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Balsam fir sawfly defoliation effects on survival and growth quantified from permanent plots and dendrochronology

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Summary

Balsam fir sawfly (*Neodiprion abietis* (Harris)) has become a serious pest of young managed balsam fir (*Abies balsamea* (L.) Mill.) stands in western Newfoundland, Canada. During 1991–2008, a total area of 561 000 hectares was moderate to severely defoliated. We quantified impacts (growth and survival) using data from permanent sample plots (PSPs) and dendrochronology and related these impacts to defoliation severity determined from aerial defoliation data, in order to provide input into a Decision Support System. We analyzed 67 Newfoundland Forest Service PSPs, selected based on severity of defoliation (classes 1–6), stand age and management interventions (pre-commercially thinned *vs* natural) and measured before and after defoliation (1996–2008). We used Bayesian statistics to combine information from different sources, each having their own limitations and associated uncertainty. No mortality was observed in immature plots 12 years after defoliation, but survival was 54 per cent lower in mature defoliated than in non-defoliated plots. Plots in defoliation class 1 (1 year of moderate, 30–70 per cent, defoliation) showed 22 per cent cumulative growth reduction and complete recovery to pre-defoliation growth increment after 5 years. Plots in defoliation classes 2–6 (one to three consecutive years of severe, 71–100 per cent, defoliation) had mean cumulative growth reductions of 26–40 per cent and did not recover to pre-defoliation levels even 9 years after defoliation ceased. Natural and thinned plots responded similarly to defoliation severity. These results suggest that proactive control measures need to be implemented since impacts are severe, even with only 1 year of severe defoliation.

Introduction

Defoliating insects have considerable impacts on tree growth and prolonged severe defoliation can lead to tree mortality. Balsam fir sawfly (*Neodiprion abietis* (Harris)) is an insect defoliator native to eastern Canada. Outbreaks of balsam fir sawfly have historically been short in duration (Martineau, 1984), but it has become a serious pest of young managed balsam fir (*Abies balsamea* [L.] Mill.) stands in western Newfoundland, Canada, with the current outbreak, which began in 1991, being the longest ever recorded (Piene *et al.*, 2001; Moreau, 2006). During 1991–2008, a total area of 561 000 hectares was moderately to severely defoliated (Canadian Council of Forest Ministers, 2009). The long duration of the current balsam fir sawfly outbreak has been attributed to extensive pre-commercial thinning, with higher egg densities and defoliation measured in thinned than in unthinned stands (Ostaff *et al.*, 2006). Balsam fir sawfly feeds primarily on balsam fir needles of all age-classes except current-year foliage (Martineau, 1984). Larvae hatch in late June to early July, and, besides feeding gregariously on its primary host, balsam fir, it also feeds on white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) B.S.P.) and eastern larch (*Larix laricina* (DuRoi) K. Koch) (Carroll, 1962). The larvae feed on the outside edges of the needle, leaving the central filament. By the time the larvae have finished feeding, the remaining portion of the needle shrivels, turns yellow to brick red and then drops off. In the fall and winter, trees attacked in the previous season are bare of all but the current year foliage. Damage caused by balsam fir sawfly to a tree takes three forms: defoliation, reduced vigor and growth, and tree mortality.

Parsons *et al.* (2003) quantified volume growth reduction in balsam fir to be 12 and 35 per cent, respectively, during the first and second year of balsam fir sawfly defoliation, while Piene *et al.* (2001) estimated 78–81 per cent growth reduction after 4 years of defoliation. Both studies recommended that growth reduction be incorporated into wood supply analyses because the outbreak will reduce the amount of wood available for future harvest. To reduce effects of balsam fir sawfly defoliation, operational biological control programs with nucleopolyhedrovirus are available. These have been found to be safe, efficacious and economical for suppression of outbreak balsam fir sawfly populations (Lucarotti *et al.*, 2007). Spray programs with Abietiv™ (Sylvar Technologies Inc., Fredericton, New Brunswick, Canada) were conducted from 2006 to 2009 to control the damage (Hubert Crummey, personal communication).

In order to estimate potential and actual reductions caused by balsam fir sawfly and help make decisions related to control programs, a Decision Support System (DSS) is needed. To assist insect and forest management decision making for spruce budworm (*Choristoneura fumiferana* (Clem.)), a spruce budworm Decision Support System (SBWDSS) was developed by the Canadian Forest Service (MacLean and Porter, 1995). In the SBWDSS, annual defoliation data obtained from aerial surveys and various projected defoliation scenarios are converted into cumulative 5-year defoliation estimates. These estimates are used to model tree growth reduction and mortality in a stand inventory database within a Geographic Information System (GIS) (MacLean *et al.*, 2001). The SBWDSS helps forest managers predict budworm outbreak effects on forest structure and productivity, forecast forest growing stock and sustainable harvest levels, optimize insecticide protection programs and use silviculture and harvest scheduling to restructure forest management to reduce future damage (Hennigar *et al.*, 2007).

To develop a comparable DSS for balsam fir sawfly, the fundamental requirement is detailed quantified impacts on growth reduction and survival of various defoliation levels. Although impacts due to balsam fir sawfly defoliation quantified by Piene *et al.* (2001) and Parsons *et al.* (2003) provide some data, the current DSS framework requires longer term (at least 5 years and ideally incorporating tree recovery) relationships between defoliation and growth reduction and survival, to mesh with 5-year forest management planning periods. Although some data exist for growth reductions, no data were available to quantify effects of balsam fir sawfly defoliation on tree survival. Iqbal and MacLean (2010) determined a method to estimate cumulative multi-year defoliation from annual aerial defoliation survey data, and since defoliation data for large forest areas used in DSS comes from aerial defoliation surveys, it was desirable to establish relationships between growth reduction and survival to cumulative defoliation measured from aerial surveys. Similarly, growth recovery rates following severe balsam fir sawfly defoliation are slow compared with those of spruce budworm due to the absence of bud destruction that triggers epicormic shoot production and facilitates foliage recovery (Piene *et al.* 2001), and recovery rates needed to be quantified over a longer time scale.

The present study was designed to address the need for detailed long-term balsam fir sawfly defoliation impact relationships, using data from Newfoundland and Labrador Department of Natural Resources permanent sample plots (PSPs) and dendrochronology. Both PSP data and dendrochronology have advantages and disadvantages; while PSP remeasurements are efficient and provide a valuable temporal trend that can be related to a variety of site and stand factors, including defoliation, dendrochronology provides annual growth data but cores are time consuming to obtain and analyze, and taking multiple cores repeatedly over time may affect tree health. In order to obtain accurate inference, it is best to utilize all available information so we used both PSP and dendrochronological methods, linked using Bayesian statistics. Prior growth and survival data from PSP remeasurements were combined with more detailed information from dendrochronology using Bayesian statistics to get posterior inferences (McCarthy and Masters, 2005) (i.e. estimates of survival and growth reduction with confidence envelopes) about impacts due to balsam fir sawfly defoliation. Bayesian analysis treats all parameters as random, assigns prior distributions to characterize knowledge about parameter values prior to data collection and uses the joint posterior distribution of parameters given the data as the basis of inference.

Objectives of this study were to (1) quantify effects of balsam fir sawfly defoliation on survival in immature and mature plots and (2) quantify growth reduction in immature plots using both PSP and dendrochronology data and Bayesian inference procedures, for a range of aerial defoliation survey severity classes.

