and lack of manipulative studies (Miller

Received 31 July 2014. Accepted 16 November 2014.

G.B. Sainte-Marie and D.D. Kneeshaw. NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, UQAM, C.P. 8888 Succ. Centre-ville, Montréal, QC H3C 3P8, Canada; Center for Forest Research, UQAM, C.P. 8888, Succ. Centre-Ville, Montréal, QC H3C 3P8, Canada.
D.A. MacLean and C.R. Hennigar. Faculty of Forestry and Environmental Management, University of New Brunswick, P.O. Box 4400, Fredericton, NB E3B 5A3, Canada.
Corresponding author: Guillaume B. Sainte-Marie (e-mail: sainte-marie.guillaume@courrier.uqam.ca).

 Published at www.nrcresearchpress.com/cjfr on 17 November 2014.

and Rusnock 1993; Koricheva et al. 2006; but see Robert et al. 2012), this hypothesis has been operationally implemented, often to a great extent and with large investments (Chabot et al. 2013; Gagnon and Chabot 1991). The main prophylactic treatments against SBW include replacement of natural balsam fir with spruce plantations (Hennigar and MacLean 2010), precommercial thinning (PCT) to increase spruce content and reduce competing vegetation (Pothier 2002; Pothier et al. 2012), and the promotion of hardwood content (Chabot et al. 2013). In recent decades, large-scale forest management has considerably modified forest cover in parts of SBW-susceptible forests, reducing mean stand age and altering tree species composition (Belle-Isle and Kneeshaw 2007; Blais 1983; Cyr et al. 2009), characteristics that essentially determine stand vulnerability to SBW outbreaks (Erdle and MacLean 1999; MacLean 1980).

In addition to forest management, the severe 1967–1992 SBW outbreak caused extensive tree mortality and stand renewal (Blais 1983). The most vulnerable mature stands composed of balsam fir and white spruce (*Picea glauca* (Moench) Voss) are now less abundant, younger, and, therefore, less vulnerable to the SBW than at the time of the last outbreak (Bouchard et al. 2006). A large amount of SBW-killed or timber-harvested stands also regenerated with a higher proportion of nonhost species such as paper birch (*Betula papyrifera* Marshall) and trembling aspen (*Populus tremuloides* Michx.) (Bouchard et al. 2006; Spence and MacLean 2012). Evidence suggests that these species and other hardwood species could reduce defoliation and SBW susceptibility, due either to the increased diversity of the SBW's natural enemies or to dispersal barriers generated by nonhost tree species (Campbell et al. 2008; Cappuccino et al. 1999; Su et al. 1996).

Severe SBW outbreaks, as well as forest management, also generate younger and consequently less vulnerable forest cover (Bouchard et al. 2007; Etheridge et al. 2005; MacLean 1988). Severe SBW outbreaks cause partial mortality in immature cohorts (MacLean and Andersen 2008; Ruel and Huot 1993), which increases the time necessary for mature balsam fir dominated forest cover to re-establish after the outbreak, thereby reducing forest vulnerability for intervals of 50 years or more (Blais 1981; Bouchard et al. 2006; Erdle and MacLean 1999). It has been reported that the three previous SBW outbreaks in Quebec followed such a cyclical pattern, with the 1909–1920 outbreak being severe, the 1938–1958 outbreak being less severe than its predecessor, and the 1967–1992 outbreak being severe (Bouchard et al. 2006; Bouchard et al. 2007). This natural cycle along with the impression of having created forests of lower vulnerability due to preventive silviculture has led to the expectation that the next SBW outbreak will be less severe than the 1967–1992 outbreak (Coulombe et al. 2004; James W. Sewall Company 2011; Morin et al. 2007); however, this assertion remains to be tested.

From 1973 to 1992, a severe SBW outbreak occurred in the Gaspé region in eastern Quebec, Canada, and caused tree mortality across 47% of the area. Objectives of this study were to (*i*) determine how forest species composition and age have changed since the last SBW outbreak in a severely impacted forest, (*ii*) simulate effects of SBW outbreak scenarios, with and without hardwood reduction of defoliation, on volume reduction during the last outbreak and under current forest conditions, and (*iii*) estimate effectiveness of preventive forest management measures (plantation, PCT, and hardwood retention) in modifying forest composition and age and, consequently, decreasing volume reductions under SBW outbreak scenarios.

Methods

Study area

The 104 000 ha Gaspé management unit study area is comprised of natural forests dominated by balsam fir mixed with hardwoods (Fig. 1). SBW host species present in the area, in decreasing order of susceptibility (Hennigar et al. 2008), are balsam fir, white spruce, red spruce (*Picea rubens* Sarg.), and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb). Hardwood species were, from the most to the least abundant, white birch, trembling aspen, maple (*Acer* spp.), pin cherry (*Prunus pensylvanica* L. f.), and yellow birch (*Betula alleghaniensis* Britton). Nonhost conifers such as eastern white cedar (*Thuja occidentalis* L.), tamarack (*Larix laricina* (Du Roi) K. Koch), and jack pine (*Pinus banksiana* Lamb.) accounted for less than 1% of the total volume.

The use of intensive forest management in the study area was relatively high, with 15% of the area treated with PCT by 2004 and 7% of the study area in plantations, mostly black and white spruce (white spruce (42%), black spruce (31%), and Norway spruce (*Picea abies* (L.) Karst.) (12%), jack pine and tamarack (6%), and unknown species (9%)) according to the SIFORT database "Système d'Information FORestière par Tesselle", a large-scale, 14 ha resolution systematic sampling grid based on stand information interpreted from aerial photos (Pelletier et al. 2007). A total of 80% of the study area was disturbed from 1958 to 2004 by either SBW, harvesting (mostly clearcutting, see below), or intensive management (plantation and (or) PCT); other disturbances affected <1% of the study area.

Forest inventory data

Stand characteristics in the Gaspé management unit were determined using 7399 sample points from the SIFORT database (Pelletier et al. 2007). Forest species composition and age per sample point were determined from successive inventories in 1985–1986, 1992–1993, and 2004 (hereafter referred to as the 1985, 1992, and 2004 inventories, respectively). A previous inventory (1974) conducted prior to the start of the 1973–1992 SBW outbreak (the first large-scale inventory undertaken in Quebec) was also initially included in our analysis but was removed due to stand age related inconsistencies. In addition to having only three different stand age classes (10, 30, and 90 years), the 1974 inventory for the study area had 20% of stands reporting a stand age > 2 age classes younger (>21 years) than in the 1985 inventory (11-year interval) (vs. 8% in 1992 and 5% in 2004).

Inventory-derived data on forest composition and stand age change for the same period were compared with the Quebec Ministry of Natural Resources (QMNR) permanent sample plot (PSP) database. PSPs were measured in 1974–1977, 1981–1986, 1995–1997, and 2003–2005 (hereafter referred to as 1974, 1981, 1995, and 2003, respectively), which covers the 1973–1992 SBW outbreak period in the region. The PSP network in Quebec is not subject to protection from forest management, which makes its disturbance history similar to that of the study area. A total of 219 plots were selected either within the study area or up to 75 km outside but within the same bioclimatic domain as in the study area (Fig. 1).

The dominant stand age, forest cover composition, initial disturbance (severe SBW outbreak, wildfire, or clearcut + plantation), and partial disturbance (light or moderate SBW outbreak, wildfire, PCT, or partial cut) were recorded for each stand in the SIFORT database within the study area. Sampling methods were generally similar between inventories, with minor inconsistencies regarding stand composition and uneven-aged stands. We summarized stand composition data into three stand types: balsam fir stands (>75% in basal area), spruce–fir stands (spruce ≥50% and balsam fir <50%), and mixedwood stands (hardwood–softwood; hardwoods ≥25%). Categories of young and old uneven-aged stands, based on the estimated age of the oldest stems, differed between 1985 (<60-year vs. >60-year inventories) and 2004 (<80-year vs. >80-year inventories). For simulation purposes, the young and old uneven-aged stands were assumed to be 40 and 80 years old in 1985 and 50 and 90 years old in 2004, respectively. Therefore, in all cases, uneven-aged stands were considered to be mature (>40 years) with regards to SBW, which reduced the consequences of this inconsistency in our analyses.

Fig. 1. Map of the Gaspé Peninsula and study area (separated into two bioclimatic domains).

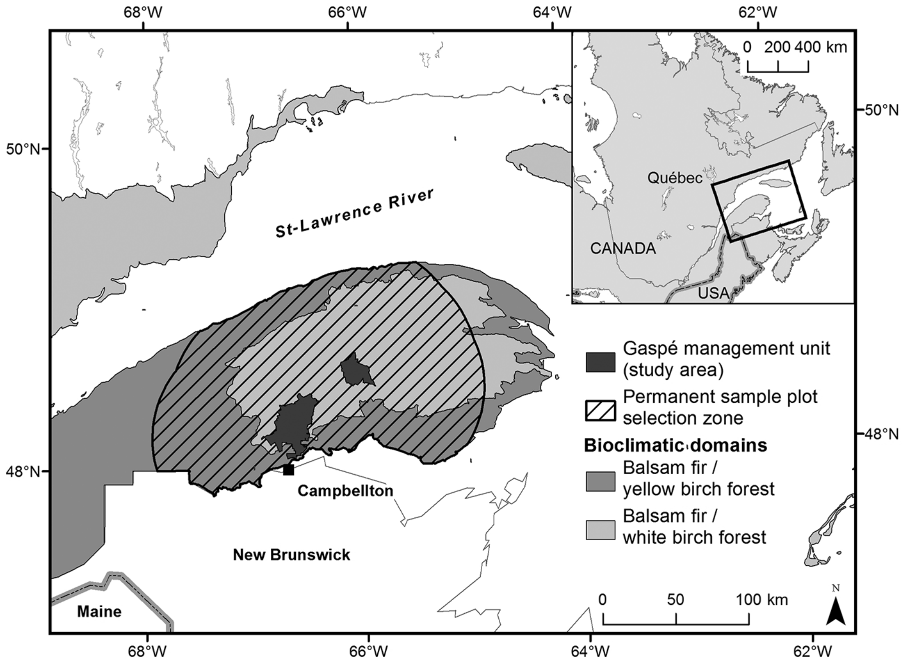
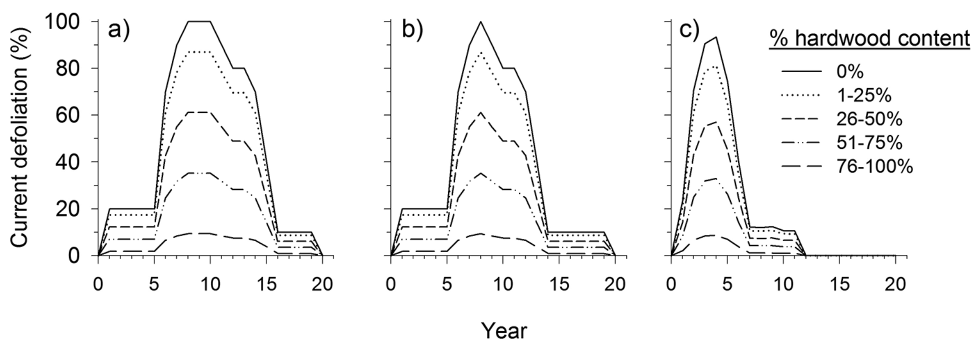


Fig. 2. Hardwood content (%) effect on balsam fir defoliation due to spruce budworm given (*a*) severe (MacLean et al. 2001), (*b*) moderate (MacLean et al. 2001), or (*c*) light (modified from Gray et al. 2000) outbreaks. Hardwood effects were assumed to be constant throughout the outbreak and directly proportional to stand hardwood content, based on Su et al. (1996).



Simulation of SBW outbreak scenarios

We used the Accuair ForPRO system (Forus Research 2010; McLeod et al. 2012), commonly known as the Spruce Budworm Decision Support System (SBWDSS), to analyse stand vulnerability to the SBW. This tool is made up of four components: (*i*) a defoliation and damage database (Erdle and MacLean 1999); (*ii*) an estimated volume reduction database as a function of cumulative defoliation and stand type (i.e., the Stand Impact Matrix (SIMPACT)) (MacLean et al. 2001); (*iii*) a timber supply model (in our case, the Remsoft Spatial Planning Framework) (Remsoft Inc. 2008); and (*iv*) the ForPRO system to link the previous three components. Timber yields were estimated using the Quebec PSP network and the ARTEMIS–2009 tree-level growth model (Fortin and Langevin 2010). Because the Remsoft Spatial Planning Framework has a deterministic framework (no form of uncertainty is integrated), ForPRO is usually used in a scenario planning approach, with a range of optimistic to pessimistic future scenarios (MacLean et al. 2001). Scenarios help overcome the absence of uncertainty in deterministic models as long as a plausible range of possibilities is used (Schoemaker 1995).

Simulations of effects of light, moderate, and severe SBW outbreak scenarios (Fig. 2) on potential timber volume were initialized using SIFORT forest inventory characteristics in 1985 and in 2004. The resulting peak SBW outbreak caused timber volume reductions (after 10 years for the light outbreak scenario and after 15 years for moderate and severe outbreak scenarios) were compared to determine how forest vulnerability to SBW changed over this period. With average intervals between SBW outbreaks of approximately 30 years (Bouchard et al. 2006; Robert et al. 2012), a SBW outbreak could possibly occur in 2004 (31 years after the start of the 1973–1992 outbreak. However, our objective was to use ForPRO simulations of the 1985 and the 2004 forest conditions as a measure of effectiveness of forest management actions in reducing vulnerability.

The three SBW outbreak severity scenarios simulated (Figs. 2*a*–2*c*) were as follows: (*i*) a light outbreak present in the Gaspé region during the 1973–1992 SBW outbreak (Gray et al. 2000), characterized by 5 years of moderate defoliation (30%–70%) and 1 year of severe defoliation (>70%); (*ii*) a moderate outbreak including 3 years of moderate defoliation and 5 years of severe defoliation (MacLean et al. 2001); and (*iii*) a severe outbreak including 3 years of moderate defoliation and 7 years of severe defoliation (MacLean et al. 2001). Outbreak duration varies considerably within outbreaks; the last SBW outbreaks lasted more than 20 years in some places and much less in other places (Gray et al. 2000). The 10-year maximal duration simulated here is a typical outbreak duration at a given site; however, because ForPRO uses cumulative defoliation values, 6 additional years of defoliation are also considered in the simulated outbreak duration. Nevertheless, specific outbreak duration was not fundamental here as we did a comparative analysis across three outbreak severities and durations, forest conditions, and management scenarios. Unlike MacLean et al.'s balsam fir defoliation estimates, Gray et al. (2000) used aerial defoliation estimates, i.e., defoliation is averaged over the stand and potentially underestimates balsam fir defoliation in all stand types except pure balsam fir stands. Furthermore, they used class midpoints and likely underestimated maximum annual defoliation by about 20% (Campbell 2008). Therefore, we modified the light outbreak scenario by increasing annual defoliation values by 20% during the outbreak rise and by 10% during the outbreak decline (MacLean et al. 2001) to account for the buildup of natural enemy populations as the outbreak progresses (Royama 1992). Collectively, the three SBW outbreak patterns define a plausible range of defoliation severity. Given that most trees sampled for monitoring SBW populations were balsam fir, outbreak scenarios primarily represent defoliation trends on balsam fir. Based on Hennigar et al. (2008), defoliation on white, red, and black spruce was recalculated throughout the outbreak as 72%, 41%, and 28%, respectively, of that on balsam fir. Mean 5-year cumulative defoliation per SBW outbreak scenario by hardwood content class and 5-year periods is presented in Table 1.

Because hardwood content has been identified as reducing stand-level vulnerability to the SBW, we tested effects of incorporating defoliation reductions related to stand hardwood content based on averaged balsam fir defoliation in a 3-year period before outbreak decline in New Brunswick from Su et al. (1996). Given the widely held observation that natural enemies have a relatively constant impact throughout outbreak duration at many spatial scales (Campbell et al. 2008; Cappuccino et al. 1998), we assumed a constant hardwood content effect, reducing spruce–fir defoliation throughout the outbreak (Figs. 2*a*–2*c*).