Methods

Aerial defoliation survey data

Aerial defoliation surveys are commonly used to assess annual defoliation over large areas and are currently the only operational method to provide such data (MacLean and MacKinnon, 1996). The Newfoundland and Labrador Department of Natural Resources conducts annual aerial defoliation surveys and records balsam fir sawfly defoliation and severity level (nil 0–30 per cent, moderate 31–70 per cent or severe 71–100 per cent of visible crown foliage) on sketch maps. Aerial defoliation surveys are conducted during a 1- to 3-week period after the completion of feeding (usually from mid-late August) using helicopters (Hubert Crummey, personal communication). A distinct reddish-brown coloration of foliage due to desiccation of damaged needles (MacLean and Ebert, 1999) helps observers judge the area and severity of defoliation. In other areas like New Brunswick, fixed-wing aircraft along flight lines 2–5 km apart are used (Miller and Kettela, 1975) for spruce budworm aerial defoliation surveys, and these have been found to be 82–85 per cent correct in differentiating three defoliation classes 0–30, 31–70 and 71–100 per cent defoliation (MacLean and MacKinnon, 1996; Taylor and MacLean, 2008) compared with ground-based defoliation estimates. No measure of accuracy is available for aerial surveys conducted with helicopters, but they are assumed to be of higher accuracy based on low altitude, slow speed flights and means of closer observation in case of doubt.

Records from the sketch maps are digitized and stored in Arc/Info GIS format (Environmental Systems Research Institute). Data on spatial accuracy and transfer error rates are not available but would be included in the overall aerial defoliation survey accuracy assessments reported above. All areas that sustained balsam fir sawfly defoliation during 1996–2008, and not defoliated by other insects, on the island of Newfoundland were overlaid using ArcView GIS 9.2 (Figure 1), to assign multi-year defoliation severity classes. Considering multiple years and defoliation levels, a total of six defoliation severity classes were distinguished (Table 1), ranging from 1 year of moderate to 3 successive years of severe defoliation.

PSP data

The Newfoundland and Labrador Department of Natural Resources has collected data from ~1000 fixed area, rectangular shaped PSPs across Newfoundland since 1985, in order to provide stand growth data that can be used to calibrate and validate stand growth projection models. Plot size is 0.04 ha for mature (>60 years age) stands and is determined by a minimum of 75 plot trees for immature stands (≤60 years age), typically 0.002–0.02 ha for very dense to open immature stands. The PSPs are located in forests encompassing the full range of developmental stages, ecoregions (Meades and Moores, 1994) and disturbance regimes. PSPs are remeasured every 4–5 years, when all tagged trees are measured for status (live/dead), diameter growth at breast height (d.b.h.) and other characteristics. Ingrowth was not distinguished from new trees tagged as plot areas were extended after extensive suppression-related mortality in immature plots. Using ArcView GIS 9.2, the PSP locations shape file was overlaid with defoliation severity classes determined from the aerial defoliation survey. A total of 67 PSPs were selected, with 59 defoliated

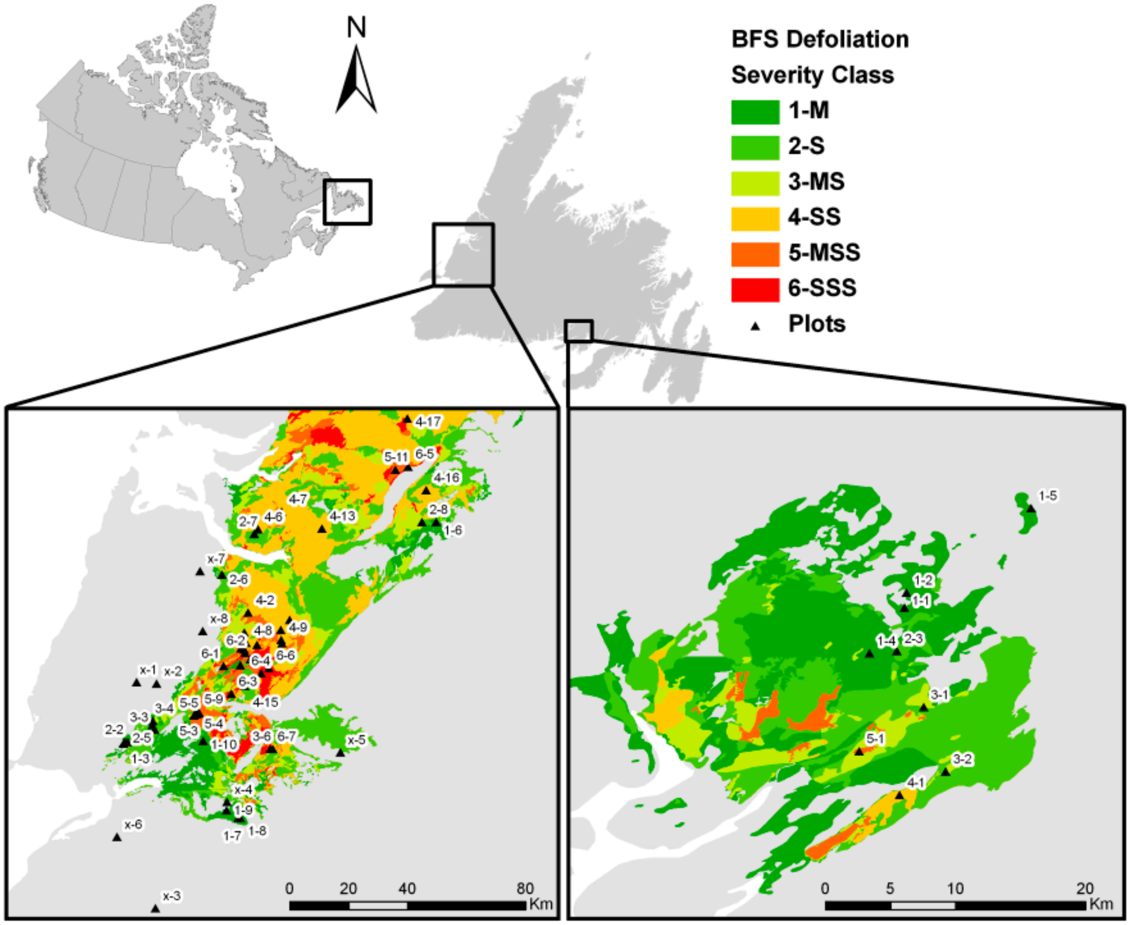

Figure 1. Map of plot locations and balsam fir sawfly defoliation in Newfoundland from 1996 to 2008. Six defoliation severity classes were based on levels of defoliation in up to 3 years, with 'M' denoting moderate (31–70%) and 'S' severe (71–100%) defoliation. Details of sampled plots are presented in Table 1.

Table 1: Details of 67 PSPs in Newfoundland used in analysis. Plots are categorized based on severity and duration of defoliation

Severity Class	Plot ID	Defoliation year (severity)[*]	Thinned/Natural	Stand age (yrs)
1 (M)	1-1[†]	2001(M)	Thinned	41–60
	1-2[†]	2001(M)	Thinned	41–60
	1-3[†]	1997(M)	Natural	21–40
	1-4[†]	2000(M)	Natural	41–60
	1-5[†]	2001(M)	Natural	41–60
	1-6	2006(M)	Natural	41–60
	1-7	1997(M)	Natural	61–80
	1-8	1997(M)	Natural	81–100
	1-9	1997(M)	Natural	81–100
	1-10	1997(M)	Natural	81–100
2 (S)	2-1	1996(S)	Thinned	21–40
	2-2[†]	1997(S)	Natural	21–40
	2-3[†]	2000(S)	Natural	41–60
	2-4[†]	1996(S)	Natural	41–60
	2-5[†]	1997(S)	Natural	41–60
	2-6[†]	2002(S)	Natural	41–60
	2-7	2002(S)	Natural	81–100
	2-8	2005(S)	Natural	81–100
3 (MS)	3-1[†]	1999(M), 2000(S)	Thinned	21–40
	3-2[†]	2000(M), 2001(S)	Thinned	41–60
	3-3[†]	1996(S), 1997(M)	Natural	41–60
	3-4[†]	1996(M), 1997(S)	Natural	41–60
	3-5[†]	1996(M), 1997(S)	Natural	41–60
	3-6	2000(M), 2001(S)	Natural	81–100
4 (SS)	4-1[†]	1999,00(S)	Thinned	21–40
	4-2[†]	2001,02(S)	Thinned	21–40
	4-3[†]	2000,01(S)	Thinned	21–40
	4-4[†]	2000,01(S)	Thinned	41–60
	4-5[†]	2000,01(S)	Natural	21–40
	4-6	2002,03(S)	Natural	21–40
	4-7	2002,03(S)	Natural	21–40
	4-8[†]	2000,01(S)	Natural	41–60
	4-9	2001,02(S)	Natural	41–60
	4-10	2001,02(S)	Natural	41–60
	4-11	2001,02(S)	Natural	41–60
	4-12[†]	2000,01(S)	Natural	41–60
	4-13[†]	2002,03(S)	Natural	41–60
	4-14	2000,01(S)	Natural	61–80
	4-15	2000,01(S)	Natural	81–100
	4-16	2005,06(S)	Natural	81–100
	4-17	2006,07(S)	Natural	81–100
5 (MSS)	5-1	1998,99(M), 2000(S)	Thinned	21–40
	5-2	1996,97(S), 1998(M)	Thinned	21–40
	5-3	1996,97(S), 1998(M)	Thinned	21–40
	5-4[†]	1996,97(S), 1998(M)	Thinned	21–40
	5-5[†]	1996,97(S), 1998(M)	Thinned	21–40
	5-6[†,‡]	2000(M), 2001,02(S)	Thinned	21–40
	5-7[†,‡]	2000(M), 2001,02(S)	Thinned	21–40
	5-8[†]	1998(M), 1999,00(S)	Thinned	41–60
	5-9	1996,97(S), 1998(M)	Natural	21–40
	5-10	2000(M), 2001,02(S)	Natural	41–60
	5-11	2004(M), 2005,06(S)	Natural	81–100
6 (SSS)	6-1[†,‡]	1997,98,99(S)	Thinned	21–40
	6-2[†,‡]	1998,99,00(S)	Thinned	21–40
	6-3[†,‡]	2000,01,02(S)	Thinned	21–40
	6-4[†,‡]	2000,01,02(S)	Thinned	21–40
	6-5	2004,05,06(S)	Thinned	21–40
	6-6[†,‡]	2000,01,02(S)	Natural	21–40
	6-7	2000,01,02(S)	Natural	81–100

Table 1: Continued

Severity Class	Plot ID	Defoliation year (severity)*	Thinned/Natural	Stand age (yrs)
X	x-1§	Not defoliated	Natural	81–100
	x-2§	Not defoliated	Natural	61–80
	x-3§	Not defoliated	Natural	81–100
	x-4§	Not defoliated	Natural	81–100
	x-5§	Not defoliated	Natural	81–100
	x-6§	Not defoliated	Natural	81–100
	x-7§	Not defoliated	Natural	81–100
	x-8§	Not defoliated	Natural	81–100

* Defoliation from aerial defoliation survey; M = Moderate (31–70%) and S = Severe (71–100%).

† Plots for which cores for dendrochronology analysis were extracted.

‡ Plots established other than PSPs.

§ Mature plots that were not defoliated.

by balsam fir sawfly along with eight mature non-defoliated PSPs close to and with similar site quality to defoliated plots. Since thinning began in Newfoundland during the mid to late 1980s and no mature thinned plots could be located, all non-defoliated mature plots were natural. For each selected PSP, one to three measurements were available before and after defoliation. Survival was calculated as percentage of living trees with d.b.h. ≥ 7 cm that survived during the measurement period compared with the number of living trees before defoliation; trees <7 cm d.b.h. were omitted to remove suppression-related mortality. Data from the PSPs were used to: (1) determine survival rates before and after defoliation in immature and mature plots; (2) compare survival rates in defoliated and non-defoliated mature plots, to quantify age- *vs* defoliation-related mortality; and (3) estimate growth (basal area increment/ha/year) before and after defoliation in immature plots. Details of the 67 analyzed PSPs are listed in Table 1. In summer 2009, all selected PSPs were remeasured, and increment cores from 33 PSPs (at least 5 randomly selected plots per defoliation severity class in immature stands) were sampled for dendrochronological analysis.

Dendrochronology data

Two increment cores were extracted using an increment borer at breast height perpendicular to each other from 12 to 15 dominant or co-dominant balsam fir trees within 33 immature plots. In addition, cores were sampled from three to five black spruce and three to five white birch (*Betula papyrifera* Marsh.) trees in or close to each plot where possible. Cores were mounted onto boards and sanded to a grit of 800, as per standard dendrochronology preparation procedures (Swetnam *et al.*, 1985). Growth rings were examined and measured to the nearest 0.01 mm using a WinDENDRO (Version 2009, Regent Instruments Inc., Blain, Quebec, Canada) scanner-based image processing tree-ring measurement system (Guay *et al.*, 1992). Core series were amalgamated and signal homogeneity was verified using COFECHA (Holmes, 1983). Poorly correlated tree series (i.e. R < 0.42 for a 30-year time span with 15-year lag) were checked for errors. ARSTAN (Cook, 1985) was used to generate a mean standardized chronology of individual species ring widths using a two-stage detrending method, which applies a negative exponential or linear trend for each tree-ring series and then cubic-smoothing spline to remove remaining age or growth trends (Holmes *et al.*, 1986) to produce dimensionless growth index values. Standardized master chronologies were produced for each plot. These chronologies were studied for growth trends 6 years before and 5–13 years after defoliation up to the year of core collection in 2009. Growth changes (per cent) were measured comparing total growth increment in the plot from all sample trees in a given year after defoliation to growth before defoliation (5 years average).

Statistical analyses

The data have a repeated measures design, for which mixed-model analysis provides more convenient ways of modeling error structures. To investigate the relationship between per cent survival of immature and mature defoliated plots and mature non-defoliated plots, we used linear regression using uninformative priors as no previous detail was available about survival relationships. This analysis modeled a linear regression relationship between mean per cent survival (Survival_k) and an explanatory variable (years after defoliation) separately for immature and mature defoliated *vs* mature non-defoliated plots. The Bayesian model can be specified as:

$$\text{Survival}_k = \alpha + \beta \times \text{YAD}_k, \tag{1a}$$

with prior distributions on the intercept α and slope β modelled as

$$\alpha \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2) \tag{1b}$$

$$\beta \sim \text{Normal}(\mu_{\text{YAD}}, \sigma_{\text{YAD}}^2), \tag{1c}$$

where α is the regression intercept and β, the regression slope between the per cent survival in any plot k and the year after defoliation (YAD) for that plot.