Because all spruce species were combined within our set of yield curves and because there are substantial, known differences in vulnerability between spruce species, we had to consider them as one of the two most abundant spruce species in the Gaspé region, i.e., either white or black spruce. In determining the effectiveness of intensive management (objective *iii*), we simulated SBW impacts using black spruce and white spruce alternatively (see below). In evaluating the comparative impacts of SBW outbreaks on the 1985 and 2004 forest composition (objective *ii*), the choice of spruce species was of minor importance because we looked at relative, not absolute, SBW damage. For the latter objective, we chose black spruce as the default spruce species for the simple reason that it was more abundant than white spruce in the Gaspé region (51%–59% of merchantable spruce stems in the PSPs vs. 48%–32% for white spruce, 1%–3% for red spruce, and 0%–6% for Norway spruce in 1974 and in 2003, respectively). As white spruce is usually more productive than black spruce, we expected our combined spruce yield to slightly underestimate and overestimate white and black spruce yields, respectively.

Table 1. Mean cumulative balsam fir defoliation (%) for the severe, moderate, and light spruce budworm outbreak scenarios as a function of stand hardwood content, based on relationships from Su et al. (1996).

Outbreak scenario	Hardwood content class (%)[a]	Mean periodic cumulative defoliation (%)[b]	
		Period 1	Period 2
Severe	Pure SW	67	85
	SW dominated	59	74
	SW–HW	41	52
	HW dominated	24	30
	Pure HW	6	8
Moderate	Pure SW	65	63
	SW dominated	59	55
	SW–HW	40	38
	HW dominated	23	22
	Pure HW	6	6
Light	Pure SW	45	39
	SW dominated	39	34
	SW–HW	28	24
	HW dominated	16	14
	Pure HW	4	4

[a]Hardwood (HW) content classes, in percentage of total stand volume: pure softwood (SW) (0% hardwood), softwood-dominated (1%–25%), softwood–hardwood (26%–50%), hardwood-dominated (51%–75%), and pure hardwood (>75%).

[b]Outbreak patterns in Fig. 2 were converted into two 5-year simulation periods: period 1: years 6–10 (severe and moderate outbreaks), years 1–5 (light outbreak); period 2: years 1–15 (severe and moderate outbreaks), years 6–10 (light outbreak).

Silvicultural treatments description, impact evaluation, and assumptions

We compared effectiveness of silvicultural treatments in decreasing volume reductions following a SBW outbreak and in increasing postoutbreak softwood yield. Some of the harvesting was done with partial cutting (20% of harvested area), but most was done by clearcutting (80% of harvested area). All treatments were done after harvest but were grouped into either extensive management (harvesting only and natural regeneration) or preventive (i.e., intensive) management, which included PCT (mechanical thinning of competing vegetation), plantation (black or white spruce and no subsequent thinning), and cleaned plantation (combined use of plantation and PCT).

About 20% of managed stands were also affected by SBW mortality; however, the SIFORT inventory likely underestimated their abundance as it records only one major and one minor disturbance per measurement year. There was no difference in the 1985–2004 composition change between managed-only stands and stands affected by both SBW and management, and therefore, we grouped all managed stands whether also affected by SBW or not.

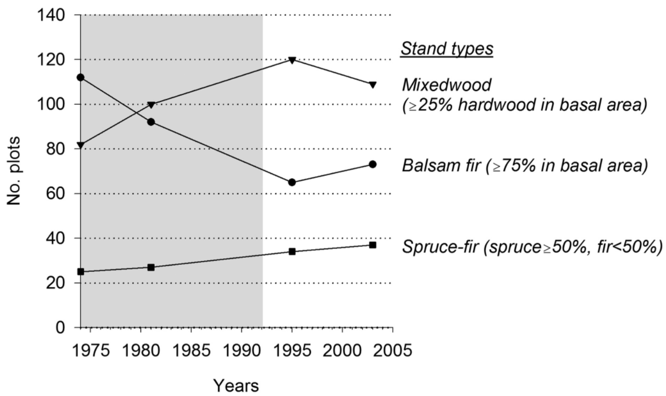
We evaluated the effect of silvicultural treatments from 1985 to 2004 on species composition in 2004 by selecting stands that were balsam fir stand type in 1985. The resulting forest composition for each treatment type was then used to assess the effectiveness of past forest management in decreasing volume reductions and in increasing softwood yields following a severe SBW outbreak scenario (10-year duration, including the hardwood content effect) for mature, 70-year-old stands. We grouped silvicultural treatments in terms of their impact on forest composition: increased mixedwoods, increased spruce, balanced composition, and unmanaged. Silvicultural treatments were also evaluated with regards to the spruce species used, whose vulnerability to SBW vary substantially. Therefore, we conducted and compared two simulations in which spruce volume was either exclusively composed of white spruce, a preferred host, or black spruce, a minor host.

Results

Change in forest composition and age from 1985 to 2004

In 1985, the 103 600 ha study area had 43 600 ha of balsam fir stands (the most vulnerable stand type to SBW outbreaks; 48% of the study area with known composition), 33 400 ha of mixedwood (37%), 13 800 ha of spruce–fir stands (15%), and 12 800 ha with unknown composition. By 2004, balsam fir had decreased by 26 000 ha to 17 600 ha (20% of the study area with known composition), mixedwoods increased by 20 600 ha to 54 000 ha (63%), and spruce–fir increased by 1300 ha to 15 100 ha (17%).

Fig. 3. Species composition of 219 permanent sample plots located within a 75 km radius of the study area by stand type from 1974 to 2003. Shaded area represents the spruce budworm outbreak period (1973–1992).



Changes in stand type in the Gaspé region (see Fig. 1 for area delimitation) during the 1981–2003 period based on PSP data showed similar (albeit slightly smaller) patterns to the stand-level data for the 1985–2004 period: balsam fir abundance decreased from 42% to 33% in the plots vs. 48% to 29% of stands, spruce–fir increased from 12% to 17% in the plots vs. 15% to 16% of stands, and mixedwood increased from 46% to 50% in the plots vs. 37% to 56% of stands (Fig. 3). The stand type change in PSPs from 1974 to 1981 (during the initial phase of the 1973–1992 SBW outbreak) was substantial, with a 9% decrease for balsam fir plots, a corresponding increase of 1% for spruce–fir plots, and an 8% increase for mixedwood plots. The balsam fir – mixedwood proportion thus decreased throughout the 1974–1995 period: however, the trend was inverted for the 1995–2003 period, i.e., after the 1973–1992 SBW outbreak, as balsam fir increased by 3% and mixedwoods decreased by 5%.

These trends were also present with softwood volume in the study area, but in that case, balsam fir stands still remained the dominant source of softwood timber by 2004, with 50% of total softwood yield relative to 63% in 1985. The fact that balsam fir stands had the highest softwood yield of all stand types is responsible for this disparity relative to area proportion changes.

Overall, the balsam fir stand age structure remained similar between 1985 and 2004, with a dominance of mature, 41- to 60-year-old and 61- to 80-year-old age classes, whereas the age structure in the other stands (mixedwood and spruce–fir stands) went from a relatively uniform distribution to an inverse-J structure dominated by young stands (Figs. 4*a*–4*b*). In terms of stand maturity, the extent of mature (>40 years) balsam fir stands, more vulnerable to SBW outbreaks than immature (≤40 years) stands, remained similar at 77% and 78%, respectively, of total fir stands (Figs. 4*c*–4*d*). In comparison, other stand types had fewer mature stands, with 63% mature in 1985 and 58% in 2004.

Simulation of SBW outbreaks effect on volume yields – no hardwood content effects

Actual softwood volume in the study area decreased from 7.5 million m³ to 6.5 million m³ between 1985 and 2004 (starting point of simulations in Fig. 5). This initial difference increased during the 15-year simulation period due to higher mean softwood productivity (i.e., slope of the undefoliated lines in Fig. 5) in the undefoliated 1985 simulation (77 500 m³·year⁻¹) than in the undefoliated 2004 simulation (47 500 m³·year⁻¹). This was essentially due to the older age of spruce–fir and mixedwood stands in 1985 relative to 2004 and the fact that balsam fir stands, which had the highest softwood yield among all stand types in 2004 (balsam fir, 118 m³·ha⁻¹; spruce fir, 77 m³·ha⁻¹; and mixedwood, 38 m³·ha⁻¹), had declined relative to 1985.