All Bayesian analyses were performed in WinBUGS v.3.0.3 (Spiegelhalter *et al*., 2004), which has become the standard software for Bayesian analysis using source codes from McCarthy (2007). All posterior distributions were generated by WinBUGS using 100 000 Markov chain Monte Carlo samples after discarding an initial 10 000 samples. Parameter estimates for the regression were based on the mean of the posterior Bayesian estimates and 95 per cent credibility intervals were estimated. As a cross-check to the results, data were also analyzed using a linear mixed model fit in the R statistical package (R Development Core Team 2008, http://www.r-project.org) with plot specific regression coefficients and corresponding α and β values compared with Bayesian estimates.

For growth response, informative priors of mean per cent growth change (basal area increment per hectare per year compared with pre-defoliation growth) and precision ($\tau = 1/\sigma^2$) in different defoliation severity classes, as measured from PSPs, were used. These were combined with growth response of respective severity and years after defoliation, as estimated from dendrochronology. Posterior mean per cent growth change was assumed to be drawn from a normal distribution and 95 per cent Bayesian credible intervals annually were estimated until 9 years after defoliation.

To test whether responses to defoliation differed between thinned and natural plots a linear mixed-effects model, fitted using the lme function (Pinheiro and Bates, 2000) in the R statistical package, related per cent growth change to years after defoliation. Defoliation severity classes (1–6), and management (thinned *vs* natural) were treated as random effects in the models. Models were compared using analysis of variance and the best fit model that showed the best BIC (Bayesian Information Criterion) and log-likelihood was selected. This selected model worked as one multi-level regression where severity classes were included as an ordinal covariate. The basic linear mixed-effects model was specified as:

$$\begin{aligned}\%\mathrm{Growth}_k = {} & (\beta_0+\beta_1\mathrm{Year}_k+\beta_2\mathrm{Year}_k^2) \\ & + (b_{0,\mathrm{sev}}+b_{1,\mathrm{sev}}\mathrm{Year}_k+b_{2,\mathrm{sev}}\mathrm{Year}_k^2)+e_k \end{aligned} \quad (2)$$

where the β_i's are fixed parameter estimates and the $b_{j,\mathrm{Sev}}$ represents the group level random effects. No significant autocorrelation (even for simpler models using plot as a grouping variable as opposed to severity class) was detected. While inclusion of all random effects were significant ($P < 0.05$), based on log-likelihood tests, $b_{0,\mathrm{Sev}}$ and $b_{2,\mathrm{Sev}}$ accounted for almost 80 per cent of the variation explained by random effects. Other fixed effects model forms were explored; however, the above model form (equation (2)) was the best fit in terms of several goodness-of-fit criteria including BIC, significance of parameter estimates and residual distributions. To test whether responses differed between species, a similar method was used where severity classes (1–6) and tree species (balsam fir, black spruce and white birch) were treated as random effects in the models. Defoliation severity class was treated as a grouping variable along with species.

Results

Survival of balsam fir after defoliation

Immature plots

Eighty-nine per cent of immature plots (39 in total) in the severely defoliated classes (5 and 6) were thinned, whereas 73 per cent of plots in severity classes 1–4 were natural (unthinned). Balsam fir survival did not decline after defoliation in immature plots. Only 18 per cent of plots (all natural) showed reduced survival by a maximum of 20 per cent, but the trend does not appear to have initiated with defoliation. Trees in immature thinned plots across all defoliation severity classes survived during the measured period of 8–12 years after defoliation. The intercept and slope values from Bayesian and linear mixed model were almost the same (99.36 intercept and −0.26 slope for Bayesian *vs* 99.39 intercept and −0.32 slope for mixed model) and were not significantly different from zero.

Mature plots

Relatively few mature plots (13 in total) were found in defoliated areas, in comparison to immature plots (39 in all). Survival of trees in non-defoliated mature plots declined by 21 per cent over 12 years, in comparison to over 60 per cent reduction in survival in defoliated plots (Figure 2). Variability in survival was high in defoliated plots relative to non-defoliated plots. Three plots, one in each of defoliation severity classes 3, 4 and 6, showed complete mortality ~7 years after defoliation began.

Linear regression with uninformative priors showed that after 4 years, mature defoliated plots had statistically different survival rates (0.73 95% confidence interval (CI) 0.58–0.88) than non-defoliated plots (0.94 (CI 0.89–1.00 CI)) (Figure 3). Variability in survival in mature defoliated plots was high compared with the non-defoliated plots, and after 12 years, mean survival in mature plots was 54 per cent lower (82 per cent in non-defoliated *vs* 28 per cent in defoliated plots). Immature defoliated plots showed little variability and survival remained almost the same 12 years after defoliation. As expected, the intercept and slope values from Bayesian and linear mixed model were almost the same in both cases of mature non-defoliated plots and defoliated plots with plots explaining >50 per cent of the total variance in each case.

Growth

Growth effect on balsam fir as determined from PSPs (prior)

There was little change in growth (basal area increment, square metre per hectare per year) over time for balsam fir trees in severity class 1 (1 year of moderate defoliation), with only one-third of plots demonstrating growth reduction after defoliation (Figure 4). In other defoliation severity classes (2–6), trends of reduced growth resulting from defoliation were much clearer, and almost all plots showed reduced growth in the year after defoliation,