Softwood volume yield for the undefoliated scenario was 8.7 million m³ and 7.3 million m³ at the end of the 1985 and 2004 simulations, respectively. Total volume reductions caused by SBW outbreak scenarios (with no hardwood content effect on spruce–fir defoliation) for the study area (i.e., undefoliated scenario volume minus the minimum yield; see black dots in Fig. 5) were higher in the 1985 simulation than in the 2004 simulation: 1.2 and 1.0 million m³ for the light outbreak, 2.9 and 2.4 million m³ for the moderate outbreaks, and 3.9 and 3.3 million m³ for the severe outbreak scenarios, respectively (Fig. 5).

However, in terms of percentage volume reduction, the difference between the 1985 and 2004 simulations (no hardwoods effect scenario) was almost nil, with 15% vs. 15%, 33% vs. 34%, and 45% vs. 46% volume reductions for the light, moderate, and severe outbreak scenarios, respectively.

Simulation of SBW outbreaks effect on volume yields – hardwood content effects

The difference in percentage volume reduction between the 1985 and the 2004 simulations was higher but still low when including the hardwood content effect to reduce spruce–fir defoliation at 14% vs. 13%, 30% vs. 29%, and 41% vs. 39% volume reductions for the light, moderate, and severe outbreak scenarios, respectively. Because these differences in percentage volume reduction were insignificant, we chose to present only one of the two periods, the 2004 simulation, to simplify.

Simulated volume reductions, with and without hardwood content effects on reducing spruce–fir defoliation, were 13% and 15%, 29% and 34%, and 39% and 46% of undefoliated softwood yield volume reductions for light, moderate, and severe outbreak scenarios, respectively (Fig. 6). Total softwood volume "saved" by the protective effect of hardwoods increased with outbreak severity, totaling 11%, 13%, and 16% of the maximal losses (i.e., in the no hardwood content effect) for light, moderate, and severe outbreak scenarios, respectively.

The hardwood content effect substantially reduced mixedwood stand losses relative to the no hardwood content effect 2004 simulations, with 9% vs. 12%, 22% vs. 35%, and 25% vs. 47% volume reductions for simulations with and without hardwood content effect during light, moderate, and severe outbreak scenarios, respectively (Fig. 7). Black spruce – balsam fir stands were generally the least affected stand type, with <2% difference in volume reductions compared with mixedwoods (Fig. 7). Balsam fir stands, which had the highest volume reductions in all scenarios, had little difference between the simulations with and without hardwood content effect (<1% difference in volume reduction), with 16%, 38%, and 52% volume reductions including the hardwood content effect in light, moderate, and severe outbreaks, respectively. When using white spruce as the default spruce species during a severe outbreak scenario including the hardwood content effect, mixedwood stands were the least affected stand type with 30% volume reduction, followed by white spruce – fir stands with 41% volume reduction, and lastly balsam fir with 58% volume reduction (data not shown). In 1985, balsam fir stands accounted for 63% of total softwood volume, and despite the fact that their abundance had decreased by 2004, they still accounted for a majority of total softwood volume in the study area at 50%, mostly due to the increase in mixedwood stand abundance and their lower softwood yield. This partially explains why the volume reduction level stagnated between 1985 and 2004 in the study area. We did not find an improved softwood volume by 2004 either. With a maximum "saved" softwood volume of 0.53 million m³ simulated during a severe outbreak scenario including the hardwood content effect, the protective effect of hardwoods did not maintain sufficient softwood volume to offset the reductions associated with the softwoods being replaced by hardwoods, i.e., 1.4 million m³ from 1985 to 2004.

Fig. 4. Age class distribution (*a* and *b*) by area (per thousand hectare; '000 ha) and percentage of area by maturity class (*c* and *d*) (immature, ≤40 years; mature, >41 years) for balsam fir stands and other stands (mixedwood and spruce–fir) in the study area in 1985 and in 2004. Uneven-aged stands, rare in 1985 (<5% of study area) but more frequent in 2004 (35% of balsam fir stands, 11% of other stands), were excluded from *a* and *b* but included in the simulations and in *c* and *d* as mature stands (see Methods).

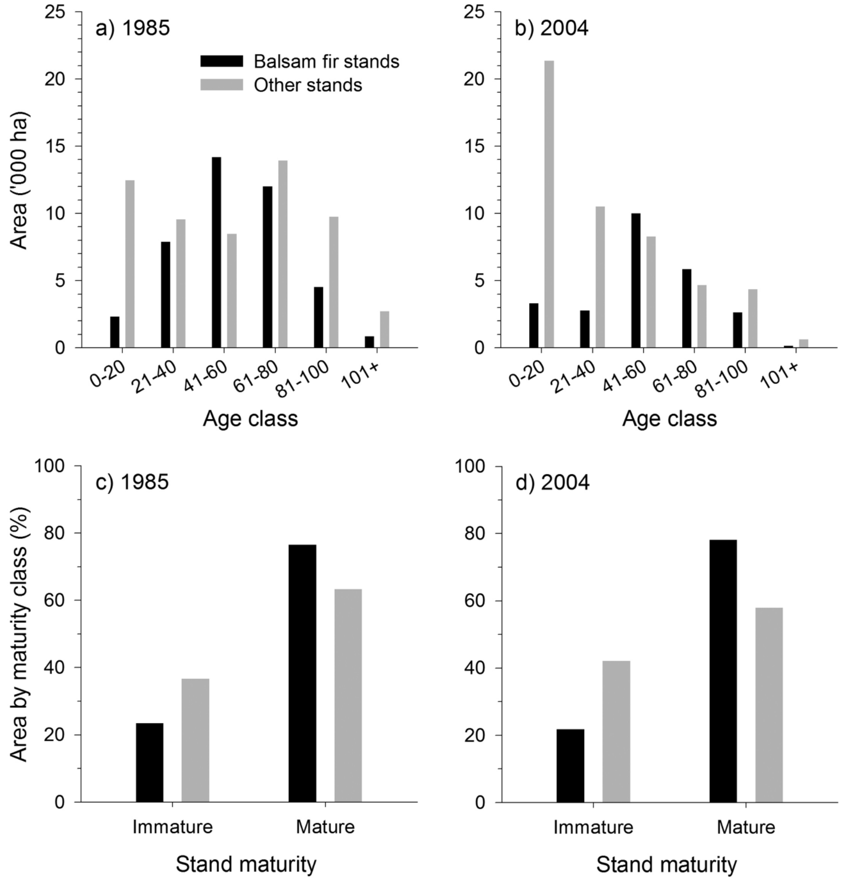
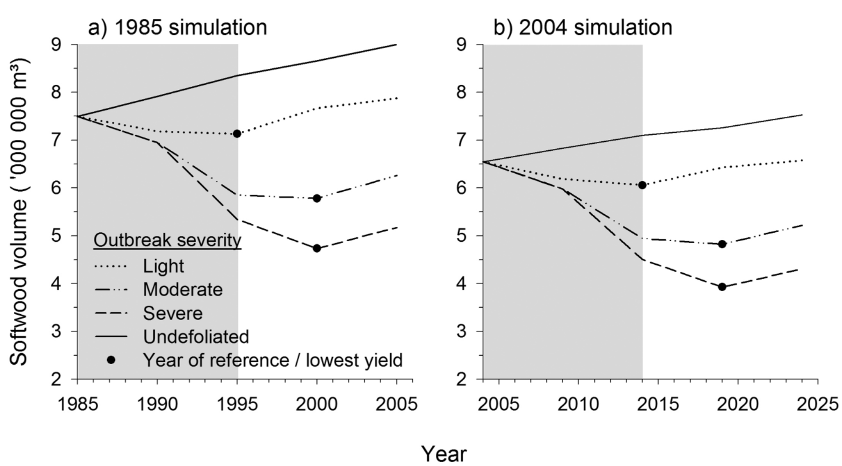


Fig. 5. Softwood volume yield (per million m³; '000 000 m³) for 20-year simulations initiated using (*a*) 1985 and (*b*) 2004 Gaspé management unit forest conditions, under undefoliated and three spruce budworm outbreak severities (outbreak, 10-year duration; shaded area) with no hardwood content effect on defoliation. Spruce yield (planted and natural regeneration) is composed of black spruce only (see Methods). Black circles represent the year of lowest yield, when SBW-caused volume reduction was calculated.



Effectiveness of silviculture in changing forest composition and limiting potential volume reductions

From 1985 to 2004, 33 900 ha of the study area were undisturbed, whereas the remainder was disturbed by SBW, intensive management, extensive management, or a combination of SBW and forest management. Specifically, 30 300 ha were affected by SBW only, 20 000 ha by intensive management (12 200 ha PCT, 4500 ha plantation, and 3300 ha of cleaned plantations), and 19 400 ha by extensive management. A proportion of managed stands was also affected by SBW, but as explained in the Methods, we grouped all managed

Fig. 6. Softwood volume reductions (%) for simulations starting in 2004 given (*a*) light, (*b*) moderate, and (*c*) severe spruce budworm outbreak scenarios (outbreak, 10-year duration; shaded area) with and without hardwood content effect reducing spruce–fir defoliation. Hardwood effects were assumed constant throughout the outbreak and directly proportional to stand hardwood content, based on Su et al. (1996).

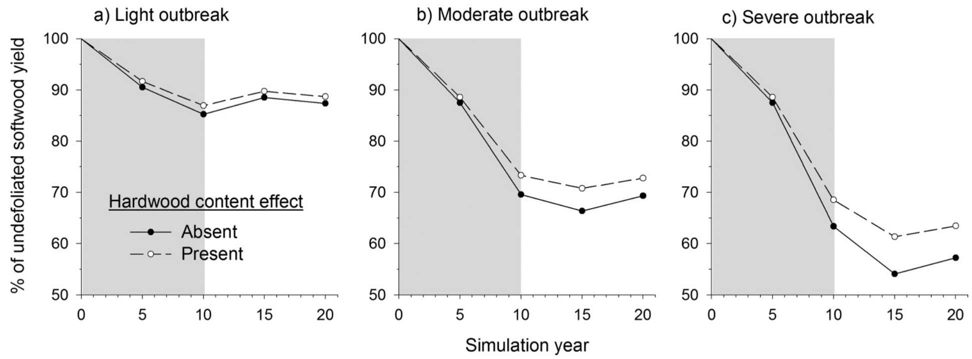
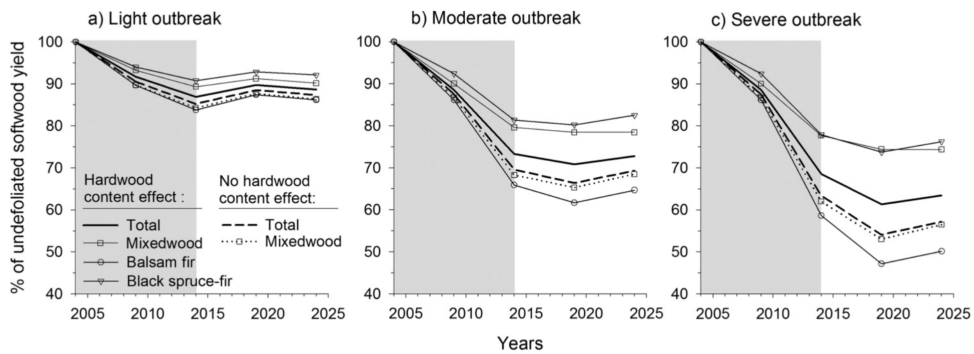


Fig. 7. Softwood volume reductions (%) per stand type for simulations starting in 2004 with and without hardwood content effect in reducing spruce–fir defoliation. The following three spruce budworm outbreak scenarios were simulated: (*a*) light, (*b*) moderate, and (*c*) severe (outbreak, 10-year duration; shaded area). Spruce yield (planted and natural regeneration) was assumed to be composed of black spruce only (see Methods).

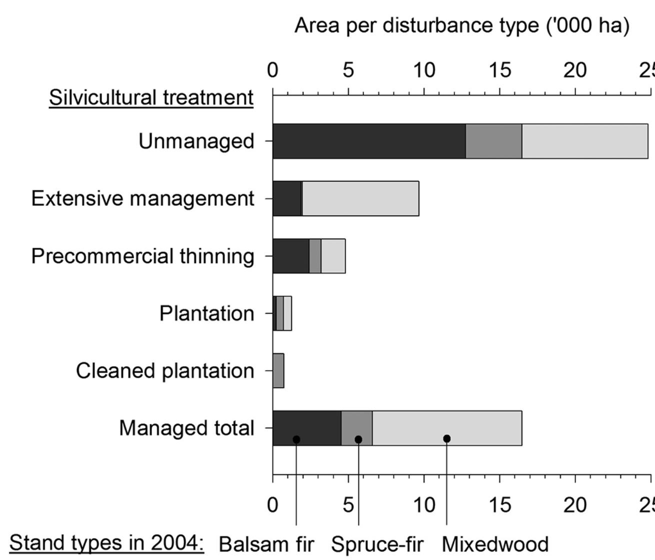


stands, whether also affected by SBW or not, based on the limited influence of SBW on the 1985–2004 composition change within managed stands.

Balsam fir stands in 1985 composed 42% of the study area, and by 2004, there were substantial species composition changes depending on the type of disturbance (Fig. 8). Only 39% of spruce plantations (uncleaned, i.e., without PCT) were still classified as having a spruce–fir composition, whereas the others became dominated either by a hardwood–conifer mix (43%) or by balsam fir (18%) (Fig. 8). PCT stands were slightly better than uncleaned plantations in limiting hardwood encroachment, with 33% of PCT stands having a mixedwood composition by 2004. With 17% of PCT stands being classified as spruce–fir stands by 2004, PCT did not significantly increase the proportion of spruce–fir stands relative to extensive management and unmanaged stands, which had 1% and 15% spruce–fir stands by 2004, respectively. In contrast, cleaned plantations (i.e., combined with PCT) were the most effective of the evaluated silvicultural treatments in maintaining spruce–fir composition, with 98% of treated stands being dominated by spruce–fir in 2004. Overall, intensive management did not succeed in limiting competing vegetation as 34% of PCT stands became mixedwoods, 62% of uncleaned plantations became either balsam fir or mixedwood stands, and a total of 29% of treated stands were spruce–fir stands by 2004. Hardwood encroachment was greatest on extensively managed sites, with 80% of treated stands having a mixedwood composition by 2004 (Fig. 8). However, stands unmanaged between 1985 and 2004 still experienced substantial hardwood encroachment, with 34% of stands having a mixedwood composition by 2004 (51% balsam fir and 15% spruce–fir).

Based on the effect of silvicultural treatment on forest composition presented in Fig. 8, we evaluated the volume reduction and softwood yield 15 years after a severe SBW outbreak simulation

Fig. 8. Effect of silvicultural treatment from 1985 to 2004 on species composition in 2004 of stands that were balsam fir stand type in 1985 (42% of the study area). Stands unmanaged between 1985 and 2004 were either undisturbed or affected by spruce budworm only. Extensive management excludes intensive treatments such as precommercial thinning, plantation, or both (cleaned plantation).



(10-year duration) applied to 70-year-old stands (Fig. 9). The following four silvicultural regime effects were simulated: increased mixedwoods (from extensive management), increased spruce (from cleaned plantation), balanced composition (from plantation or PCT),