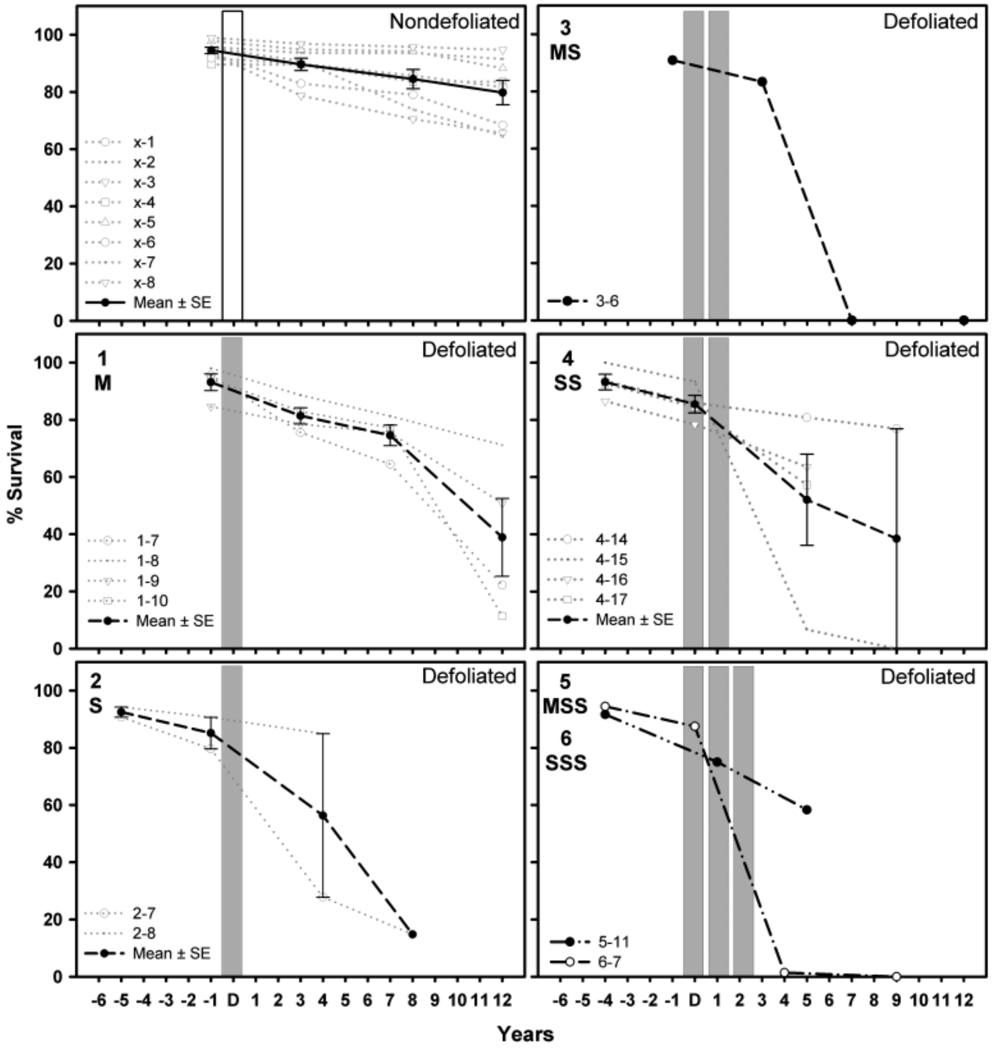

Figure 2. Mean ± standard error per cent survival of balsam fir in 21 mature (stand age > 60 years) plots, by defoliation severity class and in non-defoliated mature plots. Per cent survival was calculated before and after years of defoliation 'D'; years of moderate (M) to severe (S) defoliation are shaded grey.

followed by recovery after defoliation ceased. Both thinned and natural plots responded similarly to defoliation. Mean growth reduction as compared with pre-defoliation growth and precision (1/variance) were calculated for each defoliation severity class (not presented here) each year after defoliation and were used as priors in subsequent Bayesian analysis.

Growth effect on balsam fir as determined from dendrochronological analysis (data)

Annual growth data in the form of standardized growth chronologies for all plots (Figure 5) showed clearer trends of reduced growth after defoliation, in comparison to data from PSPs measured only every 4–5 years (Figure 4). Comparing different defoliation classes, severely defoliated classes (3–6) showed less variability in their growth reduction and recovery in comparison to the less severely defoliated classes (1–2, which sustained only 1 year of defoliation).

To detect differences in growth response resulting from severity of defoliation or management (i.e. thinned *vs* natural plots), the linear mixed-effects model that showed the best BIC (Bayesian information criterion) and log-likelihood was selected. Here, defoliation severity as a random effect showed better values (BIC value of 2706). Severity classes 1 and 3 did not show any differences in growth between thinned *vs* natural plots. Severity class 4 thinned plots showed less growth reduction than natural plots, and in severity class 6 natural plots showed lower growth reduction initially after defoliation then increased to more than that of the thinned plots 3–4 years after defoliation began. Since no thinned plots could be found in severity class 2 and no natural plots in severity class 5, effects of management could not be evaluated in these classes.

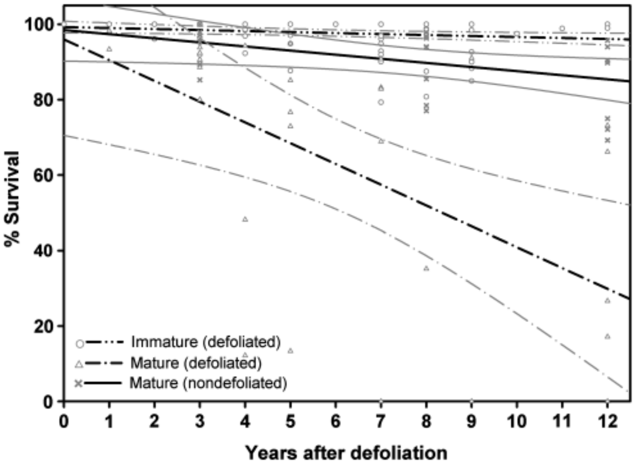

Figure 3. Linear regression (black lines) and 95% Bayesian credible intervals (grey lines) using uninformative priors for per cent survival of immature and mature defoliated plots and mature non-defoliated plots.

Overall, the growth response of thinned and natural plots appeared similar.

Growth effects on balsam fir using Bayesian inference (posterior)

Using Bayesian statistics, both the prior (information from PSP data) and the likelihood (information from dendrochronological analyses) were combined to estimate annual mean posterior growth responses and 95 per cent Bayesian credible intervals for up to 9 years after defoliation (Figure 6). The growth information presented in Figure 4 showed variability in response to balsam fir sawfly defoliation, although some trends of reduced growth could be seen and quantified in the form of a prior. The dendrochronology data (Figure 5) provide more detail and also show variability at plot level. Ignoring prior information will result in inference based on only dendrochronology data that would result in wide credible intervals. Growth analysis from the PSPs (prior), when used together with the growth reduction data from dendrochronology, resulted in improved precision of growth reduction estimates (Figure 6). Mean cumulative growth reduction increased progressively from 22 per cent (15–29 per cent) for severity class 1 to 43 per cent (35–50 per cent) in defoliation severity class 6. Balsam fir recovered completely only in severity class 1, 5 years after defoliation ceased. None of the other severity classes had completely recovered to pre-defoliation growth even 9 years after defoliation. After maximum growth reduction, a partial recovery occurred for 3 years in severity classes 2 and 3 and for 4 years in severity classes 4–6. There was steady growth after this phase of 3–4 years recovery. Towards the end of the measurement period (9 years after defoliation), growth was still 20 per cent less than pre-defoliation levels in severity classes 2–4 and ~40 per cent less in severity classes 5–6, differentiating those that had sustained three consecutive years of defoliation.

Growth effects on black spruce and white birch

When using species as a random effect, the BIC values were better (6412) than when considering species as a fixed effect (6489). The baseline model (data for all species pooled) differed significantly for the different species (Figure 7). White birch, a non-host species, showed no negative growth response resulting from defoliation, and small declining growth trends during a few years may have resulted from either climatic effects or perhaps a stand-opening response. Black spruce showed relatively little decline in growth as compared with balsam fir in all defoliation severity classes (Figure 7). Growth recovery in black spruce was relatively slow compared with balsam fir and in four of six severity classes (1, 2, 4 and 6) balsam fir had higher growth than that of black spruce 9 years after defoliation.