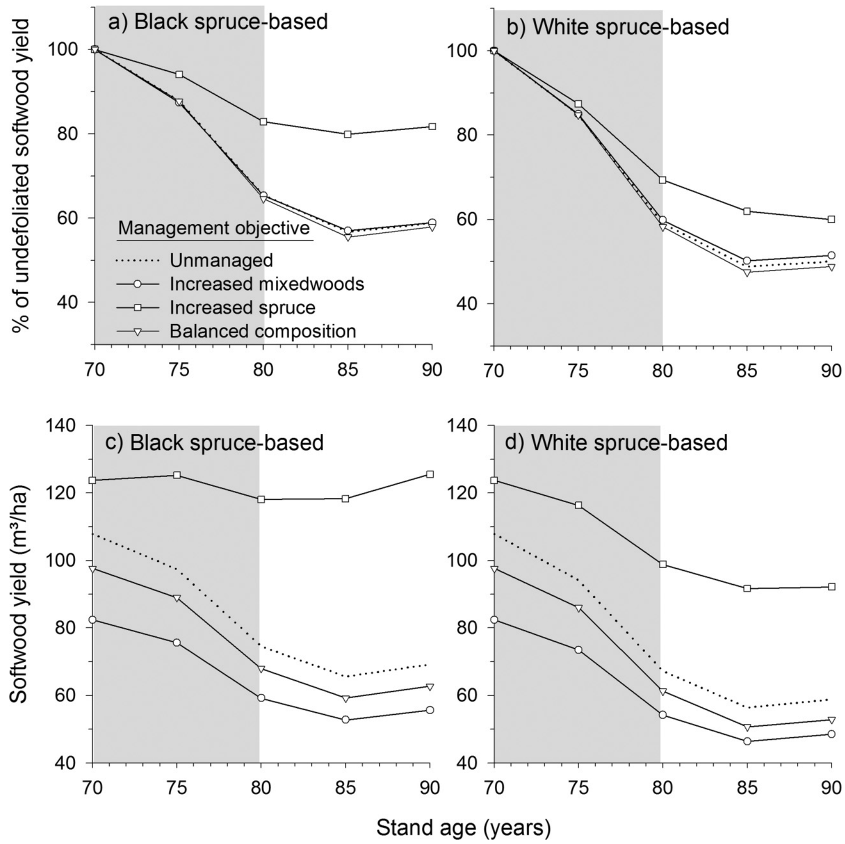


Fig. 9. Volume reduction (*a* and *b*) and softwood yield (*c* and *d*) simulated for 70-year-old stands representing different past silvicultural treatments during a severe spruce budworm outbreak scenario (including the hardwood content effect, 10-year duration; shaded area). Silvicultural treatments are as presented in Fig. 8: increased mixedwoods = extensive management; increased spruce = cleaned plantation; balanced composition = precommercial thinning or plantation; and unmanaged stands. Simulations consider all spruce as either black spruce (*a* and *c*) or white spruce (*b* and *d*).

and unmanaged stands. By the end of the outbreak simulation, treatments in black spruce based simulations had lower volume reductions than in white spruce based simulations, with 43% and 51% mean volume reductions, respectively (Figs. 9*a*–9*b*). Volume reduction was least under the increased spruce objective, assuming black spruce, at 20% by the end of the outbreak simulation (Fig. 9*a*) vs. a volume reduction of 38% assuming that spruce was white spruce (Fig. 9*b*). In comparison, volume reductions for unmanaged stands, increased mixedwood, and balanced composition objectives were 43%–44% assuming that spruce was black vs. 50%–53% assuming that spruce was white.

Before the outbreak simulation, softwood yield of 70-year-old stands was highest under the increased spruce management regime at 124 $m^3 \cdot ha^{-1}$ (Figs. 9*c*–9*d*). Due to a lower softwood and spruce content, the balanced composition (plantation or PCT) management regime had substantially lower softwood yields at 98 $m^3 \cdot ha^{-1}$ than both increased spruce management and unmanaged stands at 108 $m^3 \cdot ha^{-1}$. The increased mixedwood management regime yielded the lowest volume of 82 $m^3 \cdot ha^{-1}$ before the outbreak simulation. Postoutbreak softwood yields were higher assuming black spruce based management regime simulations rather than white spruce based simulations, with means of 62 and 54 $m^3 \cdot ha^{-1}$ by the end of the outbreak simulation, respectively. Yet, in both cases, the increased spruce (black or white) management had the highest postoutbreak softwood yield at 118 and 92 $m^3 \cdot ha^{-1}$, respectively, compared with 59 and 51 $m^3 \cdot ha^{-1}$, respectively, postoutbreak yield for balanced composition management and 53 and 46 $m^3 \cdot ha^{-1}$, respectively, for increased mixedwood management simulations (Figs. 9*c*–9*d*).

Discussion

Variability of host resource abundance and vulnerability

It has been suggested that over a large spatial scale, an increase in hardwood content, reduction in large balsam fir accumulation, and younger stand age following severe SBW outbreaks and forest management could reduce forest vulnerability to the following SBW outbreak (Bouchard et al. 2007). We found substantial reductions in balsam fir and increases in hardwood content and observed reductions in stand age, especially for mixedwood and spruce–fir stand types, which would reduce forest vulnerability to the SBW. There were relatively low levels of regenerating pure balsam fir stands (Fig. 4) as a consequence of the abundant conversion to mixedwood composition following harvesting. Nevertheless, with the low spruce stand abundance and age and the low softwood productivity of mixedwood stands, balsam fir stands remained the main source of softwood volume in 2004 (50% of total softwood volume; see Results). A combination of these factors explains why we did not find large differences in overall volume reduction levels between the 1985 and the 2004 simulations.

This limited impact of forest management on forest vulnerability to the SBW over the medium term contrasts with correlative studies relating high SBW outbreak severities during the 20th century to large-scale increases in the abundance of balsam fir following forest management (Blais 1983; Jardon et al. 2003; but see Boulanger et al. 2012). However, our results may not entirely address this question as host connectivity or forest contiguity, which were not accounted for in our model, could play a role in determining the damage generated by the SBW at the landscape scale (Robert et al. 2012). Nevertheless, our results suggest that variability in host resource abundance and age might not be as high as expected immediately following a severe SBW outbreak and that such high variability, if ever present, may be more visible over a multiple outbreak time frame.

In this study, we applied three SBW outbreak scenarios of varying severity on the forest resource in a top-down manner as input to SBWDSS projections; however, host resource abundance and susceptibility at the landscape scale (as defined by host species and age) also determine regional SBW outbreak patterns (Cooke et al. 2007). Future studies could thus make use of bottom-up approaches such as regeneration or succession studies and process-based modeling to explore the role of feedbacks between forest resource and SBW outbreak patterns in determining forest vulnerability to SBW.

Role of hardwoods and intensive management in preventive strategies against SBW

Needham et al. (1999) found that optimum hardwood levels depend on the severity of SBW attack; below 45% defoliation (5-year average), the amount of balsam fir volume lost to increased hardwood growing space exceeded the amount of volume protected, but as defoliation severity increased above 45%, the optimal hardwood levels increased. At severe levels of defoliation (>75%), optimal hardwood content was approximately 50% of initial standing volume (Needham et al. 1999). The mortality levels simulated by Needham et al. (up to 94% mortality) are most likely rare at the landscape level (but see MacLean and Ostaff (1989); average of 87% fir mortality in Cape Breton) as they are higher than the most affected stands in our study area (average of 52% volume reduction in the most vulnerable balsam fir stands in the severe outbreak without hardwood content effect). Although our results also suggest a positive correlation between outbreak severity and hardwood content effect and despite mixedwoods being substantially less vulnerable when considering the protective effect of hardwoods (Fig. 7), we found that softwood stands still produced more softwood timber than mixedwood stands. Thus, increased hardwood content resulted in fewer softwood trees in the landscape, a loss of softwood timber that was never compensated for by the protective effect of hardwoods.

In unmanaged, SBW-prone forests, increases in hardwood content are temporary as the shade-tolerant balsam fir eventually takes over while the hardwood cohort gradually disappears (Holling 1973; Marchand 1991). However, the use of clearcut harvesting, which tends to promote shade-intolerant species (Harvey and Bergeron 1989), without plantation or competing vegetation control over successive forest rotations could maintain forest composition in an early successional stage. Our results suggest that intensive management with cleaning or vegetation management is necessary to limit hardwood encroachment and that the current rate of use of extensive management will eventually affect the sustainability of softwood timber production in the study area.

Most forest composition changes (mixedwood stand abundance increase and balsam fir stand abundance decrease) that occurred in the study area were unplanned, i.e., they resulted from earlier SBW outbreaks or from natural regeneration following harvesting. The relatively limited extent of "planned" forest composition changes resulting from intensive management did not increase softwood volume in managed stands relative to unmanaged stands, but it contributed to limiting hardwood encroachment and softwood decline following harvesting (Fig. 8). This effect was particularly true for PCT, which maintained a balanced composition between the three stand types. In that sense, these results are in agreement with Belle-Isle and Kneeshaw (2007), who suggested that PCT in boreal mixedwoods can limit hardwood encroachment and emulate natural forest dynamics in terms of forest composition. This is especially the case for jurisdictions such as Quebec where herbicides (frequent alternatives to PCT) have been banned (Belle-Isle and Kneeshaw 2007; Gouvernement du Québec 1998; Harvey and Brais 2002). Nevertheless, the failure of intensive management to increase spruce–fir stand abundance in the study area was clear and largely attributable to the low use of vegetation management treatments in plantations (combined plantation and PCT treatments), which is a main factor determining intensive management effectiveness (Thompson and Pitt 2003). This raises questions about how preventive management against SBW and intensification of forest productivity are currently implemented in the boreal mixedwoods of Quebec. Plantations must be successfully established and PCT must shift species composition from balsam fir toward spruce to be effective landscape-scale factors.

White spruce and especially black spruce plantations increased the postoutbreak softwood yield, with 33% and 45% increases, respectively, in postoutbreak yields relative to PCT (during a severe outbreak scenario with hardwood content effect; Fig. 9), but were often invaded by balsam fir and intolerant hardwoods, stressing the need for effective vegetation management or cleaning (Thompson and Pitt 2003; Wagner et al. 2006). Considering that economic constraints might limit the use of cleaning treatments on all plantations, it becomes necessary to evaluate the risk of hardwoods or balsam fir taking over the plantation. For instance, either site quality or the preharvest hardwood content could serve as indicators of high competition risks (Harvey et al. 1995; Laflèche et al. 2000), and combined with cost–benefit analyses (Thompson and Pitt 2003), managers could thus make use of our softwood yield projections to select the best cost-effective intensive management treatment in the context of SBW-prone forests.

White spruce is often preferred to black spruce for its higher wood value and productivity; however, because we did not look at wood value and because of the identical black and white spruce undefoliated yield in our model, it is difficult to reliably recommend the best choice between black or white spruce because it depends on the given situation. Nevertheless, the high postoutbreak softwood yields of cleaned and uncleaned black spruce plantations found here and their lower vulnerability suggest that a balanced mix of plantations of black and white spruce, as well as minor or nonhost conifer species as in the study area (i.e., 32% black spruce, 41% white spruce, 12% Norway spruce, and 15% other species), represent a conservative and reasonable approach.

We did not observe significant effects of the 1985–2004 forest management activities on overall forest vulnerability to the SBW due to factors including the following: the ineffectiveness of PCT and plantations in increasing spruce–fir content, the effective but limited use of cleaned plantation treatments, and the considerable softwood yield reduction that followed the large hardwood content increase. Rather, we observed a large decrease in softwood timber supply from 1985 to 2004, which was attributable to both SBW and hardwood encroachment. Although the hardwood content effect was the highest in severe outbreaks, the protective effect never compensated for the loss of softwood growing space to hardwoods. Therefore, we question the strategy of increasing hardwood content in forests to reduce SBW damage and also question the widespread use of extensive management, which generates a strong hardwood encroachment in boreal mixedwoods. Although we cannot recommend the most profitable option between black and white spruce plantation in revenue terms, our results suggest that the combination of black and white spruce plantation and cleaning treatments is currently the most effective solution to increase softwood yield and reduce forest vulnerability to SBW. Therefore, we stress the need for a more effective competing vegetation control and an increased abundance of spruce species and nonhost softwoods in SBW prevention strategies.

Acknowledgements

Financial support for this research was provided by the Fonds de Recherche Québécois sur la Nature et les Technologies (FRQNT), the Center for Forest Research (CFR), and by the Spray Efficacy Research Group (SERG). We thank Frédéric Raulier and Philippe Marcotte for technical assistance, Louis Morneau and Cédric Fournier at the Quebec Ministry of Forest, Fauna and Parks, and Elizabeth Campbell and David R. Gray at the Canadian Forest Service for data sharing. We also thank Michel Huot and three anonymous reviewers for helpful comments on this manuscript.

References

Baskerville, G.L. 1975. Spruce budworm: the answer is forest management: or is it. For. Chron. **51**: 157–160. doi:10.5558/tfc51157-4.

Belle-Isle, J., and Kneeshaw, D. 2007. A stand and landscape comparison of the effects of a spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak to the combined effects of harvesting and thinning on forest structure. For. Ecol. Manage. **246**(2–3): 163–174. doi:10.1016/j.foreco.2007.03.038.

Blais, J.R. 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**(3): 620–629. doi:10.1139/x81-085.

Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. **13**(4): 539–547. doi:10.1139/x83-079.

Blum, B.M., and MacLean, D.A. 1984. Silviculture, forest management, and the spruce budworm. *In* Spruce budworms handbook: managing the spruce budworm in eastern North America. *Edited by* D.M. Schmidt, D.G. Grimble, and J.L. Searcy. USDA Forest Service, Washington, D.C. pp. 83–102.

Bouchard, M., Kneeshaw, D., and Bergeron, Y. 2006. Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. Ecology, **87**(9): 2319–2329. doi:10.1890/0012-9658(2006)87[2319:FDASSB]2.0.CO;2.

Bouchard, M., Kneeshaw, D., and Messier, C. 2007. Forest dynamics following spruce budworm outbreaks in the northern and southern mixedwoods of central Quebec. Can. J. For. Res. **37**(4): 763–772. doi:10.1139/X06-278.

Boulanger, Y., Arseneault, D., Morin, H., Jardon, Y., Bertrand, P., and Dagneau, C. 2012. Dendrochronological reconstruction of spruce budworm (*Choristoneura fumiferana*) outbreaks in southern Quebec for the last 400 years. Can. J. For. Res. **42**(7): 1264–1276. doi:10.1139/x2012-069.

Campbell, E.M. 2008. Temporal and spatial patterns in the severity of spruce budworm outbreaks in relation to bioclimatic conditions in eastern Canada. Département des sciences biologiques, Université du Québec à Montréal, Montréal, Québec.

Campbell, E.M., MacLean, D.A., and Bergeron, Y. 2008. The severity of budworm-caused growth reductions in balsam fir/spruce stands varies with the hardwood content of surrounding forest landscapes. For. Sci. **54**(2): 195–205.

Cappuccino, N., Lavertu, D., Bergeron, Y., and Régnière, J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. Oecologia, **114**(2): 236–242. doi:10.1007/s004420050441.

Cappuccino, N., Houle, M.J., and Stein, J. 1999. The influence of understory nectar resources on parasitism of the spruce budworm *Choristoneura fumiferana* in the field. Agric. For. Entomol. **1**(1): 33–36. doi:10.1046/j.1461-9563.1999.00009.x.

Chabot, M., Boulet, B., and Morneau, L. 2013. La tordeuse des bourgeons de l'épinette. *In* Le guide sylvicole du Québec, tome 1; Les fondements biologiques de la sylviculture. *Edited by* B. Boulet and M. Huot. Les publications du Québec, Québec. pp. 400–414.

Cooke, B.J., Nealis, V.G., and Regniere, J. 2007. Insect defoliators as periodic disturbances in northern forest ecosystems. *In* Plant disturbance ecology: the process and the response. *Edited by* E.A. Johnson and K. Miyanishi. Academic Press. pp. 487–525.

Coulombe, G., Huot, J., Arseneault, J., Bauce, É., Bernard, J.-T., Bouchard, A., Liboiron, M.-A., and Szaraz, G. 2004. Rapport de la commission d'étude sur la gestion de la forêt publique québécoise. Bibliothèque nationale du Québec.

Cyr, D., Gauthier, S., Bergeron, Y., and Carcaillet, C. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front. Ecol. Environ. **7**(10): 519–524. doi:10.1890/080088.

Erdle, T.A., and MacLean, D.A. 1999. Stand growth model calibration for use in forest pest impact assessment. For. Chron. **75**(1): 141–152. doi:10.5558/tfc75141-1.

Etheridge, D.A., MacLean, D.A., Wagner, R.G., and Wilson, J.S. 2005. Changes in landscape composition and stand structure from 1945–2002 on an industrial forest in New Brunswick, Canada. Can. J. For. Res. **35**(8): 1965–1977. doi:10.1139/x05-110.

Fortin, M., and Langevin, L. 2010. ARTEMIS-2009: un modèle de croissance basé sur une approche par tiges individuelles pour les forêts du Québec. Gouvernement du Québec, Ministère des ressources naturelles et de la faune, Direction de la recherche forestière, Mémoire de recherche no. 156.

Forus Research. 2010. Forus Simulation Framework user guide. Fredericton, New Brunswick, Canada.

Gagnon, R., and Chabot, M. 1991. Prévention des pertes de bois attribuables à la tordeuse des bourgeons de l'épinette. Gouvernement du Québec, Ministère des Forêts, Direction des programmes, Service d'aménagement forestier.

Gouvernement du Québec. 1998. Mise à jour du régime forestier / Document de référence / Bilan – Enjeux – Orientations. Gouvernement du Québec, Ministère des ressources naturelles.

Gray, D.R., Régnière, J., and Boulet, B. 2000. Analysis and use of historical patterns of spruce budworm defoliation to forecast outbreak patterns in Quebec. For. Ecol. Manage. **127**(1–3): 217–231. doi:10.1016/S0378-1127(99)00134-6.