Discussion

Bayesian statistics have been found to be very cost-effective for increasing confidence in ecological research (McCarthy and Masters 2005). Since prior information was available in the form of growth analyses from PSPs before the dendrochronology analyses, we used Bayesian analysis in this study. Variability in tree response to balsam fir sawfly over a large landscape area exists as a result of variability in defoliation level, limitations of defoliation estimation (Iqbal and MacLean, 2010), and differences in site and stand characteristics. Similar to some previous studies (Ellison, 2004; McCarthy and Masters, 2005), use of prior information improved the precision of parameter estimates. Although the purpose of this study was to quantify defoliation impacts on tree growth and survival and not to demonstrate the capabilities of Bayesian statistics, there is a growing literature that has applied Bayesian statistics in ecology. Our conclusion is that the Bayesian approach used here did improve the estimation of survival (Figure 3) and growth (Figures 6 and 7) caused by balsam fir sawfly defoliation.

Since tree mortality continues for a number of years after an insect outbreak collapses even though there was no defoliation (Hudak *et al*., 1978), long-term study was needed in order to quantify survival differences after defoliation. This study fills the gap by providing long-term survival effects for balsam fir sawfly. We found no mortality in young balsam fir trees (immature plots) 10 years after balsam fir sawfly defoliation, but for mature plots, survival reduction occurred such that 60 per cent more trees had died 12 years after defoliation relative to non-defoliated mature plots. Since photosynthetic capacity differs with age of foliage (e.g. Clark, 1961), the effect of defoliation on tree growth is determined not only by the amount of foliage consumed or destroyed by the insect but also by the age of the foliage destroyed. Balsam fir sawfly larvae prefer 1-year-old foliage (Moreau *et al*., 2003; Parsons *et al*., 2003; Iqbal and MacLean, 2010) and defoliation of old foliage may have less impact on tree growth because current-year foliage, although lower initially, has the highest level of photosynthetic activity later in the growing season (Clark, 1961). Trees hence can get enough starch

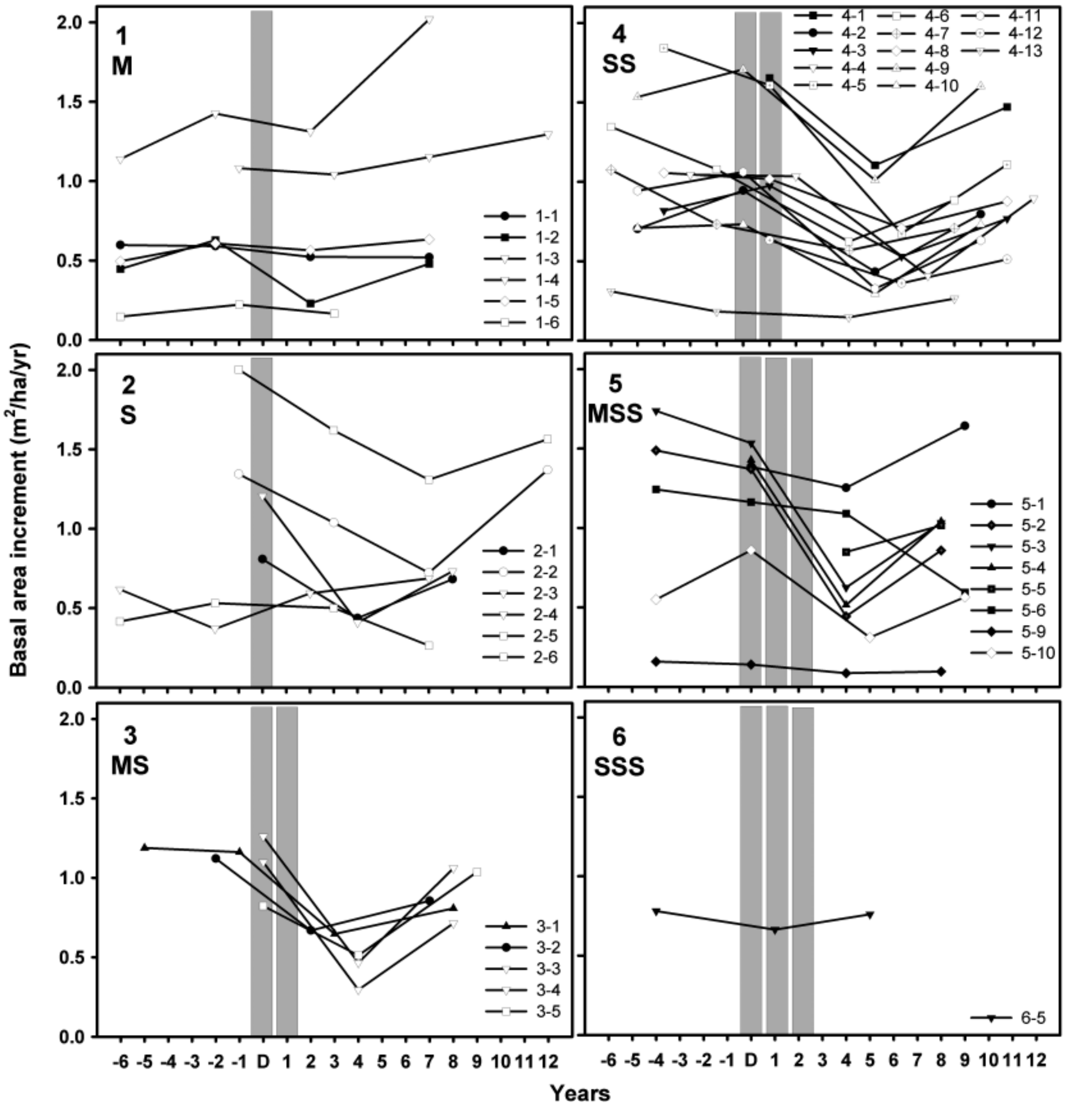

Figure 4. Growth (basal area increment) of balsam fir in 39 immature plots in thinned (filled symbols) and natural (open symbols) stands by six defoliation classes, before and after defoliation. Years of moderate (M) to severe (S) defoliation are shaded grey.

to keep them living at a young age, but for mature trees that have higher maintenance needs from assimilation of produced starch to sustain themselves, food produced by the new foliage alone is insufficient and hence mortality occurs. Similarly, stress created by defoliation increases chances of other pests like balsam woolly adelgid (*Adelges piceae* (Ratz.)) attacking the trees and hence indirectly contributes to mortality. No balsam wooly adelgid damage was observed in the sampled plots at the time of remeasurements or mapped in provincial surveys, and thus it is unlikely that it was a cause of mortality.

Growth reduction was estimated only for immature plots. Such estimation from PSP data was not possible in mature plots because of low survival in mature defoliated plots (i.e. 0 per cent survival in three plots and an average of 20–40 per cent survival in others (Figure 2), relatively few mature defoliated plots (13 in total) and small numbers of trees in each plots. Therefore, insufficient sample trees were available for growth analyses from mature sample trees. In addition, it is difficult to separate growth reduction caused by defoliation from natural age-related growth reduction. Since balsam fir sawfly prefers immature stands (Piene *et al.*, 2001), which are important in forest growth and yield analysis, our dendrochronology analyses for growth reduction estimates focused on immature stands. As reported by Parsons *et al.* (2003), the immediate and severe reduction in growth due to defoliation by balsam fir sawfly is a direct result of the lack of an apparent compensation mechanism, i.e. release of suppressed buds (Piene, 1989) in the host species balsam fir. Growth reduction as measured by Parsons *et al.* (2003) (12 per cent first year, 35 per cent second year) and Piene *et al.* (2001) (46 per cent after 2 years of

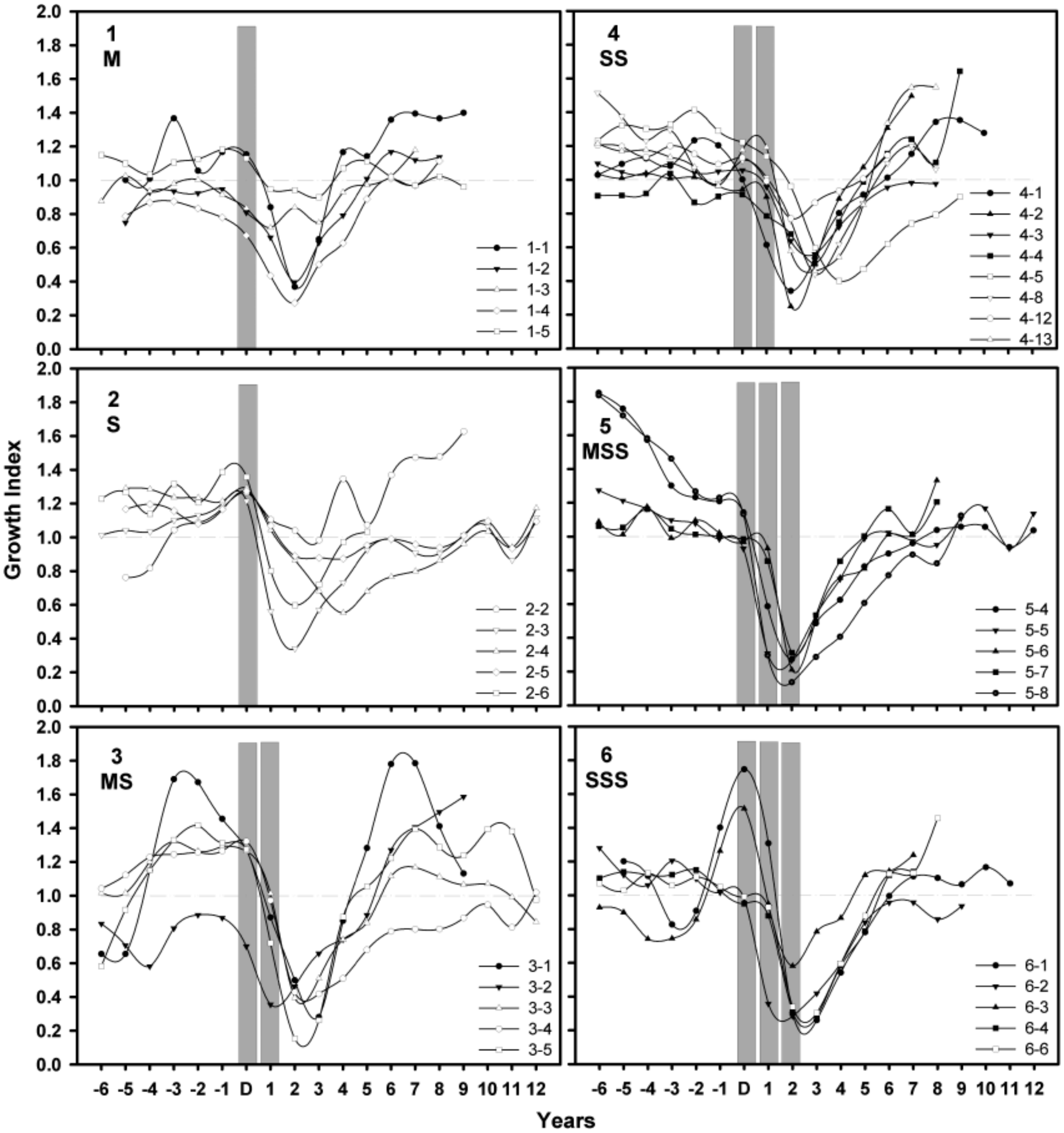

Figure 5. Standardized growth chronologies of balsam fir for 33 plots in thinned (filled symbols) and natural (open symbols) stands, by six defoliation classes. Years of moderate (M) to severe (S) defoliation are shaded grey; 'D' indicates the initial year of defoliation.

outbreak) are fairly close to the values that we found, 22–26 per cent after 1 year of moderate or severe defoliation, 29–34 per cent after 2 years and 40–43 per cent after 3 years (Figure 6).

Growth reduction of black spruce during the initial years after defoliation was relatively less than for balsam fir (Figure 7), consistent with the fact that balsam fir sawfly prefers balsam fir for feeding (Carroll, 1962). In higher defoliation severity classes, more growth reduction occurred in black spruce, probably because of a spillover effect where, when all the 1 year and older age classes of foliage are consumed on balsam fir sawfly larvae start feeding on black spruce.

Recovery of balsam fir following defoliation by balsam fir sawfly is slow compared with that following spruce budworm and hemlock looper defoliation (Iqbal *et al.*, 2011b), especially in severely defoliated plots. Except for severity class 1, none of the plots in defoliation severity class 2–6 showed full recovery 9 years after defoliation. In the years following spruce budworm defoliation, small leaves were produced (Quiring and McKinnon, 1999); similarly, reduced needle biomass (Piene and Little, 1990; Piene and MacLean, 1999) was recorded. Although spruce budworm, hemlock looper and balsam fir sawfly differ in age-classes of foliage consumed, all three feed on balsam fir as their primary host. Balsam fir sawfly do not destroy buds or shoots during feeding and consequently do not stimulate release of suppressed buds, unlike current-year foliage feeders like spruce budworm (Batzer, 1973;