Harvey, B.D., and Bergeron, Y. 1989. Site patterns of natural regeneration following clear-cutting in northwestern Quebec. Can. J. For. Res. **19**(11): 1458–1469. doi:10.1139/x89-222.

Harvey, B., and Brais, S. 2002. Effects of mechanized careful logging on natural regeneration and vegetation competition in the southeastern Canadian boreal forest. Can. J. For. Res. **32**(4): 653–666. doi:10.1139/x02-006.

Harvey, B.D., Leduc, A., and Bergeron, Y. 1995. Early postharvest succession in relation to site type in the southern boreal forest of Quebec. Can. J. For. Res. **25**(10): 1658–1672. doi:10.1139/x95-180.

Hennigar, C.R., and MacLean, D.A. 2010. Spruce budworm and management effects on forest and wood product carbon for an intensively managed forest. Can. J. For. Res. **40**(9): 1736–1750. doi:10.1139/X10-104.

Hennigar, C.R., MacLean, D.A., Quiring, D.T., and Kershaw, J.A. 2008. Differences in spruce budworm defoliation among balsam fir and white, red, and black spruce. For. Sci. **54**: 158–166.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. **4**: 1–23. doi:10.1146/annurev.es.04.110173.000245.

James W. Sewall Company. 2011. Spruce–fir resource in the state of Maine. Maine Department of Conservation. Available from www.maine.gov/dacf/mfs/archive/pubs/pdf/spruce_fir_resource_rpt.pdf.

Jardon, Y., Morin, H., and Dutilleul, P. 2003. Périodicité et synchronisme des épidemies de la tordeuse des bourgeons de l'épinette au Québec. Can. J. For. Res. **33**(10): 1947–1961. doi:10.1139/x03-108.

Koricheva, J., Vehviläinen, H., Riihimäki, J., Ruohomäki, K., Kaitaniemi, P., and Ranta, H. 2006. Diversification of tree stands as a means to manage pests and diseases in boreal forests: myth or reality? Can. J. For. Res. **36**(2): 324–336. doi:10.1139/x05-172.

Laflèche, V., Ruel, J.-C., and Archambault, L. 2000. Evaluation de la coupe avec protection de la regeneration et des sols comme methode de regeneration de peuplements melanges du domaine bioclimatique de la sapiniere a bouleau jaune de l'est du Québec, Canada. For. Chron. **76**(4): 653–663. doi:10.5558/tfc76653-4.

MacLean, D.A. 1980. Vulnerability of fir–spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. **56**: 213–221. doi:10.5558/tfc56213-5.

MacLean, D.A. 1988. Effects of spruce budworm outbreaks on vegetation, structure, and succession of balsam fir forests on Cape Breton Island, Canada. *In* Plant form and vegetation structure. *Edited by* M.J.A. Werger, P.J.M. van der Aart, H.J. During, and J.T.A. Verhoeven. SPB Academic Publishing, The Hague, Netherlands. pp. 253–261.

MacLean, D.A. 1996. Forest management strategies to reduce spruce budworm damage in the Fundy Model Forest. For. Chron. **72**(4): 399–405. doi:10.5558/tfc72399-4.

MacLean, D.A., and Andersen, A.R. 2008. Impact of a spruce budworm outbreak in balsam fir and subsequent stand development over a 40-year period. For. Chron. **84**(1): 60–69. doi:10.5558/tfc84060-1.

MacLean, D.A., and MacKinnon, W.E. 1997. Effects of stand and site characteristics on susceptibility and vulnerability of balsam fir and spruce to spruce budworm in New Brunswick. Can. J. For. Res. **27**(11): 1859–1871. doi:10.1139/x97-146.

MacLean, D.A., and Ostaff, D.P. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. Can. J. For. Res. **19**(9): 1087–1095. doi:10.1139/x89-165.

MacLean, D.A., Erdle, T.A., MacKinnon, W.E., Porter, K.B., Beaton, K.P., Cormier, G., Morehouse, S., and Budd, M. 2001. The spruce budworm decision support system: forest protection planning to sustain long-term wood supply. Can. J. For. Res. **31**(10): 1742–1757. doi:10.1139/x01-102.

Marchand, S. 1991. Dynamique de la régénération naturelle de jeunes sapinières boréales du centre du Québec. M.Sc. thesis, Université Laval, Québec City, Québec.

McLeod, I., Lucarotti, C.J., Hennigar, C.R., MacLean, D.A., Holloway, A., Cormier, G., and Davies, D. 2012. Advances in aerial application technologies and decision support for integrated pest management. *In* Integrated pest management and pest control. *Edited by* S. Soloneski and M.L. Larramendy. InTech Open Access Publisher, Rijeka, Croatia. pp. 651–668.

Miller, A., and Rusnock, P. 1993. The rise and fall of the silvicultural hypothesis in spruce budworm (*Choristoneura fumiferana*) management in eastern Canada. For. Ecol. Manage. **61**(1–2): 171–189. doi:10.1016/0378-1127(93)90197-U.

Morin, H., Jardon, Y., and Gagnon, R. 2007. Relationship between spruce budworm outbreaks and forest dynamics in eastern North America. *In* Plant disturbance ecology: the process and the response. *Edited by* E.A. Johnson and K. Miyanishi. Elsevier, New York. pp. 555–564.

Needham, T., Kershaw, J.A., MacLean, D.A., and Su, Q. 1999. Effects of mixed

stand management to reduce impacts of spruce budworm defoliation on balsam fir stand-level growth and yield. North. J. Appl. For. **16**: 19–24.
Pelletier, G., Dumont, Y., and Bédard, M. 2007. SIFORT: Système d'Information forestière par tesselle. Manuel de l'usager. Ressources naturelles et Faune, Québec.
Pothier, D. 2002. Twenty-year results of precommercial thinning in a balsam fir stand. For. Ecol. Manage. **168**(1–3): 177–186. doi:10.1016/S0378-1127(01)00738-1.
Pothier, D., Elie, J.G., Auger, I., Mailly, D., and Gaudreault, M. 2012. Spruce budworm-caused mortality to balsam fir and black spruce in pure and mixed conifer stands. For. Sci. **58**(1): 24–33. doi:10.5849/forsci.10-110.
Power, J.M. 1991. National data on forest pest damage. *In* Canada's timber resources. *Edited by* D.G. Brand. Canadian Forest Service, Petawawa National Forestry Inst., Chalk River, Ontario, Canada. pp. 119–129.
Remsoft Inc. 2008. Spatial Woodstock 2008.12 user guide. Remsoft Inc., Fredericton, New Brunswick, Canada.
Robert, L.-E., Kneeshaw, D., and Sturtevant, B.R. 2012. Effects of forest management legacies on spruce budworm (*Choristoneura fumiferana*) outbreaks. Can. J. For. Res. **42**(3): 463–475. doi:10.1139/x2012-005.
Royama, T. 1992. Analytical population dynamics. Chapman & Hall, New York.
Ruel, J.C., and Huot, M. 1993. Impact de la tordeuse des bourgeons de l'épinette [*Choristoneura fumiferana* (Clem.)] sur la régénération des sapinières après la coupe à blanc. For. Chron. **69**(2): 163–172. doi:10.5558/tfc69163-2.
Schoemaker, P. 1995. Scenario planning: a tool for strategic thinking. Sloan Management Review (winter): 25-40.
Spence, C.E., and MacLean, D.A. 2012. Regeneration and stand development following a spruce budworm outbreak, spruce budworm inspired harvest, and salvage harvest. Can. J. For. Res. **42**(10): 1759–1770. doi:10.1139/x2012-121.
Su, Q., MacLean, D.A., and Needham, T.D. 1996. The influence of hardwood content on balsam fir defoliation by spruce budworm. Can. J. For. Res. **26**(9): 1620–1628. doi:10.1139/x26-182.
Thompson, D.G., and Pitt, D.G. 2003. A review of Canadian forest vegetation management research and practice. Ann. For. Sci. **60**(7): 559–572. doi:10.1051/forest:2003060.
Wagner, R.G., Little, K.M., Richardson, B., and Mcnabb, K. 2006. The role of vegetation management for enhancing productivity of the world's forests. Forestry, **79**(1): 57–79. doi:10.1093/forestry/cpi057.