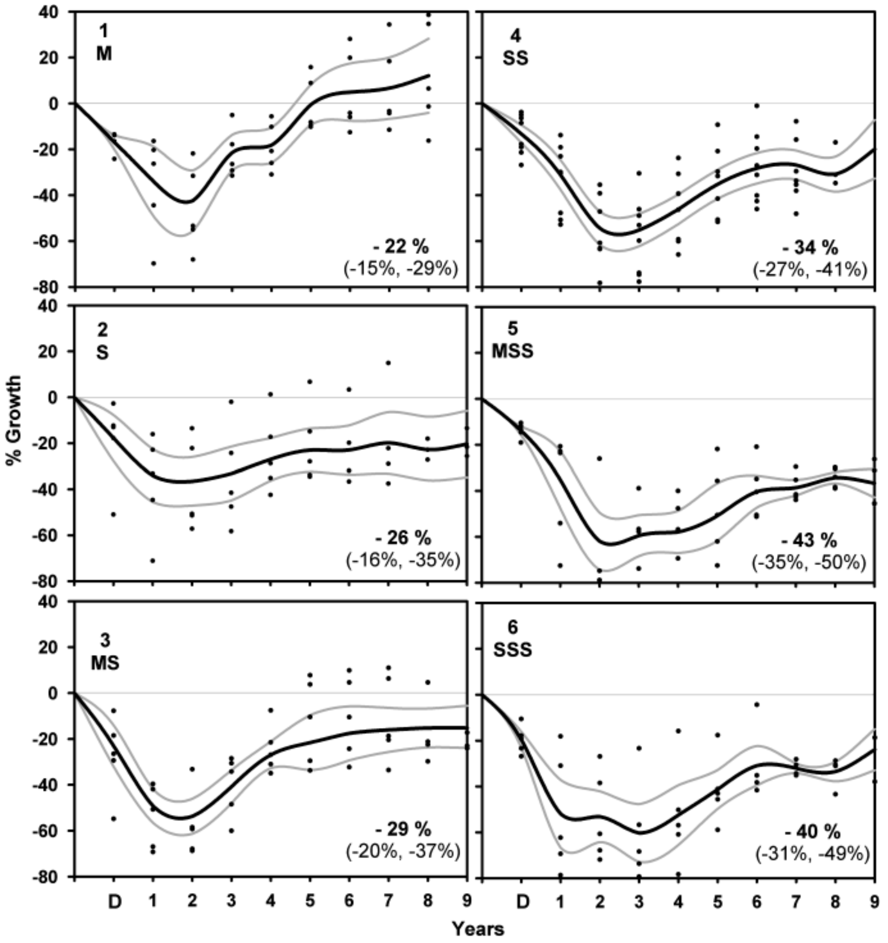

Figure 6. Mean percentage growth reduction compared with pre-defoliation growth (0%) of balsam fir with 95% Bayesian credible intervals using prior from PSP growth reduction analysis for the six defoliation classes (as described in Table 1). 'D' indicates the initial year of defoliation. Values at the bottom right are mean and 95% credible interval cumulative growth reduction, compared with the 10 previous years (including the first year of defoliation).

Piene *et al*., 2001) or all age class defoliators like hemlock looper, which greatly increases tree recovery from defoliation (Piene, 1989). Poor recovery as observed in black spruce (Figure 7) could partly be explained by the slow growth and longer needle retention (8 years; Kayama et al., 2007) characteristic of black spruce compared with that of balsam fir.

Although pre-commercially thinned stands sustain more balsam fir sawfly defoliation than natural stands (Ostaff *et al*., 2006), growth responses after defoliation are not different. This could be due to the fact that trees in thinned stands, even though more defoliated, are also more evenly spaced, getting more light and are less stressed. Hence the losses expected from higher defoliation may be countered by better growing conditions.

Our results strongly suggest the value of establishing a successful proactive pest management program for balsam fir sawfly. Substantial tree mortality in mature plots after balsam fir sawfly defoliation is important for forest pest managers. Because balsam fir sawfly feed upon multiple age-classes of foliage in 1 year, there is less time for managers to react than for spruce budworm, which typically feeds only on current-year foliage and takes up to 4 years for tree mortality to occur. In contrast, 1–3 years of severe balsam fir sawfly defoliation can cause large long-term losses to stand growth and yield from both tree mortality in mature plots and slow growth recovery.

The growth and survival *vs* defoliation relationships were a key component towards our development of a DSS for balsam for sawfly (Iqbal *et al*., 2011a). The DSS uses species-specific growth and survival *vs* defoliation level relationships (i.e. Figures 3, 6 and 7) to convert measured defoliation from aerial surveys, overlaid onto a GIS-based forest inventory for all stands and possible future defoliation and management strategies portrayed in scenarios (MacLean *et al*., 2001) into effects on stand growth and yield. These are then integrated into a forest estate model to project effects on timber supply for 25 years. Results suggested that the defoliation levels observed in the past would reduce total operable

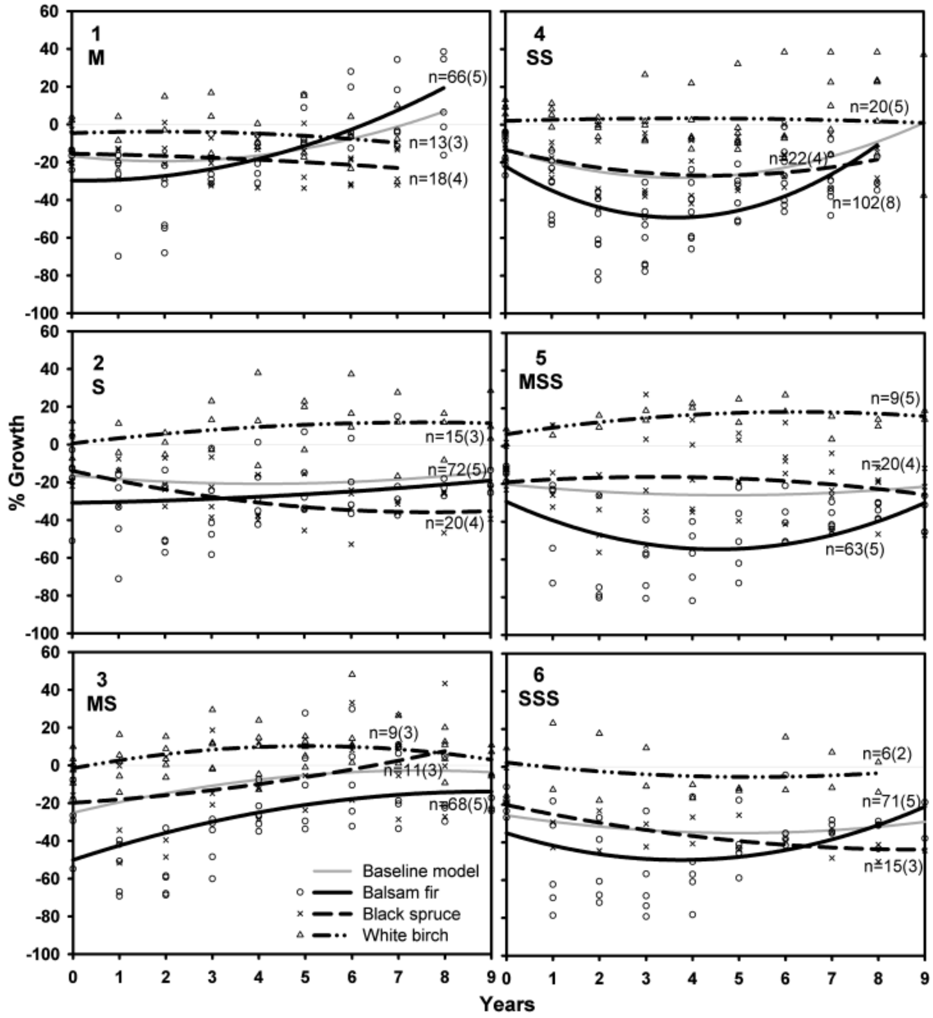

Figure 7. Effect of species (balsam fir, black spruce and white birch) on per cent growth change compared with pre-defoliation growth (0%), 9 years after defoliation using a mixed-effect model. The baseline model represents output where all the data for a specific severity class were pooled. '0' on the x-axis denotes the initial year of defoliation. Number of trees cored is shown as '*n*' with respective number of plots (in brackets) for each species.

softwood growing stock and softwood harvest level by 26 and 31 per cent, respectively, for balsam fir sawfly (Iqbal *et al.*, 2011a). Sensitivity analysis using different defoliation scenarios suggested that maximum reductions in harvest levels could be reduced from 40 to 17 per cent by protecting the most susceptible 25 per cent of the landbase using biological insecticide and minimized further to 9 per cent by re-optimization of harvest schedules to reduce losses (Iqbal *et al.*, 2011a). Such DSS assist forest managers in making decisions about implementing a control program, quantifying forest-level losses due to the balsam fir sawfly and adjusting sustainable harvest levels after defoliation.

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Conflict of interest statement

None declared.

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